

Dental ontogeny of the woolly rhinoceros *Coelodonta antiquitatis* (BLUMENBACH, 1799)

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SUMMARY

A study has been made of 267 skulls and 160 mandibles of the woolly rhinoceros, *Coelodonta antiquitatis* Blumenbach. From these it can be shown that there is a marked similarity in certain developmental peculiarities of the dentition to the living African rhinoceroses *Diceros bicornis* and *Ceratotherium simum* Burchell. The presence of the milk-tooth D1, the condition of D2-D4, as well as some morphological peculiarities in the molar rudiments in maxillae of woolly rhinoceros, would seem to indicate that developmental phases in the milk-teeth of *C. antiquitatis*, *D. bicornis* and *C. simum* are similar. The rudimentary incisors dI1 - dI2 in adult individuals of woolly rhinoceros and contemporary African ones are met with the same frequency. The peculiarities of initiation, development and eruption of P4 and M3 for the woolly rhinoceros are identical with those in the living species. The abnormalities, irregular eruption of P4 and supernumerary P4 and M3, are found both in recent and extinct rhinoceros of the genera *Coelodonta* and *Dicerorhinus*. From this morphological analysis it can be concluded that the dentition of the family Rhinocerotidae was not subject to rigid specialization during evolution, but retained a plasticity and ability for rapid reconstruction.

SAMENVATTING

267 schedels en 160 onderkaken van de wolharige neushoorn, *Coelodonta antiquitatis* Blumenbach werden door de auteur bestudeerd. Hieruit kon worden geconcludeerd dat er wat betreft de ontwikkeling van het gebit een duidelijke gelijkenis bestaat met de levende Afrikaanse neushoorns *Diceros bicornis* en *Ceratotherium simum* Burchell. Dit geldt voor verschillende kenmerken. De aanwezigheid van de melkkies D1, de conditie van D2-D4 en enkele morfologische kenmerken in de rudimentaire kiezen in de maxillae van de wolharige neushoorn, duiden erop dat de ontwikkelingsfasen in de melkkiezen van *C. antiquitatis*, *D. bicornis* en *C. simum* gelijk zijn. De rudimentaire incisieven dI1 - dI2 bij volwassen individuen van de wolharige neushoorn en de recente Afrikaanse soorten komen met de zelfde frequentie voor. De kenmerken van aanleg, ontwikkeling en doorkomen van P4 en M3 bij de wolharige neushoorn zijn identiek met die van de levende soorten. De afwijkingen, het onregelmatig doorkomen van P4, de extra P4 en M3, worden aangetroffen zowel in recente als in uitgestorven neushoorns van de geslachten *Coelodonta* en *Dicerorhinus*. Uit deze morfologische analyse kan geconcludeerd worden dat in het proces van evolutie het gebit van de Rhinocerotidae niet onderhevig was aan strikte specialisatie. Het behield een zekere mate van flexibiliteit en het vermogen tot snelle aanpassing.

Introduction

The woolly rhinoceros, *Coelodonta antiquitatis* Blumenbach, was the most widely distributed species of large Pleistocene Mammalia in the Middle and Late Pleistocene, being found throughout most of Eurasia. Its skeletal remains - skulls, mandibles, bones of the postcranial skeleton - are often well preserved in large numbers and are often found in Quaternary deposits together with bones of other Pleistocene Mammalia. They are well represented in fossil collections. Despite the vast osteological material accumulated in the collections of zoological and geological museums of Russia through several centuries, the woolly rhinoceros is still the most poorly understood species of all the Pleistocene Mammalia of the 'mammoth complex'. Neither the cranial morphology, dentition nor variation between individuals is well studied at present, so there is no description available in the literature on the ontogeny of woolly rhinoceros dentition, despite the predominance of cranial material in collections. The majority of papers include only the most general description and measurements of single finds of skulls and teeth. The dental ontogeny of extinct rhinoceroses of the *Dicerorhinus* genus has not been investigated at all. Their skeletal remains are scarcely found in the territory of Russia, but are numerous

elsewhere in the Western, Eastern and Southern parts of Europe.

There is little work on the dental ontogeny of recent rhinoceroses, although the contemporary African species - the black narrow-nosed *Diceros bicornis* L. (SHANZTE, 1966; DITTRICH, 1974) and white wide-nosed rhinoceros *Ceratotherium simum* Burchell (HILLMAN-SMITH *et al.*, 1986) - have been studied relatively well. Developmental studies of living rhinoceros have been conducted primarily for practical purposes. During the last 25 years the populations of all species of living rhinoceros have been sharply reduced. The problem of conservation of extant species in nature has become acute and so for registration and regulation of rhinoceros numbers within the limited areas of national parks, the individual age of animals should be known exactly.

Some data on the eruption and change of milk-teeth for calves of African rhinos *D. bicornis* and *C. simum* are available. Observation of eruption and development of teeth has been conducted on animals born in zoos. However, it has been restricted to the period when young animals allow investigation of their mouths.

This information on dental ontogeny has been supplemented by X-ray data on the maxillae of young African rhinos that died in zoos. Furthermore, the rudiments of molars concealed in alveolar pockets of maxillae have been studied (SHANZTE, 1966; DITTRICH, 1974), as have the teeth of white African rhinos shot in the wild, whose individual age was approximately known. Simultaneously with the investigation of macromaterial (crania and mandibles with teeth), there has been a study and calculation of microscopic growth lines of seasonal accumulation of dentine in thin sections of upper M1 (HILLMAN-SMITH *et al.*, 1986). For more precise determination of animal age, the results obtained from both methods have been compared.

The information on dental ontogeny of living Asian rhino species is extremely scarce and has been concerned only with growth as recorded by dentine microstructures of the upper M1.

The results of the investigation of dental ontogeny in living African rhinos have shown that the development, time of eruption and replacement of teeth, for rhinos of the *Diceros* and *Ceratotherium* genera, are basically similar. However, the timing of tooth eruption and replacement does not remain constant even for individuals of the same species. It is subject to individual variability and depends upon the animal's habitat, condition and nutrition. It causes some inaccuracy in the determination of individual animal age by estimates of tooth wear. The information on maximum life duration of living rhinos both in the wild and zoos shows that it is approximately the same for African and Asian species and ranges between 40-45 years. These data are confirmed by calculation of the maximum number of microscopic seasonal growth layers of dentine in sections of the upper molars M1 for old individuals of the African white rhino *Ceratotherium simum* and the Indian 'one-horned' rhino *Rhinoceros unicornis* (HILLMAN-SMITH *et al.*, 1986).

From a large number of specimens, the author has studied the dental variation of woolly rhinos *C. antiquitatis* according to age stages that correspond to certain ontogenetic phases. For comparison, data on the dental ontogeny of living rhinos similar in ecology to *C. antiquitatis* have been used, especially the African white rhino *Ceratotherium simum* Burchell.

The investigation of dentition ontogenesis of woolly rhinos involves: a) - the development of a method of individual age determination of *C. antiquitatis* based on the degree of molar wear; b) - revealing the individual variation in dental structure; c) - the study of specific peculiarities in dental ontogeny of woolly rhinos.

Material

For the woolly rhino *Coelodonta antiquitatis* Blumenbach, 268 skulls, 160 mandibles and 35 isolated teeth from collections of the Zoological Institute of the Russian

Academy of Sciences (RAN) in Saint Petersburg (ZIN), the Geological-Mineralogical Museum of Kazan State University (GM - KGU), and the Institute of Geology and Geophysics of the Siberian department of the RAN in Novosibirsk (IGG), have been studied.

In addition, material from Moscow Academic institutes - the Geological Institute (GIN) and the Institute of Animal Evolution, Morphology and Ecology (IEMEG) - have been investigated. Regional material has been studied in the museums of 30 towns of Russia and Ukraine. For comparison with living rhinos, a series of skulls and complete mandibles (70 specimens) of living African rhinos - black narrow-nosed *Diceros bicornis* Linnaeus and white wide-nosed *Ceratotherium simum* Burchell - from collections of ZIN, RAN and the Zoological department of the Museum of Natural History of Humboldt University, Berlin (Germany) has been investigated.

Methods

Teeth from the skulls and mandibles of rhinos were measured. The measurements have been made with calipers to an accuracy of 0.1 mm.

The following measurements have been made: length and width of the crown at the masticatory surface, height (only for unworn teeth) from the enamel edge of the crown base to the top of the most protruding crest.

The plates have been taken from the masticatory surface of the right and left tooth row. The standard plates of upper and lower tooth rows correspond to definite age stages and ontogenetic phases in tooth development, and were taken for determination of the individual age of woolly rhinos according to the degree of tooth wear.

For white African rhinos *Ceratotherium simum*, 16 age stages have been recognised by HILLMAN-SMITH *et al.* (1986), according to individual skulls whose age was exactly known in most cases. They included the earliest stages of milk age (from 1.5 month to 1.5 year). Comparing the plates from molars of the upper tooth row of woolly rhinos with the image of the upper tooth rows of *C. simum* which correspond roughly to the same age stage, the author has marked out 10 age stages for *C. antiquitatis*. For woolly rhinos the earliest age stages corresponding to suckling calves are absent.

For designation of the age stages the following conventional abbreviations are used:

C-I, juvenile, corresponding to the individual age of 1-1.5 years; C-II, juvenile, 2-3 years; C-III, juvenile, 3-4 years; C-IV, semiadult, 8-11 years; C-V, semiadult, 10-15 years; C-VI, adult, 15-20 years; C-VII, adult, 20-25 years; C-VIII, adult, 25-30 years; C-IX, old, 35-40 years; C-X, old, 40-45 years.

Upper teeth have been designated with capital letters - (D)I, C, D, P, M; lowers with lower-case letters - (d) i, c, d, p, m. The upper teeth are more suitable for deter-

mination of the individual age of woolly rhinos, because the age changes are displayed most clearly by the upper molars. The designation of principal morphological details of rhino teeth follows the scheme of E.J. BELJAEVE (1966) (Fig. 1).

Single or multiple protuberances of dentine growth are often found on the upper molars of woolly rhinos and those of *Dicerorhinus*. Since previous authors have not recorded such details of rhinos teeth, the author has designated these growths as *petiolus mastoideus* (Fig. 1, 16).

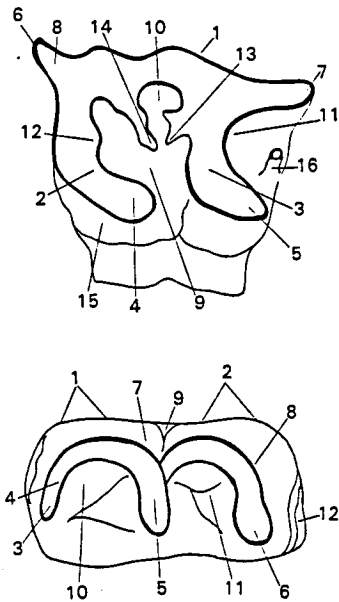


Fig. 1:
Nomenclature of the upper molars: Nomenclature of the lower molars:
Nomenclatuur van de molaren uit de bovenkaak: Nomenclatuur van de molaren uit de onderkaak:
(E.J. BELJAEVE, 1966) (E.J. BELJAEVE, 1966)

1. ectoloph	1. metalophid
2. protoloph	2. hypolophid
3. metaloph	3. paraloconid
4. protocone	4. parastylid
5. hypocone	5. metaconid
6. parastyle	6. ectoconid
7. parastyle form/ parastyle-achtige vorm	7. protoconid
8. metastyle	8. hypoconid
9. middle part/ middelste deel	9. outer synclinal/ buitenste synclinale
10. added part/ toegevoegde deel	10. vallee anterieure/ voorste deel
11. outer part/ buitenste deel	11. vallee posterieur/ achterste deel
12. anticroche	12. cingulum
13. croche	
14. crest/ kam	
15. cingulum	
16. petiolus mastoideus	

Results

Being firmly and closely embedded in the alveolae, the molars of extinct rhinos are more often found in place within skulls and jaws than isolated. However, finds of milk teeth are extremely rare. More often they are found separately. This results from the fact that the skulls and maxillae of milk and juvenile individuals (younger than 3 years) are rapidly degraded during burial and are badly preserved as fossils.

Milk incisors

These are represented by 3% of the total amount of investigated material.

Upper incisors (*dentes incisivi*) are sometimes found in skulls of adult individuals of woolly rhinos. Their frequency is no more than 4 % of the *C. antiquitatis* sample.

The incisors DI1 of woolly rhinos are rudimentary, very small (from 4 x 5.5 mm to 10 x 16 mm) and of spherical or pear-shaped form with reduced roots. In the process of evolution they lost the morphological structural features that are typical for these teeth. In adult individuals the rudimentary incisors have time to resorb, but their alveolae remain in the premaxillary. The incisors DI1 are not found in pairs, only in one half of the premaxillary and generally the right one.

Lower incisors di1, di2. These are present in the premaxillary bone of the mandible of juvenile individuals of woolly rhinoceros specimen IEMEG N3751-35, from the Shikotan Peninsula (east coast of the Laptev Sea).

According to the wear on the milk molars d1-d4 in the mandible it could be concluded that the age of the individual was no greater than 1-1.5 years. The lower incisors of woolly rhinos have the same morphological peculiarities as the upper ones. They are very small and heavily reduced. They differ from the upper incisors in their alveolar cavities. They are always present in pairs in the premaxillary.

In living African rhinos *D. bicornis* and *C. simum*, the rudimentary incisors are laid or erupted at late stages of embryogenesis, but shortly before birth or in the first months after birth they are resorbed (SHANZTE, 1966; DITTRICH, 1974). In the maxillae of adult individuals of African rhino species the incisors are rarely found, as in the case of woolly rhinos.

Upper milk molars

The detailed description of the morphology of milk molars D1-D4 of woolly rhinos is not available in the literature.

Isolated milk molars, similar to woolly rhinos of the early Pleistocene species from Zabaikalje (location Tologoy) of the Tologoyan rhinos *Coelodonta tologojensis*, are described by E.J. BELJAEVA (1966).

The milk molars of *C. antiquitatis* in the sample studied by the author are represented by complete upper maxil-

lary fragments. Where the milk molars D1-D4 are in the alveolar pockets, the permanent premolars P2-P4 have been preserved as rudiments. Besides the morphology of the milk teeth these data have permitted the author to study also the early ontogenetic stage of joint development of milk and permanent premolars for woolly rhinos. In all there are four such specimens in the sample. Two of them (from the GIN RAN collection, GIN N1, N2, find location unknown) belong to individuals of age stage C-I. The foundations of the molars are not preserved in these samples. The specimen IEMEG

N3128-23, from the River Jana basin, represents the skull of a juvenile individual of age stage C-II. In the internal alveolar pockets, the very delicate rudiments of the permanent premolars are preserved, not covered by enamel. The fourth sample IGG N9201, Kuznetzk hollow, belongs to an individual of age stage C-III. The milk molars D1-D3 of this specimen are heavily worn: of the original crown height less than one third remains. Their roots are largely resorbed, but still firmly hold the tooth crowns in the alveolae. The premolar D4 is worn somewhat more than half. Its long roots are submerged

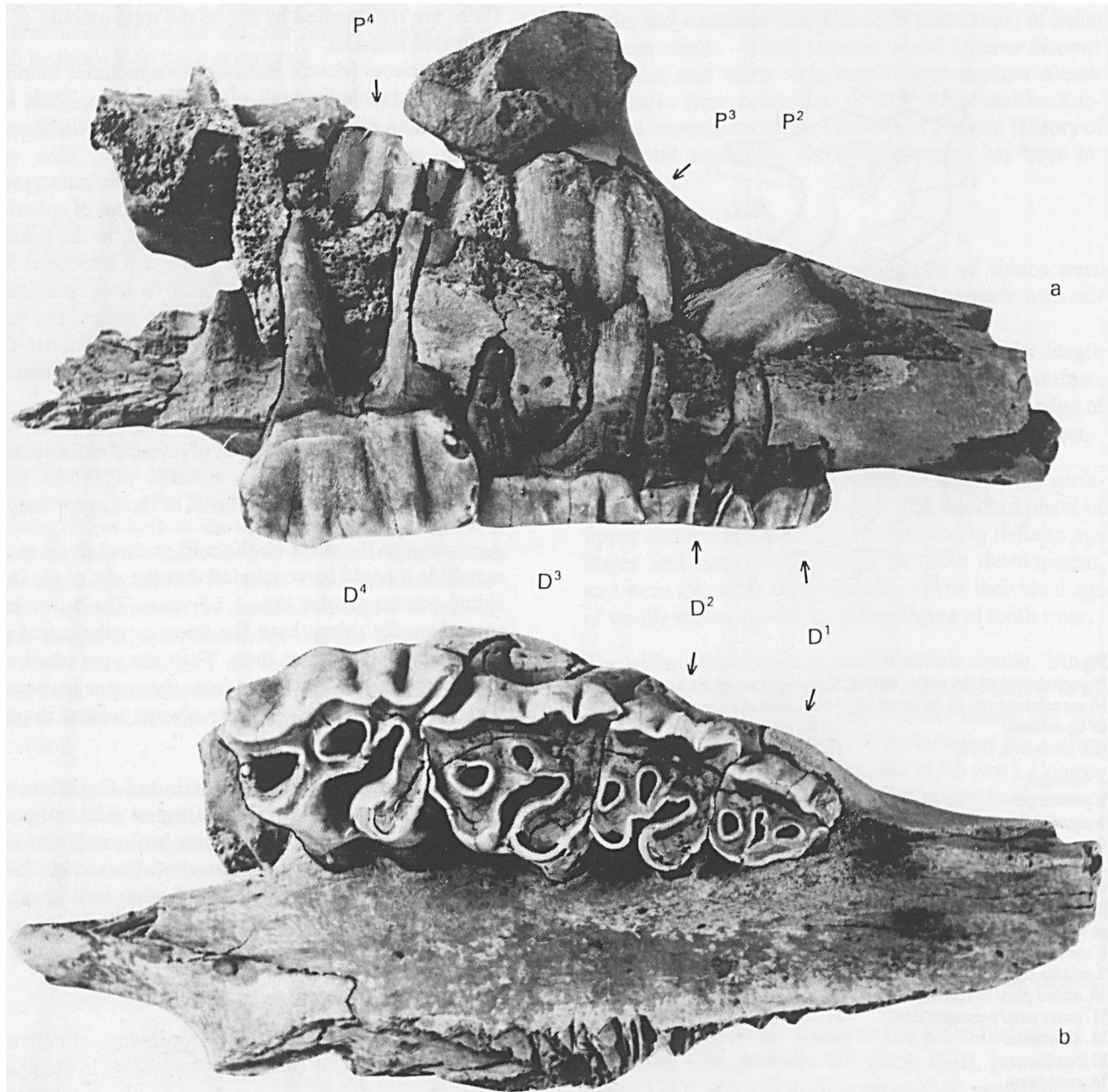


Fig. 2 a, b: N 9201 Kuznetzk, West Siberia.

Fragment of the upper maxilla of a juvenile rhinoceros with the milk teeth D1-D4 and initiation of the permanent P2-P4 above them. Note that D1-D4 and P2-P4 in the figure are similar to D1-D4 and P2-P4 in the text.

a. Side-view b. View from above

Fig. 2 a, b: N 9201 Kuznetzk, West-Siberië.

Fragment van de bovenkaak van een jonge neushoorn met de melkkiezen D1-D4 en aanleg van de permanente P2-P4 erboven. D1-D4 en P2-P4 in de figuur zijn gelijk aan D1-D4 en P2-P4 in de tekst.

a. Zijaanzicht b. Bovenaanzicht

deeply into the maxilla. The masticatory surface of all four premolars is at one level and forms a common flat surface (Fig. 2a, b inset). D1 (N4) is of small dimensions with indications of considerable reduction. The crown is triangular in form, stretched longitudinally and somewhat flattened from the sides. The external wall of the ectoloph has a distinct front and back rib and is raised slightly above the transverse crests (protoloph and metaloph). The protoloph is oriented with a backward slant to the longitudinal tooth axis, somewhat exceeding the length of the metaloph. In D1 samples of GIN N1 and N2 a small anterior valley is present. This detail has also been registered by E.J. BELJAEVA (1966) in the teeth of Tologoyan rhinos as an index of archaism typical for early ancestral rhinos forms. The enamel is thin, the pattern of enamel prisms (wrinkles of the enamel) is clearly exposed and similar to that on the enamel of permanent premolars of woolly rhinos, but somewhat shallower. The dimensions of D1 are smaller in comparison with genuine ones, because the measurements have been carried out on heavily worn crowns. The genuine dimensions of D1 in woolly rhinos exceeded the dimensions of such teeth for Tologoyan rhinos and approached nearer to the teeth D1 of woolly rhinos from Nihowan, China.

As for formation and replacement of D1 in living rhinos, it is known that for Asian species, *Didermoceros sumatrensis* Fischer, *Rhinoceros unicornis* Desmarest and *Rhinoceros sondaicus* Linnaeus, both D1 and the P1 replacing it are preserved in ontogenesis. For the black African rhino *Diceros bicornis*, the replacement of D1 by the first permanent premolar P1 does not occur, but sometimes the retained D1 functions together with the permanent premolar briefly and then falls out (DITTRICH, 1974). For white African rhinos *C. simum*, the first premolar is heavily reduced and never replaced by a permanent one (HILLMAN-SMITH *et al.*, 1986).

In all species of Rhinocerotidae, both extinct and living, the first milk molar D1 and the one that replaces it, the permanent premolar P1, have in their structure visible indices of reduction: greatly reduced dimensions of crowns in comparison with other teeth of premolar row, and simplified in structural details. In D1 formation and further P1 reduction in the permanent teeth of extinct rhinos of *Coelodonta* and *Dicerorhinus* genera, we encounter the phenomenon of palingenesis (formation and development of rudimentary organs), and the mechanism of embryo-adaptation expressed in a breach of further formation of rudimentary structures and their destruction. In ontogenesis of the dentition of living rhinos this is accomplished by means of heterochrony of teeth rudiment formation and their eruption. Function is established first before eruption. Their rudiments take more room and therefore receive more nutrition to promote growth and development. From observation on development and eruption of the teeth of African rhinos *D. bicornis* and *C. simum*, it is known that in new-

born rhinos, first D3 teeth erupt, then D2 (in the mandible the milk premolars erupt several days earlier but with the same sequence). For a nine-month old calf of *D. bicornis* the following teeth are present: D22; D33; D44 - however, D1 at that time is still absent and it only erupts at the age of 12-14 months (DITTRICH, 1974).

Such ontogenetic peculiarities in the development and eruption of the first milk molar D1 as seen in living African rhinos, were apparently also inherent for the D1 of woolly rhinos.

Thus, in the sample IGG N9201, the second permanent premolar P2 is situated above the first milk molar D1 in the alveolar pocket. Its crown has a slanting orientation with the peak directed toward the roots of the second milk molar D2 (Fig. 2a, b, inset). It is clearly seen that the large crown of D2 occupies the whole of the small space under the roots of D1 and D2. There is no place for the formation of the first premolar P1, even if it would have been able to be laid. The absence of P1 in the permanent teeth of woolly rhinos confirms the fact visually.

Apparently all above-mentioned peculiarities of structure, development and eruption of first milk molar D1, as well as reduction of P1 in permanent teeth of living African and woolly rhinos, demonstrates the minor functional importance and rudimentary nature of these teeth for rhinos throughout this subfamily of Rhinocerotidae.

In D2-D4 the tooth crowns are molarized and trapeziform. The front and back ribs of the ectoloph are equally well developed. The protoloph and metaloph are strongly deflected backwards. The antecrochet and crochet are locked early and form an additional alveole. The middle valley is narrow and slants forward. The enamel is thin, and the pattern of enamel prisms is clear. The typical line of milk molars of woolly rhinos is oblong parastyle and metastyle folds. The parastyle fold of the back tooth goes behind the metastyle of the previous one.

According to crown form, development and orientation of parastyle and metastyle fold, and degree of inclination of transversal crests, the milk molars of *C. antiquitatis* bear resemblance to these teeth in extinct rhinos of the *Dicerorhinus* genus. This is not evidence of their phylogenetic propinquity, rather indicative of the fact that these features are typical for ancestral forms of Rhinocerotidae.

The upper milk molars D1-D4 of *C. antiquitatis* bear great resemblance to the premolars of Tologoyan rhinos *C. tologojensis* and apparently differ slightly from these teeth of woolly rhinos from the Early- and Middle Pleistocene. During ontogenesis the milk teeth always preserve many signs of archaism inherited from their far ancestors.

There are outgrowths of small dentine stems (*petiolus mastoideus*) on D3 and D4 of the specimen IEMEG N 3128-23 in the area of the back valley. The stems are more typical for the permanent upper molars and are often met in P4-M3 of rhinos of the *Dicerorhinus* genus. For samples of upper back molars of *Dicerorhinus kirchbergensis* Jäger (from the collection of the Institute of Quarternary Palaeontology of Weimar, Germany and the Zoological Institute of Kazakh Academy of Sciences, Alma-Ata), the dentine stems are localized not only in the area of the back, but also in the middle valley, with several on one tooth. Often these small stems are covered by enamel. The presence of dentine stems is recorded also in the milk teeth of Tologoyan rhinos *C. tolojoensis* (BELJAEVE, 1966).

In upper molars of the woolly rhino *C. antiquitatis*, the dentine stems are more rare. The author has found a different frequency of this feature in teeth of *C. antiquitatis* from various geographical regions. Thus, for samples from Middle Volga, North-East Siberia and Zabaikalje, the frequency of dentine stem occurrence is higher than for samples from the Central-European part of Russia.

It is difficult to explain what biochemical function such dentine outgrowths could perform. Perhaps, the dentine stems are connected with hyperfunction of secretory activity of dentine and enamel organs forming the teeth in embryogenesis. This, in its turn, could reflect favourable natural conditions under which the given rhino population developed.

Lower milk molars

There is one mandible of woolly rhino with molars in the sample, IEMEG N3751-35, from the Shikotan peninsula, east coast of the Laptev Sea.

d1. This does not show wear. The selenodont tooth has an intensely developed protoconid and one back internal alveole of oval form. The crown is condensed from the sides. The labial and lingual sides are smooth, without folds. There are two roots accreted at the base. The enamel is fine, the pattern of the enamel prisms is clear. The crown length is 20 mm, width 11 mm, height 17 mm.

d2. Only the peaks of the protoconid and hypoconid cones are worn down. There are grooves at the buccal surface of the metalophid and the hypolophid. As in d1 the crown of d2 is somewhat condensed from the sides. There are small knobs on the lingual surface of the protoconid. The front internal valley is only slightly outlined, the back internal valley is well developed to a round form. The crown length is 28 mm, width 16 mm, height 26.5 mm.

d3. The peaks of the protoconid and the hypoconid are worn down more than d2. The crown bears more resemblance to the permanent lower molar. The front and

back crest are clearly divided by an external valley. The front internal valley is well developed but shallow. The crown length is 37 mm, width 20 mm, height 30 mm.

d4. The tooth crown is worn down. According to the tooth fragments preserved in the two halves of the maxillae, it was determined that the roots d4 were not yet closed. The entrance in the internal cavity of the tooth crown is wide, the tooth is not completely formed and erupted, but the protoconid peak is already produced to the common level of the masticatory surface of the tooth row. The tooth is not worn down.

For living African rhinos *D. bicornis* and *C. simum*, d3 erupts first at the age of 2 months, then D2. D3 begins to function first, d2 joins in later. In the first year of a rhino's life the milk molar d1 merely begins to erupt and is already in function at 1.5 years.

According to the wear and condition of the milk teeth of the woolly rhino mandible IEMEG N3751-35, it can be concluded that the sequence of lower milk tooth eruption and the beginning of their wear for *C. antiquitatis* correspond to those for living rhinos.

Based on the data obtained during investigation of upper and lower milk teeth of woolly rhinos, it can be concluded that the tooth formula for milk replacement in *C. antiquitatis* was: di12; dc00; d44.

Age determination according to milk teeth

For African rhinos (*Diceros bicornis* and *Ceratotherium simum*), the replacement of the milk teeth by permanent ones occurs, for D2 at the age of 2.5-3 years, and for D3 at the age of 3-4 years. The difference in timing is not more than 6-12 months. The milk teeth D1-D3 of rhinos function for a short time, not more than 4-6 years. The fourth milk molar D4 alone functions for a long time. For *D. bicornis* and *C. simum* it erupts at the age of 1 year and functions until 8-15 years (DITTRICH, 1974; HILLMAN-SMITH *et al.*, 1986).

Supposedly the eruption, function and replacement of the milk teeth for woolly rhinos was somewhat more prolonged. All the same, this period in the life of the animal was much shorter than the time of function of the permanent teeth. Therefore the degree of inaccuracy is less in the determination of individual age according to milkteeth.

By comparing the maxillary fragments containing milk teeth of woolly rhinos (sample: GIN N1, N2; IEMEG N3128-23; IGG N9201) with images of upper tooth rows of juvenile individuals of white African rhinos, and taking into account data on eruption time and replacement of D1-D4 for these species, the author has marked out for the juvenile woolly rhinos three age stages:

C-I: juvenile corresponding to an age of 1.5-2.0 years. There are milk teeth D1-D3 in the maxilla. The degree of wear is average (they are half worn from the initial

crown height). In the teeth the middle and back valleys are not closed, the parastyle and metastyle folds of the ectoloph are strongly stretched. The crocket and antecroket are nearly closed.

In the samples GIN N1, N2, D4 and formation of the permanent premolars in the internal alveolar pockets were not preserved.

For *D. bicornis* and *C. simum* at the age of 1.5 years, the fourth premolar does not erupt completely. In X-ray photographs of white rhino maxillae it is seen that the rudiments of permanent premolars in rhinos of this age are not formed yet, they are very small and the roots are not developed (SHANZTE, 1966; DITTRICH, 1974; HILLMAN-SMITH *et al.*, 1986).

These data confirm the author's supposition that the milk tooth D4 and the rudiments of the permanent teeth in the samples of collection GIN RAN have not been preserved merely because of their fragility and delicacy.

C-II: juvenile, corresponding to an age of 2-3 years. There are milk teeth D1-D4 in the maxilla. A molar ready for eruption, M1, is found in the alveole. In the internal alveolar pockets the unripe, delicate and fragile initial stages of the permanent premolars P2, P3, P4 are located. The crowns of the milk teeth D1-D3 are worn more than half, and D4 is at an initial stage of wear (the peaks of the principal crests are worn). The middle and back valleys are closed in D2, the middle valley is closed in D3 but the back one is not yet closed.

C-III: juvenile, corresponding to an age of 3-4 years; Fig. 2a, b, inset). The milk teeth D1-D2 are intensely worn, D3 is worn more than half. The back valley is closed in all three teeth. D4 is worn less than half. The entrance in the middle valley is wide, the back valley is not closed. The crocket and antecroket are nearly closed. M1 was not preserved in sample IGG N9201. The foundations of the permanent premolars P2-P3, ready to replace the worn milk teeth, are seen in the alveolar pockets. The rudimentary P4 is not formed yet; the crown is not covered by enamel, the roots are closed, and the entrance into the internal cavity of tooth is wide.

Permanent teeth

The tooth formula of permanent teeth in woolly rhinos is I00; C00; P33; M33.

Upper premolars and molars

P2-P4. These are molarized, hypsodont, and have a prismatic crown form. The parastyle and metastyle folds of the ectoloph are developed only in the very initial stages of wear and wedge out rapidly. The crocket and antecroket are closed early and form an additional alveole.

For living forms of the African rhino *Diceros bicornis* and *Ceratotherium simum*, the eruption of P2 begins within 2.5-3 years, P3 in 3-4 years. The final eruption of

these teeth ends at 6-7 years (DITTRICH, 1974; HILLMAN-SMITH *et al.*, 1986).

In the first two to three years, the P2 and P3 that begin to function are worn faster because of the principal load distributed among them; then the back molars M2 and M3 finally erupt and begin to function. As M2 and M3 are engaged in work, the wear of the P2 and P3 tooth crowns is retarded. Since the eruption time of the back molars varies in different individuals of the same species depending on habitat conditions, the degree of wear of P2 and P3 is identical for the same age.

Thus, observation of eruption and development of teeth in rhinos living in captivity has shown that their teeth erupt significantly later than for animals living in natural conditions (DITTRICH, 1974; HILLMAN-SMITH *et al.*, 1986). By examining a large series of woolly rhino skulls, the author has revealed an analogous discrepancy in the degree of wear of the first premolars compared to the rest of the teeth. All this complicates the determination of the individual age of woolly rhinos based on the degree of wear in P2 and P3. The principal peculiarities of crown changes in P2 and P3 for woolly rhinos according to age stages could be traced only roughly.

C-IV. The initial stage of P2 and P3 crown wear (the major crests show slight wear). Intense crown wear of the fourth milk molar is still found in the maxilla. The crocket and antecroket are closed. The middle and back valleys are not closed, the entrance in the middle and back valleys is wide. M2 and M3 do not erupt and are concealed in alveoles.

C-V. In P2 the locking of the back valley has occurred, in P3 it is nearly closed. The middle valley is not closed in either tooth. In P3 the parastyle fold of the ectoloph is lengthened and goes behind the metastyle of P2. The crowns of P2 and P3 are worn less than half. At that time the milk tooth still remains, or the permanent fourth molar P4 appears, but its crown does not yet rise to the common level of the tooth row. In M1 the middle valley is not closed. The parastyle fold of the ectoloph of M1 is lengthened. M2 is at the initial stage of wear. M3 is concealed in the alveole, but it is ready for eruption.

C-VI. In P2 and P3 all valleys are closed. The form of the crowns is close to a rectangular prism. At that time the P4 crown is at the common level of the masticatory surface.

The middle valley of P4 is not closed, the additional and back ones are closed or nearly closed. In M1 the middle valley is not closed, but is narrowed considerably. The back valley is not closed. In M2 the additional valley is closed, the middle and back ones are not closed. M3 is at the beginning of peak wear of major crests.

C-VII. In P2 and P3 the enamel edge of the ectoloph is levelled; the enamel becomes thin. In P4 and M1 the back valley is closed, the entrance in the middle valley is

narrowed. In M2 the middle and back valleys are not closed. M3 is in the initial stage of wear.

C-VIII. The crown of P2 is shortened in the longitudinal direction. In P2 and P3 the enamel is fragmentary. The alveoles are reduced in dimensions. In P4 and M1 the valleys are closed. In M2 the back valley is closed. In M3 the back closed valley appears.

C-IX. The enamel in the crowns of P2 and P3 is absent or fragmentary. The form of the masticatory surface is irregular. Reduced to a single dimension, the basic al-

veole is present in the crowns of P2 and P3. The crowns of P2 and P3 are worn down to the base. In P4 the alveolar dimensions are reduced, the enamel edge of the ectoloph is smoothed. In M1 only the middle and back alveoles, greatly reduced in size, are present. In M2 all valleys are closed, the enamel edge of the ectoloph is smooth. C-X. P2 and P3 fall out. P4 and M1 are worn down to the root.

P4. Of all teeth of the premolar row, P4 is formed and erupted with great retardation. At that time the permanent premolars P2 and P3, and the first back molar M1,

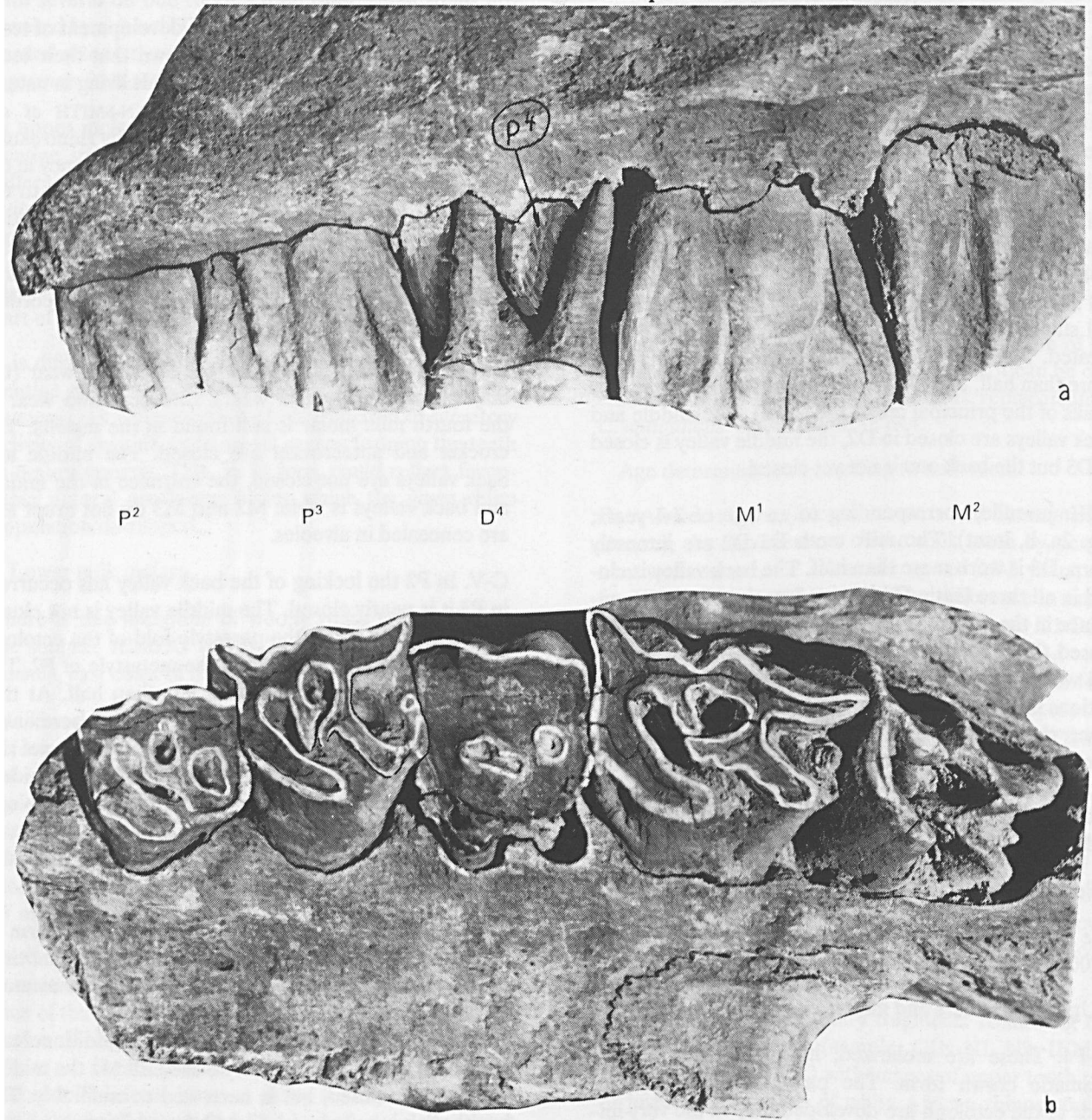


Fig. 3 a, b: N 3389 Fragment of the upper maxilla of *Coelodonta antiquitatis*. Intensely worn crown of the milk tooth D4 with long roots. The permanent tooth P4 can be seen under it. Note that D4 and P4 in the figure are similar to D4 and P4 in the text.
a. Side-view b. View from above

Fig. 3 a, b: N 3389 Fragment van de bovenkaak van *Coelodonta antiquitatis*. Sterk versleten kroon van de melkkies D4 met lange wortels. De permanente kies P4 is eronder te zien. D4 en P4 in de figuur zijn gelijk aan D4 en P4 in de tekst.
a. Zijaanzicht b. Bovenaanzicht

have already begun to function. The crown of D4 is still present and worn only by half. At this time the permanent molar is still in the alveole, incompletely formed. And only when M2 begins to function and M3 is ready for eruption, does the premolar P4 replace the milk D4. At that time the crown of the milk molar D4 is worn down to the root so that only a flat dentine disc covering P4 is left. The roots of milk D4 are resorbed very slowly and remain for a very long time (up to 60-70 mm) for the intensely worn tooth (Fig. 3a, b, inset).

Due to the late initiation of rudiments of the permanent premolar P4 and their slow development, which is stretched in time for in total 8-9 years, abnormalities arise and are often found in the development and eruption of the tooth. During such long periods of time the animals could be subjected to illnesses and injuries which would affect negatively the developing tooth and promote the origin of abnormalities. The first type of abnormality, which is met in woolly rhinos and living rhino species, is the irregular eruption of the P4 crown. Thus, for the specimen ZIN N10 818, West Africa, the skull of an adult individual of *D. bicornis*, the crown of the left P4 is turned at 90 degrees around its axis relative to the neighbouring teeth P3 and M1 (Fig. 4a). The crown of P4 of the right tooth row occupies the normal position. An analogous anomaly is met in the specimen ZIN N10705, woolly rhino skull where a slanting eruption is observed in the yet unworn crown of the left P4 (Fig. 4b). The second type of anomaly described by the author earlier (GARUTT, 1990) is the occurrence of supernumerary P4 and M3. It is manifested in the formation of extra tooth rudiments and their eruption simultaneously with a complete tooth. If there is no place for the supernumerary tooth, it erupts alongside through the palate bones.

Anomalies of the first type apparently occur because the roots of the milk D4 are abnormally slow in being resorbed and are held in the maxilla for a long time, preventing normal eruption of the permanent premolar P4. Set in the maxillary alveolar pocket, the rudiment of the permanent molar P4 is not fixed by anything, as the previous premolars have been erupted for some time. If P4 cannot push out the remains of the milk tooth D4 then with considerable mobility the crown of P4 moves aside in eruption.

As for the supernumerary teeth of woolly rhinos, it should be noted that in the skull of *C. antiquitatis* GM KGU N732 (Fig. 4c), in addition to the supernumerary molar P4 there is an osteoma at the top of the occipital bone. Pathological peculiarities of the osteoma indicate that it was formed in the young animal at the site of a bone fracture. It is possible that this could affect and promote the pathological development of P4.

In the determination of individual ages of woolly rhinos at stages C-V-VI it is necessary to consider the great individual variability in the time of eruption of P4, and

hence the different degree of wear of the P4 crown relative to those other maxillary teeth. At later age stages C-VII-X, the wear rate of the P4 crown becomes even, and the precision of age determination according to wear of the crown of P4 is higher.

At the age stage C-VI, the crown of P4 is worn noticeably less than half. At stage C-VII the crown P4 is worn half or slightly less than half. At stages C-IX-X the crown of P4 is worn practically down to the root.

M1. In the African species *D. bicornis* and *C. simum* the eruption of M1 begins at an age of 1.5-3 years. At that time the intensive growth of facial skull bones begins. The maxillae are lengthened so that an additional area and support for mastication become necessary.

In the dentition of woolly rhinos, the functional importance of M1 increases when the eruption of the fourth molar P4 occurs. At that moment the crown of P4 has not yet risen to the level of the masticatory surface of the tooth row. A temporary 'diastema' is formed between P3 and M1. At that time the crown of M1 is worn less than half. The parastyle of the ectoloph of M1 is strongly lengthened and broadened, and directed toward the 'diastema' formed. Thus the empty space is reduced. For a short time the crown of P4 comes completely out the alveole and closely fits between the teeth P3 and M1 in the tooth row - compensatory broadening disappears (Fig. 5a-d).

M2. The crown is large and trapeziform. The front and back ribs are well developed at the external surface of the ectoloph.

In the recent African rhinos *D. bicornis* and *C. simum*, the back molar M2 erupts at the age of 6-8 years (DITTRICH, 1974; HILLMAN-SMITH *et al.*, 1986).

The slight irregularity of the back molars M2 and M3 in the right and left maxillary halves of the same individual is typical both for living and woolly rhinos. Often the teeth in the right part of the maxilla are worn more than in the left one. This results from the different times of eruption of permanent teeth in right and left halves of the maxilla, which never appear simultaneously in both halves. Accordingly, these teeth begin to function at various times and will be worn to differing degrees. If the habit of the individual animal to masticate food at one part of maxilla is taken into account, the difference in the degree of wear of the teeth is strengthened. As the gap in time of eruption of milk teeth of a given generation between the two halves of the maxilla is much less (from 2 to 8 days), so the difference in wear of the right and left teeth is less and is not so noticeable. The irregular timing of eruption of the back molar teeth increases and therefore the difference in degree of tooth wear in the right and the left maxillae is more clearly expressed in the teeth of that generation.

The difference in wear of the teeth M2 and M3 between

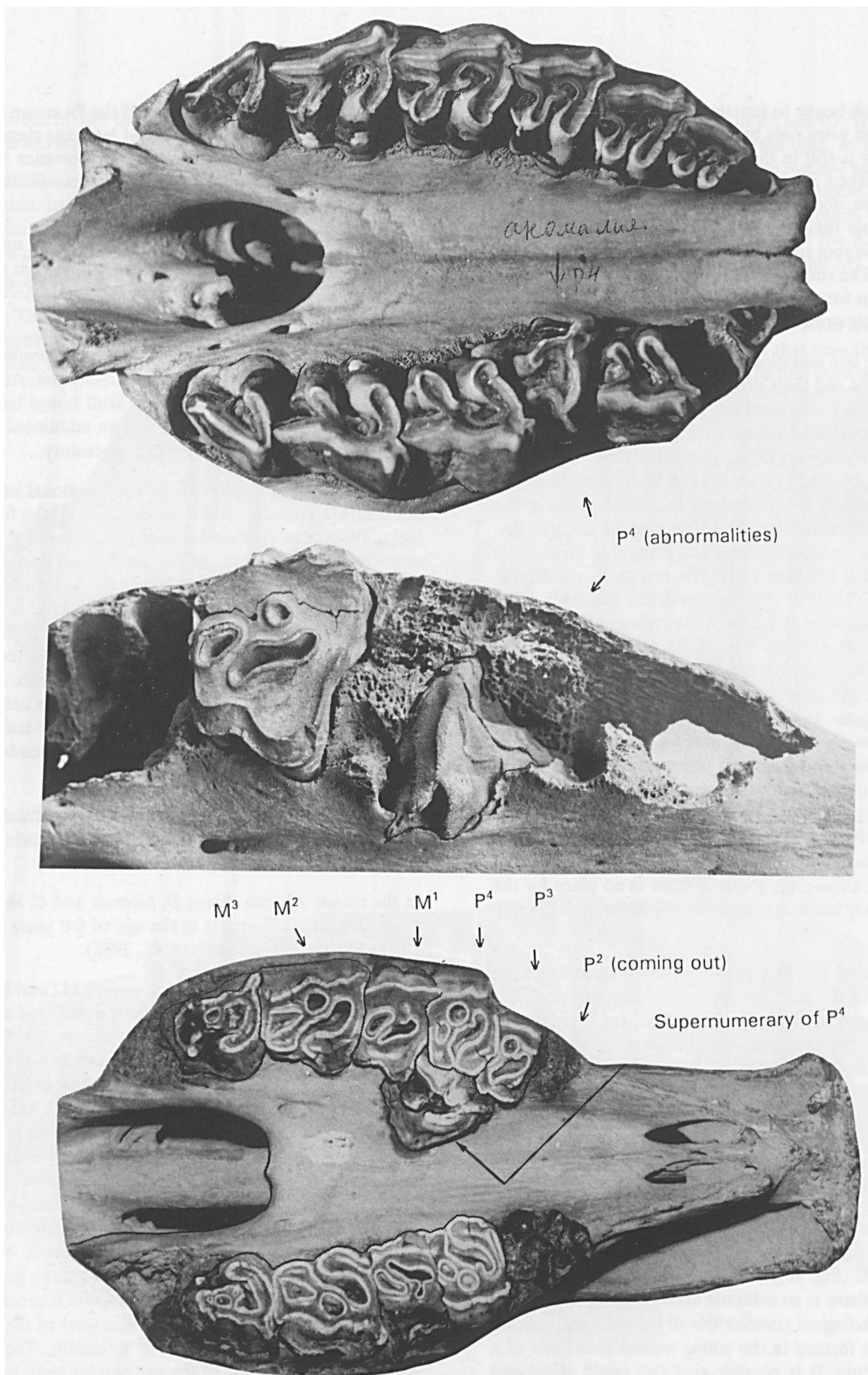


Fig. 4 a, b, c: Abnormal position of P4 (P4 in the figure).
 Fig. 4 a, b, c: Afwijkende positie van P4 (P4 in de figuur).
 a. ZIN N 10.818 *Diceros bicornis*
 b. ZIN N 10.705 *Coelodonta antiquitatis*
 GMKGU N 732 *Coelodonta antiquitatis*

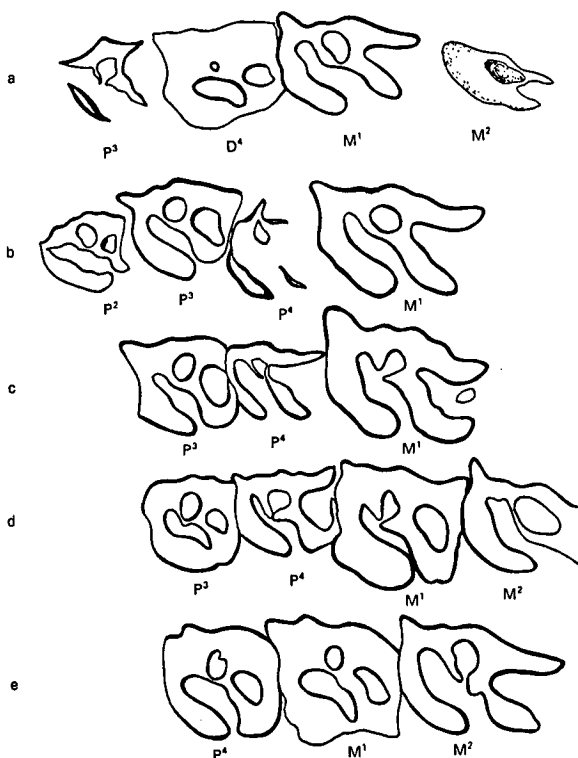


Fig. 5 a-e: The change of form of the masticatory surface of the M1 crown during the eruption of P4. Note that M1 and P4 in the figure are similar to M1 and P4 in the text.

Fig. 5 a-e: De verandering van vorm van het kauwvlak van de M1 kroon tijdens het doorkomen van P4. M1 en P4 in de figuur zijn gelijk aan M1 en P4 in de tekst.

- a. GMKGU N715 Tatarstan
- b. GMKGU N716 Tatarstan
- c. GMKGU N729 Tatarstan
- d. ZIN N14100 Yakutia
- e. GMKGU N735 Tatarstan

right and left sides is well seen in the back molars M2 and M3 of *C. antiquitatis*, nos. GM KGV N737, Tatarstan and ZIN N14 100, Yakutija. In the first specimen, the right M2 back valley is not closed completely, and in the M3 not all of it comes out of the alveole (only the peaks of the principal crests are touched with wear). In M2 of the left side, the back valley is closed completely, and in M3 the middle valley and the closed additional valley are expressed distinctly. Conversely, in the second specimen M2 and M3 of the right teeth are worn stronger relatively to the left one (Fig. 6a, b).

Taking into account the above-mentioned peculiarity in the development of woolly rhino dentition, the conclusions of B.S. RUSANOV (1968) that in the Early Pleistocene form of *C. antiquitatis* in M2 the back valley was not closed till complete tooth wear, appears hasty.

For the Early Pleistocene, B.S. Rusanov has defined the subspecies of woolly rhino *Coelodonta antiquitatis pristinus*, from the shore of River Milkere, which in his opinion has such a peculiarity in the structure of the upper back molar M2. Only one skull and one isolated tooth of this form of rhino has been examined.

The other skull of woolly rhino is regarded by B.S. Rusanov as a Late Pleistocene form and is described by him as *Coelodonta antiquitatis humilis*. For this form, in his opinion, the back valley is closed early in M2. The teeth of the right and left rows were not preserved completely in any of the compared specimens, and those which are in the maxillae indicate different individual ages.

Thus, the Milkereanian skull of *Coelodonta antiquitatis pristinus* has P2-M2 of the left tooth row and only M3 of the right. If the wear of M3 is taken into account (incompletely erupted from the alveole, only the peaks of the principal peaks worn) and the wear degree of the preserved teeth, then at this stage of wear (VI), the un-

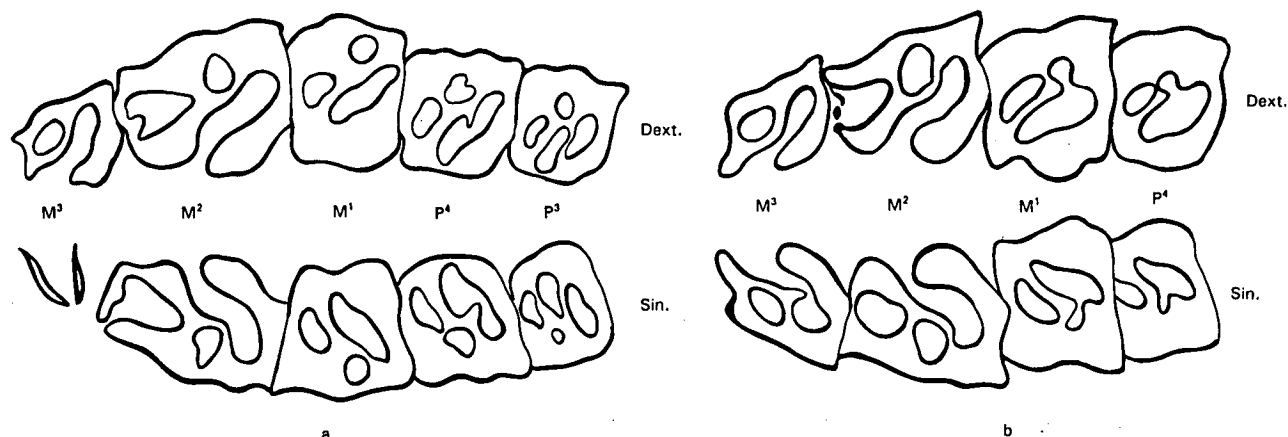


Fig. 6 a, b: Irregular wear of the teeth of the right and left side of the upper maxilla of *Coelodonta antiquitatis*. Note the different dental nomenclature.

Fig. 6 a, b: Onregelmatige afslijting van de rechter en linker kiezen uit de bovenkaak van *Coelodonta antiquitatis*. De nomenclatuur verschilt met die in de tekst.

- a. NGMKGU 737 Middle Volga, Tatarstan
- b. NZIN Yakutia, Verkhoyansk region N14.100

closed back valley of M2 is quite possible. Judging by its dimensions, form and depth, the back valley was already worn to the beginning of closure. The separate and isolated tooth M2, no. N901 from the valley of the River Omoloi, with an unclosed back valley worn to an even greater degree, is insufficient to serve as the basis for determination of an independent subspecies.

Adduced in comparison to the Milkerenian skull of *Coelodonta antiquitatis humilis*, specimen N104/5 has only M1-M3, strongly worn. The crown of M1 is strongly shortened in the longitudinal direction, which is typical for the final stage of tooth wear. Only two alveoles, heavily reduced in dimensions, have remained of the principal valleys of M1. It is not strange that at such a late stage of wear (VIII-IX), the back valley is closed in M2.

The presence of additional folds in the additional and middle valleys of M2 of *C. antiquitatis pristinus* is regarded by B.S. Rusanov as another typically archaic trait confirming, in his opinion, the Early Pleistocene age of these woolly rhinos. However, by studying large series of skulls of *C. antiquitatis* from different geographical regions, the author has noted that the given index is not frequently met in woolly rhinos, not only in the back molars M2 and M3, but more often in premolars P3 and P4. The dimensions and morphological peculiarities of the skull do not influence the frequency of occurrence of this index.

Previously, A.K. AGADJANJAN (1972) and N.M. ERMOLOVA (1973) investigated skulls of *C. antiquitatis* from Jakutija and Pribaikalje, using a larger sample than B.S. Rusanov. They noted the considerable individual variation of the enamel pattern and crown form of the molar teeth at different stages of wear. They cast doubt on Rusanov's conclusions and noted correctly that it is impossible to reach such conclusions without an understanding of woolly rhinos dental ontogenesis.

The closing of the antecrochet, crests, and crocket, protoloph with the metaloph, and metaloph with metasyle in woolly rhino teeth are transitional and abbreviated in the development of the upper molars, and as the author is convinced, are subject to great individual variability. Therefore, it is necessary to have a sample with preserved teeth of the right and left parts of the maxilla, and not one but a series of specimens in order to recognize these indices as diagnostic of a subspecies.

M3. The pyramidal form of the crown is typical. Before the beginning of tooth wear its crests are closely fitting at the crown peak.

For African rhinos *D. bicornis* and *C. simum*, M3 erupts at the age of 8-15 years. At not later than 15 years, M3 comes out of the alveole and begins to wear. Since M3 erupts late, with its rudiment, like the rudiment of P4, in the alveolar pocket, it occupies much space and the crown is not fixed. Abnormalities in development are

typical for M3 also. The occurrence of a supernumerary M3 is registered for African white rhinos (HILLMAN-SMITH *et al.*, 1986). The author has found supernumerary M3 in skulls of woolly rhino, no. GM KGU N737, Tatarstan, and Merck's rhino from the Halle Museum, Germany.

Lower premolars and molars

Lower premolars and molars are hypsodont, with a clear pattern of enamel prisms.

The formation and eruption of the lower molars occurs earlier than for the upper molar teeth. Correspondingly both their wear and loss occur earlier. Thus, at the stage of replacement of milk D4 by the permanent P4, the first premolars p2 and p3 in some individuals of woolly rhino are already intensely worn. The older the individual, the stronger the expression of difference in degree of tooth wear in the upper and lower jaw. Individual variation in the teeth of the mandible during wear is expressed to a greater extent. It is impossible to identify the age stages of upper tooth wear with those for the lowers, due to the small number of woolly rhinos skulls with complete mandibles. The peculiarities in development of p4 and m3 are the same as for P4 and M3 of the maxilla, excluding the abnormalities of irregular eruption and supernumerary teeth typical for the upper jaw.

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