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The functional significance of wear-induced change in the occlusal morphology of herbivore cheek teeth, exemplified by *Dicerorhinus etruscus* upper molars

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Wear has traditionally been seen as a problem affecting comparability of teeth in functional analysis, and analyses have usually been restricted to single stages of wear. This paper discusses the functional implications of wear-induced change, using the upper molars of *Dicerorhinus etruscus* as an example. Wear is seen to be an integral part of tooth function and a dynamic approach to dental functional morphology is advocated as an alternative.

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1. Introduction

Wear changes the shape of all functional teeth, although some are changed rather more than others. The cheek teeth of many herbivores are particularly subject to wear, perhaps mainly because most vegetation is of a rather poor nutritive quality and has to be eaten in large quantities. As a consequence of this, most herbivores do not rely on the primary (preformed) morphology of their cheek teeth for food comminution, but on a secondary shape, produced and maintained by regulated wear. In most cases this secondary shape is not constant, but changes — anyone familiar with ageing ungulate skull material knows this well. Because of this change, functional analysis has traditionally been restricted to single stages of wear (and often single teeth: for example little-worn second molars). Sometimes this is probably the best approach and sometimes the available material does not allow any other. But often it is an unnecessary, and even potentially misleading, constraint on the understanding of tooth form.

We know that animals are able to comminute their food successfully not only at, say, peak reproductive potential, but throughout most of their lives. Thus, teeth seem to function well at most wear stages, and there is no reason to restrict analysis to any particular stage. On the contrary, since there is no a *priori* method for distinguishing between those aspects of tooth shape relating directly to food comminution and those relating to wear regulation, growth, or some other factor, a dynamic approach seems more relevant. As an example, I present a condensed analysis of wear-induced change and functional relationships in the Pleistocene rhinoceros *Dicerorhinus etruscus*.

2. Example and discussion

The Early to early Middle Pleistocene rhinoceros *Dicerorhinus etruscus* (Falconer) was a relatively brachydont animal with lophodont cheek teeth of the type found in most Rhizocerotidae. Fig. 2 shows three occlusal dimensions plotted against paracone height for a combined sample of M^1 and M^2 of this species. Each dimension is differently affected by wear. The (max) width of the phase I facet (see below) shows no significant change at all, while protoloph length increases gradually throughout. Ectoloph length first increases rapidly to its maximum as the tooth is worn in, and then slowly decreases until the base begins to wear, when decrease becomes more rapid.

These changes can be best understood in relationship to chewing. Like most mammals, lophodont rhinoceroses have a rather well developed two-phase powerstroke (see e.g. Hiiemäe 1978). Phase I involves mainly buccal contacts and has a strong dorsal component of movement, while phase II involves more lingual areas (at least for upper teeth) and horizontal or even somewhat ventrally directed movement. Of the dimensions shown in Fig. 2, ectoloph length and phase I facet width both refer to the extension and orientation of the main phase I facet complex, which thus emerges as an essentially wear-stable structure. This is in accordance with the interpretation of the buccal facets as shearing blades (see Fortelius 1981), since the main factors influencing blade function are length transversal to relative movement and the angle of the plane of contact to the force vector (Rensberger 1973).

Protoloph length increase, on the other hand, essentially reflects an increase in the phase II occlusal

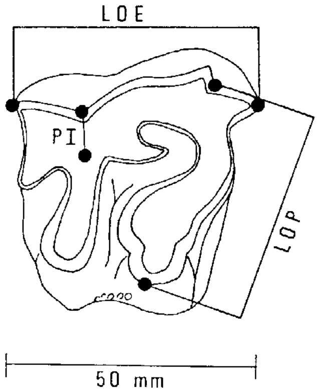

Fig. 1. M^1 of *Dicerorhinus etruscus*. LOE = ectoloph occlusal length, LOP = protoloph occlusal length, P I = phase I facet maximum length along metacone ridge. Paracone height (PAH, not shown) was measured along the paracone rib.

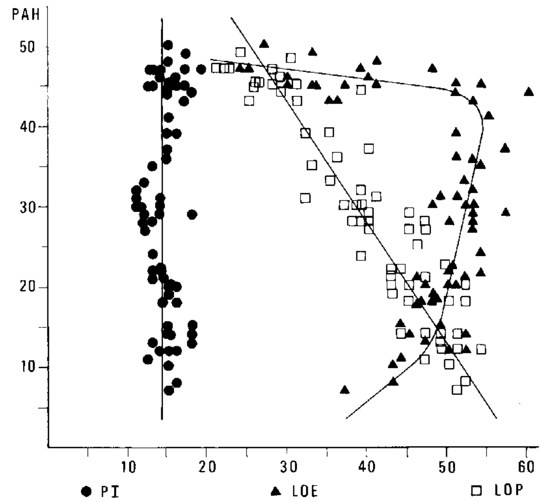

Fig. 2. Change of three occlusal dimensions with wear in a sample of M^1 and M^2, *D. etruscus*, Mauer and Mosbach (Geol. Paleont. Inst. Univ. Heidelberg, Nat. Hist. Museum Mains, Hess. Landesmuseum Darmstadt). Abbreviations as in Fig. 1, scales in mm. Straight lines are regression lines of occlusal dimensions on PAH, third curve fitted by eye. See text.

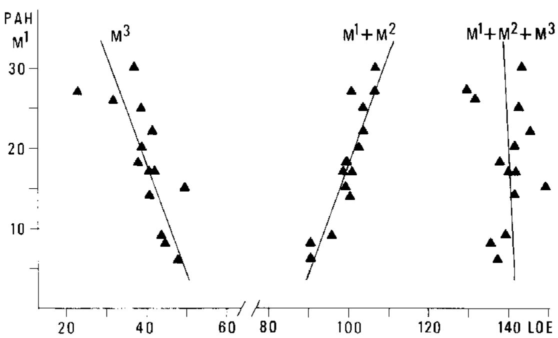

Fig. 3. Change of ectoloph length with wear in sample of associated M^1—M^3, *D. etruscus* (material as in Fig. 2). Abbreviations as in Fig. 1, scales in mm. Lines are regression lines of LOE on PAH in M^1. One sets with M^3 in wear included. See text.

area. In fact, most of the rather dramatic change during wear is due to a rapid decrease in height of the medial and lingual parts of the crown, which is what makes possible the maintenance of the stable phase I complex, as discussed by Fortelius (1982). There is relatively little direct tooth-to-tooth contact during phase II, and the so-called lingual phase I facets are also rather ephemeral phenomena in this rhinoceros. This may be taken to indicate that the lingual parts of the teeth function mainly in some way not requiring direct occlusal contact. Possibly the lingual basins function as compression chambers for rupturing cell walls, while fibre cutting takes place mainly during phase I.

The functional unit, however, is not the single tooth but the tooth row as a whole. When the upper molars are considered together (Fig. 3) it is seen that the decrease of ectoloph length observed for M^1 and M^2 (Fig. 2) is neatly compensated for by a corresponding increase at M^3. The length of the phase I blades is thus even more constant than was implied above.

3. Conclusion

In adddition to the above examples many instances of compensation and reciprocal change during wear could be cited. What has been shown, however, is sufficient to demonstrate the principle: Wear is not a problem to be somehow eliminated in analysis, it is an integral part of tooth function. The study of whole dentitions as changing systems seems at least as likely to result in an understanding of functional relationships as the traditional, more static emphasis on single wear stages. The latter often present a wealth of functionally rather incomprehensible detail, and this together with the lack of objective criteria for deciding what exactly are "comparable" stages may easily invite misunderstanding or overinterpretation.

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