A NOTE ON THE SCALING OF DENTAL WEAR (1)

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ABSTRACT: We know more about the nature of dental wear than has been recognized. By combining data on microwear and the scaling of tooth size we may conclude that dental wear (at least in herbivores) is mainly caused by discrete particles evenly distributed in the food.

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The evolution of hypsodonty in herbivorous mammals is one of the classic examples of adaptive evolution. However, the scaling of tooth size, including crown height, has not been well understood. This seems to be partly because the nature of dental wear has not been considered explicitly. In this paper I attempt to present a coherent model.

Contrary to assertions in the literature (Pilbeam and Gould, 1974; Gould, 1975) "metabolic" scaling of mammalian cheek teeth does not require positive allometry (Fortelius, 1985). The reason is briefly that the volume comminuted per chew is proportional to the volume enclosed between the occluding toothrows, which, ceteris paribus, is isometric to tooth size. The rate of chewing scales, as do other similar rates (such as heart rate and breathing), approximately as body mass to the power -0.25 (Fortelius, 1985). If the teeth are isometric to body size the amount of food comminuted per unit time is therefore proportional to body mass to the power 1 - 0.25 = 0.75, or to the metabolic rate. The empirical evidence is also overwhelmingly in favour of isometric scaling (summary in Fortelius, 1985).

Theoretically, crown height should also be isometric to body size for mammals that eat foods which induce equal amounts of wear, since life span scales approximately as body size to the power 0.25 (see Peters, 1983). Life-long energy (and food) requirements should scale as metabolic rate times life span, or as body mass to the power 0.75 + 0.25 = 1. Thus there is no need for higher tooth crowns to compensate for the longer life span (2). The number of chews during the lifetime of a mammal is, on average, a constant independent of body size. Recently Janis (in press) has accumulated data to show that relative crown height (hypsodonty) in ungulates shows no systematic relationship to body size. This was also the opinion of Simpson (1944). As it happens, this considerably limits the number of possible interpretations as to how food causes dental wear.

It would seem intuitively probable that dental wear during one unit action (one chew) depends on the nature of the food, the shape, size and composition of the teeth and the stress developed between the toothrows. The amount of food present, on the other hand, would not seem to be a critical variable, since wear obviously takes place only on the surface of the teeth. As long as there is enough food present to cover the occlusal surfaces the exact amount would appear irrelevant. Such a model of wear is, however, in stark disagreement with the relationships outlined above.

Consider geometrically similar pairs of occluding toothrows in several sizes but of identical composition. Between each pair is a sheet of food of unit thickness. Each pair is operated by "chewing muscles" such that a constant stress is developed in each case (3). Under these circumstances the increment of dental tissue lost from any corresponding dental surfaces must be a constant independent of size. In other words, small teeth lose as thick a layer of tissue as do large teeth. From this model of wear we must predict that animals eating the same food should have equally high tooth crowns regardless of body size. This prediction is obviously falsified by the most cursory inspection of empirical data (4).

The Gedankenexperiment above is grossly unrealistic in one regard only: in real animals the

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thickness of the sheet of food present between the occluding teeth is, on average, isometric to tooth size. If we assume that the food induces wear in proportion to its thickness, then the thickness of the wear increment will not be constant but rather isometric to tooth size.

If wear takes place only at the surface of the tooth, how can it matter how much food is present above that surface? The simplest answer is that food is not continuously wear-inducing, but contains discrete "wear particles" evenly distributed in it. As a body of such ideal food is compressed between the teeth approaching occlusion the probability of one wear particle making contact with any one point on the dental surface will be a linear function of the amount of particles present above this point, i.e., of the thickness of the food. If real foods have properties sufficiently similar to such an ideal food, then this would explain why the teeth of real animals are worn in proportion to tooth size, and therefore why crown height is, within dietary groups, isometric to body size.

Real foods, if sufficiently different, leave distinguishable wear patterns on the occlusal surfaces, especially on the enamel. The use of "microwear" patterns to reconstruct the diets of extinct species is based on this observation. An utterly homogeneous food will leave no signature on the surface that it is abrading, since the pattern of particle loss will depend only on the nature of the dental tissue. If the wear patterns are different, then the foods must contain individual particles responsible for the differences. This was perhaps implied by Rensberger (1978), when he stated that the "occlusal process" (which gives rise to occlusal wear) is made up of "occlusal events".

The particles responsible for wear may be of many kinds and sizes, and some may not be properly particles. Phytoliths are an obvious example, but others must be important, too. The role of contamination by soil and dust is unclear, but not obviously problematical.

The model appears plausible, at least for herbivores (5). It should be relatively simple to ascertain whether and how the thickness of food material between two occluding surfaces influences the amount of wear induced. Results of such experiments might prove very useful for the understanding of microwear patterns. If the model is falsified we shall have to rethink the problems of dental wear and scaling quite considerably (6).

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LITERATURE CITED

Chivers, D.J., Wood, B.A. and Bilsborough, A. (eds.) 1984. Food Acquisition and Processing in Primates. New York: Plenum Press.

Fortelius, M. 1985. Ungulate cheek teeth: developmental, functional and evolutionary interrelations. Acta Zoologica Fennica 180: 1-76.

Gould, S.J. 1975. On the scaling of tooth size in mammals. American Zoologist 15: 351-362.

Janis, C. (in press). An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preferences. In Proceedings of the VIIth International Symposium on Dental Morphology, Paris 1986 (D.E. Russell, ed.).

Peters, R.H. 1983. The Ecological Implications of Body Size. Cambridge: Cambridge University Press.

Pilbeam, D. and S.J. Gould. 1974. Size and scaling in human evolution. Science 186: 892-901.

Rensberger, J.M. 1973. An occlusion model for mastication and dental wear in herbivorous mammals. Journal of Paleontology 47(3): 515-528.

Rensberger, J.M. 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In Development, Function and Evolution of teeth (P.M. Butler and K.A. Joysey, eds.), pp. 413-438. London: Academic Press.

Simpson G.G. 1944. Tempo and Mode in Evolution. New York: Columbia University Press.

NOTES

1. This paper is a contribution from the Valio Armas Korvenkontio Unit of Dental Anatomy in Relation to Evolutionary Theory.
2. It is probably rare for dental wear to be an actually limiting factor for reproductive life span. If such is the case (following dietary or other shifts in adaptation, for example), then higher tooth crowns will be selected for, but this bears no systematic relation to body size.
3. For each food a critical stress exists at which it breaks. Lower stress is useless, and higher stress does not improve comminution but increases wear (Rensberger 1973). Presumably the actual stress generated to break any given food is approximately constant.
4. Our dental morphological terminology is (or could at least be) largely size-independent; it does not really require explicit testing to reject the hypothesis that absolute crown height is independent of body size. One of the best examples available is rhinos and hyraxes, which are quite similar in dental morphology (including relative crown height) and diet, but differ in linear body (and tooth) size by about an order of magnitude. Selenodont artiodactyls provide several similar examples. Whether crown height would be precisely isometric to body size given animals identical save for size is of course impossible to establish. Available data suggest that it would be at least nearly so (Janis, in press).
5. Morphologically similar teeth of different sizes are also found among carnivores, where dental wear is often light. Factors such as occlusal relief and depth of cutting blades relative to gape and bite size are probably important for carnivores, and indeed generally. Such factors cannot explain hypsodonty, however.
6. It is well known that there are body size-related dietary differences in many groups (the primates have been best studied in this respect; see e.g. Chivers et al., 1984). How such differences relate to other factors, particularly to chewing rate, is an interesting and unstudied problem. I offer these observations as a conceptual aid towards the study of such interrelations.