LETTER

REPLY TO BEN-DOR ET AL.:

# Oral bacteria of Neanderthals and modern humans exhibit evidence of starch adaptation

**Christina Warinner[a,b,1], Irina M. Velsko[a], and James A. Fellows Yates[a]**

We are pleased to see Ben-Dor et al.'s interest (1) in our study on the evolution and changing ecology of the hominid oral microbiome (2), which finds that starch-adapted oral bacteria are characteristic of the oral microbiota of *Homo*. However, in their critique, Ben-Dor et al. mischaracterize our findings by asserting claims not made in our article, and their conclusion that genetic adaptations in host microbiota have no implication for understanding hominin diets reveals misunderstandings about microbial evolution and the mechanisms of amylase-binding proteins.

Ben-Dor et al. dismiss out of hand our findings of bacterial starch adaptation in the *Homo* oral microbiome, falling back on unrelated arguments about the archaeological visibility of scavenging and human capacity for gluconeogenesis to promote an extreme vision of early *Homo* diets as carnivorous. Such arguments are largely theoretical and hypothetical and do not seriously engage with the microbial evidence presented in our study.

Specifically, we do not make quantitative claims about the frequency or amount of starch consumed during early *Homo* evolution, nor do we assert that starch alone was responsible for encephalization. Rather, we show that the oral microbiome of *Homo* is distinct from that of chimpanzees, gorillas, and howler monkeys in that it contains a high abundance of starch-adapted oral streptococci and is enriched in carbohydrate-processing genes related to oral streptococci. In particular, human oral streptococci possess genes enabling them to bind and utilize host salivary amylase for nutrient acquisition and dental colonization, a trait that is conferred by multiple independent genes (e.g., *abpA*, *abpB*, *abpC*) in an example of convergent evolution (3). Among these genes, *abpA* is noteworthy because it is only expressed in the presence of both starch and salivary amylase (4), and thus it only confers a selective advantage to the bacterium in the presence of dietary starches. We find that this apparent microbial coadaptation to dietary starches is not unique to modern humans but is also present in Neanderthals, and thus is consistent with the oral availability of starches in a common ancestor (5–7). We argue that this observation has implications for understanding earlier *Homo* diets and the energetics of encephalization, and thus warrants further study.

We understand that such findings are inconvenient for models of early *Homo* carnivory, but we reject Ben-Dor et al.'s argument that such microbial evidence should be ignored. Technical advancements in archaeological science are improving our ability to recover previously understudied and less conspicuous aspects of past diets, and are increasingly uncovering direct evidence of plant material (8–11). As such, our findings contribute to a growing body of evidence that earlier *Homo* diets may have been more varied than previously appreciated, and we look forward to future evidence-based studies that further enrich our understanding of human evolution.


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**2** J. A. Fellows Yates *et al.*, The evolution and changing ecology of the African hominid oral microbiome. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2021655118 (2021).

**3** E. M. Haase *et al.*, Comparative genomics and evolution of the amylase-binding proteins of oral streptococci. *BMC Microbiol.* **17**, 94 (2017).

**4** A. E. Nikitkova, E. M. Haase, F. A. Scannapieco, Effect of starch and amylase on the expression of amylase-binding protein A in *Streptococcus gordonii*. *Mol. Oral Microbiol.* **27**, 284–294 (2012).

**5** A. G. Henry, A. S. Brooks, D. R. Piperno, Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). *Proc. Natl. Acad. Sci. U.S.A.* **108**, 486–491 (2011).


[a]Department of Archaeogenetics, Max Planck Institute of Evolutionary Anthropology, Leipzig 04103, Germany; and [b]Department of Anthropology, Harvard University, Cambridge, MA 02138

Author contributions: C.W., I.M.V., and J.A.F.Y. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no competing interest.



[1]To whom correspondence may be addressed. Email: warinner@fas.harvard.edu.

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**6** D. C. Salazar-García *et al.*, Neanderthal diets in central and southeastern Mediterranean Iberia. *Quat. Int.* **318**, 3–18 (2013).
**7** K. Hardy *et al.*, Diet and environment 1.2 million years ago revealed through analysis of dental calculus from Europe's oldest hominin at Sima del Elefante, Spain. *Naturwissenschaften* **104**, 2 (2017).
**8** K. Hardy *et al.*, Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. *Naturwissenschaften* **99**, 617–626 (2012).
**9** A. G. Henry, A. S. Brooks, D. R. Piperno, Plant foods and the dietary ecology of Neanderthals and early modern humans. *J. Hum. Evol.* **69**, 44–54 (2014).
**10** R. C. Power *et al.*, Dental calculus indicates widespread plant use within the stable Neanderthal dietary niche. *J. Hum. Evol.* **119**, 27–41 (2018).
**11** D. C. Salazar-García *et al.*, Dietary evidence from Central Asian Neanderthals: A combined isotope and plant microremains approach at Chagyrskaya Cave (Altai, Russia). *J. Hum. Evol.* **156**, 102985 (2021).