

FUNCTIONAL ASPECTS OF OCCLUSAL CHEEK-TOOTH MORPHOLOGY IN
HYPSODONT, NON-RUMINANT UNGULATES

by

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SUMMARY

Hypsodonty is usually regarded as an evolutionary response to increased dental wear, and "functional" hypsodonty has been defined by VAN VALEN (1960) in terms of general tolerance to wear rather than crown height. Much less seems to be known about the function of the teeth themselves. This paper discusses the occlusal morphology of ungulate teeth in relation to the properties of foods, the principles of comminution and the process of mastication.

INTRODUCTION

Brachyodonty and hypsodonty are primarily words that describe teeth with respect to crown height. Although they are sometimes used in a purely relative sense, more often only the prism-shaped cheek teeth of some herbivores, mainly rodents and ungulates, are called hypsodont (e.g. ROMER, 1970:305; VAUGHAN, 1978:20). Hypsodonty is thus basically a morphological concept, but it has long carried strong functional implications (cf. OSBORN, 1903:106). Very often hypsodonty is interpreted as an adaptation to grass eating, "...for grass is a hard, gritty material that rapidly wears down the surface of a grinding tooth." (ROMER, 1970:305). Hypsodonty has also been regarded as a response to generally increased wear, and VAN VALEN (1960:532) proposed a "functional" index of hypsodonty, taking into account the size of the animal and the amount and wear-resistance of the exposed enamel as well as the height of the crown. Despite being somewhat difficult to use, this index is potentially a useful measure of relative wear-tolerance and of hypsodonty in that functional sense.

Increased dental wear may be caused by more abrasive food (the most common explanation), tougher food demanding higher occlusal pressures during mastication, food of a lower nutritive quality or relatively increased energy-requirements of the animal (e.g. increased body size) - the last two because the animal must chew relatively more food than before (RENSBERGER, 1975:18ff). Thus in terms of ecology or diet, the function of hypsodonty does not seem to be particularly specific.

However, the function of mastication seems to be to com-

minute food, and that of the teeth not primarily to resist wear but to serve as the vehicles of comminution. The understanding of mastication and dental functional morphology has increased considerably over the past decades (e.g. BUTLER & JOYSEY, 1978), and it now seems possible to consider the functional aspects of the occlusal morphology of hypsodont teeth apart from increased wear-tolerance.

The masticatory apparatus is only part of the digestive system, which is only part of the organism. Dental function can not be discussed successfully in isolation of its context, and tooth form can not be properly understood in functional terms alone. "Organisms are not optimizing machines; they are historical objects, constrained by inherited *Baupläne*, modes of development, and mechanical properties of building materials." (GOULD, 1980:111). Except for factors relating to wear resistance and comminution (including food transport, stable loading etc.), the enamel patterns of the occlusal surfaces are probably influenced by such things as resistance to breakage and stress distribution, as well as by ontogenetic and phylogenetic backgrounds.

Despite this complexity, or rather because of it, a certain amount of "functional reductionism" is of the essence when dental function is discussed. It is obviously impossible to observe mastication in an extinct animal, and even in living animals it is far from easy to find out what happens between the teeth during chewing. The functional principles are therefore usually inferred from form by analogy, either with other teeth or with man-made equipment. Words such as "slicing", "shearing", "shredding" and "grinding" are thus usually descriptions of inferred rather than known function, and although useful as such they are not explanations of how teeth work (LUCAS, 1979:488). Further, unless the mechanical principles involved are understood, there is always a risk that the similarity of essentially non-functional features is taken as evidence of similar function.

One of the main difficulties seems to be a general ignorance of how foods actually break (LUCAS, 1979:486), and detailed analysis must await the appearance of relevant data. The present (and somewhat hypothetical) discussion attempts to summarize briefly some data concerning the properties of foods, the dietary strategies of animals, the principles of comminution and the process of mastication, and to relate features of occlusal morphology to these. The text is primarily concerned with non-ruminant ungulates and leans heavily on rhinoceroses for examples. Ruminants, because of their fundamentally different digestive strategy (JANIS, 1976), provide interesting possibilities for comparison.

FOODS AND DIETS

Although there is some information available about both the diets of living ungulates and the chemical composition of various species of food plants (e.g. DOUGALL et al., 1964), data on the mechanical properties of plant foods seem largely to be lacking. Further, taxonomic data are not applicable as such, as differences between parts and growth stages are considerable (DOUGALL et al., 1964:88).

The food of ungulates is often referred to as either graze

(monocotyledonous plants) or browse (dicotyledonous plants) (e.g. LEUTHOLD, 1977:249). The difference, however, is perhaps not so much taxonomic as related to spatial and temporal mode of occurrence, and to nutritive and mechanical properties (cf. LEUTHOLD, 1977:249; JANIS, 1976:761f). Thus grazers are essentially animals that feed on mature grasses and similar fibrous "bulk" foods with a high cellulose content, while browsers mainly utilize more scattered "quality" foods with higher contents of soluble carbohydrates and proteins. In general terms, graze is tough, consists mainly of thin rods, and must be eaten in large quantities to provide adequate nutrition. Browse is more variable but generally softer and consists of sheets (leaves), thicker rods (twigs, branches) or bulky three-dimensional objects (fruits etc.). Because of its higher nutritive quality, browse does not have to be eaten in as large quantities as graze.

This is obviously a grossly simplified view of ungulates and

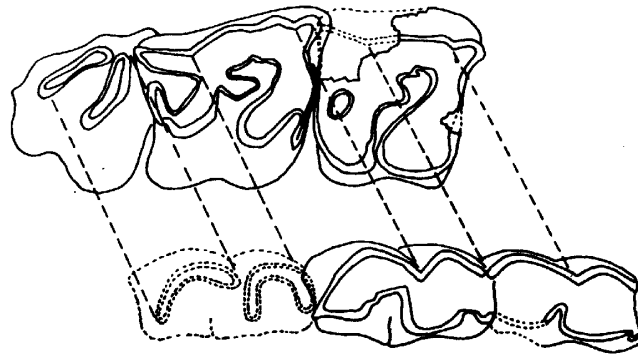


Fig. 1: Occlusal view of the right molars of a Pleistocene lophodont rhinoceros (*Dicerorhinus hemitoechus*). Dashed lines indicate the direction of occlusal motion and approximate occlusal relationships. Upper teeth above, lower teeth (reversed for pictorial purposes) below. Buccal up, lingual down. Note reciprocally curved enamel crests of upper and lower teeth.

their foods, but as will be seen it is useful for the discussion of differences in occlusal morphology.

TEETH

Crown shape is used independently of crown height as a basis for naming teeth. In ungulates, three main types are distinguished: bunodont, lophodont and selenodont. The crowns of unworn bunodont teeth are systems of cusps and cuspids that occlude in a "pestle-and-mortar" fashion (cf. LUCAS, 1979:497), but the occlusal surfaces of worn bunodont teeth are systems of dentine basins surrounded by enamel crests (the walls of the partly worn-away cusps and cuspids). As indicated by the name, the cusps and cuspids of lophodont teeth have merged into lophs and lophids, with the result that the enamel crests are longer and straighter (fig.1). Lophodont upper teeth are relatively broader than bunodont upper

teeth, and the occlusal stroke, directed anteromedial, is correspondingly longer. The enamel crests on upper teeth run in two main directions: parallel to the axis of the toothrow and posteromedial to it. The enamel in the medial parts of the upper occlusal surface is thin, and wear is concave (fig.2A,B).

Selenodont teeth *sensu stricto* occur in pecorans and tylopods, but the teeth of most hypsodont equids are also called selenodont. Whereas the teeth of selenodont ruminants may be either low-crowned or high-crowned, selenodont teeth in perissodactyls seem always to be fairly high-crowned, and the teeth of modern horses are much higher-crowned than the teeth of any ruminant. The selenodont teeth of e.g. horses are derived from lophodont ones by a rearrangement of the lophs and lophids so that all the enamel crests are orientated parallel to the axis of the toothrow. Wear resistance is more uniform, the occlusal surfaces are flat, and cementum is incorporated into the crown, which thus becomes massive. A few

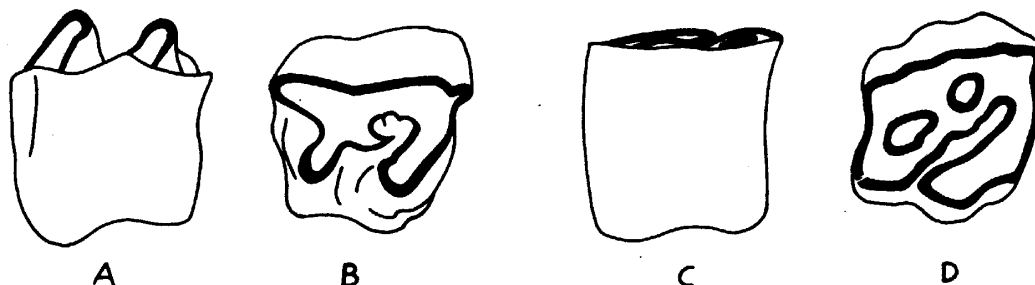


Fig. 2: Buccal and occlusal views of lophodont and "selenodont" rhinoceros first upper molars. A&B: *Dicerus bicornis*, C&D: *Ceratotherium simum*. In the former, the enamel is thin medially and the occlusal surface is strongly concave. In the latter the enamel crests are of roughly equal thickness and sub-parallel orientation, and the occlusal surface is nearly planar.

rhinoceroses (e.g. *Ceratotherium simum*, *Coelodonta antiquitatis*) have essentially similar teeth, although they are not usually called selenodont (fig.2C,D).

A selenodont tooth is clearly more hypsodont *sensu* VAN VALEN (1960) than a lophodont tooth of the same height, but the amount of exposed enamel is not the only functionally relevant difference between the two.

COMMINUTION

The enamel crests of the occlusal surfaces may be considered as blades (LUCAS, 1979:497), and plant foods may in a very general way be classified as soft solids. For a blade to divide a soft solid, it must pass completely through this, since cracks are not propagated as they are in hard solids (LUCAS, 1979:495). Com-

minution of food by blades, therefore, can only occur when tooth-to-tooth contact is achieved and when the blades are long enough to divide the entire food object.

The enamel crests of upper and lower teeth are usually reciprocally curved or arranged obliquely to each other, so that the area of potential occlusal contact, largely between these relatively slow-wearing enamel crests, is small during every instant of the stroke. Because occlusal pressure is inversely related to the area of contact, a minimal area gives a maximal pressure for a given masticatory force (RENSBERGER, 1973:518). Larger food objects are probably cut by progressive deformation as the point of contact moves along the crests (cf. ATKINS & MAY, 1979:2747).

A blade can not pass through a solid unless pressure is equal to or higher than the failure threshold of the food material. If occlusal pressure is too low, chewing will result only in deformation of the food but not in comminution (RENSBERGER, 1973:518). Tough, fibrous foods like mature grass probably require high occlusal pressures for comminution, and it is interesting to note that while wear in brachyodont rodents seems to be primarily due to food and detrital abrasion, wear in hypsodont rodents appears to result mainly from tooth-to-tooth attrition due to high occlusal pressure and great chewing activity (RENSBERGER, 1978:436).

Occlusal pressure is, of course, directly proportional to the masticatory force normal to the plane of contact as well as inversely proportional to the area of contact, and pressure is potentially different at occlusal surfaces orientated differently with respect to the direction of the masticatory force vector. Thus, except for deformation of food compressed between the teeth, which is here ignored for simplicity, three variables seem to influence occlusal pressure: the area of contact, the magnitude of the force vector and the angle between this and the plane of occlusal contact.

MASTICATORY FORCE

The masticatory force is generated by the elevator muscles of the mandible, the most important of which are the temporalis, the masseter and the medial pterygoid (fig.3)(HIIEMÄE, 1978:381).

The temporalis is said to be of relatively small importance in herbivores in which lateral movements of the mandible are essential (CROMPTON & HIIEMÄE, 1969:30). The masseter and the medial pterygoid originate rather symmetrically anteriorly on the zygomatic arch and the skull base, and insert on the outer and inner surfaces of the angle of the mandible, respectively. Thus the masseter pulls the mandible upwards, forwards and outwards, and the medial pterygoid correspondingly upwards, forwards and inwards.

Ungulates are anisognathous as a rule, and occlusion during mastication is unilateral and unidirectionally anteromedial. The part of the chewing cycle when upper and lower teeth are in contact, either directly or *via* food, is known as the power stroke. It is divided into two phases, denoted by the numerals I and II. These phases have been identified in a wide range of mammals, both directly from recorded motion and indirectly from corresponding wear facets (HIIEMÄE, 1978:371ff). The orientation of phase I and phase II surfaces on the upper tooth is given schematically in

fig.3B.

As strong contraction of the muscles on the balancing (non-occluding) side would seemingly necessarily interfere with unilateral occlusion, these probably have an essentially passive, stabilizing function (cf. HIIEMÄE, 1978:391). For simplicity, muscular activity is here discussed only on the working side. A full discussion of the motion and forces involved in mastication is possible only in three dimensions, but consideration of the horizontal and vertical components is potentially clarifying.

In an imaginary transversal section of the masticatory apparatus (fig.3B), the horizontal force components of the masseter and pterygoid have opposite directions. The vertical components of both are directed upwards, and when the plane of occlusal contact is inclined dorsomedial, as during phase I, part of the vertical force is parallel to it. This component provides the force for occlusal motion, the component normal to the plane of contact being responsible for occlusal pressure.

The masseter is generally larger and stronger than the pterygoid (BECHT, 1953:521), and it seems probable that the net force vector has an outwards component when both muscles contract maxi-

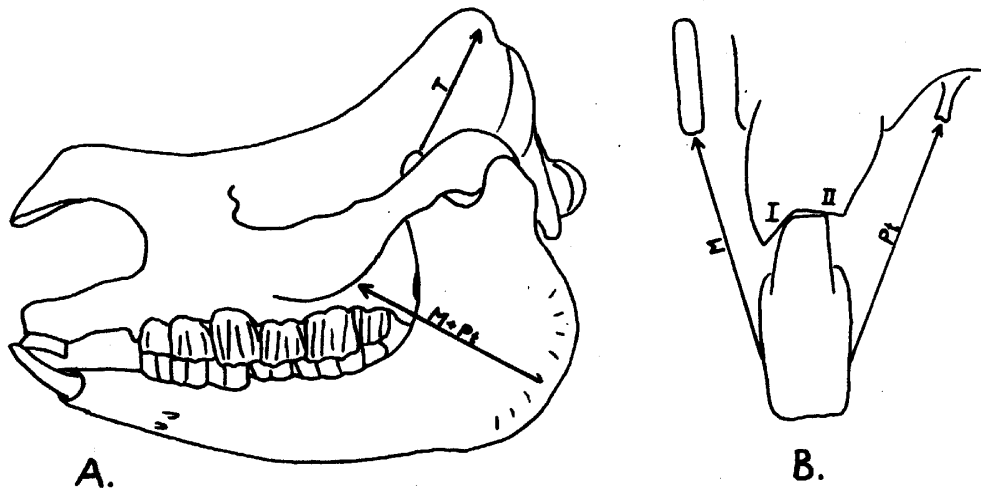


Fig. 3: Highly simplified representation of the muscular forces involved in mastication. Arrows denote only approximate direction, not magnitude. A: *Rhinoceros unicornis*, lateral view. B: Imaginary transversal section through the jaws and molars of a lophodont rhinoceros. M = masseter, Pt = medial pterygoid, T = temporalis. I and II correspond to phases of the power stroke (see text).

mally. Ventrad or ventromedial motion can not occur when the masseter is contracting strongly enough to override the inwards pull of the medial pterygoid. The fact that motion does not stop in mid-

stroke but continues from phase I into phase II indicates that the masseter is not contracting strongly during the latter. This implies less masticatory force during phase II than during phase I, and indirectly less occlusal pressure.

FUNCTIONAL IMPLICATIONS

Dental wear in the form of facets indicates contact or near-contact between occlusal surfaces (RENSBERGER, 1978:426), and thus high occlusal pressure relative to the failure threshold of the food. Phase I surfaces on the teeth of lophodont rhinoceroses or paleotheres, for instance, occur as well developed facets, whereas the phase II surfaces are morphologically more diffuse, indicating wear primarily by food abrasion and thus lower pressure. Wear is also faster buccally than lingually in some lophodont rhinoceroses (FORTELIUS, in press); and as the upper tooth is worn it gradually erupts, turning mediad on its longitudinal axis (cf. fig.4A). This accords well with the discussion of the muscular forces involved, which predicts higher pressure during phase I (above).

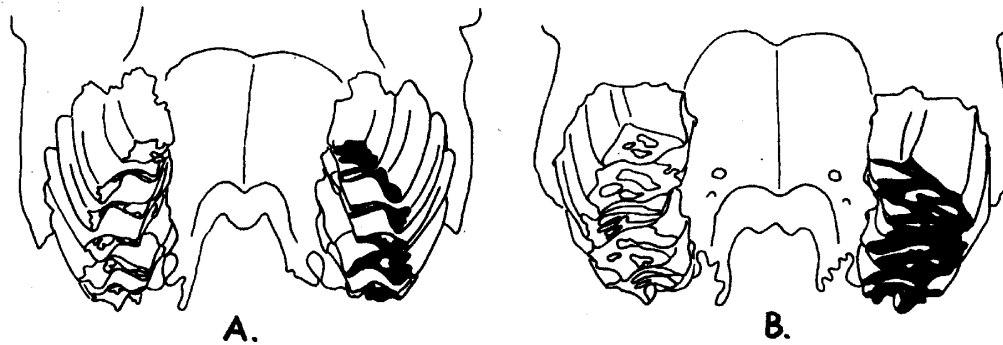


Fig. 4: Antero-inferior view of the upper cheek teeth of two rhinoceroses. A: *Diceros bicornis* (lophodont), B: *Ceratotherium simum* ('selenodont'). Occlusal surfaces shown black on the right. Note concave versus flat wear patterns and curved versus straight buccal walls. The last molar is just reaching occlusion in both dentitions. Cf. fig.2. Discussion in text.

According to JANIS (1979:56), a progressive loss of phase II occurs in ungulates as the teeth become more hypsodont. Although her phase II concept seems to be different from that of e.g. HIEMÄE (1978:368) and RENSBERGER (1978:419ff), this is probably true in principle. In forms with flat-wearing and dorsomedial inclined occlusal surfaces on the upper teeth (fig.4B), the power stroke may well be said to consist of one long phase I motion. The functional implication of this is that high pressure may be maintained during the entire power stroke.

Phase I occlusion in lophodont forms is essentially the interaction of the long blade formed by the buccal enamel crests of the lower teeth with the buccal enamel and dentine surfaces of the upper

teeth (fig.5A). Selenodont teeth have several shorter blades, parallel to each other and arranged in serial fashion (fig.5B). The number of high-pressure crest-to-crest contacts is much greater during a single stroke than in lophodont teeth, indicating that more tough food may be comminuted per stroke. On the other hand, lack of long blades probably limits the size of objects that may be cut during a single stroke. While allowing the animal to comminute sufficiently large volumes of tough, low-quality graze to maintain itself on this food, selenodontology probably also limits it to such food, as much of the browse is of unsuitable size or shape for the relatively short blades.

Ruminants do not more than cursorily masticate plants as they occur in nature, but literally "chew the cud". This pre-digested material is probably of much more uniform mechanical properties than the original vegetation, and tough tissues probably become softer. The cheek teeth of grazing ruminants are not as

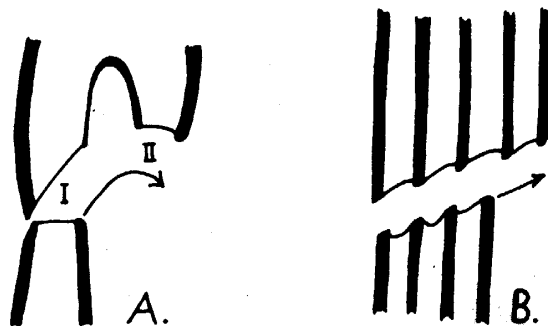


Fig. 5: Sections through idealized upper and lower lophodont (A) and selenodont (B) cheek teeth. Arrows indicate approximate path of occlusal motion. In (A) both phases of the power stroke are well developed, in (B) high-pressure phase I occlusion dominates. Note the long single-blade contact in (A), contrasting with the serial blade interaction of (B). Discussion in text.

high-crowned as those of modern horses, for instance, indicating relatively less wear. The jaws are more slender and the masticatory muscles smaller - the mandibular elevators of a bison weigh only about one third of what they do in a horse (BECHT, 1953:521). Therefore it seems that high occlusal pressure is not a characteristic of hypsodont ruminants to the same extent as it is of hypsodont non-ruminants.

CONCLUSIONS

The changes in occlusal morphology accompanying the development of hypsodontology in non-ruminant ungulates have definite functional significance apart from the increased wear-resistance. The flat-wearing, dorsomedial inclined occlusal surfaces with parallel

enamel crests transversal to the direction of occlusal motion indicate that hypsodont teeth are primarily adapted to rapid comminution of foods requiring high occlusal pressure, and that wear is primarily caused by tooth-to-tooth attrition due to the high pressure and probably great chewing activity. In hypsodont ruminants, occlusal pressure seems to be lower, and wear in these must be explained in terms of chewing activity and probably abrasiveness as well. Abrasiveness is probably a factor of some importance in non-ruminants, too, but its effect is obscured by the high occlusal pressure.

The development of the selenodont pattern usually accompanying hypsodonty in ungulates involves shortening of the long buccal blade pair characteristic of lophodonty. Functionally, lophodont dentitions are probably more versatile than the specialized selenodont ones, involving both high- and low-pressure mastication and allowing food objects of a variety of sizes and shapes to be cut and possibly otherwise broken. OSBORN (1903:106) regarded brachydonty and hypsodonty in rhinoceroses (i.e. lophodonty and selenodonty *sensu lato*) as mutually exclusive dietary adaptations. The present discussion seems to support his conclusion, although the transition may be more or less gradual and intermediates seem to exist (e.g. *Rhinoceros unicornis*). Particularly, true hypsodonty with a well developed selenodont pattern is probably more or less an exclusive grazing adaptation.

ABSTRACT

Dental functional morphology is better discussed in relation to the physical principles of food breakdown than in vague terms derived from analogy with man-made equipment. Functional analysis of the occlusal morphology of hypsodont, non-ruminant ungulates indicates that dental wear is caused primarily by high occlusal pressure during mastication and by great chewing activity, and that abrasiveness of the food is of secondary importance rather than the main cause, as is often claimed.

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REFERENCES

- ATKINS, A.G. & MAY, Y.W. 1979. On the guillotining of materials. *J. Materials Sci.* 14, pp. 2747-2754.
- BECHT, G. 1953. Comparative biologic-anatomical researches on mastication in some mammals I and II. *Proc.Ned.Acad.Wet.Ser. C* 56, pp. 508-527.

- BUTLER, P.M. & JOYSEY, K.A. (eds.) 1978. *Development, Function and Evolution of Teeth*. Academic Press, London.
- CROMPTON, A.W. & HIIEMÄE, K. 1969. How mammalian molar teeth work. *Discovery* 5 (1), pp. 23-34.
- DOUGALL, H.W., DRYSDALE, U.M. & GLOVER, P.E. 1964. The chemical composition of Kenya browse and pasture herbage. *East African Wildlife J.* 2, pp. 86-126.
- FORTELIUS, M. (in press). Ecological aspects of dental functional morphology in the Plio-Pleistocene rhinoceroses of Europe. In: Kurtén, B. (ed.): *Teeth: Form, Function, and Evolution*. Columbia Univ. Press, New York.
- GOULD, S.J. 1980. The promise of paleobiology as a nomothetic, evolutionary discipline. *Paleobiology* 6 (1), pp. 96-118.
- HIIEMÄE, K. 1978. Mammalian mastication: a review of the activity of jaw muscles and the movements they produce in mastication. In: Butler, P.M. & Joysey, K.A. (eds.): *Development, Function and Evolution of Teeth*. Pp. 359-398. Academic Press, London.
- JANIS, C.M. 1976. The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. *Evolution* 30, pp. 757-774.
- JANIS, C.M. 1979. Mastication in the hyrax and its relevance to ungulate dental evolution. *Paleobiology* 5 (1), pp. 50-59.
- LEUTHOLD, W. 1977. *African Ungulates*. 307 pp. Springer Verlag, Berlin.
- LUCAS, P.W. 1979. The dental-dietary adaptations of mammals. *N. Jb. Paläont. Mh.* 1979 (8), pp. 486-512.
- OSBORN, H.F. 1903. The extinct rhinoceroses. *Mem. Amer. Mus. Nat. Hist.* 1 (3), pp. 75-164.
- RENSBERGER, J.M. 1973. An occlusion model for mastication and dental wear in herbivorous mammals. *J. Paleont.* 47 (3), pp. 515-528.
- RENSBERGER, J.M. 1975. Function in the cheek tooth evolution of some hypsodont geomyoid rodents. *J. Paleont.* 49 (1), pp. 10-22.
- RENSBERGER, J.M. 1978. Scanning electron microscopy of wear and occlusal events in some small herbivores. In: Butler, P.M. & Joysey, K.A. (eds.): *Development, Function and Evolution of Teeth*. Academic Press, London. Pp. 415-438.
- ROMER, A.S. 1970. *The Vertebrate Body*. 4th ed., 601pp., W.B. Saunders, Philadelphia.
- VAN VALEN, L. 1960. A functional index of hypsodonty. *Evolution* 14 (4), pp. 531-532.
- VAUGHAN, T.A. 1978. *Mammalogy*. 2nd ed., 522 pp., W.B. Saunders, Philadelphia.