

The *Hadropithecus conundrum* reconsidered, with implications for interpreting diet in fossil hominins

Elizabeth R. Dumont^{1,*}, Timothy M. Ryan² and Laurie R. Godfrey³

¹221 Morrill Science Center, Department of Biology, University of Massachusetts, Amherst, MA 01003, USA

²Department of Anthropology and Center for Quantitative Imaging, EMS Energy Institute, 409 Carpenter Building, Pennsylvania State University, University Park, PA 16802, USA

³Department of Anthropology, University of Massachusetts, 240 Hicks Way, Amherst, MA 01003, USA

The fossil ‘monkey lemur’ *Hadropithecus stenognathus* has long excited palaeontologists because its skull bears an astonishing resemblance to those of robust australopiths, an enigmatic side branch of the human family tree. Multiple lines of evidence point to the likelihood that these australopiths ate at least some ‘hard’, stress-limited food items, but conflicting data from *H. stenognathus* pose a conundrum. While its hominin-like craniofacial architecture is suggestive of an ability to generate high bite forces, details of its tooth structure suggest that it was not well equipped to withstand the forces imposed by cracking hard objects. Here, we use three-dimensional digital reconstructions and finite-element analysis to test the hard-object processing hypothesis. We show that *Archaeolemur* sp. cf. *A. edwardsi*, a longer-faced close relative of *H. stenognathus* that lacked hominin convergences, was probably capable of breaking apart large, stress-limited food items, while *Hadropithecus* was better suited to processing small, displacement-limited (tougher but more compliant) foods. Our suggestion that *H. stenognathus* was not a hard-object feeder has bearing on the interpretation of hominin cranial architecture; the features shared by *H. stenognathus* and robust australopiths do not necessarily reflect adaptations for hard-object processing.

Keywords: *Hadropithecus*; *Archaeolemur*; robust australopiths; gape; mechanical advantage; finite-element analysis

1. INTRODUCTION

The skull of the fossil ‘monkey lemur’ *Hadropithecus stenognathus* bears an astonishing resemblance to that of robust australopiths, an enigmatic side branch of the human family tree (figure 1). Similarities include a functionally short palate, steep facial profile, enlarged P4 and molars, diminutive incisors, incisiform upper canines and a thick mandibular corpus. Multiple lines of evidence from skull shape, tooth macro- and microstructure, and tooth enamel chipping, microwear and texture analysis support the hypothesis that robust australopiths consumed at least some ‘hard’ (fail to fracture under high loads) or stress-limited (non-compliant, i.e. stiff and brittle or stiff and tough) foods [1–8] (but see [9]). As in these hominins, the relatively enlarged and heavily pitted molars in *H. stenognathus* suggest that it too ate stress-limited food items [10–12]. However, its moderately thin and non-decussating molar enamel suggest that its teeth were not well suited to resist fracture. These conflicting signals from different components of the *H. stenognathus* masticatory system are the ‘*Hadropithecus conundrum*’ [13]: is it possible that, despite its strikingly hominin-like cranial architecture and dental proportions, this fossil lemur was not a hard-object feeder? The puzzle becomes all the more intriguing when *H. stenognathus* is compared with its close relative *Archaeolemur* sp. cf. *A. edwardsi*—a

longer-faced lemur with similarly pitted but distinctly non-hominin-like dental proportions, whose thick and strongly decussated molar enamel clearly points to a diet that included stress-limited food items [14]. *Archaeolemur*, in contrast to *Hadropithecus*, has small molars, relatively large premolars, low-relief post-canine teeth, a robust upper canine and enlarged, procumbent, pitheciin-like incisors. The palate of *Archaeolemur* is narrower relative to its length, and its rostrum projects further beyond the anterior roots of the zygoma. Differences in the stable carbon isotope signatures of *Archaeolemur* and *Hadropithecus* affirm that they had very different diets [15], with *Archaeolemur* consuming predominantly C₃ foods and *Hadropithecus* consuming CAM or C₄ plants. By themselves, the stable isotope data suggest that *Hadropithecus* could not have consumed large seeds or hard fruits, because the latter derive virtually exclusively from C₃ plants.

The cranial and dental morphology of *Hadropithecus* can be interpreted in two very different ways. If *Hadropithecus* generated very high bite forces that were efficiently transmitted to its expanded molar battery, these forces could have been high enough to cause failure in foods such as fruit with resistant pericarps or seed coats. These and other stress-limited foods fracture when sufficient stress is applied but maintain structural integrity prior to that point. In this scenario, the expanded molars might also serve to protect the integrity of the thin-enamelled teeth themselves by reducing stress in the teeth through an increased tooth–food contact area [16]. While molar expansion could have protected the teeth, without a concomitant increase in bite force, it

* Author for correspondence (bdumont@bio.umass.edu).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2011.0528> or via <http://rspb.royalsocietypublishing.org>.

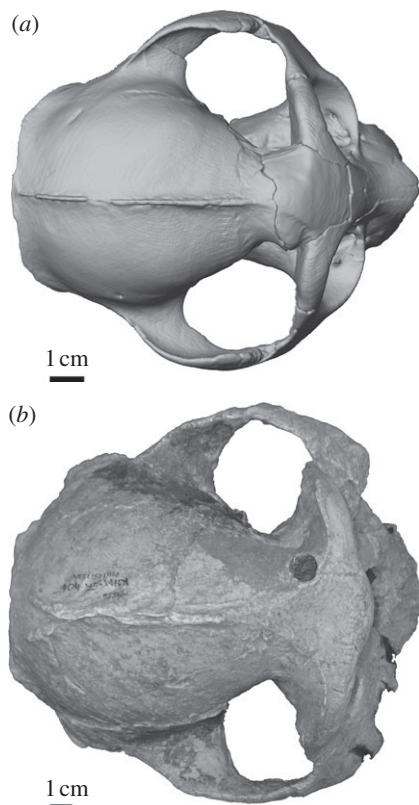


Figure 1. Dorsal views of the skulls of (a) *H. stenognathus* (Vienna cranium NHMW 1934 IV 1) and (b) *Paranthropus boisei* (KNM-ER 406). Both species have been interpreted as hard-object feeders, although contradictory signals exist for each [6,8,9,12,13].

also would have decreased the magnitude of stress imposed on the food, thus limiting the ability to access stress-limited foods.

The second interpretation of craniodental architecture in *Hadropithecus*, supported by the isotope data, is that it reflects adaptations for processing displacement-limited (perhaps tough but compliant) food items. Here, the relatively short palate, small incisors and expanded molars of *Hadropithecus* may indicate efficient mastication of large quantities of displacement-limited foods that require little incisal preparation, as was initially suggested by Walker [17] for fossil hominins. Some displacement-limited foods include parts of plants that contain a relatively large proportion of indigestible material and must be thoroughly pulped to release nutritious components. Such foods are tough; they deform and absorb a great deal of energy before fracturing and are most effectively processed by large, planar post-canine teeth with embedded shearing surfaces [18]. Notably, the posterior premolar (P4) and molars of *Hadropithecus* are large and wear quickly to expose 'ribbons' of enamel that form sharp, intersecting surfaces [14]. Lucas [18] also suggests that large teeth are better than small teeth at fracturing small particles and thin sheets or rods, such as the blades of grass or leaves. By contrast, many stress-limited foods, whether brittle or tough, are also large or blocky, and may require initial cracking by incisors or premolars.

Here, we test the hypothesis that despite its superficial resemblance to hard-object-feeding robust australopiths, *H. stenognathus* was better suited to consuming large

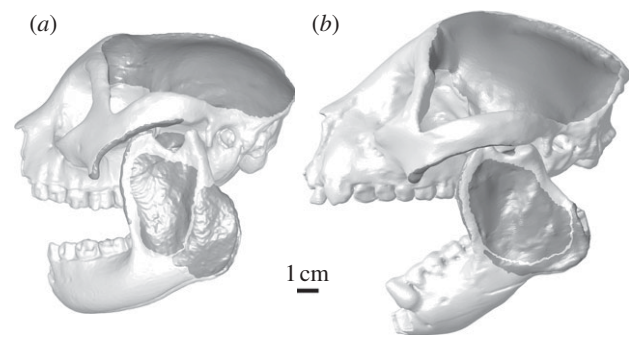


Figure 2. Estimated jaw positions at maximum gape and muscle attachment areas for (a) *H. stenognathus* and (b) *A. sp. cf. A. edwardsi*. (Additional details of muscle attachments are provided in the electronic supplementary material, figures S1 and S2.)

quantities of food items that were small or thin and displacement-limited. In keeping with data from dental morphology and microstructure as well as stable isotopes, we hypothesize that the longer-faced (relative to skull width) *A. sp. cf. A. edwardsi* was better able than *H. stenognathus* to break apart large, stress-resistant food items with its smaller, low-crowned posteriormost premolars and molars. These hypotheses lead to a series of specific and testable predictions. Relative to *A. sp. cf. A. edwardsi*, we predict that *H. stenognathus* had an absolutely narrower maximum gape, more efficient transfer of muscle to bite force (higher mechanical advantage), especially during molar biting, and lower magnitudes of bite force per unit of occlusal surface. On the other hand, relative to *H. stenognathus* we predict that *A. sp. cf. A. edwardsi* was capable of an absolutely wider gape, structurally stronger (i.e. capable of withstanding relatively higher forces) and able to deliver more bite force per unit of occlusal surface area under P4 (and perhaps also M2) loading. We tested these predictions using three-dimensional modelling and finite-element (FE) analysis, a technique recently borrowed from engineering and widely used to evaluate the biomechanical implications of morphological variation among living and extinct organisms (e.g. [19]).

2. MATERIAL AND METHODS

(a) *Specimens and digital reconstruction*

Our analyses were based on digitally reconstructed models of *H. stenognathus* [20] and *A. sp. cf. A. edwardsi* produced from medical computed tomography (CT) scans (figure 2). We used different threshold settings for extracting images from the two sets of CT scans as they were scanned in different scanners using different settings and reconstructed using different software. Although this could have introduced geometric errors into the reconstructions, we do not believe this was the case. Both sets of CT scans were of high quality, with crisp contrast between the bone surfaces and adjacent matrix and air. In addition, the surface models were extracted by experienced personnel who were supervised by experts in the anatomy of these species and the two models include comparable levels of anatomical detail.

The *A. sp. cf. A. edwardsi* skull was found in 1996 entirely embedded in flowstone on the cave floor at Anjohibe [21]. When the flowstone matrix was removed, the skull and

mandible were nearly whole. They were scanned on the HD350 CT scanner (Universal Systems, Cleveland, OH, USA) at the Center for Quantitative Imaging (CQI) at Penn State University. The cranium and mandible were scanned together at 130 kV and 100 mA with an inline pixel size of 0.293 mm and a slice thickness of 1.0 mm, resulting in a dataset of 281 slices. Reconstructions were completed using MIMICS v. 13.0 (Materialise, Ann Arbor, MI, USA) and GEOMAGIC STUDIO v. 12.0 (Research Triangle Park, NC, USA) to extract and edit a surface model.

Details of the scanning and reconstruction of the *Hadropithecus* skull can be found in [20]. In brief, the cranium of a young adult (NHMW 1934 IV 1, found at Andrahomana in 1899) was scanned in Vienna using a Philips medical CT scanner in helical mode using the ear kernel at 140 kV and 53 mA, and two orbital processes belonging to this skull but found in 2003 [20] were scanned on the HD350 CT scanner at the Penn State CQI. The entire dataset consisted of 221 slices reconstructed with a matrix size of 512×512 pixels, resulting in voxel dimensions of $0.293 \times 0.293 \times 0.40$ mm. The mandibular fragments (NHMW 1934 IV 2/1a,b) were also scanned on the Philips scanner in Vienna using the ear kernel with energy settings of 120 kV and 108 mA. The mandibular dataset consisted of 194 slices with voxel dimensions of $0.211 \times 0.211 \times 0.4$ mm. The frontals were repositioned into the Vienna cranium *in silico*, without scaling, using anatomical clues and the imaging program AMIRA 3.1.1 (Visualization Sciences Group, Burlington, MA, USA). Following reconstruction with AMIRA 3.1.1, binary stereolithography models of the cranium and mandible were extracted for cleaning with GEOMAGIC STUDIO v. 12.0.

(b) Gape estimates

For each species, we aligned the mandible as far anteriorly within the glenoid fossae as was permitted by the articular eminences while maintaining a small gap between the condyles and glenoid fossae (figure 2). The mandibles were depressed as far as possible while keeping the articular surfaces of the condyles aligned with the glenoid fossae and maintaining small spaces between the posterior edges of the ascending rami and the post-glenoid processes. We measured absolute gapes from the three-dimensional models as the distances between the P4 paracone and the anterior margin of the m1 trigonid and between the M2 paracone and the posterior margin of the m2 trigonid. Gape angle was measured as the angle included by lines drawn from each pair of points to the apex of the mandibular condyle.

(c) Finite-element model construction and analysis

From the surface models, we used MIMICS v. 13.0 (Materialise) to generate solid FE models composed of four-noded tetrahedral elements (*H. stenognathus* = 854 273 elements; *A. sp. cf. A. edwardsi* = 904 464 elements). Both cortical and trabecular bones were assigned isotropic material property values (cortical: $E = 17.3$ GPa, $\nu = 0.28$; trabecular: $E = 2.23$ GPa, $\nu = 0.28$ [22,23]). Each model was constrained from rigid body motion by fixing one node in each glenoid fossa and at the interface between either a right P4 or a right M2 and a food item [24]. We limited constraints only to those sufficient to prevent rigid body motion [25].

It is impossible to know either the absolute values of forces that were produced by the masticatory muscles of extinct animals or the bite forces that resulted. Nevertheless,

Table 1. Estimates of total masticatory muscle force (predicted total force) under three different body mass scenarios, the contribution of each muscle to total force (% of total force) and the ratio of working/balancing side muscle force applied to the models (W/B ratio). We compared the following pairs of models: an average-sized *Hadropithecus* and the estimated size of this *Archaeolemur* specimen; equal sizes (a small *Hadropithecus* and a large *Archaeolemur*); and two models in which the effect of body size on stress state was mitigated by applying equal ratios of applied force to total surface area.

	predicted total force (N)	% of total force	W/B ratio
<i>Hadropithecus</i>			
average mass = 35.4 kg	1157		
small individual = 30 kg	1374		
equal force : surface area	1374		
temporalis		62.1	1.1
superficial masseter		11.4	1.3
deep masseter		15.8	1.3
medial pterygoid		10.7	5.04
<i>Archaeolemur</i>			
average mass = 27.3 kg	1277		
large individual = 30 kg	1374		
equal force : surface area	1769		
temporalis		65.1	1.1
superficial masseter		5.3	1.3
deep masseter		19.4	1.3
medial pterygoid		10.1	5.04

data derived from living primates that describe the capacity of masticatory muscles to produce force, the osteological correlates of that capacity and the ratio of working to balancing side force production during biting permit an informed estimate of muscle forces. We began estimating the total force generated by the superficial and deep masseter, temporalis and medial pterygoid muscles by using published body mass estimates and a regression equation to predict the total reduced physiological cross-sectional area (rPCSA) of these muscles. We used the estimated mean body mass for both species (35.4 kg for *Hadropithecus*; 27.3 kg for *Archaeolemur*; both based on postcranial data), as well as an intermediate body mass (30 kg) that could have been exhibited by a small adult *Hadropithecus* and a large adult *Archaeolemur* [26]. We used a regression equation derived from platyrrhine primates [27] because these animals resemble *Hadropithecus* and *Archaeolemur* in symphyseal fusion and some have *Archaeolemur*-like molar form and microstructure, unlike living strepsirrhines. The resulting total rPCSA values were multiplied by a muscle stress value of 30 N cm^{-2} [28] to estimate total maximum muscle force production (table 1).

Perry [29] reported significant correlations between specific masticatory muscle attachment regions and rPCSA in a broad sample of strepsirrhine species. We identified the relevant muscle attachment regions (the insertion of superficial and deep masseter and medial pterygoid, and the origin of temporalis) on our three-dimensional digital models based on previous work [30] and our own inspection of fossils, casts and the digital reconstructions (figure 2; electronic supplementary material, figures S1 and S2), and used the relative size of the attachment areas reported by

Perry to partition total maximum force among the muscles (table 1). We then used published ratios of working to balancing side muscle force derived from electromyographic studies of peak masticatory force reported for *Cebus* (masseter and temporalis [31]) and *Macaca* (medial pterygoid [23]; table 1) to adjust the working and balancing side forces. Finally, we distributed muscle force vectors on the cranium directed towards the three-dimensional centroid of each muscle's insertion area on the dentary using the program CENTROID and the tangential traction option in the program BONELOAD v. 6.0 [32] (programs available on www.biomech.org and upon request from E.R.D.).

We compared the relative performance of the two models during separate simulations of unilateral biting with the P4 and M2 at the maximum gape angle using two performance metrics: von Mises stress and mechanical advantage. von Mises stress addresses the concept of structural strength by providing a metric that reflects the ability of structures composed of ductile materials to resist fracture. We compared the average magnitude of von Mises stress in *Archaeolemur* relative to *Hadropithecus* in seven anatomical regions: the zygomatic arches, the superolateral orbital margins and post-orbital bar, the inferomedial orbital margins and the frontals. Mechanical advantage was calculated simply as bite force (reaction force in the z -direction at the P4 or M2 constraint) divided by muscle force. Higher ratios of mechanical advantage indicate more efficient transfer of muscle force into bite force. Bite force at the P4 and M2 was divided by the area of these teeth (length \times width) in *Archaeolemur* and *Hadropithecus* to estimate force per unit of occlusal surface area.

We solved the models in three ways: for their estimated mean size, their range of size overlap and with size 'removed'. Given the importance of bite force in feeding ecology [33] and the general interest in estimating bite forces in extinct animals, we recorded bite force derived from the first two analyses. However, because there is uncertainty in estimating body mass and muscle forces in fossils, no matter how carefully it is done, we also took the conservative approach of comparing von Mises stress between the two models based solely on their shapes. We did that by using identical ratios of applied force to total surface area (table 1) [34]. This allowed us to assess the impact of differences in morphology on structural strength without regard to model size. The loaded FE models, along with still images and videos of the analysis results, are archived and freely available on www.biomech.org.

3. RESULTS

(a) Gape

We found marked differences in gape at both P4 and M2. *Archaeolemur* sp. cf. *A. edwardsi* had a larger estimated maximum gape angle (28° versus 17°) and an absolutely wider gape at P4 (29.5 versus 19.0 mm). *Archaeolemur* sp. cf. *A. edwardsi* also had a higher maximum gape angle at M2 (25° versus 14°) and, again, a similarly wider absolute gape (20.8 versus 13.1 mm). The magnitudes of these differences clearly demonstrate that *A. sp. cf. A. edwardsi* was capable of a much wider absolute gape than was *H. stenognathus*.

(b) Structural strength

In the analyses of the models at estimated body size, the lower von Mises stress values exhibited by the *A. sp. cf.*

A. edwardsi model under both loading conditions indicate that it was structurally stronger than that of *H. stenognathus* (figure 3 and table 2). The magnitudes of stress during P4 biting were most divergent in the superolateral aspect of the orbit and post-orbital bar on the working side and the temporal region of the balancing side. Stress contours and average von Mises stress under M2 loading also revealed a large discrepancy in stress magnitude between the two models (figure 4 and table 2). *Hadropithecus stenognathus* exhibited higher stress than *A. sp. cf. A. edwardsi* on both the working and balancing sides. Higher magnitudes of stress in the *Hadropithecus* model were also present in comparisons at equal intermediate body mass. In comparisons of models adjusted for size, stress values in *Hadropithecus* and *Archaeolemur* were similar under P4 loading, but *Hadropithecus* again displayed higher stresses under the M2 loading regime. (Note that because all analyses were linear, the patterns of stress distribution did not vary among comparisons; only the magnitudes changed.)

(c) Mechanical advantage

A comparison of mechanical advantage (bite force/muscle force) confirmed that *H. stenognathus* exhibited 16 per cent higher mechanical advantage than *A. sp. cf. A. edwardsi* during molar biting (table 3). Despite marked differences in facial structure between the two species, mechanical advantage differed little between them during P4 biting. Overall, *H. stenognathus* exhibited a more substantial increase in mechanical advantage at M2 relative to P4 (39%) than did *A. sp. cf. A. edwardsi* (32%). Given its higher mechanical advantage, the *Hadropithecus* model returned higher bite force estimates at both body sizes and under both loading regimes (P4 bite force: *Hadropithecus* at 35.4 kg = 421 N, *Hadropithecus* at 30 kg = 371 N; *Archaeolemur* at 27.3 kg = 321 N, *Archaeolemur* at 30 kg = 345 N; M2 bite force: *Hadropithecus* at 35.4 kg = 682 N, *Hadropithecus* at 30 kg = 602 N; *Archaeolemur* at 27.3 kg = 474 N, *Archaeolemur* at 30 kg = 510 N). However, when bite forces were divided by P4 and M2 area, values for *Archaeolemur* were consistently higher (10 and 11% at estimated body size; 30 and 34% at 30 kg).

4. DISCUSSION

The narrow gape, relatively low structural strength, high mechanical advantage in M2 loading and lower bite force per unit of occlusal area of the *H. stenognathus* model support the hypothesis that this species was well-suited to processing large quantities of small and/or flat, displacement-limited foods. Rather than invoking a diet of resistant, stress-limited foods, we suggest that the pitting found on the molar teeth of *H. stenognathus* was caused by either exogenous grit [35] or biominerals [36]. One possibility is that *Hadropithecus* ate underground storage organs (USOs) of C₄ plants (see also [20]). *Hadropithecus* lived in environments in which the bulbs and corms of grasses and sedges could have sustained it through the portions of the year when the leaves turn brown and lose their nutrient content—much in the way that Amboseli baboons (*Papio cynocephalus*) spend up to 70 per cent of their time foraging on the small USOs of grasses [37,38]. The consumption of large quantities of bulbs and corms compensates for their

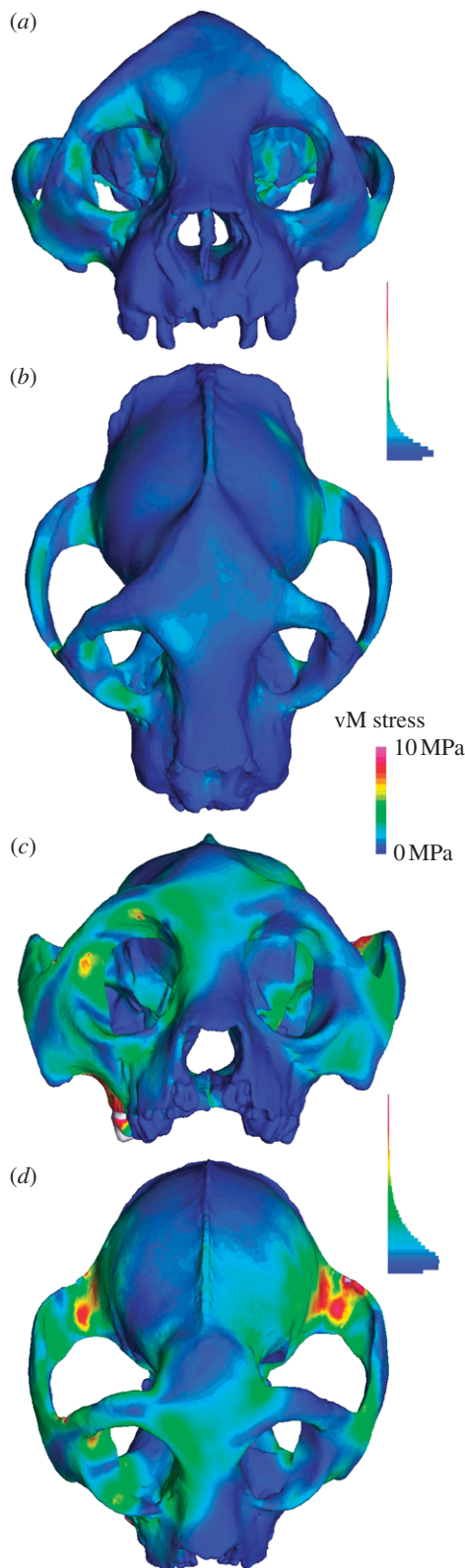


Figure 3. The predicted distribution of von Mises stress in models of (a,b) *A. sp. cf. A. edwardsi* and (c,d) *H. stenognathus* during P4 biting at maximum gape. These models were scaled to predicted body size. Histograms illustrate the distribution of stress across the volume of each model. White areas indicate stresses that exceed the maximum value depicted in the stress histogram (10 MPa). These differences persisted but were smaller in magnitude when the models were scaled to equal body size and when equal ratios of applied force to total surface area were used in order to remove the effects of size on the stress results [34].

Table 2. A comparison of average von Mises stress of the *Hadropithecus* and *Archaeolemur* models at estimated body sizes in seven anatomical regions and under premolar (P4) and molar (M2) loading. Values represent the percentage of stress in *Archaeolemur* relative to *Hadropithecus* (i.e. values under 100 indicate that *Hadropithecus* was more stressed than *Archaeolemur*).

anatomical region	P4	M2
working side		
zygomatic arch	59	67
superolateral orbit and post-orbital bar	37	43
inferomedial orbit	56	66
balancing side		
zygomatic arch	50	51
superolateral orbit and post-orbital bar	64	77
inferomedial orbit	60	62
forehead	57	47

low nutritional quality. Materials testing has recently demonstrated that USOs exhibit a wide range of material properties [3]. As Dominy *et al.* [3] point out, while rhizomes are stiff and tough, other USOs are more compliant and less tough. Bulbs and corms of C_4 grasses and sedges fall into the latter category; tubers exceed bulbs and corms in fracture toughness. A diet of C_4 bulbs or corms is consistent with the strong C_4 signal provided by carbon isotope analyses of *Hadropithecus* material [10,14,15,39]. Among other primates, USOs of grasses are processed by baboons whose molars have enamel comparable in relative thickness to that of *Hadropithecus* [40].

A second possibility is that *Hadropithecus* consumed the leaves or roots of succulent CAM plants [15,41]. In fact, once they are corrected for trophic enrichment, the combined stable carbon and nitrogen isotope values of *Hadropithecus* more closely match those of some CAM plants (e.g. *Alluaudia procera*) that are very common in the spiny thickets of southern Madagascar than they do the grasses or sedges measured thus far, whose stable nitrogen isotope values are too low (B. E. Crowley 2010, personal communication). Unlike the leaves of grasses, succulent leaves of many CAM plants are available year-round in the arid south. Thus, for example, despite the dry season dormancy, which causes *Alluaudia* to drop its mature leaves, young leaves emerge at the height of the dry season. The leaves of succulent plants such as *Alluaudia* have mechanical defences against herbivory [42], which could have caused heavy microwear pitting. Whether *Hadropithecus* ate bulbs, corms or leaves, these foods are nutrient-poor and large quantities may have been required to meet its nutritional needs.

In contrast to *H. stenognathus*, the absolutely wider gape, relatively higher structural strength of the skull and higher bite force per unit of P4 and M2 occlusal surface area in *A. sp. cf. A. edwardsi* suggest that it was well equipped to break apart large, stress-limited food items. This, in conjunction with its C_3 diet, low-relief molars, very thick and heavily decussated molar enamel, and the presence of woody fruit exocarps and parts of seeds in coprolites ascribed to it [43], is consistent with the inference that it consumed large, stress-limited fruits and/or seeds at least facultatively, and perhaps as staple

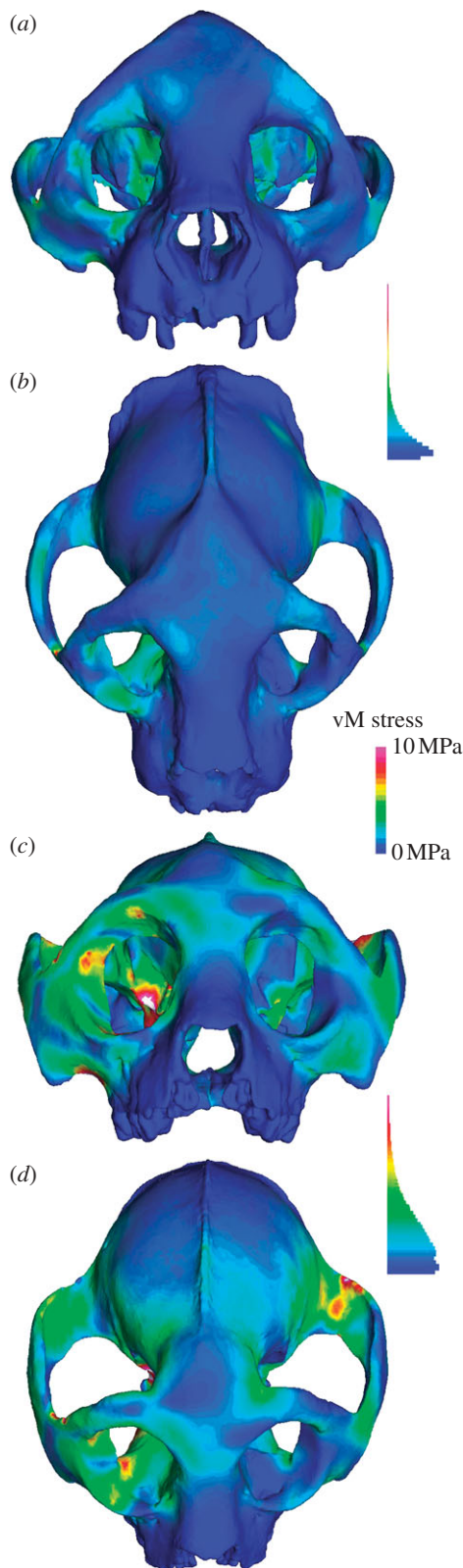


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Table 3. A comparison of mechanical advantage (bite force/muscle force) in models of *Archaeolemur* and *Hadropithecus* at maximum gape during simulated P4 and M2 biting. Higher values indicate greater mechanical advantage. The percentage differences in mechanical efficiency between the two species under each loading condition (difference) and the percentage increase in efficiency of M2 over P4 loading within each species (increase P4 to M2) are also reported.

loading condition	<i>Archaeolemur</i>	<i>Hadropithecus</i>	difference
P4	0.25	0.27	7%
M2	0.37	0.44	16%
increase P4 to M2	32%	39%	

resources. Even in the most arid regions of Madagascar, trees yielding such fruits have C_3 photosynthesis [15].

Our data affirm that the processing of foods that require heavy mastication but little incisal preparation may have influenced the evolution of hominin-like dental and facial features in *Hadropithecus*. However, the broader implication of our research is that the length of the face *per se* has little bearing on the material properties of foods consumed; short-faced species (such as *Hadropithecus*) did not necessarily consume stress-limited foods, while longer-faced animals (such as *Archaeolemur*) may well have. Species with short, hominin-like faces may be mechanically efficient, but those capable of generating and withstanding high bite forces should also exhibit relatively low von Mises stresses. Controversy still reigns over the diets of short-faced hominins (e.g. [1,6,8,9]); our data affirm that gross morphological clues can be inconclusive.

Our data also affirm that one must be careful in using microwear to assess diet, as heavy pitting can result from a variety of causes [35]. Dental microstructure (relative enamel thickness, enamel prism decussation) and antemortem chipping may be more informative. In the case at hand, *Hadropithecus* has relatively thin enamel while *Paranthropus* has exceptionally thick enamel. A specialized diet of bulbs or succulent leaves for *Hadropithecus*, as well as the inclusion of harder USOs and other mechanically resistant foods in the diets of robust australopithecids, might explain both their observed differences in molar microstructure and similarity in facial architecture.

This work was supported by NSF DBI-0743460. We thank I. Grosse for many discussions about FEA, D. Pulaski for help with model development, and W. Jungers and two anonymous reviewers for thoughtful and constructive criticisms. The *Archaeolemur* specimen was prepared by V. Heisey, Stony Brook University. Field discoveries of the skull and mandible of the *Archaeolemur* and portions of the skull of the *Hadropithecus* used here were supported by NSF grants SES-8912867, BSR-9025020 and DEB-9306603 to D. A. Burney, and BCS-0129185 to D. A. Burney, L.R.G. and W. L. Jungers. We thank A. Walker for general assistance during the reconstruction of the skull and mandible of *Hadropithecus*, U. Göhlich for providing access to the *Hadropithecus* skull and mandible in Vienna, G. Weber for CT scanning the material in Vienna, and C. Shaw for transporting specimens. We also thank Dr H. Imhof and S. Plischke (University Clinic for Radiology, Medical University of Vienna) for help with the CT scanning. High-quality casts were made in Vienna by

A. Fürtst and A. Englert. Scanning in Vienna was supported by a grant from the European Union (MRTN-CT-2005-019564).

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