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21. THE RHINOCEROTIDAE

KURT HEISSIG

The phylogeny and classification of the Rhinocerotidae are revised on the basis of the newly introduced characters presented by Prothero, Manning, and Hanson (1986) and Groves (1983) and my own observations since the revised classification of Heissig (1973a). The characters used here are discussed in detail, especially to avoid too many parallelisms. The presence of a functional fifth metacarpal in the two fore feet of *Juxia sharamurunense* Chow and Xiu in the American Museum serves the key to the controversy over whether the first true rhinoceroses had a tridactyl or tetradactyl manus. The evidence of a strong relationship of the American *Diceratherium* group with the basic stock of the rhinoceroses, especially the genus *Trigonias*, and on the other hand, the fundamental differences from *Menoceras*, as stated by Prothero, Manning and Hanson (1986), have modified our knowledge of the early history of the family. The hypothesis of a common ancestry of the Teleoceratini and the Rhinocerotinae, brought forward by the same authors, is rejected here. Some characters limiting the adaptational potential of subfamilies and tribes are analyzed in relation to the behavior of the animals.

Introduction

During the nearly thirty years in the middle of our century, when no specialists in the western world were concerned with detailed study or classification of the rhinoceroses, a huge mass of undescribed material was stored in the museums and collections all over the world. Modern means of transportation led to more extensive digging, and as a result, vast and only partially identified collections of fossil rhinoceroses were waiting for their adequate descriptions or monographs. Since the group was again taken into consideration in the beginning of

the 1970s by Guérin, Ginsburg, and Heissig in Europe, Radinsky a little earlier in the United States, and, later, Fortelius in Finland, all authors have felt that a thorough revision of the classification was needed. The basis of the classification was fixed by Radinsky (1966) by restricting the family to members with the chisel-tusk shearing complex of I_2 and I^1 , and their descendants. The later attempts by Heissig (1973a) as well as the phylogenetic and systematic hypotheses presented in this volume, must remain provisional until the materials already collected are described and used as a base of a new classification. We are still far from this goal, but we now need a classification to work with and to arrange our materials. A revised version of my classification (1973a) is presented here, changed by a better understanding of the American species and some strong arguments of my American colleagues.

Characters and parallelisms in the Rhinocerotidae

Using characters for a phylogenetic analysis means avoiding parallelisms. Most gradually changing characters are an expression of a general tendency among the whole group whereas discrete characters, especially when new structures are formed, may be unique and therefore key characters for the analysis. The loss of an element or a structure may occur very easily and is always suspected to be subject to parallelisms. Nevertheless, we can even use parallel evolved structures, if they follow different ways in different subgroups. In the following list, a lot of single characters currently

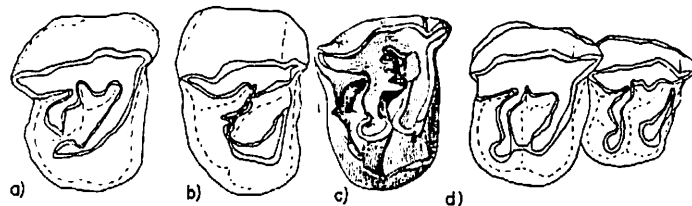


Fig. 21.1. Molarization stages of premolars: a) pre-molariform b) sub-molariform c) paramolariform d) semimolariform and molariform

used in the literature, and most of the characters used by Groves (1983) and Prothero, Manning, and Hanson (1986) are arranged in classes of significance. Some missing characters may be ascribed to a supergroup of characters reflecting merely one general tendency. The general significance of others is not sufficiently known to me.

General trends

Skull shortening-- can be used on the specific, and possibly on the generic level. Single traits of this tendency may have systematic value, as in the shortening of the basicranium. In most cases, we have to consider allometric shortening of face, cranium, and even smaller parts of the skull.

Skull broadening-- mainly, but not exclusively, combined with shortening. I have found no means to detect parallelisms.

Deepening of the nasal notch-- occurs in most lineages at different times. Forms with strong horns must solve mechanical problems and may be distinguished by the special features of the construction of the nasal bones.

Molarization of premolars-- a general tendency in all tribes, but very slow and subject to a high degree of variation in the maxillary. In the mandible, it is completed early. In the advanced forms, it is delayed and possibly even reversed in high-crowned forms. Most, but not all, Rhinocerotini and Dicerotini follow a different way of molarization, passing through a paramolariform instead of a semimolariform stage (Fig. 21.1).

The complication of the crown pattern

of upper teeth by secondary folds as crista and crochets-- occurs in most lineages, but may follow different patterns. Parallelisms are extensive, high variability allows reversals. Primitively there is a crochet present in the molars, a crista in the premolars. The crochet arising with molarization in premolars is often split in several short folds in the early stages of molarization, but may unite as a single fold with the crista. The crista of molars is not homologous with the crista of tapiroids, but arises between paracone and metacone.

Limb shortening-- is correlated as a general character with the increase of body weight. If exceeding the limits of mediportal conditions it can be used as a character of a group.

The increase of crown height of the cheek teeth-- is confined to progressive forms in most groups and may indicate a change of diet, but not necessarily grazing. In most cases it causes a delay of molarization and the formation of cement. In the Elasmotheriini it is a general character, exceeding the degree reached in other groups.

The reduction of the posterior cingulum in M³-- is a general character in Rhinocerotidae. It is a good character if reversed. The specific morphology reached by this process differs considerably in several lineages.

The reduction of the lingual cingula in upper premolars-- occurs in most, but not all tribes at different times, to a different degree. Reversals of the trend are possible.

The reduction of the metacone rib of up-

per teeth-- occurs earlier in molars than in premolars. Timing and degree are different in the lineages, but it is going on in nearly all tribes. There is no known reversal.

The closure of the subaural channel-- a single trait of skull shortening and therefore occurring in several tribes, but sometimes significant within a lineage. There are no reversals.

The reduction of the anterior crest of the paralophid in dP₃-- is evolved several times in single genera of different tribes. There are no reversals. In *Coelodonta* it is compensated by a splitting of the paralophid in dP₂.

Some characters may be differentiated in divergent directions coming from an intermediate primitive stage. They are listed here, being equally widespread and gradual in change:

The direction of the premaxillae-- originally downsloping to enable the contact of the incisors, may be changed to horizontal, when the lower incisors are coming up by curving or by a more upright implantation. In some early genera, such as *Ronzotherium*, there seems to be a slight development in the opposite direction.

The orientation of the occipital plate-- reflects the normal skull position and is dependent upon feeding habits. There are deviations from the right angle in both directions, but overhanging of the occipital crest is more widespread and stronger developed, because of its correlation with grazing (Fig. 21.2).

The articulation of the fibula with the femur-- may be a primitive feature as indicated by its presence in the tapirs. It is suppressed in different tribes, but the present knowledge of its occurrence is still insufficient. Its occurrence is suppressed in the fossil *Diceros neumayri*, but still developed in both recent Dicerotini. So we must assume the possibility of reversals.

Trends observed only in single groups

Further shortening of the limbs, exceeding mediportal conditions-- is a typical feature in the Teleoceratini. Only

the distal limb segments are shortened.

Shortening of the whole limb length-- is confined to the *Chilotherium* group, including some *Peraceras* of the Aceratheriini.

Size increase of the I₂-- is a trend observed in all other subfamilies except Rhinocerotinae.

The gradual reduction of P₁-- is a character quite different from its early loss in ontogeny. It is observed in most derived genera of the Aceratheriinae and several Diceratheriinae and Elasmotheriini.

The reduction of protocone constriction from behind and merging of protocone and antecrochet-- occurs as a general trend among Rhinocerotini and Dicerotini, but is observed in one single species of *Subchilotherium* too.

The strengthening of the posterior protocone fold-- the opposite trend, coming from the intermediate primitive condition, occurs as a group tendency independently in Aceratheriinae and Elasmotheriini.

The loss of characters or elements

The loss of the distal part of metacarpal V and its digit-- occurs in all tribes except the stem group Trigoniadini, mostly in the advanced members. In the Rhinocerotinae alone it is a general character of the whole subfamily.

The loss of all incisors-- is confined to the Rhinocerotinae, but not as a general character. The reduction is normally rapid, but can be followed in some lineages (Fig. 21.2).

The loss of I₁-- is correlated with the increase of I₂ and a narrow symphysis. It occurs several times in distantly related genera.

The early loss of P₁-- is a highly variable character and may be subject to reversals easily. The same is true of its prolonged retention.

The loss of the median lower crest of the mandibular symphysis-- occurs early in the history of the family, but may be useful to separate lineages in the early evolution.

Aceratheriinae (incisors strong, horn weak)		Rhinocerotinae (horn strong, incisors weak or lost)					
Teleoceratini (short limbs)		Aceratherini (slender limbs)		Rhinocerotini and Dicerotini (primitive)		Elasmotheriini (early derived)	
Grazers	Teleceras (Miocene)	Acerorhinus (Mio-Pliocene)	Rhinoceros unicornis (Recent)	Hispanotherium (Miocene)	Ceratotherium (Recent)	Irranotherium (Miocene)	Elasmotherium (Pleistocene)
	Aprotodon (Oligo-Miocene)		Chilotherium (Miocene)				
Type of adaptation	Limb shortening	Limb shortening	Teeth hypsodont Head upturned	Head lowered Incisors reduced	Head lowered Incisors lost	Head lowered Incisors lost	Head lowered Incisors lost
	Incisors diverging, symphysis broad	Limb shortening and incisor divergence	Incisors lost	Head lowered	Head lowered	Head lowered	Horn shifted posteriorly
Example for browsers	Brachypotherium (Miocene)	Aceratherium (Miocene)	Rhinoceros sondaicus (Recent)	Unknown	Dicerotinus (Recent)		
	Prosantorhinus (Miocene)	Mesaceratherium (Oligo-Miocene)	Dicerotinus (Recent)				
Stem group Browsers only		Diceratheriinae (no known adaptation to grass diet) (balance of horn and incisors, or hornless)					

Fig. 21.2. The adaptation of the Rhinocerotidae to a grass diet.

The loss of the horn-- is confined to the Aceratheriinae, occurs in most, not in all lineages at different times.

Single characters with some parallelisms

The formation of a horn-- occurs three times independently, but may be distinguished by the type of horn, which is unique in each case (Fig. 21.2).

The reduction and loss of the third articulation between radial and intermedium-- occurs twice, at the base of the Aceratheriini and the Elasmotheriini, as specialization of the more long-legged slender limbs of these tribes.

The broadening of the mandibular symphysis-- occurs twice as an extreme form of specialization in Aprotodon and Chilotherium sensu stricto but combined with a different position of the incisors.

The sharpening of the ventral edge of the vomer-- a character found in Rhinoceros only by Groves (1983) is paralleled by Chilotherium sensu stricto and may be due to facial shortening.

A long parolophid in lower molars (and premolars)-- is a progressive character of Rhinocerotinae, but also present in some unrelated forms. It can be reduced again.

The closing of the mediusinus in upper molars by swollen lingual cusps-- occurs several times in rather high-crowned forms. It is formed by an antecrochet in Chilotherium, by the protocone in Rhinoceros and Ceratotherium.

The formation of a postorbital process-- occurs in several genera, but may be significant in a single lineage.

A convex lower margin of the mandible-- was achieved by some unrelated genera, but is of high generic value.

The inclination of the ramus mandibulae-- depends upon skull shortening and skull position. Reversals of a tendency are possible.

Characters with no or rare parallelisms

The articulation of the ulna with the intermediate-- is a character uniting all Rhinocerotinae, but never observed in any

other tribe.

The double-rooted P₁-- is an apomorphic character, even if the function is not clear. It is observed in all Rhinocerotinae, where it is retained, and in some specimens of Subhyracodon.

The craniocaudal elongation of the distal facet of the intermedium for the ulnar-- unites the Rhinocerotini and Dicerotini and is not observed in any other tribe.

The loss of the naso-lacrimal contact -- is an autapomorphy of Dicerotini.

The short trochiter of the caput humeri (tuberculum maius) - also in the Dicerotini, is autapomorphic.

There are many characters of this class, autapomorphic for single genera. They are not treated here, because the present knowledge does not yet allow a cladogram of all genera. For the Rhinocerotini see Groves (1983).

Origins

Within the Rhinocerotidae, the Rhinocerotidae are defined by Radinsky (1966) by the unique shearing complex of I₂ against I₁. There are many other synapomorphies uniting the family, as shown by Prothero, Manning, and Hanson (1986). The origin of the family was a mystery for a long time because of its retention of a fourth digit in the manus, which was not known in any suspected ancestor, and was definitely lost in all known hyracodonts. The idea of the reappearance of this digit in the Rhinocerotidae is rejected here because it is in the most primitive members of the family where it occurs, being lost in many advanced genera.

Two fore feet of *Juxia sharamurunense*, that I found in the immense treasures of Osborn's Mongolian expeditions, housed in the American Museum of Natural History, show clearly a fully developed fifth metacarpal and its phalanges. So we must now consider the indricotheres as the sister-group of Rhinocerotidae, bound together by a primitive tetradactyl manus, a similar molar and premolar pattern of their earliest members

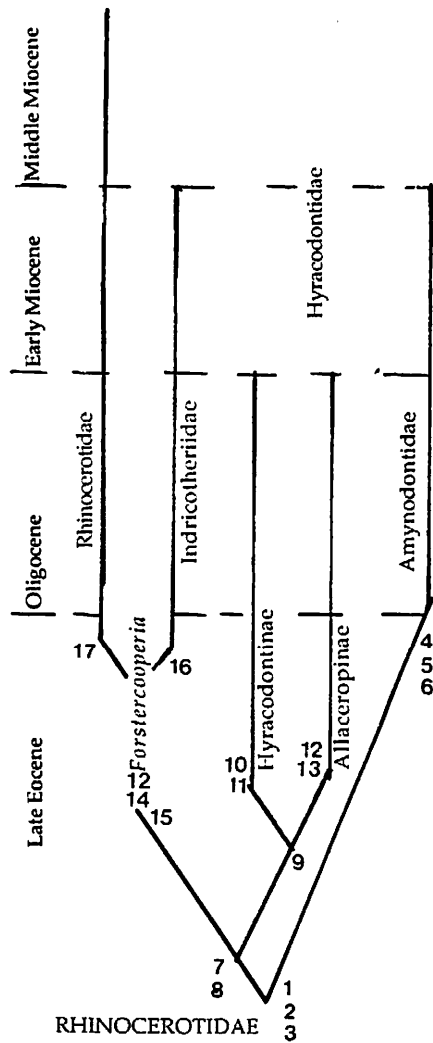


Fig. 21.3. The origin of the Rhinocerotidae. Characters: 1) M_3 hypoconulid lost; 2) trigonid lengthened in lower molars; 3) parastyle fused to ectoloph; 4) extreme lengthening of molars; 5) strong canine; 6) limbs massive; 7) lower premolars lengthened; 8) upper premolars broadened; 9) tridactyl manus; 10) diastema shortened; 11) incisiform canine; 12) reduced metastyle of M^3 ; 13) I_3 lost; 14) patella broadened asymmetrically; 15) I^1 enlarged; 16) I_1 enlarged; 17) I_2 enlarged.

and the enlarged I^1 . Both are together the sister-group of the remaining Hyracodontidae *sensu stricto*. It is therefore necessary to exclude the Indricotheriidae again from the hyracodonts and to keep them separate on a family level (Fig. 21.3).

The earliest Rhinocerotidae

With the beginning of the Oligocene, we find a pair of genera in both North America and Europe. Their common features may represent characters of the common ancestor of the whole family. The skull is narrow and long with tapering hornless nasals and a rather shallow nasal notch. The enlarged lower I_2 is straight and nearly horizontally implanted. The upper first incisor is less enlarged and meets the lower one. The upper dentition is still complete. Canine and third incisors are lost in the mandible. The outer wall of the premolars is undulating in the same way as in the indricotheres, with broad paracone and metacone ribs. Sometimes there are sharp metacone ribs in the molars. The premolars are faintly or not molarized. Even in the lower premolars, the entoconid may be isolated or lacking entirely.

The smaller genera of both continents represent the main evolutionary lineages, *Trigonias* Lucas (1900) in America, and *Epiaceratherium* Abel (1910) in Europe. They have larger, more elongate I^1 , similar to all later Rhinocerotidae, but retain I^3 and upper canines. The lower big incisor is rather short with a trigonal outline of the crown and a trigonal cross section. The larger genera *Amphicaenopus* Wood, 1927, in America and *Ronzotherium* Aymard, 1856, in Europe are also similar to each another. The I^1 is less elongate, still nearly conical in *Ronzotherium*, but I^3 and canine are lost. The first upper incisor in *Amphicaenopus* is intermediate, but more primitive than in *Trigonias*. Both genera have straight, elongate lower tusks with an oval cross section. They disappear during the Oligocene without descendants.

The first evolutionary lineages

The record of the early rhinoceroses is poor in the Old World, and rich in America. It is easy to follow the lineage from *Subhyracodon* Brandt, 1878, to *Diceratherium* Marsh, 1875, a sister-group of *Trigonias* with tridactyl manus and without I^3 and upper canine. The structure of the upper premolars is very similar to *Trigonias* and the primitive arrangement of the ridges on the outer wall is preserved. In *Diceratherium* the first horns in rhinoceros evolution are formed as lateral protuberances at the sides of the nasals. These groups, mainly known from America, should be united on the subfamilial level as two tribes: Diceratheriini Dollo, 1885, and Trigoniadini nov. trib. (Fig. 21.4).

The Diceratheriini found their way to the Old World only for a short time. In the upper Oligocene of France, a single skull was found and named "*Rhinoceros pleuroceros*" by Duvernoy (1853). It shows clearly the lateral protuberances of *Diceratherium*, but at the moment it is not clear if it should retain its generic name *Pleuroceros* Roger, 1904, or if it would be better to include it in *Diceratherium*.

Besides the rapidly growing *Ronzotherium* and smaller hyracodonts of the genus *Eggysodon* Roman, 1912, the rhinoceros fauna of the European Oligocene is scarce. The first genus arising from the main stock after *Epiaceratherium* is *Protaceratherium* Abel, 1910, with its more primitive species *albigense* Roman, 1912, from the base of the upper Oligocene. In contrast to the American evolutionary lineage it has not lost its fourth digit in the manus. The metacone rib is flattened even in the premolars. This points to a relationship with the Aceratheriinae. Also in contrast to the American Diceratheriini, the sharp outer protoconid edge is flattened, a character arising already in *Epiaceratherium*. In this species the I^1 is still triangular, but reaches the typical blade-like form in the later *Protoceratherium minutum* (Cuvier, 1822), the type species. In this species the premolars are

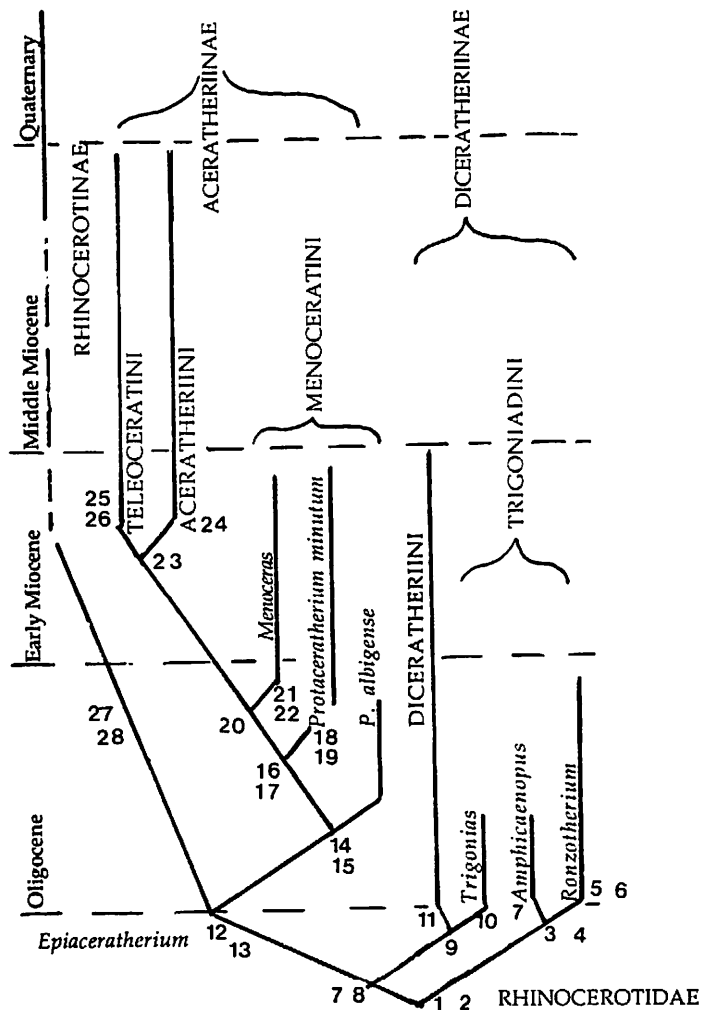


Fig. 21.4. The diversification of the Rhinocerotidae. Characters: 1) incisor shearing complex, $I^1/2$; 2) general tendency toward deepening of nasal notch; 3) I_2 straight and long; 4) I^3 and canine lost; 5) symphysis massive and high; 6) size increase; 7) I^1 trigonal, elongate; 8) incipient molarization of upper premolars; 9) metacone ribs lost in upper molars; 10) nasals short; 11) tridactyl manus; 12) median lower crest of mandible lost; 13) basicranial axis short; 14) I^2 lost; 15) I_2 lanceolate, curved; 16) I^1 blade-like; 17) metacone rib reduced in premolars; 18) molarized premolars; 19) I^1 smaller; 20) split median horn base; 21) tridactyl manus; 22) horn enlarged; 23) nasal notch deepened; 24) posterior articulation of radiale with intermedium lost; 25) limbs massive and short; 26) I^1 broad and low; 27) strong subterminal undivided horn base; 28) tridactyl manus, P_1 double rooted.

semimolariform to molariform and the angulate lanceolate lower incisors curve upwards, at least in males. The sexual dimorphism is accentuated in the incisors: the females have shorter crowns, whereas the males have long crowns with a loss or thinning of enamel on the lingual side. The limb proportions and a lot of derived characters of the skeleton, especially the form of tarsal 1, are very similar to *Menoceras* Troxell, 1921.

Unfortunately, we cannot follow the steps from this first genus, which shows clear affinities to all modern rhinocerotoid genera, to the later tribes dominating the Palearctic Neogene. The skull is not yet sufficiently investigated to know whether the basicranium is already as short, as it is according to Prothero, Manning, and Hanson (1986), in all higher rhinoceroses.

In the terminal Upper Oligocene, a second immigration wave of rhinoceroses occurred in Europe. Besides the first Aceratheriinae, a *Menoceras*-like animal also occurs, described by others as "*Diceraotherium zitteli*" Schlosser, 1902, or "*Diaceraotherium florsheimense*" Heller, 1933. Teeth are the majority of remains known, but a well-preserved skull from the Wischberg in Switzerland exhibits the split terminal horn bosses of the *Menoceras*-type. The postcranial skeleton is unknown. Shortened limb bones that may belong to this animal have also been discovered, but whether these are actually part of the same animal remains to be proven.

The evolutionary lineage, from which *Protacraotherium* and later *Menoceras* and the Aceratheriinae split, must have evolved outside of Europe. It must have separated from the ancestral stock of the Rhinocerotinae before curving its lower incisors upwards, before separating the antecrochet of the upper molars by a sharp groove from the protocone. According to Prothero, Manning, and Hanson (1986), this small group should be taken as a separate subfamily, the Menocerotinae. In my opinion, this sister-group of the Aceratheriini and Teleocerotini, without closer relation-

ship to one or the other, should be kept within the Aceratheriinae as a third tribe, Menocerotini.

The different members of the subfamily Aceratheriinae exhibit a different rate of molarization of the premolars. At the end of the Oligocene, all Menocerotini have reached semimolariform to molariform conditions. In the Aceratheriini it is the semimolariform stage that is generally adopted, but the linguodistal edge of the premolars is still rounded and not square. In the lower second premolar there is still an isolated entoconid. The Teleocerotini still exhibit submolariform conditions. In both tribes there are lineages with delayed molarization.

The Aceratheriini

The less specialized tribe of the advanced Aceratheriinae offers a very complicated phylogeny. Only the morphological characters of the skull, the incisors, and the mandibular symphysis are generally useful, including the presence or absence of upper incisors. The limb bones may be used in more specialized genera.

The earliest known acerathere is *Mesacraotherium* Heissig, 1969, from the upper Oligocene. Its slender limbs and narrow skull are primitive, as are the premolars. A rather peculiar feature is the broad mandibular symphysis with strong upwards curved incisors, shearing against large, chisel-shaped upper ones. These characters are unique in aceratheres and link this genus to *Alicornops* Ginsburg and Guérin, 1979, in the middle Miocene and possibly to *Aceratherium* Kaup, 1834, in the upper Miocene. This may be the only endemic group of aceratheres in Europe.

Another immigration near the end of the lower Miocene brings the third rhinoceros wave to Europe. It comprises another type of acerathere. All forms of this second branch are characterized by the tendency to reduce the upper incisor after the loss of its shearing function, the lower incisor working against a prehensile upper lip. Whereas in *Mesacraotherium* and *Al-*

icornops the nasals are still unknown, we know that in at least one line of this second branch a small horn base like those of female *Menoceras* is retained. The first genus to appear is *Plesiaceratherium* Young, 1937, with four species known from China to Spain. It is hornless with a narrow skull and a narrow symphysis. The small upper incisors seldom have traces of wear. The lower ones are flattened and only slightly upturned. The genus disappears during the middle Miocene without descendants.

In the middle Miocene a somewhat later immigration brings *Hoploaceratherium tetradactylum* (Lartet 1837; see Ginsburg and Heissig, this volume, Chapter 22) with a small horn base on unfused nasals, and no upper incisors. The nasals are primitively long and the skull is narrow. The narrow symphysis and the thick, moderately-curved lower incisors, are of the uniform shape uniting *Hoploaceratherium* Ginsburg and Heissig (this volume) with the so called "*Aceratherium*" species of Asia and early *Aphelops* Cope, 1873, and *Peraceras* Cope, 1880. All these forms are somewhat later and therefore have shorter nasals. "*Aceratherium*" *depereti* Borissiak, 1927, also has a small horn that may reflect a real relationship. The American genera seem to be earlier offshoots of this group if they are really homogenous. In Europe the genus terminates with the upper Miocene *H. bavarium* (Stromer, 1902), with markedly shortened nasals and a broader skull.

In Africa, the genus *Chilotheridium* Hooijer, 1971, with shortened tetradactyl limbs and a small horn far back on the long nasals, seems to be nearer to *Hoploaceratherium* than to *Chilotherium*. The skull form of "*Turkanatherium*" *acutirostratum* Deraniyagala, 1951, points to the same group, but the nasal notch is rather shallow. Both genera occur in the middle and upper Miocene.

The group around *Chilotherium* Ringström, 1924, may have originated from the same group as indicated by the form of the lower incisors. It begins in the early

middle Miocene of South Asia with *Subchilotherium* Heissig, 1972, from the lower Siwalik series. Unfortunately, the only known skulls of this genus are of considerably younger age, so that the most primitive condition is unknown. The symphysis is moderately broad as in *Aceratherium*, and the medial flanges of the incisors are not upturned. The structure of the cheek teeth is very near that of the later *Chilotherium* species. The premolars, especially the P₂, are shortened in the same way. The limb bones are shortened as in *Chilotherium*, but not in the same degree. The manus is not completely known.

The second genus of this group, *Acerorhinus* Kretzoi, 1942, is better known. It starts in the late middle Miocene with *A. palaeosinensis* (Ringström, 1924) with still rather long nasals and a narrow skull. The general tendencies of broadening of the skull and deepening of the nasal notch can also be seen in this genus. The lower incisors are similar to *Subchilotherium* but less curved. Their medial flanges are upturned as in *Chilotherium* and the mandibular symphysis is hollowed from below. A broadening of the symphysis is not observed. The distance from the nasal notch to the orbit is short, and the facial crista is confluent with the anterior rim of the orbit, forming a nearly vertical straight line. This genus is evolving rapidly during the upper Miocene leading to very complicated structures in the upper cheek teeth (*Sinorhinus brancoi* Schlosser, 1903). In my opinion, the narrow zone of rugosities along the anterior rim of the nasal cannot be interpreted as a horn base. The limbs are shortened, but more massive than in *Chilotherium*, and the manus remains tetradactyl. This genus persists up to the lower Pliocene and comprises the latest *Aceratheriini* of the Old World.

Chilotherium sensu stricto begins in the upper Miocene and exhibits the typical broadened symphysis already in the first species. The medial flanges of the incisors are upturned and the symphysis is hollow below. In contrast to *Acerorhinus*, the skull is broad and the distance between the orbit

and the nasal notch is longer. The facial ridge is clearly in front of the orbit and forms a right or obtuse angle. The skull narrows from the frontals to the nasals, not abruptly as in *Acerorhinus*, but gradually. These characters may indicate a long separate history of both genera. The limbs are shorter than in any other genus of the *Aceratheriini*, but remain slender. Some species show a lateral shifting of tarsal elements. The manus is tridactyl, at least in the type species. In the other species it is not sufficiently known. A general increase in size and a trend to facial shortening is observed during the upper Miocene. The genus disappears, as does *Subchilotherium*, at the end of the Miocene. In spite of the rather high-crowned cheek teeth, there is no sign of neck bending, as in other grazing rhinoceroses. I suppose that in all forms fighting with enlarged incisors instead of horns, the head position was horizontal, and that the grazing was possible only by shortening of the limbs to bring the head nearer to the ground. Nevertheless, it remains questionable if *Chilotherium* was a true grazer.

The Teleoceratini

Whereas the *Aceratheriini* have always retained rather slender limbs, even while undergoing shortening, the *Teleoceratini* show the tendency to massive and short distal limb segments throughout their history. In contrast to the *Aceratheriini*, they never lose their upper first incisor pair and retain their shearing function.

The first representative of this tribe is *Brachydiceratherium* Lavocat, 1951, with the single species *B. lemanense* Pomel, 1853, from the upper Oligocene of France. Its long and narrow skull is quite similar to the *Aceratheriini* in the long and tapering nasals with the small, divided horn base at the tips. The nasal incision is deep. The lower incisors are strongly curved and the symphysis is rather broad. The limbs are more massive than in the early *Aceratheriini* but only slightly shortened. The manus is tetradactyl and shows the

primitive third articulation between radial and intermedium. This facet on the radial is replaced in all *Aceratheriini* by a rough protuberance, indicating the former presence of a facet.

Somewhat later, at the beginning of the lower Miocene, a second genus *Diaceratherium* Dietrich, 1931, came to Europe as an immigrant. The skull is smaller and horned, but the cheek teeth show a divergent morphology and the limbs are more shortened. Both genera coexisted during the lower Miocene in western Europe for some time. The large *Brachydiceratherium* has broad premolars with heavy lingual cingula and broad, low-crowned molars. Also the lower cheek teeth are broad and have strong cingula. The genus disappeared in the upper part of the lower Miocene, probably giving rise to *Brachypotherium* Roger, 1904, in the middle Miocene. This genus is tridactyl in the manus and is widespread in the Old World during the middle and upper Miocene with several species. It persists into the late Pliocene in East Africa. The skull is broad and short, with reduced, hornless nasals and strong premaxillae, bearing a strong upper incisor. The heavy mandible has a curved lower margin and strongly curved, but nearly horizontal implanted incisors. In the upper premolars, the molarization is complete, but the morphology of the other teeth is nearly unchanged. There is a slight shortening of the premolars, especially the first, and the second shows signs of reduction. The limbs are short in the distal segments, the proximal ones being larger. The genus reaches the maximum size of brachyodont rhinoceroses in its Indian species, *B. perimense* (Falconer and Cautley, 1847).

The smaller *Diaceratherium* outnumbered *Brachydiceratherium* during the lower Miocene. It shortened its limbs more rapidly, and shows a moderate increase of crown height of the cheek teeth. It retains a nasal horn, and shows only a weak molarization of the premolars and no reduction of the fifth metacarpal. Its evolutionary steps are marked by several species names, *D. as-*

phaltense (Depéret and Douxami, 1902), *D. aginense* (Repelin, 1917) and *D. aurelianense* (Nouel, 1866), all in the lower Miocene. The last species, with a moderately shortened skull, extremely shortened limbs, but a tetradactyl manus, tends to develop very high-crowned teeth. It gave rise to the tridactyl genus *Teleoceras* Hatcher, 1894, in America, where it reached hippopotamus-like proportions. In Europe, this lineage disappeared at the end of the lower Miocene.

Contemporaneous to *D. aurelianense*, there existed a smaller offshoot of this lineage, *D. douvillei* (Osborn, 1900). It leads to the genus *Prosantorhinus* Heissig, 1973b, characterized by a saddle-shaped skull with upturned nasals and the fusion of the nasal rugosities to one strong globular horn base. This lineage underwent a slight size reduction combined with the final molarization of the premolars. The crown height is less than than in *D. aurelianense* and does not change. The shortening of the limbs was continuous, but the genus remained tetradactyl. It disappeared in the middle Miocene. There are questionable remains of other species, possibly related to this group. The species *tagicus* Roman, 1907, may be related to *Prosantorhinus* if the similarity of the upper cheek teeth is reliable. It is considerably smaller than all known Teleoceratini.

A third lineage of Teleoceratini remains confined to Asia. It parallels *Chilotherium* in the extreme broadening of the symphysis early in the upper Oligocene, and the early Elasmotheriini in the crown height of the cheek teeth, the low degree of molarization, and the high posterior cingulum of the premolars. This genus *Aprotodon* Forster Cooper, 1915, starts with *A. aralense* (Borissiak, 1944). The skull is entirely primitive with long, slender nasals, but no horn base. The nasal notch is progressive and reached its furthest retraction over the end of the premolar series. These features are contrasted by the specialization of the symphysis. It is very broad and the incisors are curved outwards.

During the history of this genus, known mainly in the Siwalik series, the crown height increased considerably. The premolar molarization is weak but finally reached the semimolariform stage, with a straight metaloph and a simple postfossette. Single teeth and bones are known up to the basal upper Miocene of the Nagri Formation, but the evolution of the skull and mandible are not known.

The Rhinocerotinae

All living rhinoceroses have horns as their most conspicuous weapons. Nevertheless, the Asiatic species fight against predators, including man, with their large tusk-like incisors, sharpened by the contact with the upper ones. This behavior was already noticed in the seventeenth century. The horn is used mainly against conspecific rivals. It may have been formed in analogy to the cervid antlers to make fighting less dangerous and to prevent fights by an impressive display.

In the early rhinoceroses, such as *Diceratherium* or *Menoceras*, we find a balance of equally important incisors and horns. Later, the Teleoceratini and Aceratheriini strengthened the incisors, and the Rhinocerotinae strengthened the horn. The alternative structure was lost or reduced, because the skull position for the use of one is incompatible with the use of the other. The Aceratheriini and Teleoceratini retained the primitive horizontal skull position and had to shorten limbs to be able to eat small plants. So we rarely find grazers in these tribes (e.g., *Teleoceras*).

The Rhinocerotinae, comprising also fossil Elasmotheriini, have strengthened their horns. The incisors remained in the primitive stage of early Diceratheriinae or even vanished. They lowered their skull position in order to use their horn, and the muscles once adapted to this position could easily bring the muzzle down to the ground. So the tendency to a grazing diet was followed independently in several lines during this process.

The Elasmotheriini

The first group undergoing this specialization has reached the highest degree of adaptation to hard and abrasive diet in all large ungulates of the Old World. They finally evolved ever-growing, rootless prismatic cheek teeth. The history of this tribe is dominated by this tendency. The earliest member of this tribe is described as *Caementodon* sp. from the lower Miocene of the Tugiti beds. This smallest known member of the Rhinocerotinae showed the first formation of cement in the tooth grooves and an elongation of the molar ectoloph. *Caementodon* Heissig, 1972, from the Siwalik series is a first side branch, characterized by an elongation of molars, heavy cement covers on the cheek teeth, and rather high crowns. The upper and lower incisors are small but present, resembling the incisors of the first rhinoceroses *Trigonias* and *Epiacreratherium*.

The main lineage is represented at the same time by the larger *Beliajevina* Heissig, 1974, from the middle Miocene of Bjelometschetskaja and Anatolia. These animals still have a small incisor, but the crowns of the cheek teeth are higher. In all these genera the molarization of the premolars is delayed and remains on the submolariform stage. From this genus we know the earliest elasmotheriine skull. It was not figured, but in his description Borissiak, 1935, mentions a dome-like horn base at the nasofrontal suture. The limbs are high and show no third articulation of radius with intermedium.

Since the phylogenetic study of Heissig (1976), the number of known elasmotheres has considerably increased. These "newcomers," mainly from China, offer the impression that the position of the horn is rather variable and may have not shifted backward only once to reach the frontals. A second character seems to be more reliable. The zygomatic arches are high and broad, ascending backwards over the level of the skull roof in *Iranotherium* Ringström, 1924, faint and not spreading laterally in *Elasmotherium* Fischer, 1808. In this first char-

acter the early genera show an intermediate homogenous type. Most early forms are found in Asia, but there are some offshoots in Europe and Africa. *Tesselodon* Yan, 1979, from the middle Miocene of China is known only by teeth, which are similar to *Beliajevina*. *Shennongtherium* Huang and Yan, 1983, also from the Chinese Miocene, is a high-crowned member of the Rhinocerotini. The better-known genera from the middle Miocene, *Hispanotherium* Crusafont and Villalta, 1947, and *Begertherium* Beliajeva, 1971, both with an intermediate horn position, show only reduced or vestigial incisors and stronger hypsodonty. The zygomatic arch is still unknown in both. *Kenyatherium* Aguirre and Guérin, 1974, known only by teeth from the upper Miocene of Africa, is similar to both, but a relationship to *Iranotherium* cannot be excluded.

With *Iranotherium* from the middle Miocene of the Gobi starts a branch of Elasmotheriini leading to the huge upper Miocene terminal species *I. morgani* Mecklenem, 1929, from Maragheh. It has a strong terminal horn on the nasals and a high ascending zygomatic arch. The incisors are totally lost, and the hypsodonty of the cheek teeth reaches the same degree as the contemporaneous forms of the other branch. These are best known from China and were named *Sinotherium* by Ringström (1924). The only known skull fragment points to a frontal or nasofrontal horn position. Some new species from China may represent the transition from very high-crowned teeth with delayed root formation to the final rootless prismatic stage. At the same time, the fine plication of the enamel is accentuated. A complete skull recently found in the upper Miocene of China shows a terminal horn like *Iranotherium* but faint, straight, zygomatic arches like *Elasmotherium*. It raises the possibility that there was a transition from one genus to the other by reduction of the zygomatic arch and backward shifting of the horn. This genus, *Ningxiatherium* Chen, 1977, may include some of the species known only by teeth.

Elasmotherium, the terminal form with

a shortened skull, a domed frontal and an extreme enamel plication, reaches its maximum size in the early Pleistocene and shows some size decrease before dying out. It was confined to the steppes of Asia, and only one specimen is recorded from Europe. It became extinct with the first severe cooling in the middle Pleistocene.

The Rhinocerotini

The earliest Rhinocerotini occur in Europe and Asia with the third rhinoceros wave, at the proboscidean datum. That may suggest an African origin, but there are no earlier faunas from Africa containing rhinoceroses. This tribe comprises the more primitive members of the subfamily, but was more diversified and successful than the groups discussed previously. Both tribes are linked by a double-rooted P_1 , the articulation of the ulna with the intermedium, the presence of one or two strong median horns, and medium-sized to vestigial incisors, horizontally implanted in a long symphysis. Less important similarities are the rather strong metacone ribs, mainly in the upper premolars, and the tridactyl, unspecialized limbs.

In contrast to the Elasmotheriini, most Rhinocerotini remain browsers with a primitive dentition and no marked increase in crown height. The loss of incisors occurs independently in several lines, but not in all. In the manus, the third articulation of the radial with the intermedium is preserved, and the intermedium shows a third facet for the ulna, or at least a lengthening of the distal facet. In this feature, the difference between Aceratheriini and Teleoceratini is paralleled by the difference of the Elasmotheriini and Rhinocerotini and Dicerotini, on the other hand. The origin of this group probably occurs near the *Trigonias-Epiacatherium* stage of evolution. Most likely the shortening of the basicranium, which it shares with the Aceratheriinae, occurred before the separation of both subfamilies. The upper incisor evolved to its typical blade-like form after the separation of the Elasmoth-

eriini, and the lower incisor is not lengthened in most genera.

The first radiation of the tribe must have occurred before the first record of the group. There are several side branches showing single remaining primitive traits, already lost in the contemporaneous members of the main stock. All these characters are dental, since nothing is known about limb bones and horn formation. In the following, I discuss only the named species.

Dicerorhinus abeli (Forster Cooper, 1915) is the best known species of this type. The mandible and lower incisors are of rhinocerotine type, but Forster Cooper was misled by the strong lingual cingulum of the upper premolars and the marked anterochet constriction in the upper molars, paralleling the aceratheres. In the last premolar there is a faint trace of a bridge uniting the lingual cusps as in a semimolariform stage, unlike the paramolariform condition of most Rhinocerotini, where the cusps are united by their bases. The skull is broad, even if there is a sagittal crest. The same characters as in the early Miocene form from the Bugti beds we find in the smaller *Dicerorhinus steinheimensis* (Jäger, 1835) from the middle Miocene of Europe, except the presence of stronger metacone ribs.

The central stock of the tribe begins with *Lartetotherium* Ginsburg, 1974, in the lower Miocene (Burdigalian) of Europe. The nasals have a conical, subterminal horn base as in *Dicerorhinus*. The frontals show a second horn in the type but not in all referred specimens. The upper incisors are chisel-shaped, the lower ones spatulate and implanted horizontally, even in males. The upper premolars are paramolariform with strong, narrow ribs on the outer wall, widely separated but converging to the ectoloph crest. There is no trace, or only faint traces, of a lingual cingulum. In the molars, the anterochet and its lingual constriction are faint.

During the middle Miocene, we find rhinoceroses of similar dental type widespread in the Old World. In the Siwa-

li series of India, *Gaindatherium* Colbert (1974), with its single horn foreshadows the later *Rhinoceros*, but the skull is still long, and the low-crowned teeth are nearly identical to *Lartetotherium*. We can follow this line up to the upper Miocene Nagri beds. From this time onwards, the evolution in South Asia was separate from the rest of the Old World except China. The transition from the *Gaindatherium* lineage to the modern and Pleistocene *Rhinoceros* species is insufficiently known. The upper cheek teeth are high-crowned and block-shaped in the younger genus. There are several side branches, including the huge *Punjabitherium* Khan, 1971, with two horns, showing that the number of median horns is not a reliable character. *Rhinoceros sondaiensis* Desmarest, 1822, on the other hand, remains primitive in the dentition, but shares the skull shortening and the upslanting head with the type species, *R. unicornis*. In South Asia, *Dicerorhinus sumatrensis* (Fischer, 1814) persisted nearly unchanged with a dentition like *Lartetotherium*.

In the middle Miocene of Africa, we find *Dicerorhinus leakeyi* Hooijer, 1966, related undoubtedly to the central stock, but a little more primitive in the stronger lingual cingula of the upper premolars and the more primitive stage of molarization, varying between the submolariform and the paramolariform type. The skull is long and low and resembles the other middle Miocene species. The incisors are of the same type. It is possible to trace the second main lineage of the Rhinocerotini back to this species. This lineage is represented mainly by the genus *Stephanorhinus* Kretzoi, 1942, beginning with the species *pachygnathus* Wagner, 1848, from the upper Miocene of Mediterranean area, but also by *Dicerorhinus schleiermacheri* Kaup, 1832, from the same time in Western Europe.

While the first species has nearly completely reduced incisors, the second one is larger and more primitive and shows no reduction. Both still have a lingual cingulum in the upper premolars and long, strong

nasals with tandem horns. The nasal notch is somewhat retracted. The first species continues during the early Pleistocene with the species *S. etruscus* (Falconer, 1859). It supported its strong horn with an ossified septum to allow further deepening of the nasal notch. The second one continues to the Pliocene *D. megarhinus*, with no septum and reduced, but still relatively large, lower incisors. From *D. megarhinus* De Christol, 1835, we can follow the line to *D. jeanvoireti* Guérin, 1972, decreasing in size relative to the large earlier species. A third species in the late upper Miocene, *D. ringstroemi* Arambourg (1959) is a large form without incisors or lingual cingulum. It is possibly a side branch of one of these two species.

During the middle and late Pleistocene, the severe climatic changes caused a permanent shifting, dividing, and reuniting of species areas. There are several well-known species, but their phylogenetic arrangement is still a problem. Both lineages converged in characters with the complete loss of incisors and the development of an ossified nasal septum. So the origins of the steppe-adapted *D. hemitoechus* Falconer, 1868, and the bigger *D. kirchbergensis* Jaeger, 1839, are still unknown. In China *Dicerorhinus choukoutiensis* Wang, 1931, and *D. yunchuchensis* Chow, 1963, are similar and may be related to *D. kirchbergensis* of Europe. The most specialized offshoot of the tribe, *Coelodonta* Bronn, 1831, may be related to this lineage also, as is indicated by the loss of the incisors and the ossified septum. The skull is broad, but in contrast to *Stephanorhinus* and its relatives, very low. There is no form bridging the gap in dental morphology. *Coelodonta* was the only typical grazer of this lineage, with rather high-crowned teeth and a very peculiar morphology, including the newly formed metastyle of the M^3 in some specimens. The whole group went extinct during the late Pleistocene without descendants.

The Dicerotini

The last tribe to appear is the African branch of the tandem-horned rhinoceroses.

Its apomorphic characters set it far apart from the younger Rhinocerotini, but in the middle Miocene of Africa, some poorly-known species seem to bridge the gap.

The earliest known specimens come from the middle Miocene of Anatolia and Chios, a little earlier than the first named species, *Paradiceros mukirii* Hooijer, 1968, from the late middle Miocene of Fort Ternan and Beni Mellal. It is primitive in most dental characters, but in the skull it already shows the characters of the tribe. These include the anteriorly shortened nasals, the outwards-inclined lower border of the orbit, and the lack of functional incisors. The skull resembles the living *Diceros*, but the mandible resembles *Ceratotherium*. The upper premolars already have reduced metacone ribs.

During the upper Miocene, there were two lineages. The more primitive is *Diceros primaevus* (Arambourg, 1959), very similar to *Paradiceros*, with strong lingual cingula in the premolars and low crowns on the cheek teeth. The second species, *Diceros neumayri* (Osborn, 1900) may be its descendant. It expanded its range over western Asia and the southern part of Europe, where it differentiated into ecological types and underwent some evolutionary changes during the upper Miocene. It developed rather high-crowned teeth and an overhanging occipital crest, similar to *Ceratotherium* in its most advanced specimens. Comparable tendencies are observed in *Diceros douariensis* Guérin, 1966, from Tunisia, a rather large animal with high-crowned cheek teeth. The skull morphology is incompletely known.

During the Plio-Pleistocene, the tribe is restricted to Africa again. *Ceratotherium* Gray, 1867, is reported earlier than typical *Diceros* Gray, 1821. It is not yet clear if the splitting up into the living browser-grazer pair occurred in the Pliocene or if the diversification in the upper Miocene led directly into the separate lineages. In this case *D. douariensis* should be suspected to be ancestral to *Ceratotherium*, whereas the living *Diceros bicornis* remained at the

evolutionary stage of the more primitive specimens of *D. neumayri*. It is puzzling that in the the living genera the presumed primitive condition of an articulation of the fibula with the femur is retained, whereas it was lost in the upper Miocene species.

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