

A brief review of the recent evolution of the human mouth in physiological and nutritional contexts

Peter W. Lucas^{a,*}, Kai Yang Ang^b, Zhongquan Sui^c, Kalpana R. Agrawal^d, Jonathan F. Prinz^e, Nathaniel J. Dominy^f

^a Department of Anthropology, George Washington University, 2110 G Street NW, Washington DC 20052, USA

^b Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore

^c Department of Botany, University of Hong Kong, Pokfulam Road, Hong Kong

^d Department of Anatomy, University of Hong Kong, 21 Sassoon Road, Hong Kong

^e Wageningen Centre for Food Sciences, Diedenweg 20, 6703 GW, Wageningen, The Netherlands

^f Anthropology Department, University of California, Santa Cruz, 1156 High Street, Santa Cruz, CA 95064, USA

Received 28 November 2005; received in revised form 6 March 2006; accepted 7 March 2006

Abstract

One of the defining characteristics of humans, one that could also explain our species' success, is probably our ability to cook food. A brief review of the literature suggests several adaptations of the mouth can be interpreted to support this. All probably enhance the efficiency of the physical treatment of food in the mouth.

© 2006 Elsevier Inc. All rights reserved.

Keywords: Evolution of humans; Mastication; Starch; Stickiness

1. Introduction

What makes *Homo sapiens* distinct from all other organisms? For biological anthropologists, the search for a single distinctive characteristic with sufficient power to explain the success of our species is proving rather difficult. For a long time, tools were thought to be crucial to the geographical spread of the genus *Homo* in the last two million years. However, it is now known that some populations of all the great ape genera make and use tools of some sort [1–4] and there is also evidence for rudimentary tool use in some monkey species [5,6]. None of these primates has a geographical range that rivals ours. While no other living primate fashions stone tools, though chimpanzees make use of stones [7], the earliest archaeological site at which stone tools have been found has no representative of our genus in its bone collection [8]. It is thus entirely possible that other hominins, like robust australopithecines that were at that site, but which died out more than one million years ago, were skilled toolmakers too.

Other much-vaunted human characteristics include our brain size and distinctive mode of locomotion. Until recently, the definition of the genus *Homo* stipulated a minimum brain size (600+ cm³) for the inclusion of fossils within it. However, a dwarf *Homo* species that lived until 12,000 years ago was recently found that has a much smaller brain, similar in size to that of a chimpanzee [9]. We move bipedally, but so did all extinct hominins going back to more than six million years ago [10]. Recent evidence suggests that our genus may be distinct in being born to run, not to walk [11], but this is far from being confirmed. Accordingly, anthropologists are now looking for new definitions of humanity.

One characteristic that has gained a lot of attention in the last six years is our diet. Compared to that of other large primates, the diet of modern humans is quite extraordinary. Even human populations still reliant on hunting and gathering consume discrete meals of cooked meat, grains and root vegetables. In contrast, other large primates continually consume snacks of raw fruits and leaves [12]. This is a caricature of course – there is some overlap – but even considered in detail, the contrast is very sharp. So why, when and where did such a drastic dietary transition take place? The answer has to lie in the relative

* Corresponding author. Tel.: +1 202 994 6964; fax: +1 202 994 6097.

E-mail address: pwlucas@gwu.edu (P.W. Lucas).

abundance of food resources. Most primates lacking a fermenting gut must search for food for much of the day because the patchy distribution of resources means that they need considerable foraging time before they are satiated. In contrast, present human behavior has more in common with that of carnivores. We can restrict ourselves to brief bouts of feeding, allowing considerable time to be devoted to other matters. Undoubtedly, meat has played a role in this radical reduction in foraging time, but intensive research on hunting and gathering [13] suggests that plant foods must have been paramount in the diet.

It is now contended that, nearly two million years ago in sub-Saharan Africa, early *Homo* switched from an energy base of fruit sugars to the large starchy underground storage organs (corms, bulbs, tubers etc.) that plants often form in exceptionally dry climates. Cooking is hypothesized to have developed simultaneously as a way of improving the digestibility of such foods [14–16].

The evidence for cooking being such an ancient activity is largely indirect. A mutation in the myosin of the jaw muscles (not in any other muscle apparently) that has greatly reduced the bite force potential of humans compared to other mammals is dated to just over two million years [17]; it must certainly have occurred in Africa. Also, the fossil record documents that, by about 1.5 million years ago, there had been considerable reduction in the size of the chewing (premolar and molar) postcanine teeth [18]. Both trends are plausibly linked to the effects of cooking on food, which generally eases mechanical particle size reduction [19]. There has also been a relatively recent triplication in the salivary amylase genes in human evolution [20], which is indicative of a high starch intake.

All herbivorous mammals seem to be able to digest starches to some degree, but the enzymatic digestion of raw starches by amylases is generally low. Instead, microorganisms in the large intestine break much of it down, liberating fatty acids that can be absorbed. However, these fatty acids have a much lower energy content than the starch from which they were derived [21] and there must also be a time cost in employing microbial help. Cooking substantially increases subsequent amylase activity on starch, particularly if the food is eaten while still hot [22], and it makes sense that duplications of the amylase gene family would increase enzymatic output to assist this. The perplexing thing though is why such duplications are only expressed in the saliva, and not the pancreas.

2. Models of the mammalian gut

The whole ‘ancient cooking’ argument would be much more convincing if the above oral adaptations could be understood in relation to gut activity as a whole. The problem though is that current understanding of mammalian gut physiology seems to lack any significant involvement of the mouth. Both theoretical [23–28] and practical [29,30] models tend to lack a mouth altogether, ingestion being directly into a ‘stomach.’ The understanding of the evolution of mammalian from reptilian guts has centered on adaptations of the small intestine [31]. Yet the mouth is arguably the most distinctive feature of mammals because it is not just responsible for food ingestion and transport

to the abdominal gut, but involves considerable mechanical processing and chemoreception, as testified to by many other papers in this summit. Which of the above oral adaptations might improve the digestion of cooked starchy foods?

‘Masticatory’ myosin loss in jaw-muscle [17] must relate to the lower forces generally experienced in eating less tough cooked food. However, rather than suggest that the mutation reflects redundancy of the musculature, it is just as probable it represents the body’s need to sense forces and displacements during mastication accurately. Mammalian muscles contain muscle spindles (and sometimes Golgi tendon organs) that sense the state of a muscle contracting against a load. However, just like the load-sensing technology employed by an engineer or materials scientist, if the device is not gauged to the size of the problem, then insensitivity results. We would argue that the change in jaw muscle size reflects reduction to a scale consistent with the forces required for eating cooked food. Reduction in tooth size is more difficult to understand in a adaptationist paradigm, but Lucas [19] offers various possibilities for how tooth size should match diet. The cooking of food produces much more complex changes than just reduction in toughness, involving changes in the shape of the stress–strain relationship [19].

One of the key functions of mastication is not just to reduce food particle size, but to bind those particles together with fluid (principally saliva) into a cohesive aggregate, the food ‘bolus,’ that can be swallowed [32]. Unlike the rest of the gut, which is fluid-rich, the mouth is somewhat dry and the small particles that comminution processes produce can be difficult to clear. The bolus mechanism achieves this. Many raw plant tissues are difficult to bind together. Some leaves are like this, their surfaces often being super-hydrophobic (i.e. definitively ‘non-stick’ — [33]). The problem with cooked starch is that it is just the opposite and was used in ancient times as an adhesive because of this. Cooked starch not only sticks together, but sticks all around the mouth: starch granules can be retrieved from dental plaque and calculus, not just by dentists but also by archeologists [34]. Could the triplication of salivary amylase simply be part of an evolutionary attempt to improve the self-cleaning ability of the mouth from the completely novel threat of ingested glue? There are, of course, chemical alternatives to this physical model. Cooked starches can be digested quickly enough by salivary amylase to generate the cephalic phase responses associated with sugars [35]. However, the response to potato, the food in the study of Read et al. that most resembles the underground storage organs of the cooking model, is relatively small. Salivary amylase itself can survive the acidic environment of the stomach sufficiently to pass through into the intestines intact, so enhancing digestion [36], but it seems odd that pancreatic enzymatic output has not also been genetically expanded if that were to be the main reason to boost salivary production.

3. Conclusion

If there is a single point that a short review like this could make, it would be to advance the idea that the physical

treatment of foods in the mouth is far more important than gut physiologists and even dentists appear to realize. The principal adaptation of mammals, including humans, to the physical form of their diets is via the shape and size of their teeth. Even the most humble of teeth, the incisors, have proved amenable to analyses of their form and orientation with regards to diet [37,38]. Most of the tools made by great apes, and many of the simpler (and more ancient) tools made by humans, are or were designed as accessories for food acquisition and processing. So there is now a need to try to incorporate such physical analyses into general models of digestive rate.

References

- [1] Boesch C, Boesch-Achermann H. The Chimpanzees of Tai Forest: Behavioral Ecology and Evolution. Oxford: Oxford University Press; 2000.
- [2] Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, et al. Cultures in chimpanzees. *Nature* 1999;399:682–5.
- [3] van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, et al. Orangutan cultures and the evolution of material cultures. *Science* 2003;299:102–5.
- [4] Breuer T, Ndooundou-Hockemba M, Fishlock V. First observation of tool use by wild gorillas. *PLoS Biol* 2005;3:e380.
- [5] Chiang M. Use of tools by wild macaque monkeys in Singapore. *Nature* 1967;214:1258.
- [6] Frigaszy DM, Izar P, Visalberghi E, Ottoni EB, Gomes De Oliveira M. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *Am J Primatol* 2004;64:359–66.
- [7] Mercader J, Panger M, Boesch C. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 2002;296:1452–5.
- [8] Semaw S, Renne P, Harris JWK, Feibel CS, Bernor RL, Fesseha N, et al. 2.5 million-year-old stone tools from Gona, Ethiopia. *Nature* 1997;385:333–6.
- [9] Brown P, Sutikna T, Morwood MJ, Soejono RP, Wayhu Saptomo E, Rokus Awe Due. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 2004;431:1055–61.
- [10] Zollikofer CPE, Ponce de León MS, Lieberman DE, Guy F, Pilbeam D, Likius A, et al. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. *Nature* 2005;434:755–9.
- [11] Bramble DM, Lieberman DE. Endurance running and the evolution of *Homo*. *Nature* 2004;432:345–52.
- [12] Rodman P. Plants of the apes: is there a hominoid model for the origin of the human diet? In: Ungar PS, Teaford MF, editors. *Human Diet: Its Origin and Evolution*. Westport, CT: Bergin & Garvey; 2002. p. 77–109.
- [13] Lee RB, Devore I. *Man the Hunter*. Aldrich: Chicago; 1968.
- [14] Wrangham RW, Jones JH, Laden G, Pilbeam D, Conklin-Brittain NL. The raw and the stolen: cooking and the ecology of human origins. *Curr Anthropol* 1999;40:567–94.
- [15] O'Connell JF, Hawkes K, Blurton Jones NG. Grandmothering and the evolution of *Homo erectus*. *J Hum Evol* 1999;36:461–85.
- [16] Conklin-Brittain NL, Wrangham RW, Smith CC. A two-stage model of increased dietary quality in early hominid evolution: the role of fiber. In: Ungar PS, Teaford MF, editors. *Human Diet: Its Origin and Evolution*. Westport, CT: Bergin & Garvey; 2002. p. 61–76.
- [17] Stedman HH, Kozyak BW, Nelson A, Thesier DM, Su LT, Low DW, et al. Myosin gene mutation correlates with anatomical changes in the human lineage. *Nature* 2004;428:415–8.
- [18] Wood BA. Origin and evolution of the genus *Homo*. *Nature* 1992;355:783–90.
- [19] Lucas PW. *Dental Functional Morphology*. Cambridge: Cambridge University Press; 2004.
- [20] Samuelson LC, Wiebauer K, Snow CM, Meisler MH. Retroviral and pseudogene insertion sites reveal the lineage of human salivary and pancreatic amylase genes from a single gene during primate evolution. *Mol Cell Biol* 1990;10:2513–20.
- [21] Nugent AP. Health properties of resistant starch. *Nutr Bull* 2005;30:27–54.
- [22] Wursch P. Starch in human nutrition. In: Bourne GH, editor. *Nutritional Value of Cereal Products, Beans and Starches*. Basel: Karger; 1989. p. 199–256.
- [23] Penry DL, Jumars PA. Chemical reactor analysis and optimal digestion. *Bioscience* 1986;36:310–5.
- [24] Penry DL, Jumars PA. Modeling animal guts as chemical reactors. *Am Nat* 1987;129:69–96.
- [25] Alexander RM. Optimization of gut structure and diet for higher vertebrate herbivores. *Philos Trans R Soc Lond* 1991;B333:249–55.
- [26] Alexander RM. Optimum gut structure for specified diets. In: Chivers DJ, Langer P, editors. *The Digestive System of Mammals*. Cambridge: Cambridge University Press; 1994. p. 54–62.
- [27] Jumars PA. Animal guts as ideal chemical reactors: maximizing absorption rates. *Am Nat* 2000;155:527–43.
- [28] Jumars PA. Animal guts as non-ideal chemical reactors: partial mixing and axial variation in absorption kinetics. *Am Nat* 2000;155:544–55.
- [29] Minekus M, Marteau P, Havenaar R, Huis in't Held JHJ. A multi-compartmental dynamic computer-controlled model simulating the stomach and small intestine. *Altern Lab Anim* 1995;23:197–200.
- [30] Minekus M, Smeets-Peters M, Bernalier A, Marol S, Havenaar R, Marteau P, et al. A computer-controlled system to simulate conditions of the large intestine with peristaltic mixing, absorption of fermentation products and a high-density microflora. *Appl Microbiol Biotechnol* 1999;53:108–14.
- [31] Karasov WH, Diamond JM. Digestive adaptations for fueling the cost of endothermy. *Science* 1985;228:202–4.
- [32] Prinz JF, Lucas PW. Mastication and swallowing: an optimization model. *Proc R Soc Lond* 1997;B264:1715–21.
- [33] Neinhuis C, Barthlott W. Characterization and distribution of water-repellent, self-cleaning plant surfaces. *Ann Bot* 1997;79:667–77.
- [34] Torrence R, Barton H. *Ancient Starch Research*. Walnut Creek, CA, USA: Left Coast Press; 2006.
- [35] Read NW, Welch IMcL, Austen CJ, Barnish C, Bartlett CE, Baxter AJ, et al. Swallowing food without chewing, a simple way to reduce post-prandial glycaemia. *Br J Nutr* 1986;55:43–7.
- [36] Leblenthal E. Role of salivary amylase in gastric and intestinal digestion of starch. *Dig Dis Sci* 1987;32:1155–7.
- [37] Ang KY, Lucas PW, Tan HTW. Incisal Orientation and Biting Efficiency. *J Hum Evol* in press.
- [38] Sui ZQ, Agrawal KR, Corke H, Lucas PW. Biting efficiency in relation to incisal angulation. *Archs Oral Biol* in press.