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Experimental Perspective on Fallback Foods and Dietary Adaptations in Early Hominins

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Short title: Fallback Foods and Hominin Evolution

1   The robust jaws and large, thick-enameled molars of the Plio-Pleistocene hominins

2   *Australopithecus* and *Paranthropus* have long been interpreted as adaptations for hard-object

3   feeding. Recent studies of dental microwear indicate that only *Paranthropus robustus* regularly

4   ate hard items, suggesting that the dentognathic anatomy of other australopiths reflects rare,

5   seasonal exploitation of hard fallback foods. Here we show that hard-object feeding cannot

6   explain the extreme morphology of *Paranthropus boisei*. Rather, analysis of long-term dietary

7   plasticity in an animal model suggests year-round reliance on tough foods requiring prolonged

8   postcanine processing in *P. boisei*. Increased consumption of such items may have marked the

9   earlier transition from *Ardipithecus* to *Australopithecus*, with routine hard-object feeding in *P.*

10   *robustus* representing a novel behavior.

11

1. Introduction

The australopiths (genera *Australopithecus* and *Paranthropus*) represent the earliest well-documented diversification of the hominin lineage and include the ancestor of our own genus, *Homo* (Fig. 1) [1]. Understanding the paleobiological and phylogenetic implications of phenotypic variation in this group is therefore a critical step in the study of human origins [2-4]. Australopiths were characterized by numerous apomorphic craniodental features—including robust jaws and large postcanine teeth with thick enamel caps—that have long been interpreted as adaptations for countering powerful masticatory stresses associated with a diet of mechanically challenging foods, particularly hard objects [5-8]. However, this scenario has been challenged by recent studies of dental microwear, which have failed to detect signs of routine postcanine processing of hard items in most australopiths [9-11].

One hypothesis invoked to explain this discrepancy between anatomy and microwear is that australopith craniodental adaptations reflect hard fallback foods critical to surviving seasonal periods when easier-to-process preferred resources were scarce [9-10]. Accordingly, the dearth of fossil australopith teeth preserving evidence of hard-object consumption simply reflects the rarity of such fallback items [12] in the diets of these hominins. However, the role of dietary seasonality in shaping the masticatory apparatus of primates and other mammals is unclear. Indeed, there is little evidence that the highly robust jaws of the australopiths *Paranthropus robustus* and especially *P. boisei* would be required of an organism that relies only seasonally on mechanically challenging foods [13]. Here we report the results of a long-term diet-manipulation experiment conducted using an animal model that examines adaptive plasticity [14,15] in craniomandibular development vis-à-vis temporal variation in food mechanical properties. Our naturalistic, longitudinal data provide a novel perspective on debates over early hominin

1   paleoecology and have significant implications for understanding phenotypic variation in extant

2   and fossil species that experience resource seasonality.

3

4   **2. Materials and Methods**

5   White rabbits (*Oryctolagus cuniculus*) exhibit several characteristics that make them

6   excellent models for investigating questions regarding masticatory biomechanics in primates,

7   including a vertically deep face; a temporomandibular joint situated high above the occlusal

8   plane, capable of rotational and translational movements; intracortical bone remodeling; and a

9   similar pattern of covariation among jaw-muscle activity, jaw loading, and dietary properties

10   [16-20]. Our sample contained 30 five-week-old weanling male rabbits divided equally into three

11   dietary cohorts and raised for 48 weeks. *Control* subjects were fed a diet consisting solely of

12   rabbit pellets. *Annual* rabbits were given hay in addition to pellets throughout the experiment,

13   starting with two hay cubes daily for the first 18 weeks and then six hay cubes daily for the next

14   six weeks. This 24-week schedule was then repeated. *Seasonal* rabbits received pellets and three

15   hay cubes daily for the first six weeks and were then switched to an all-pellet diet for the

16   subsequent 18 weeks, mimicking seasonal reliance on fallback foods. This schedule was repeated

17   in the final 24 weeks.

18   The mechanical properties of these diets fall within the range of values for foods ingested

19   by wild primates [21,22]. Hay and pellets result in similar levels of bone strain along the rabbit

20   mandibular corpus [16]. However, hay is stiffer than pellets [22] and therefore presents a greater

21   masticatory challenge characterized by longer loading durations and greater cyclical loading.

22   Compared to pellets, hay takes rabbits approximately three times as many chewing cycles and,

23   correspondingly, three times longer to process (Ravosa *et al.*, unpublished data). Dynamic

1   alterations in dietary behaviors related to differences in the properties of experimental foods are

2   posited to induce osteogenic responses and corresponding ontogenetic changes in the proportions

3   of the feeding apparatus [17,22,23].

4   Each animal was imaged using micro-CT (Bioscan/Mediso X-CT; settings: 70 kVp,100

5   µA, with 71-µm reconstructed isometric voxel size) upon arrival and every two weeks thereafter

6   until Week 24, when they became too large to image. Rabbits were imaged a final time following

7   sacrifice at Week 48. This data set allowed us to track skull development longitudinally from

8   weaning to mature adult stages. Using the segmenting tools available in the program *PMOD*, we

9   quantified bone cross-sectional areas at three mandibular sites (symphysis, condyle, corpus) and

10   one on the cranium (palate) involved in load resistance during chewing. To control for

11   differences in organismal size that may confound our ability to detect a dietary signal among

12   cohorts at a given age, shape ratios were computed by dividing the square root of each subject's

13   cross-sectional area at a given time point by its cranial length. These ratios were logged for

14   analysis. Statistical comparisons were performed using the bootstrap to generate confidence

15   intervals for differences between groups [24]. A more detailed description of the measurements

16   and procedures is available in the electronic supplementary material.

17

18   **3. Results**

19   Mean shape ratios for the three dietary cohorts were statistically indistinguishable at the

20   onset of the experiment (Week 0). By Week 6, *seasonal* and *annual* rabbits had significantly

21   greater shape ratios at all sites—indicating relatively larger cross-sectional areas—than *control*

22   rabbits, while being similar to each other (Table 1, Fig. 2). *Annual* and *seasonal* rabbits diverged

23   rapidly following the latter's shift to a less-challenging all-pellet diet after Week 6. By Week 12,

1   means for the *annual* cohort were significantly larger than those for the *seasonal* and *control*

2   cohorts at three of the four sites. Notably, *seasonal* rabbits differed from *control* animals only in

3   relative palatal cross-sectional area. This general pattern persisted, with slight differences,

4   through the first half of the experiment (Week 24) and characterized the final set of comparisons:

5   at Week 48, *annual* rabbits had significantly larger symphyseal, palatal, and corporal relative

6   cross-sectional areas than *seasonal* and *control* groups; the latter two cohorts differed only at the

7   symphysis (*seasonal > control*). Ratios for the *annual* group at this stage were 6–17% and 4–

8   11% larger than the ratios for the *control* and *seasonal* groups, respectively. Such differences fall

9   within the range of variation observed in closely related primate species that differ in diet

10 (electronic supplementary material, table S4), indicating that phenotypic plasticity is likely an

11 important source of interspecific adaptive variation.

12

13 **4. Discussion**

14   Seasonal hay consumption resulted in adult phenotypes clearly distinct from those of

15 animals that ate hay throughout the experiment, but only minimally differentiated from those

16 associated with the less-challenging all-pellet diet. This finding indicates that the relationship

17 between dietary properties and craniomandibular morphology is highly dependent on loading

18 history, specifically the extent to which a structure is exposed to a behavioral stimulus during

19 development. With respect to linking australopith jaw robusticity to seasonal consumption of

20 hard objects, this observation implies that the more extreme australopiths would have relied on

21 such foods for a greater portion of the year than the more generalized species. It is notable,

22 therefore, that *P. boisei*, the apex of the australopith trend toward increased jaw robusticity [1,6],

23 presents molar microwear suggesting that it processed hard foods *less* frequently than the closely

1 related but less-specialized *P. robustus* [10,25], the only australopith with microwear consistent

2 with at least seasonal hard-object feeding [9]. Our results therefore suggest that the apomorphic

3 masticatory apparatus of *P. boisei* cannot be explained by a scenario in which this species fed

4 mainly on relatively easy-to-process foods throughout the year while relying on hard objects

5 during fallback episodes that were shorter in duration than was the case for *P. robustus*. Instead,

6 the remarkable jaws of *P. boisei* probably reflect regular consumption of items that required

7 intensive postcanine processing, resulting in masticatory stresses that exceeded those

8 experienced by *P. robustus*.

9   Considered within the broader context of australopith variation, the link between

10 morphology and markedly seasonal hard-object feeding in *P. boisei* appears even more tenuous.

11 In jaw robusticity, species of *Australopithecus* fall between *Paranthropus* and the geologically

12 older and more plesiomorphic *Ardipithecus ramidus* [1,3,4]. If the morphological differences

13 between *Ardipithecus* and basal australopiths signal an adaptive shift to seasonal exploitation of

14 hard objects in the latter, then our experimental evidence suggests that exaggeration of

15 australopith craniodental features in *Paranthropus* implies increased reliance on such items.

16 Microwear results for *P. robustus* fit this scenario, whereas those for *P. boisei* contradict it

17 [10,25]. Indeed, the microwear signatures of *P. boisei*, *Au. anamensis*, and *Au. afarensis* are

18 striking in their uniform lack of evidence for consumption of very hard or very tough items

19 [10,11].

20   The functional significance of this microwear signature remains enigmatic, but it may

21 result from prolonged milling and grinding, which would have been necessary when

22 australopiths consumed tough foods due to the fact that their low-cusped molars are not as well-

23 suited for shearing such items as are the high-cusped molars of extant folivorous primates [11].

1   Although speculative, this interpretation is supported by our results: because the microwear data

2   reject frequent hard-object feeding in *P. boisei*, this species must have masticated exceptionally

3   tough foods on a regular basis. The properties of foods eaten by species of *Australopithecus* are

4   more difficult to infer, but differences between these hominins and *Ar. ramidus* in jaw

5   robusticity, megadontia, and microwear [3,4], combined with the absence of a hard-object

6   microwear signature [11], suggests tough-object feeding [26], but not to the degree inferred for

7   *P. boisei*. We posit, therefore, that increases in jaw robusticity from *Ardipithecus* to

8   *Australopithecus* to *P. boisei* reflect progressively greater reliance on tough, probably ^{13}C-

9   enriched [27] foods and concomitantly elevated masticatory stresses due to higher repetitive

10   loading and longer load durations resulting from extended bouts of milling and grinding [11].

11   Under this scenario, the hard-object feeding evident in the microwear of *P. robustus* represents a

12   novel feeding strategy, perhaps indicating adoption of a broader niche facilitated by a

13   masticatory apparatus initially shaped by a diet of tough foods but nevertheless capable of

14   processing objects with a wide range of mechanical properties.

15

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10

15

16

1   **Table 1.** Comparisons among dietary cohorts. Significant differences in shape ratios among

2   dietary cohorts are indicated by different type styles; entries in the same style are not

3   significantly different. Alpha levels were adjusted for multiple comparisons using the sequential

4   Bonferroni method within each variable-week combination (i.e., each row). *P*-values and raw

5   data are provided in electronic supplementary material (tables S1, S2).

6

7   **Figure 1**. Cladistic relationships of selected australopiths. Only the five best-represented species

8   are shown here for simplicity, along with *Ardipithecus ramidus* and genus *Homo*.

9

10   **Figure 2.** Jaw growth in dietary cohorts. Logged (base *e*) square roots of bone cross-sectional

11   area versus mean cranial length: (a) condyle, (b) palate, (c) corpus, (d) symphysis. Each datum

12   represents a given week. Data are available in the electronic supplementary material (table S3).

13

14
15

1   Table 1

Time point	Variable	Direction of observed differences		
		Smallest		Largest
Week 0				
	Symphysis ratio	Annual	Control	Seasonal
	Palate ratio	Annual	Seasonal	Control
	Condyle ratio	Annual	Control	Seasonal
	Corpus ratio	Annual	Seasonal	Control
Week 6				
	Symphysis ratio	Control	**Annual**	**Seasonal**
	Palate ratio	Control	**Seasonal**	**Annual**
	Condyle ratio	Control	**Annual**	**Seasonal**
	Corpus ratio	Control	**Seasonal**	**Annual**
Week 12				
	Symphysis ratio	Seasonal	Control	**Annual**
	Palate ratio	Control	*Seasonal*	**Annual**
	Condyle ratio	Control	Seasonal	Annual
	Corpus ratio	Control	Seasonal	**Annual**
Week 24				
	Symphysis ratio	Control	Seasonal	**Annual**
	Palate ratio	Control	Seasonal	**Annual**
	Condyle ratio	*Control*	***Seasonal***	**Annual**
	Corpus ratio	Control	Seasonal	**Annual**
Week 48				
	Symphysis ratio	Control	*Seasonal*	**Annual**
	Palate ratio	Control	Seasonal	**Annual**
	Condyle ratio	Control	Seasonal	Annual
	Corpus ratio	Control	Seasonal	**Annual**

2

Figure 1

Ar. ramidus
Au. anamensis
Au. afarensis
Au. africanus
P. boisei
P. robustus
Homo
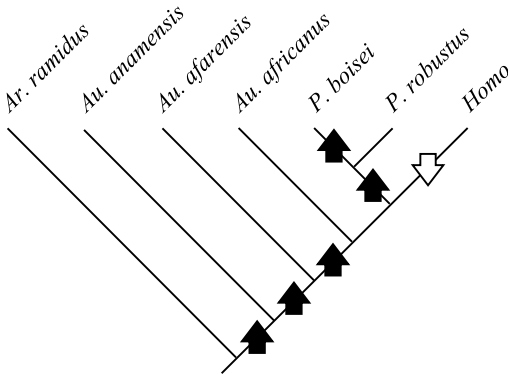
▲ Indicates increase in jaw robusticity and postcanine megadontia

▽ Indicates decrease in jaw robusticity and postcanine megadontia

Figure 2