

13. Ecological Aspects of Dental Functional Morphology in the Plio-Pleistocene Rhinoceroses of Europe

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It has been repeatedly observed that dental function in mammals is still poorly understood. Herbivore teeth particularly have been little studied from a functional viewpoint; yet there is a slowly growing body of information on the subject (Hiemäe 1967; Crompton and Hiemäe 1969, 1970; Butler 1972; Rensberger 1973, 1975; Janis 1979; Lucas 1979; and several others). The present study is an attempt to present briefly the application of such information to a specific problem, that of the ecological adaptations of the rhinoceroses of the European Plio-Pleistocene. Only the main results are given here; the methods and data will be presented later in another context, together with a more detailed discussion.

Functional morphology is a subject tinted with a quasi-teleological jargon. In reality this is, it is to be hoped, just a convenient shorthand to avoid tedious repetition of the complex and incompletely understood processes involved in evolution. In this text teleological wording is used in this "practical" sense only. The terminology employed to describe size,

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locomotory adaptations, stratigraphy, etc. is used only in a very general sense, unless otherwise specified. The rhinoceros taxonomy has been subject to some considerable disagreement. This text follows Loose (1975) for living and most Plio-Pleistocene species, otherwise "common usage."

The Plio-Pleistocene rhinoceroses have often been used as paleo-ecological indicators. "The study of the Rhinocerotidae permits prehistorians to both date the deposits and to establish the paleo-ecology of the area" (Guérin 1976:405). Yet the use of large mammals as such indicators is in many ways problematical. A case in point is that of *Dicerorhinus hemitoechus*, commonly known as the "steppe rhino" and frequently described as "hypsodont." As a matter of fact its teeth are essentially brachyodont (see p. 00), as pointed out by Osborn (1900:264)—certainly a diet of mature steppe grasses seems unlikely for this species.

The concept of the "steppe rhino" goes back to Zeuner (1934), who took it from Wüst (1922). Zeuner based his interpretation on skull morphology, not on dental criteria; yet his word is universally invoked in support of the "grazing, hypsodont steppe rhino." If this study will help to lay that unfortunate concept to rest I think it will have justified itself.

The Rhinoceros Dentition

General Features

As those of most herbivores, the cheek teeth of the rhinoceroses form a continuous row and function as a unit. In general there are three premolars (p_2^2 - p_4^4) and three molars (M_1^1 - M_3^3), which occlude in a fashion indicated in figure 13.1. The upper teeth are roughly square in occlusal view, and consist of a π -shaped arrangement of lophs: a longitudinal ectoloph and transversal proto- and metalophs (fig. 13.2a). In M_3^3 the metalop is reduced and the tooth is triangular in occlusal view (fig. 13.1, fig. 13.11). The lower teeth

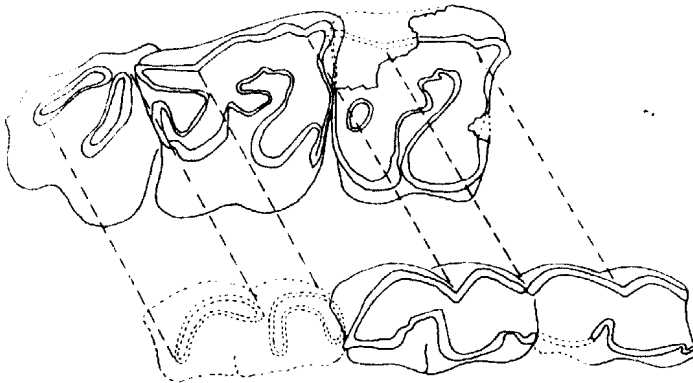


Figure 13.1. Occlusion in the molars of a rhinoceros, buccal up, lingual down.

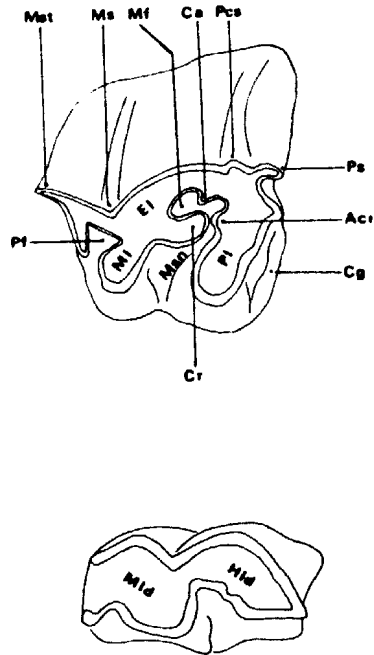


Figure 13.2. Rhinoceros dental terminology. M^2 (above) and M_2 (below).

Key: Acr = antecrochet, Ca = crista, Cg = cingulum, Cr = crochet, El = ectoloph, Hld = hypolophid, Mf = mediofossette, Ml = metaloph, Mld = metalophid, Ms = mesostyle, Msn = metaloph, Pf = postfossette, Pl = protoloph, Ps = parastyle.

are narrower, and consist of a hypo- and a metalophid behind each other (fig. 13.2b).

The occlusal motion is anteromedial and inclined upwards (fig. 13.1), as is seen from striae in the occlusal surfaces of upper teeth (fig. 13.3). The lophids of the lower teeth wear rather distinct facets into the buccal parts of the occlusal surfaces of the corresponding upper teeth. This indicates that the occlusal motion is at least loosely tracking.

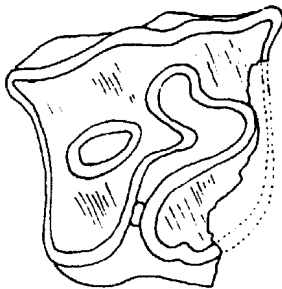


Figure 13.3. Striae in the occlusal surface of a worn M^2 dex. of *Coelodonta antiquitatis*, to show the direction of the occlusal stroke.

As most mammals investigated so far, rhinoceroses chew on one side at a time. The mandibular symphysis is firmly fused, and there is no possibility for independent movement of the two halves. During the occlusal stroke the teeth occlude only on the active side, a fact that is quite apparent even from a dried skull.

The existence of two phases of the occlusal power stroke (the part of the stroke during which the teeth are in occlusion; Crompton and Hiiemäe 1970:27f) has been argued for many primates and herbivores (Mills 1967) and for certain other groups. Kay and Hiiemäe (1974) define the two phases (I and II) as being two parts of a continuous power stroke. Janis (1979) has demonstrated, by cine fluoroscopic studies, that a minor phase II is present in *Procvavia*, but argues that, contrary to herbivorous primates, ungulates tend to reduce phase II, which may be lost altogether in grazing forms.

The power stroke of a rhinoceros is also conveniently thought of as consisting of two phases (fig. 13.4). During the stroke the masticatory force vector probably remains essentially constant (Rensberger in litt. 1979),

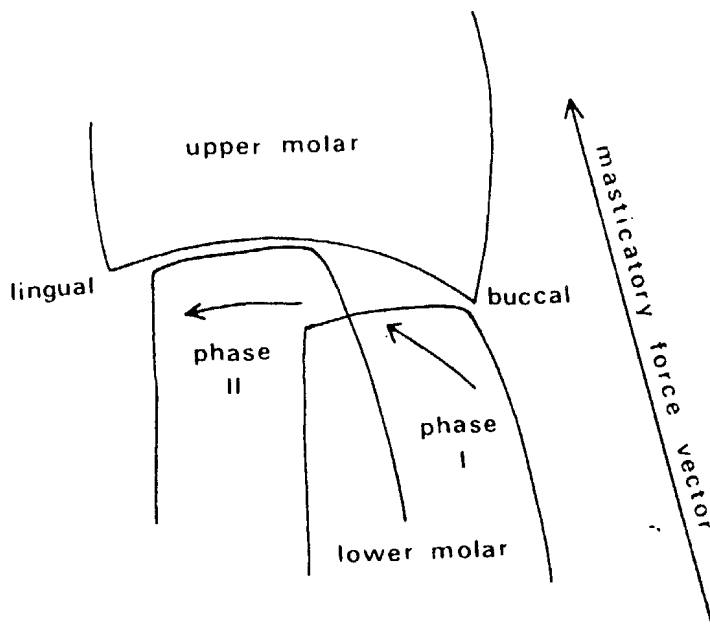


Figure 13.4. Occlusal mechanics of a brachyodont rhinoceros in relation to an imaginary masticatory force vector. The more inclined the plane of contact (and hence the path of motion) is to the force vector, the higher is the occlusal pressure and the lower the speed. As the area of contact is smaller during phase I, pressure is probably relatively uniform throughout, whereas speed is higher during phase I than during phase II. Discussion in text. Modified from sketch by John M. Rensberger.

while the motion is guided chiefly by the shapes of the occlusal surfaces, which in turn are regulated by differential wear due to structural differences, such as inequalities in enamel thickness (see below). (Naturally, the different muscular complexes involved influence the motion in different ways, and the possibility remains that the masticatory force vector varies considerably during the stroke. Rhinoceroses have well developed masseter and pterygoideus complexes, and these are important for lateral jaw movements [Crompton and Hiiemäe 1969:30]. The essentially constant masticatory force vector is used here, however, as a hypothesis with a high explanatory value.)

Initially, during phase I, only the buccal edge of the lower tooth is in contact with the corresponding upper tooth (fig. 13.4). In terms of wear facets this phase is represented by the buccal part of the occlusal surface of the upper tooth, where the ridge-and-valley structure produced by the crescent-shaped buccal edges of the lophids is clearly visible. The motion is closer to the direction of the masticatory force vector than during the following phase, and speed is high. Because of the small area of contact, pressure is probably quite high as well, and it appears that wear is fastest during phase I (see below). Further lingual, contact is made over the entire occlusal surfaces. Movement is mainly perpendicular to the masticatory force vector, and a low speed condition results. As there is a major component of masticatory force normal to the plane of contact, and the actual points of contact are few during each given moment of phase II, pressure is probably high and the comminution of food consequently efficient (Rensberger 1973:518). Phase I may perhaps be said to correspond to the shearing, phase II to the crushing/grinding component of dental function. In brachyodont dentitions both phases are well developed, whereas in hypsodont dentitions phase I is much reduced, resulting in a dominantly high pressure "grinding" type of occlusal stroke.

Words such as "cutting," "shearing," "crushing" and "grinding" have traditionally been used to describe dental function. Rensberger (1973:517) discusses the significance of these terms, and concludes that "the ability of opposing surfaces to divide food. . . seems to be a function of pressure in all four types of processes." Moreover, the function is not linear: too little pressure will only waste energy deforming the food without breaking it, while "overpressure will only needlessly wear and shorten the life of the teeth" (Rensberger 1973:517). Thus maintenance of a constant pressure during wear and consequent change in shape and area of the occlusal contact appears to be a key to understanding the functional morphology of herbivore teeth.

The jaw-joint of the rhinoceroses, as that of most herbivores, is situated above the level of the toothrows, resulting in a more equal distribution of the biting force (Crompton and Hiiemäe 1969:33) and therefore of the

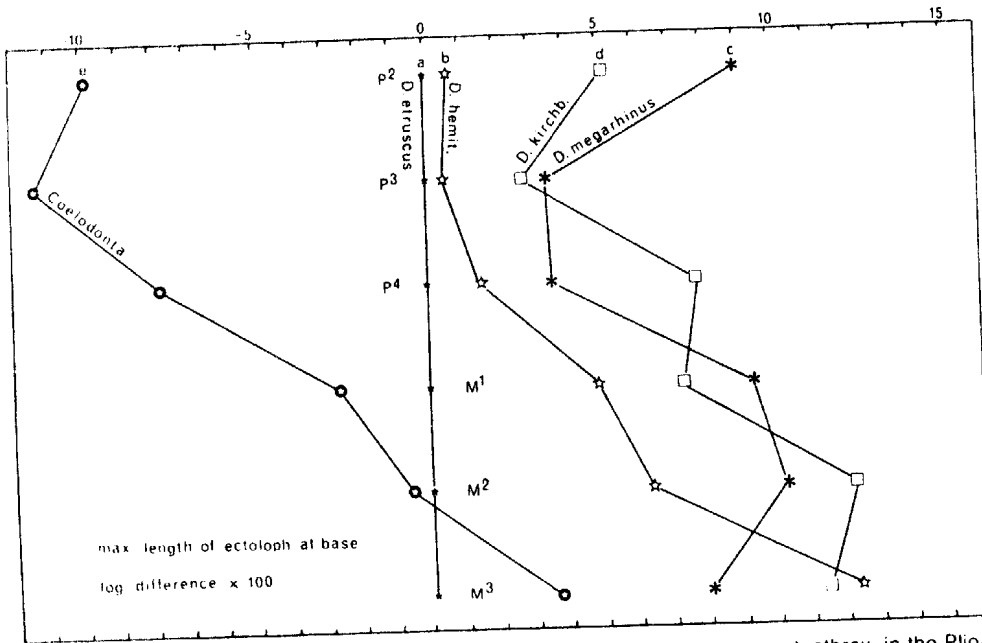


Figure 13.5. Log ratio diagram to show proportions of the upper tooththrow in the Plio-Pleistocene species discussed in the text. Note the relative enlargement of the molars in hypsodont *Coelodonta* and, to a lesser degree, in *Dicerorhinus hemitoechus*. Also note the similarity between *D. megarhinus* and *D. kirchbergensis*. Based on means of complete dentitions, except *Coelodonta* based on means of isolated teeth. From Fortelius (1979), discussion in text.

occlusal pressure. In hypsodont dentitions, where "grinding" function is important, the molars are relatively enlarged (fig. 13.5). This is related to the fact that the biting force is greatest in the posterior part of the tooththrow (close to the joint), and it means that this area is relatively more important in forms with a dominantly phase II high pressure occlusal stroke.

The terms brachyodont and hypsodont, conventionally employed to denote differences in crown height, have been used rather indiscriminately in the past, and at present they carry little information to the uninitiated reader. Usually in combinations with more, less, sub-, semi-, pseudo-, etc. they are frequently used in a relative sense only, and may even be outright misleading. (The statement "*Dicerorhinus hemitoechus* is more hypsodont than *D. etruscus* is true in a relative sense, but gives the incorrect notion that the former is hypsodont, which it is not.) The terms are used here in the sense of Osborn (1903:106), i.e., describing functionally distinct types. The morphological and structural differences between the two are summarized in table 13.1.

Table 13.1. Morphological and structural differences between brachyodont and hypsodont cheek teeth of rhinoceroses as defined in the text

<i>Brachyodont</i>	<i>Hypsodont</i>
Upper Teeth	Upper Teeth
Occlusal surface concave	Occlusal surface flat
Enamel thickness unequal	Enamel thickness uniform
Buccal and lingual walls inclined, buccal side higher	Buccal and lingual walls vertical, of subequal height
Ectoloph wear profile saw-toothed	Ectoloph wear profile straight
Secondary folds of molars separate, no mediofossette	Secondary folds of molars confluent, forming mediofossette
Styli distinct	Styli indistinct
M ³ triangular, with confluent ecto- and metalophs	M ³ square, with separate ecto- and metalophs
Lower Teeth	Lower Teeth
Lophids with crescent-shaped buccal walls	Lophids with flattened buccal walls
General	General
Crowns often lower	Crowns often higher
Cementum absent or thin ^a	Cementum thick
Enamel smooth, relatively thin	Enamel rough, relatively thick

^aNote that cementum is very capriciously preserved in fossil teeth. Rough enamel usually indicates former presence of cementum.

Brachyodont Teeth

The vast majority of the rhinoceroses have teeth that may be called brachyodont (fig. 13.6). The upper cheek teeth have characteristically projecting ectoloph edges, which form the main shearing blades of the dentition, corresponding to phase I of the occlusal stroke. The occlusal surface is concave, and the transversal lophs form a "plateau" lingually. The buccal and lingual walls slope outwards towards the base of the teeth, which are apically quite narrow.

In functional terms the key feature of the brachyodont dentition is the concave wear surface of the upper cheek tooth, which produces the shearing ectoloph edge buccally. The main factor regulating the shape of the occlusal surface is differential wear brought about (or at least influenced) by inequalities in enamel thickness: enamel is thin medially and thick buccally and lingually (fig. 13.7). In worn teeth the medial enamel ridges become thicker as the basal parts of the crown are exposed (fig. 13.8) and the relative concavity is thus decreased with wear. The functional

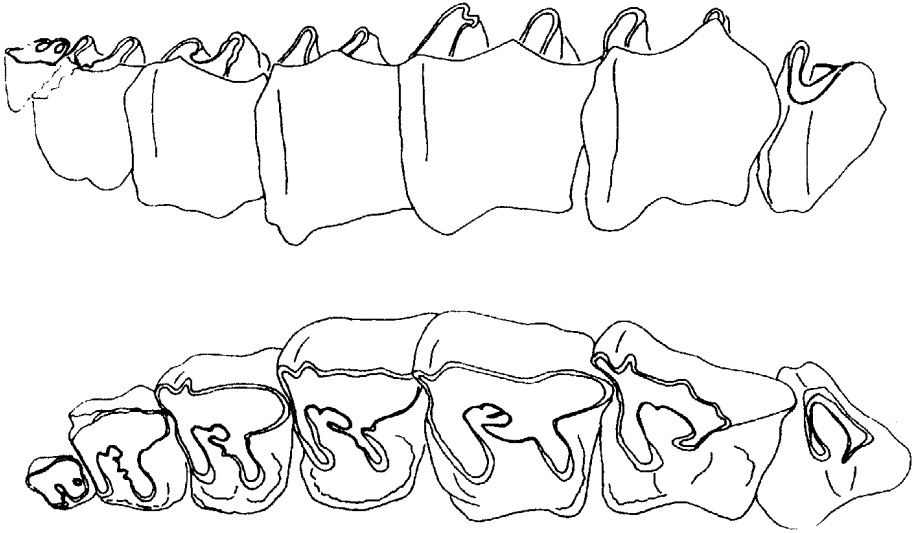


Figure 13.6. Upper cheek teeth of a brachyodont rhinoceros, *Diceros bicornis*. Buccal view (reversed) above, occlusal view below. Note the medially thin enamel ridges, the concave occlusal surface, and the saw-toothed ectoloph wear profile.

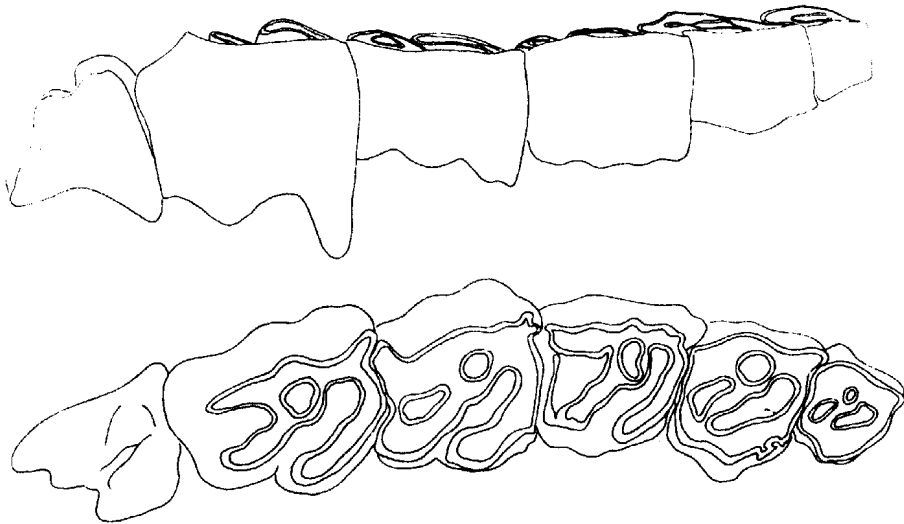


Figure 13.7. Upper cheek teeth of a hypsodont rhinoceros, *Ceratotherium simum*. Buccal view (reversed) above, occlusal view below. Note the uniform thickness of the enamel ridges, the flat occlusal surface, and the straight ectoloph wear profile.

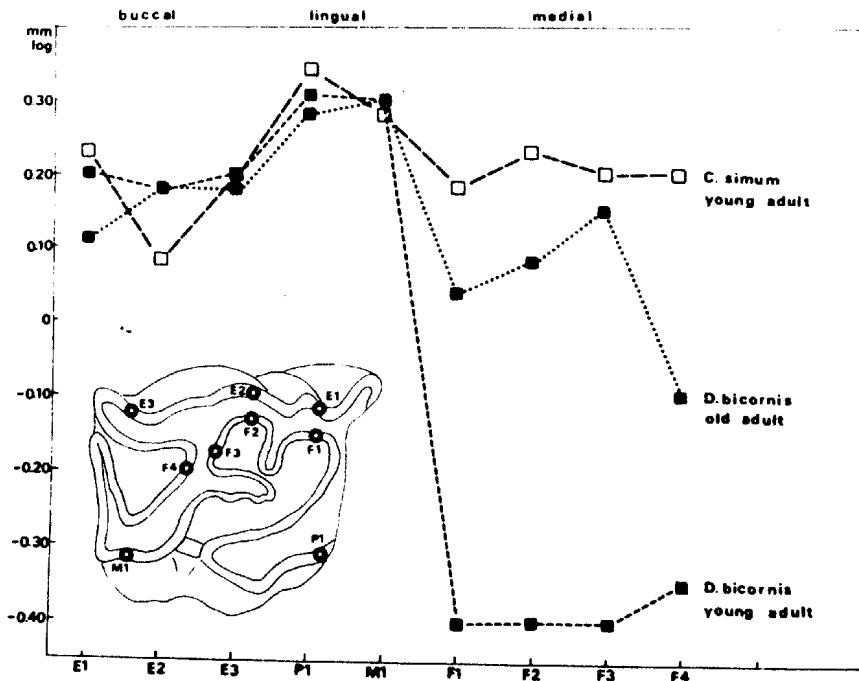


Figure 13.8. Changes in enamel thickness with wear in various parts of the crown in a brachyodont (*Diceros bicornis*) and a hypsodont (*Ceratotherium simum*) rhinoceros. In the former the medial enamel ridges become thicker with wear as the basal, thick parts are exposed, serving to reduce wear medially and to prevent exposure of the pulp cavity as well as to maintain the concavity of the occlusal surface at a functional level (see text). The "young adults" are those depicted in figures 13.6 and 13.7.

implications of this are obvious. The occlusal motion cannot, at least for any greater length, continue against the direction of the masticatory force vector. To remain functional, the upper tooth must not become too strongly concave. Moreover, if the concavity were not reduced in this way, the pulp cavity would become exposed while there was still "tooth left" buccally and lingually, which would mean a waste of dental matter and an unnecessarily reduced life span.

Wear, for some reason, is faster buccally than lingually in upper cheek teeth. Tooth morphology compensates for this. The buccal side is initially higher than the lingual side (particularly in specialized, higher crowned brachyodont species like *Diceros bicornis* and *Dicerorhinus kirchbergensis*), and the tooth is gradually rotated inwards during wear, as the curved ectoloph emerges to replace what has been worn away (fig. 13.9). This mechanism for maintaining shearing efficiency during wear is not unknown among mammals (cf. Mellett 1977:112). In senile rhinoceroses the

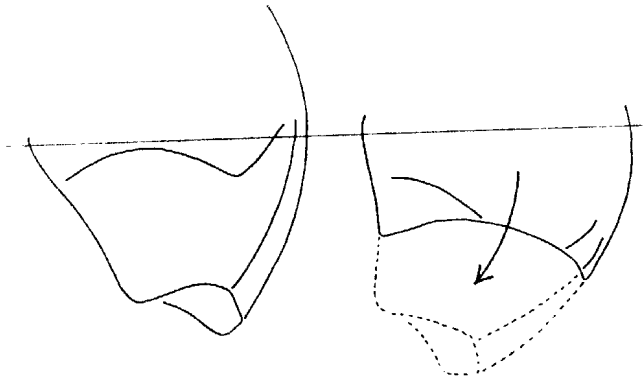


Figure 13.9. Inward rotation of a brachyodont molar to compensate for buccally faster wear and to maintain buccal shearing efficiency. anterior view (in part imaginary). Buccal right, lingual left.

teeth frequently “hang” inwards beneath the palate, showing the final stage of the process.

Brachyodont lower teeth are characterized by the smooth, crescent-shaped buccal walls of the lophids (fig. 13.1). These shear against the ectoloph edge, producing a saw-toothed ectoloph wear profile, which increases the effective length of the blade. Styli are frequently formed on the upper teeth to strengthen the structure at the critical points, and may also serve to trap food (Rensberger in litt. 1979). Cingula are frequently present when crowns are low. This may perhaps be interpreted as an adaptation to protect the gums from injury by thorns and splinters, the need for which would lessen with increasing crown height and disappear with a shift to a diet free from such components (e.g., grass).

Hypsodont Teeth

Hypsodont rhinoceros teeth differ from brachyodont teeth in having a flat, occlusal surface and a flat ectoloph wear profile (fig. 13.7). The occlusal surfaces of opposing teeth (left and right) are inclined toward each other in a tectiform fashion, much as in horses. This allows a one-phase upward-inward occlusal stroke as described below. The teeth have steep walls, and are prism-shaped in outline rather than apically constricted. Buccal and lingual sides are more equally developed than in brachyodont teeth, and the enamel is of a more equal thickness over the entire occlusal surface (fig. 13.7). Accordingly, no concave wear of the “brachyodont” kind is observed. (Interestingly, among geomyoid rodents the situation is reversed: brachyodont forms have enamel of unit thickness while hypsodont forms have strong inequalities, which in this case serve to *maintain* the

flat occlusal surface [Rensberger 1975:11f]. Function, not structure, is what differentiates the two types.)

The ectoloph edge does not project as in brachyodont teeth. Instead the wear surface is flat so that pressure is probably more uniformly high over the tooth, and on the occlusal surface there are several parallel blades (enamel ridges), which serve to comminute the food much as in modern horses (cf. Rensberger 1973:519). The molars (literally the "grinders") show the differences between hypsodont and brachyodont more clearly than do the premolars, which are relatively reduced in hypsodont forms (fig. 13.5).

Cementum, thin or absent in brachyodont teeth, is often present as a heavy coating and may fill up the fossettes, producing the characteristic wear-retarding, relief-enhancing, three-component structure found in many hypsodont forms, notably modern horses and elephants. In the Pleistocene giant rhinoceros *Elasmotherium* the cheek teeth had continuous growth, the enamel was plicated, and cementum filled all cavities (fig. 13.10d). In molar development this rhinoceros is rivaled only by a few rodents, being by far the most hypsodont of all large herbivores.

Particularly in the upper molars the effective length (perpendicular to the occlusal motion) of the enamel ridges is increased by the formation of the

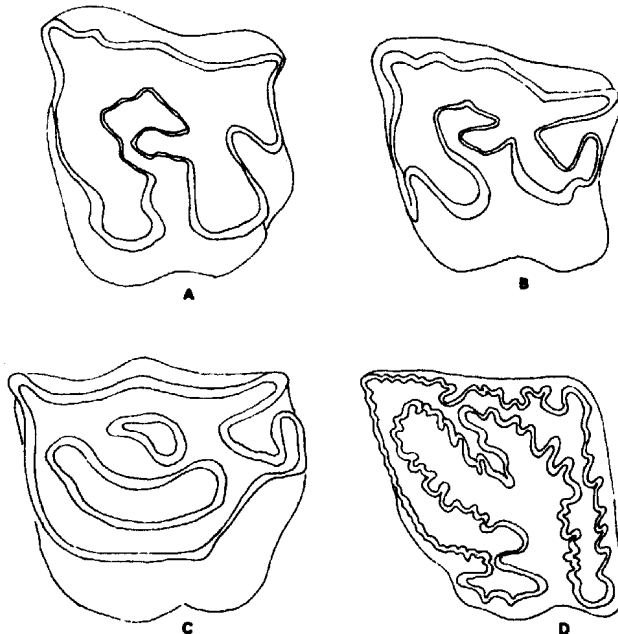


Figure 13.10. Left second upper molars of brachyodont (above) and hypsodont (below) rhinoceroses. A. *Dicerorhinus etruscus*; B. *Dicerorhinus hemitoechus*; C. *Coelodonta antiquitatis*; and D. *Elasmotherium*. Discussion in text. Not to scale.

mediofossette as crochet and crista (the two main secondary folds, fig. 13.2a) merge, and by the posterior (distal) deflection of the trasversal lophs, which may eventually become confluent (fig. 13.10c) M^3 is enlarged, and a separate metaloph is secondarily acquired by all truly hypsodont rhinoceroses, in which M^3 comes to resemble M^1 and M^2 in shape.

The lower teeth of hypsodont rhinoceroses have buccally flattened lophids, which correspond to the flat ectoloph wear profile. The ectoloph, correspondingly, is not as regularly folded as in brachyodont teeth, and the styli are indistinct. The enamel is thicker and has a rough surface, which probably is related to the presence of a cementum coating (the thinner the cementum, it seems, the smoother the enamel). Since buccal and lingual development is subequal and wear rather uniform, no marked inward rotation is observed as the upper tooth is worn down.

Functional and Dietary Considerations

Although the traditional view of hypsodonty is that it is an adaptation to grass eating (or, in functional terms, to increased abrasion), several objections have been raised to this interpretation (e.g., White 1959 and references). The rather confused debate has been much hampered by the fact that "hypsodonty" has not been adequately defined, nor have its functional implications been considered (apart from the fact that higher crowns take longer to wear down), except by a few authors (e.g., Osborn 1903; Rensberger 1973, 1975).

Increased crown height may have several causes, but can be broadly interpreted as a response to increased wear. This in turn may be a result of a need to chew more food per unit time, or food that causes more wear. The need to chew more food may be related to increased size, a more energy-consuming behavior, a colder climate, food of lower nutritive quality or some such factor. Increased wear may result directly from more abrasive food or increased contamination with extraneous abrasive material, or indirectly from food requiring higher occlusal pressures for efficient comminution (Rensberger in litt. 1979). It is argued here that true hypsodonty involves higher total occlusal pressures (a dominantly horizontal power stroke), and that it is primarily a dietary adaptation rather than a general way of increasing the life span of the animal when dental wear is limiting. Thus "indexes of hypsodonty" are of limited value: true hypsodonty is *not* just increased crown height nor yet the appearance of a cementum coating.

The combination of shearing and crushing functions implicit in the brachyodont morphology seems adapted to the comminution of bulky vegetation like twigs, fruits, and soft plants, such as is indeed the main food of living brachyodont rhinoceroses. The high occlusal pressures of the

hypsodont dentition, on the other hand, seem to be an adaptation to the rapid comminution of fibrous, thin and tough vegetation such as mature grass, which is the food of the only truly hypsodont living rhinoceros, *Ceratotherium simum*.

Thus the traditional interpretation of hypsodonty as an adaptation to grass eating is supported, but in more than the sense of increased resistance to abrasion. Rather, the high occlusal pressures enable the animals not only to eat young and tender grass occasionally (as do many bears, pigs and deer, for example), but also to specialize on old, tough and fibrous grass. (Obviously, it is more or less impossible to distinguish between the different factors influencing tooth morphology in each separate case, since many grasses, for instance, are *both* abrasive *and* tough and of a low nutritive quality to boot; and since grazing animals are frequently larger than their browsing ancestors. Still, knowledge of the existence of the various factors is of some value in discussing the ecological adaptations of brachyodont and hypsodont animals.)

Vegetation, of course, does not occur in two distinct types, and neither do rhinoceros teeth. There are intermediates between brachyodont and hypsodont, some of which are difficult to place (the living Indian "unicorn," *Rhinoceros unicornis*, for example). Despite this the two categories remain reasonably well defined, and indeed the vast majority of the rhinoceroses are clearly brachyodont, most of the remaining few being equally clearly hypsodont. Brachyodonty and hypsodonty thus probably represent mutually exclusive dietary adaptations rather than "primitive" or "advanced" conditions, although all hypsodont forms are, of course, ultimately derived from brachyodont ancestors.

The Rhinoceroses of Plio-Pleistocene Europe

The classical study concerning rhinoceros dietary adaptations is that of Zeuner (1934). Zeuner was able to demonstrate, species for species, a close relationship between skull shape and the average height of the food vegetation for living rhinoceroses. By applying the same principles to fossil species, Zeuner was able to reconstruct the "mode of life" (Lebensweise) of these. In recent years, Loose (1975) has revised the work and further developed the method. Neither author is primarily concerned with teeth, and their interpretations are based on the inferred height of the food rather than, as in the present study, on its (equally inferred) abrasive, nutritive or structural properties. In no instance do the two different approaches reach contradictory results, but a combination of both gives a more complete picture than either one alone.

In the following the ecology of the rhinoceroses of Plio-Pleistocene Europe is discussed briefly. The data concerning body size and locomotory

Table 13.2. Ecological adaptations of the European Plio-Pleistocene rhinoceroses, summary.

SPECIES	Age	Size ^a	Locomotory Adaptation ^a	Teeth	Height of Food ^b	Diet	Biotope
<i>Elasmotherium</i>	Middle	very large	?	hypodont	?	mainly	?
<i>Coelodonta antiquitatis</i>	and	medium	graviportal	brachyodont	low	grass	"cold steppe"
<i>Dicerorhinus hemitoechus</i>	Late	medium	mediportal				
<i>Dicerorhinus kirchbergensis</i>	Pleistocene	large	graviportal	brachyodont	high	browse	temperate open habitats
<i>Dicerorhinus etruscus</i>	Early Pleistocene	small	cursorial				
<i>Dicerorhinus jeanvireti</i>	Lower Villafranchian	medium	subcursorial				
<i>Dicerorhinus megarhinus</i>	Pliocene	large	mediportal				deciduous forest (?) savanna, open woodland

^a Adapted from Fortelius 1979^b Based on skull shape (Zeuner 1934, Loose 1975) (see text for explanation)

adaptations have been adapted from an unpublished manuscript (Fortelius 1979) and will be presented later elsewhere. The interpretations are summarized in table 13.2.

Dicerorhinus megarhinus (*de Christol 1834*), *Pliocene*

This large, relatively cursorially built rhinoceros had brachyodont teeth with low crowns (note that this is not tautology: functionally brachyodont teeth may be quite high crowned). The upper molars have apically constricted transversal lophs. This probably served to enhance the concavity of the occlusal surface and thus the shearing efficiency by causing rapid wear during the initial stages. Cingula are well developed, and the diet was probably similar to that of present-day browsing rhinoceroses; twigs, leaves, fruits etc. As the skeletal build suggests an open biotope, savanna-like conditions seem indicated. The same is true for the smaller and more cursorial species *D. jeanvireti* Guérin 1972, which in ecological terms appears to be rather intermediate between *D. megarhinus* and *D. etruscus*.

Dicerorhinus etruscus (*Falconer 1868*), *Early Pleistocene**

There seems to be good reason to regard *D. etruscus* as a complex of several subspecies, yet many features appear common. The following is based mainly on material from the "Cromer Forest Bed" of East Anglia, England.

D. etruscus was a very lightly built rhinoceros, with a skull shape indicative of food of intermediate height, comparable to that of *Diceros bicornis* (Zeuner 1934:49; Loose 1975:17). There are several interesting parallels between the two species in dental development as well. Both have brachyodont teeth with strong cingula and a thin cementum coating, and both have steep hypo- and metacones lacking the apical constriction found in *D. megarhinus* and *D. kirchbergensis*. This may indicate a relatively smaller importance of the shearing function (phase 1 of the occlusal stroke), and thus a functionally less extreme brachyodont condition. Compared with *D. megarhinus*, *D. etruscus* was smaller, more lightly built and probably of a less mesic dietary adaptation, and may represent an adaptation to a more cursorial mode of life and a drier, more open biotope.

Dicerorhinus hemitoechus (*Falconer 1868*), *Middle and Late Pleistocene*

Quite possibly *D. hemitoechus* is part of the same species complex as *D. etruscus*; certainly there are many common features. Two subspecies are

*I have deliberately avoided a more precise stratigraphic terminology, the European Pleistocene stratigraphy being at present subject to extensive revision. The designations "Early," "Middle," and "Late" Pleistocene are quite adequate for the present purpose.

recognized by Azzaroli (1961). The following applies mainly to the Late Pleistocene representatives, and is based primarily on material from England.

Although larger and more graviportal than *D. etruscus*, *D. hemitoechus* was the most cursorial of the Middle and Late Pleistocene rhinoceroses, with a locomotory build similar to that of *D. megarhinus*. The skull shape indicates a diet of low growing vegetation (Zeuner 1934:52, Loose 1975:22). The teeth are rather similar to those of *D. etruscus*, but the crowns are higher, cingula are reduced and there is more cementum. The molars are relatively enlarged (fig. 13.5) and M^3 is very nearly hypsodont, with a rather flat occlusal surface. In the lower teeth the lophids are perhaps more flattened buccally (cf. Staesche 1941:131). All these differences are in the direction of increased hypsodonty, and this has done much to consolidate the concept of a truly hypsodont, grazing "steppe rhino" mentioned in the introduction. The truth is that *D. hemitoechus* had mainly brachyodont teeth with some modifications toward hypsodonty, possibly indicating a shift to a diet containing more mature grasses. Probably this rhinoceros was an inhabitant of various open environments, such as the locally deforested river valley at Barrington, Cambridge (one of the main sites for remains of this species), with its rich flora of low growing vegetation (Gibbard and Stuart 1975:496).

Dicerorhinus kirchbergensis (Jäger 1839), Middle and Late Pleistocene

This large rhinoceros was of a more graviportal build than *D. megarhinus*, which is otherwise closely resembled, but still more cursorial than the larger of the living rhinoceroses. The skull shape is indicative of browsing (Zeuner 1934:52), and the species is commonly known as the "forest rhino." The teeth are brachyodont and the crown height similar to that of *D. hemitoechus*, but with a marked constriction of the transversal loph of the upper molars. As in *D. megarhinus*, this gives a more strongly concave occlusal surface and increased shearing efficiency, indicating perhaps a more mesic dietary adaptation. The unequal wear and the gradual inwards rotation of the upper cheek teeth are very marked, and the ectoloph are characteristically curved around the longitudinal axis of the teeth. Cementum is thin and the enamel smooth, and the molars are not enlarged as in *D. hemitoechus* (fig 13.5). M^3 is low crowned and generally little developed, being no higher than the corresponding tooth in *D. megarhinus*, although there is a marked difference in premolar height between the two species (Fortelius 1979:34, 41, 44). This indicates that the importance of the posterior teeth was relatively small, a view consistent with the fact that M^3 shows none of the "grinding" adaptations found in *D.*

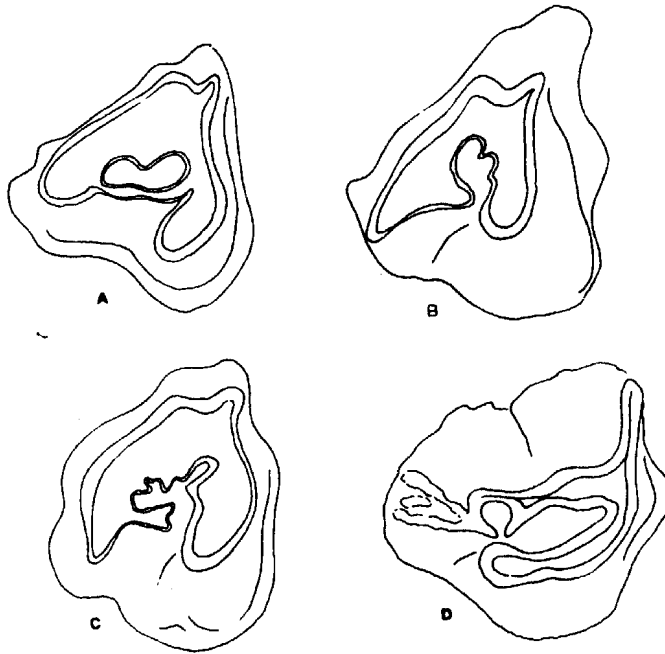


Figure 13.11. Right third upper molars of rhinoceroses. A. *Dicerorhinus etruscus*; B. *Dicerorhinus kirchbergensis*; C. *Dicerorhinus hemitoechus*; and D. *Coelodonta antiquitatis* (discussion in text). Not to scale.

hemitoechus (figs. 13.11b, 13.11c). As far as dietary adaptation is concerned, the deciduous forest appears a plausible biotope for this species. The graviportal build seems consistent with a relatively closed environment.

Coelodonta antiquitatis (Blumenbach 1799), *Middle and Late Pleistocene*

The woolly rhinoceros was a medium sized animal of compact, graviportal build, which may well reflect its relatively "cold" adaptation. Although the interpretation of the skull shape of this animal is not wholly clear, it appears to have carried its head low, at least for much of the time (Zeuner 1934:54f; Loose 1975:29). The teeth are extremely similar to those of *Ceratotherium simum* (cf. figs. 13.7, 13.10c and 13.11d), and a similar diet seems indicated. The ecological adaptation has been subject to some disagreement, and this is hardly the place to enter into that discussion. However, the teeth do indicate that the principal food of this animal was grass or some hypothetical, closely similar vegetation. Possibly the animal

was seasonal, with a different diet in summer and winter, as was suggested by Loose (1975:24).

Another hypsodont rhinoceros of the Pleistocene, which may have occurred in Europe, was *Elasmotherium*, "(un) grand mammifère le plus mystérieux du Quaternaire européen" (Guérin 1976:407). Although little is known about this animal, it appears unlikely to have been in ecological competition with any of the more "traditional" European rhinoceroses: it was a huge animal with enormous, evergrowing molars (fig. 13.10d), and its remains are mainly found in southern Russia.

Conclusion

Perhaps the most striking fact about the Plio-Pleistocene rhinoceroses of Europe is the abrupt ecological change that seems to take place at the end of the Early Pleistocene (table 13.2). Until then, it appears, Europe was witnessing a succession of species with little temporal overlap. The ecological adaptations of these species were essentially similar, although a transition from large and mediportal to small and cursorial may be observed. With the onset of the Middle Pleistocene that type of rhinoceros disappears, and instead four ecologically different species are found. It is true, of course, that of these four species *Elasmotherium*, if present at all, was probably rare in Europe, and there was a temporal alternation between *Coelodonta antiquitatis* and the two *Dicerorhinus* species, the former being mainly glacial, the latter mainly interglacial elements. Yet *Dicerorhinus kirchbergensis*, *D. hemitoechus*, and *Coelodonta antiquitatis* are known to have occurred in the same general area at the same general time (e.g., Guerin 1973), and in any case the contrast to the Pliocene and early Pleistocene is dramatic. It is very tempting to regard the increased ecological diversity as a result of the increased environmental complexity in time and space, due to the climatic "deterioration" of the Ice Age.

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