The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla)

DONALD R. PROTHERO,

Department of Geology, Occidental College, Los Angeles, California 90041

EARL MANNING

Museum of Geoscience, Louisiana State University, Baton Rouge, Louisiana 70803, U.S.A.

AND

C. BRUCE HANSON

Department of Paleontology, University of California, Berkeley, California 94720, U.S.A.

A new phylogeny of the Superfamily Rhinocerotoidea is proposed, based upon an analysis of shared derived characters of the skull, teeth and skeleton. *Hyrachyus* is considered the primitive sister-taxon of the three rhinocerotoid families (Amynodontidae, Hyracodontidae, Rhinocerotidae), and the amynodonts appear to be the sister-group of hyracodonts and rhinocerotids. The relationships of primitive hyracodonts and rhinocerotids are clarified. *Menoceras* and *Pleuroceras* (new Subfamily Menoceratinae) are removed from the Diceratheriinae, since they appear to be more closely related to higher rhinoceroses than they are to *Diceratherium*. Of the three major monophyletic groups of higher rhinocerotids (aceratherines, teleoceratines and rhinocerotines), the last two groups are more closely related to each other than either is to aceratherines. *Toxotherium* and *Schizotheroides* are tentatively removed from the Rhinocerotoidea and placed in the Lophiodontidae.

KEY WORDS:— Rhinocerotoidea – Perissodactyla – Amynodontidae – Hyracodontidae – Rhinocerotidae – phylogeny.

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INTRODUCTION

Although they are nearly extinct today, rhinoceroses were one of the most widespread and successful groups of mammals for over forty million years. They have freely circulated among the northern continents since the middle Eocene, and are known from Africa from at least the early Miocene. Rhinoceroses have occupied many diverse modes of life. There have been sheep-sized cursorial rhinoceroses (*Hyracodon*), short-limbed hippopotamus-like rhinoceroses (*Teleoceras, Metamynodon*), dwarf rhinoceroses (*Peraceras hessei* and *Teleoceras meridianum*), and rhinoceroses with tapir-like proboscies (*Cadurcodon*). The largest land mammal that ever lived (*Indricotherium*) was a hornless rhinoceros.

All five modern rhinoceros species have horns, but rhinoceroses have experimented with many different combinations of nasal and frontal horns. Such combinations include paired nasal horns (*Diceratherium, Menoceras, Pleuroceros*), tandem horns on the nasals and frontals (*Diceros, Dicerorhinus, Ceratotherium, Coelodonta*), a single nasal horn (*Teleoceras, Rhinoceros*), and a single giant frontal horn (*Elasmotherium*). In the popular mind, the distinguishing feature of a rhinoceros is its horn. The horn is not only the source of the name 'rhinoceros' but also the chief reason that rhinoceroses have been hunted to the brink of extinction. Yet, despite the popular image, most fossil rhinoceroses were hornless, and at least one of the horn combinations has evolved independently in two different groups.

One would think that such a fascinating group would be well studied and long understood. Certainly they are not uncommon or hard to find in deposits in which they occur. Fossil rhinoceroses are well represented in many museum collections. Indeed, for most rhinoceros taxa, we have not only teeth, but skulls and large quarry samples of all the skeletal elements—an unusual situation in fossil mammals. Perhaps rhinoceroses have been neglected precisely because they are too large to study anywhere but in collections. Very few rhinoceroses fit inside a briefcase. Whatever the reason, there has been relatively little serious study of fossil rhinoceroses in this century. A recent popular book on rhinoceroses (Guggisberg, 1966) cited the badly outdated information of Osborn (1923) for its discussion of fossil rhinoceroses. The most recent general reviews with detailed phylogenies of American and European fossil rhinoceroses are those of Wood (1927) and Matthew (1931). There is some recent work on Neogene rhinoceroses of the Old World (Heissig, 1973; Hooijer, 1976; Guerin, 1980), but much of the history of rhinoceroses happens outside Europe and Africa. The abundant collections of North American rhinos have been virtually ignored for over half a century. Simpson (1945: 257) characterized the state of affairs this way:

"The human factor in classification is nowhere more evident than in dealing with this superfamily [Rhinocerotoidea]. It is, as mammalian superfamilies

go, well known, but what is 'known' about it is so inconsistent in places that much of it must be wrong. Some authorities still recognize 'genera' (e.g. *Orthocynodon*, an amynodont) that are, beyond much doubt, based on slight individual variation, while others lump together in one genus a whole tribal lineage that must almost certainly include a whole cluster of genera, even if generic lines be drawn as broadly as could be desired (e.g. the supposed European *Dicerorhinus* line). Some of the most competent students (e.g., Matthew) follow very broad lines, emphasize skull and foot characters, and tend to neglect dental mutations; others (e.g., Wood) split the groups into many short, narrow sequences emphasizing minor dental characters and tending to neglect skeletal structure. Much of the published work (aside from that of Matthew, Wood, and some others) is simply incompetent and has not been revised by a properly instructed and judicious student."

Unfortunately, this statement is as accurate today as it was in 1945.

In the course of our studies of the large collections of fossil rhinoceroses in the American Museum of Natural History, we have tried to straighten out some of the problems in rhinoceros relationships. Much of our revisionary work and basic taxonomy is presented elsewhere (Prothero & Sereno, 1982; Prothero & Manning, 1986; Prothero, in review). It seems appropriate, however, to summarize here our views of rhinoceros phylogeny, so that these more restricted works can be placed in a general context.

PREVIOUS PHYLOGENIES

There are remarkably few explicit hypotheses of rhinoceros relationships in the literature, and none which attempts to discuss the entire Rhinocerotoidea. Fossil rhinoceroses were reported before 1800 (Blumenbach, 1799; '*Rhinoceros*' (= *Coelodonta*) *antiquitatis*) and by 1904 there were 42 genera and 170 species of rhinoceros named (Osborn, 1923). Most of the early hypotheses amounted to little more than a stratigraphic sequencing of the few known forms without consideration of morphology. Cope (1880), for example, presented the phylogeny shown in Fig. 1A. There is no explanation of why the genera are arranged as they are, except that they all have three digits in the manus, and are in stratigraphic order. Gaudry (1888: 131) presented a phylogenetic table of rhinoceroses and several other perissodactyls, including all the lophiodonts and 'paleotheres' known to him at the time. The groups are mostly interrelated by stratigraphic superposition, and apparently only Eurasian and African taxa are included. Thus, most of the forms discussed in this paper were not considered in Gaudry's hypothesis; many were not known until much later.

Pavlow (1892) presented a much more detailed phylogenetic diagram (simplified and updated in Fig. 1B), in which the American forms are discussed along with the European forms. Many relationships are unresolved, and biogeographic distribution appears to have been more influential than morphology. In 1892 there was still very little information about most of the American forms available to Pavlow. Thus, she did not appreciate the distinctiveness of amynodonts, or the differences between *Aphelops* and *Teleoceras* (which were lumped together in the wastebasket taxon *Aceratherium* for many more years). Pavlow was the first to recognize the relationships between
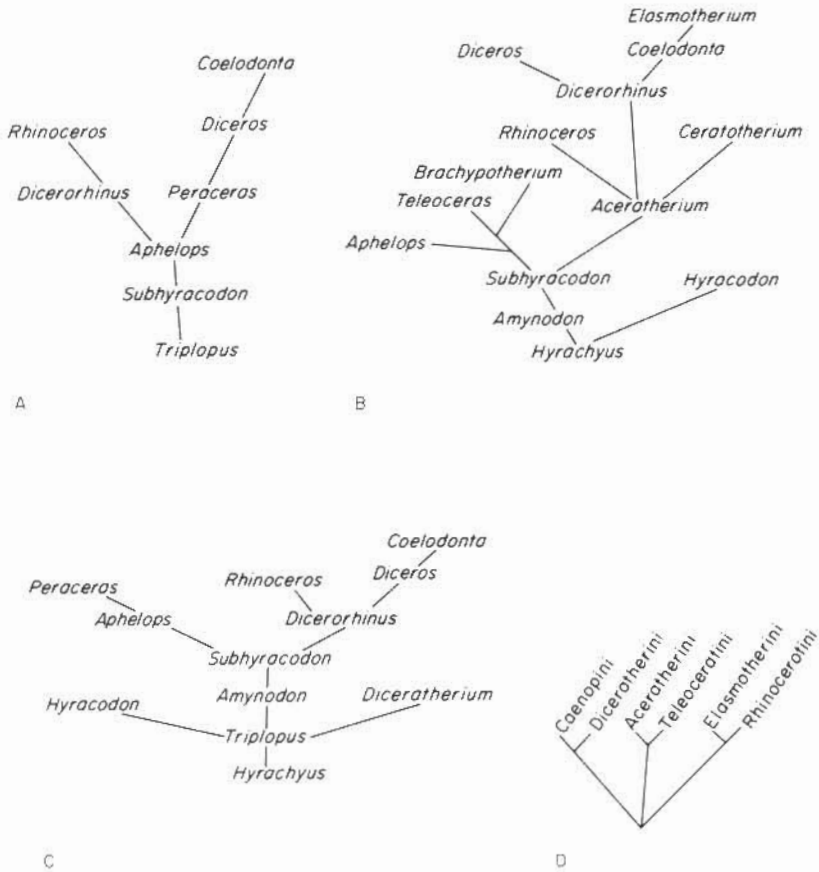
Figure 1. Simplified and updated phylogenies of: A, Cope (1880); B, Pavlow (1892); C, Scott & Osborn (1898); D, Heissig (1973).

Teleoceras and *Brachypotherium.* Surprisingly, she considered the African rhinoceroses *Diceros* and *Ceratotherium* to be of widely separate origins, an hypothesis that few have entertained since.

Scott & Osborn (1898) were the first authors to make detailed anatomical comparisons between North American forms and the known European forms. Their phylogeny (updated in Fig. 1C) does not recognize the distinctiveness of amynodonts, although they were the first authors to describe this group in detail. They also thought that the paired horn condition of *Diceratherium* justified its placement as a distinct line evolving separately from the *Hyrachyus–Triplopus* complex. They did, however, realize the distinctiveness of *Hyracodon*, and provided the first detailed description of hyracodont postcranial anatomy.

Osborn (1898: 79) was apparently the first to recognize our modern division of the rhinocerotoids into three distinct families: Hyracodontidae, Amynodontidae and Rhinocerotidae. Osborn's phylogenies emphasized what he believed to be the parallelism shown by rhinoceroses in a series of publications (Osborn, 1898, 1900, 1905, 1923). In his last work on the subject, for example, he postulated eight independent lines of rhinoceros evolution (Osborn, 1923: 213–214). Osborn explicitly stated that none of these lines has any known

relationship to any other (Osborn 1900: 229). He envisaged a very 'bushy' or 'polyphyletic' tree:

"This polyphyletic law has now been demonstrated among the rhinoceroses both of Eurasia and of North America, and is the key to the comprehension of this group; ... there are not only three families, namely, cursorial (Hyracodontidae), aquatic (Amynodontidae), and terrestrial (Rhinocerotidae), but the last family splits up into six and possibly seven phyla, many of which are contemporaneous; and the tendency of discovery will be to increase rather than to diminish the number of contemporaneous independent phyla (Osborn, 1905: 205–206)."

According to Osborn (1905: 211), the "true rhinoceroses prove to include at least seven distinct phyla corresponding to seven genera which extend back as far as the Middle Miocene if not into the Oligocene." Clearly, Osborn felt that these 'phyla' all diverged at the beginning of rhinoceros evolution and were not interrelated in any way since that time.

The next major phylogeny (Wood, 1927) concentrated on ancestor–descendant sequences of Eocene and Oligocene rhinos (Fig. 2). The main feature of Wood's phylogeny is the use of dental characters (especially the crown pattern of the upper premolars) to the exclusion of nearly all other features. This leads to a very complex pattern of ancestor–descendant relationships, with several polyphyletic taxa. Some dental characters were so variable within a species that Wood had to invoke numerous instances of parallelism. Wherever Wood could not find what he considered to be a clear ancestor–descendant relationship, he left dotted lines and 'unknown stems'.

There are several surprising features of Wood's (1927) phylogeny not seen in those of his predecessors. Wood apparently thought that two species of *Diceratherium* were independently derived from *Subhyracodon* and that *Menoceras*
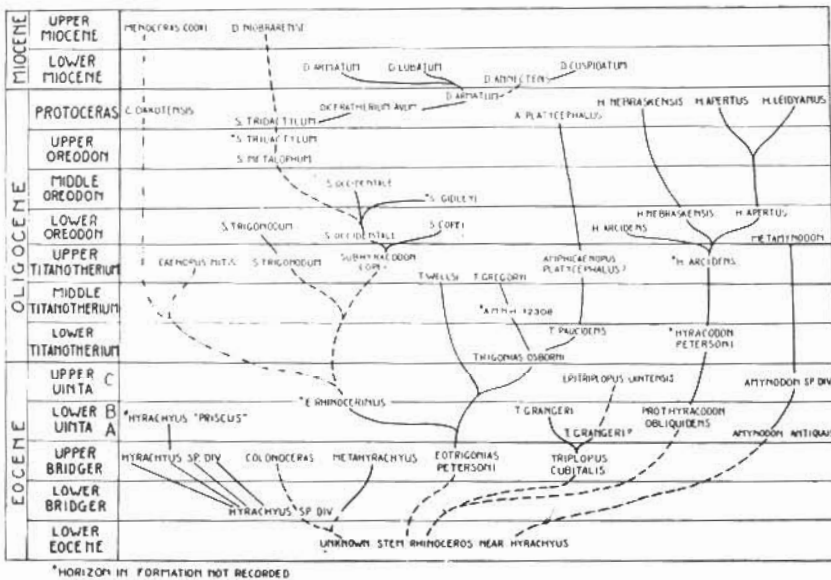
Figure 2. Phylogeny of Wood (1927: fig. 1).

was not closely related to *Diceratherium* (a view not revived until this paper). Most of the other relationships expressed in the 1927 phylogeny are in agreement with those of his predecessors. Wood continued to work on the Ceratomorpha for the rest of his life. In 1941, he commented that "my last effort at a phylogenetic tree has not been published and already seems out of date and amateurish." Although Wood continued to publish on rhinos until the 1960s, he never did put his phylogenetic ideas into print after 1927.

At the end of his brilliant career, William Diller Matthew began serious study of rhinoceroses. Although he died before much of this work could be finished, his phylogeny of 1931 (Fig. 3) is quite interesting. Horns, tusks and crown-height of the teeth are weighted more heavily than the crown patterns that Wood used. Although Matthew placed the indricotheres (here considered hyracodonts) in the Rhinocerotidae because of their enlarged tusks, he did recognize the significance of the loss of the metacone on M^3 as a rhinocerotid synapomorphy. Matthew treated all the primitive hornless Oligocene
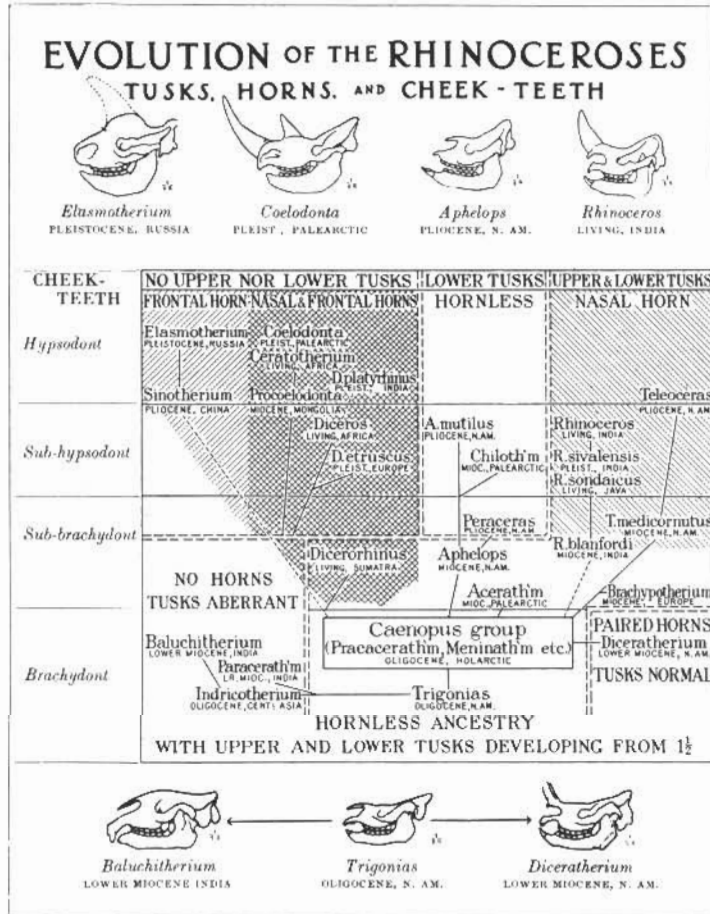

Figure 3. Phylogeny of Matthew (1931: fig. 2).

rhinoceroses as an unresolved paraphyletic '*Caenopus* group', ancestral to all the others. Matthew did not agree with Wood that *Diceratherium* and *Menoceras* were distinct. He did recognize distinct teleoceratine, aceratherine, and rhinocerotine lineages. The genus *Rhinoceros* was not placed with the rest of the rhinocerotines because of its single nasal horn. By not using many of the confusing tooth crown characters, Matthew steered clear of many of the problems that baffled Wood. Most of the groups that Matthew recognized have since turned out to be monophyletic. Unfortunately, Matthew ran into parallelisms in the characters he used as well, which misled him in a few cases.

Very few phylogenetic hypotheses about rhinocerotoids have been explicitly stated since the time of Matthew and Wood. Radinsky (1966) redefined the three major rhinocerotoid families primarily on the basis of characters of the anterior dentition. Radinsky excluded the *Allacerops* group and indricotheres from the Rhinocerotidae by restricting the definition of that family to those forms with the chisel-shaped I^1 and lanceolate I_2 specialization. Recently discovered specimens of *Teleoceras* from Poison Ivy Quarry (Clarendonian, near Orchard, Antelope County, Nebraska; Voorhies & Thomasson, 1979) seem to suggest that the lower tusk is I_3. Five of the better preserved juvenile jaws have two small peg-like deciduous teeth anterior to the lower tusk. In *Trigonias*, however, the reduction of the anterior dentition is shown by several jaws which clearly show both a canine and an I_3 behind the lower tusk (Gregory & Cook, 1928: fig. 1). In addition, it seems very improbable that occlusal relations would develop between I^1 and I_3. This suggests that the condition in the juvenile Poison Ivy Quarry *Teleoceras* represents some sort of dental atavism, or supernumerary incisor. This is much more parsimonious than postulating that the lower tusk is I_3.

Radinsky (1966, 1967) correctly realized that the indricotheres were hyracodonts and not rhinocerotids, contrary to the views of Matthew (1931) and Simpson (1945). No author since Radinsky (1966) has discussed the interrelationships of the three rhinocerotoid families, or the relationships of the primitive Rhinocerotidae. Guerin (1980) dealt only with late Tertiary European forms. Hooijer's (1976) phylogeny was restricted to Neogene African forms. Heissig (1973) grouped the rhinocerotids into subfamilies and tribes, but did not draw a phylogenetic diagram. His views are expressed in a phylogenetic diagram in Fig. 1D. Heissig's classification includes a paraphyletic wastebasket taxon ('Caenopini') and groups the paired-horned rhinoceroses ('Diceratherini'). Heissig separated the elasmotheres from the rest of the rhinocerotines on the basis of their overall phenetic dissimilarity. He considered the teleoceratines to be more closely related to the aceratherines than they are to rhinocerotines. All characters he cited for this latter relationship are either primitive for both groups (large lower tusk, absence of nasal horn, short mandibular symphysis, articulation of the radius with the cuneiform, unequally curved dorsal surfaces of the carpals and tarsals, presence of manus digit 5) or derived for the teleoceratines alone (presence of a small nasal horn, upper molars with a strong antechrochet, articulation of the ulna with the lunar, loss of manus digit 5). Heissig cited both presence and absence of this last character in his diagnosis of the Aceratheriinae.

Recently, several authors (Heissig, 1981; Guerin, 1982; Groves, 1983) have proposed phylogenies of the five recent rhinoceros species and some of their

Neogene fossil relatives. Our phylogeny (Fig. 4) follows that of Groves (1983) for the higher rhinocerotines.

A NEW HYPOTHESIS OF RHINOCEROS RELATIONSHIPS

In the hypothesis of relationships shown in Fig. 4 and Table 1, and discussed below, we have attempted to use as many different characters as possible. Many of the variations in upper premolar crown pattern that were so important to Wood (1927) have since proven to be due to intraspecific variation (Prothero, in review). For this reason we have used a greater variety of characters and de-emphasized the crown patterns of upper premolars, as did Matthew (1931). However, we have also found many characters in the postcranial skeleton that were once unknown or completely ignored by previous workers. These were added after our initial hypothesis based on tooth and skull characters and have served as a first test of our hypothesis.

We were forced by circumstances to leave many European genera out of the analysis. Many of these are inadequately described or illustrated, doubtfully valid, based on non-diagnostic or fragmentary material, or simply unavailable to us for comparison. We expect that a complete revision of the Oligocene–Miocene rhinoceroses of Europe will provide a further test of our hypothesis.

Out-group

Primitive rhinocerotoid skeletal morphology is well exemplified by *Hyrachyus*. In most respects, it differs little from more primitive ceratomorphs, such as
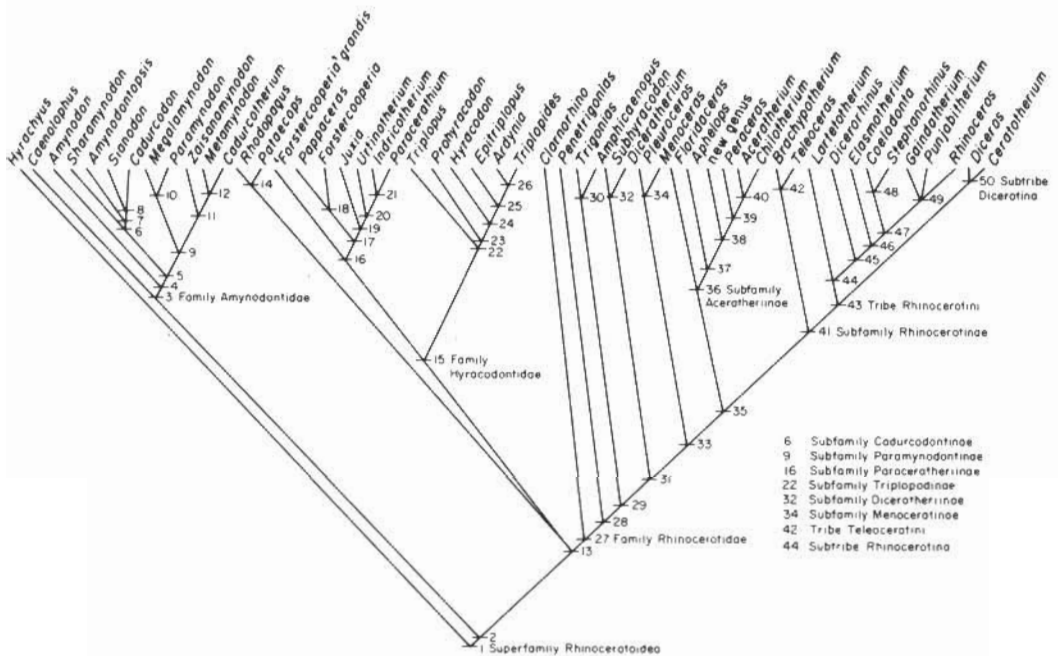

Figure 4. Hypothesis of rhinocerotoid relationships proposed here. Numbered character states listed in Table 1.

Table 1. Character states for phylogeny shown in Fig. 4: Amynodonts after Wall (1982), Rhinocerotines after Groves (1983)

1 Superfamily Rhinocerotoidea Gill, 1872: M_3 hypoconulid lost; P^4 protocone creased lingually; enlarged paralophids and metalophids; increased hypsodonty; cylindrical odontoid process on atlas.

2 Paracone near parastyle; metaloph confluent with ectoloph on M^{1-3}; P^{3-4} postprotocrista reduced; crown height index greater than 0.5; deep atlantodiapophyseal notch on atlas; fused intervertebral canal on atlas.

3 Family Amynodontidae Scott & Osborn, 1883: M^3 metacone enlarged and labially deflected; dp_1^1 lost; metaloph elongated; conical incisors; enlarged canines in males; premolars relatively reduced; elongated talonids on lower molars; preorbital fossa present.

4 Preorbital portion of skull reduced.

5 Premaxillary–nasal contact reduced or lost.

6 Subfamily Cadurcodontinae Wall, 1982 (new rank): large preorbital fossa extending medially to orbit.

7 Enlarged frontal sinus.

8 Reduced number of incisors.

9 Subfamily Paramynodontinae Kretzoi, 1942: preorbital fossa reduced; lower jaw and zygomatic arches thickened; brachycephalic skull; orbit high on skull.

10 Zygomatic arches convex laterally.

11 Reduced diastema; larger size.

12 Reduced number of incisors; narrow lower molars.

13 Reduced parastyle; increased relative length of cheek tooth series; M^{1-2} metacone flange lengthened; M^3 metacone reduced and lingually deflected.

14 Diminutive size.

15 Family Hyracodontidae Cope, 1879: tridactyl manus; long limbs and metapodials; laterally compressed carpus and tarsus.

16 Subfamily Paraceratheriinae Osborn, 1923 (= Indricotheriinae): large size; enlarged P_1; M^3 metacone reduced.

17 Conical incisors.

18 Thickened ascending ramus of premaxillary; stubby canines.

19 Increased hypsodonty; labial P^{2-4} cingulum; enlarged I^1; nasal incision retracted to posterior P^2; creased P^3 protocone.

20 I_1 enlarged and procumbent; I_{2-3}, C_1, and dp_1 reduced; overall size increased.

21 I_1^1 greatly enlarged; I_{2-3}^{2-3}, canines, dp_1 lost; nasal incision retracted to level of posterior P^4; premaxilla downturned; P^4 protocone creased posterolingually; gigantic size.

22 Subfamily Triplopodinae Osborn, 1892: flattened premolar ectolophs; parastyles further reduced.

23 Increased hypsodonty (crown height index greater than 0.75); labial cingulum on P^{3-4}.

24 P^1 replaces dp^1; P_1 rarely present; paracone folded toward parastyle on M^{1-2}; P_{2-4} labial cingula; high paralophids and metalophids; sharply constricted symphysis and rostrum.

25 C_1 reduced; elongate narrow M^2; oblique cross lophs; M^{1-2} metacones deflected labially with sharp crease; trace of M^3 metacone lost.

26 C_1 further reduced; P^1 lost; canines smaller than I_3^3.

26 Family Rhinocerotidae Owen, 1845: I^1 chisel-shaped; I_2 tusk-like; very reduced M^3 metacone; M^{1-2} cristae lost; premaxillary–nasal contact lost; reduced posterior cingulum on M^3; shorter posterior ectoloph on M^{1-2}.

28 M^{1-3} parastyle folds more open; antecrochets enlarged; M^3 metacones lost; C_1, I_3 lost in adults; metacone ribs on molars lost; paracone and metacone ribs separate and reduced on premolars; greater hypsodonty; postcotyloid process on ramus; broad ascending ramus on dentary, with straight posterior border; long, posteromedially curved process on anterolateral tuberosity of humerus.

29 Broad parasagittal crests; laterally flared lambdoid crests; concave dorsal skull profile; long nasals.

30 Extended occiput; anterodorsally inflected basicranium; long, flattened postglenoid process.

31 I_3^3, C^1 lost; metacone ribs of P^{2-4} lost; P^2 molarized; mandibular condyle broader, flat surfaced and nearly horizontal; distal condyle of humerus more asymmetrical; dorsoventrally compressed posterior articular surface on atlas; postglenoid process faces anteriorly; fifth metacarpal reduced to vestige.

32 Subfamily Diceratheriinae Dollo, 1885: long, broad supraorbital ridges; paired nasal ridges in males.

33 Strong crochet present; I^2 lost; reduced sagittal crest; premaxillary further reduced; nasal incision over posterior P^2; basicranium shortened relative to palate; upper molar lingual cingula weak or absent; shallow anteroventral notch on atlas.

34 Subfamily Menoceratinae (new taxon): bulbous terminal nasal horn bosses.

35 Upper premolars fully bilophodont; overall size increase.

36 Subfamily Aceratheriinae Dollo, 1885: medial flange of I_2 reduced; long diastema posterior to I_2; fifth metacarpal enlarged.

37 Premaxillary reduced; I^1 lost; nasal incision over anterior P^4.

Table 1. Continued

38   Dorsal skull profile flattened.
39   Nasals shortened.
40   Strong parasagittal crests; I_2 flares laterally.
41   Subfamily Rhinocerotinae Dollo, 1885: small terminal nasal horn; fused nasals; posterior articulation between scaphoid and lunar; lambdoid crests broadened laterally; bony bar between foramen ovale and foramen lacerum medium reduced or absent.
42   Tribe Teleoceratini Hay, 1902 (new rank): metapodials shortened; carpals and tarsals compressed dorsoventrally; strong antecrochets; broad zygomatic arches; lateral edge of nasals downturned and thinned, resulting in a U-shaped cross-section; calcaneal tuber elongate; brachycephalic skull; nasal incision retracted to level of anterior P^3; P_2 lost in some *Teleoceras*.
43   Tribe Rhinocerotini Dollo, 1885: nasal horn base laterally broadened, with tip of nasals extended anteroventrally beyond horn base; temporal crests slightly parasagittal.
44   Subtribe Rhinocerotina Dollo, 1885: postorbital process developed; subaural channel very narrow; posterior palatine margin moved to level of M^{1-2}; fibular head blunt, nestles under proximal head of tibia.
45   Occipital crest angle under 100°; nasal septum (cloison) tends to be ossified; foramen ovale may fuse with foramen lacerum medium; mastoids inflated; foramen magnum pear-shaped or triangular; metacone rib developed on upper cheek teeth; antecrochet lost; trochiter of humerus elongated; radius shortened; metacarpus lengthened.
46   Orbit shifts posteriorly, with anterior rim over anterior M^3; nasal incision over posterior P^4; skull dolichocephalic; corrugated enamel on molars.
47   Subaural channel closed; crochets, medifossettes develop on molars.
48   Nasal septum completely ossified; upper and lower incisors lost.
49   Vomer sharply ridged; posterior margin of pterygoid plates vertical; dp_1 retained in adulthood; M^3 subtriangular.
50   Subtribe Dicerotina Ringström, 1924 (new rank): premaxillary and symphysis greatly reduced; I_2^1 lost; frontal horn enlarged; nasals shortened and further reduced; temporal crests broadly parasagittal; lacrimal separate from nasal; infraorbital foramen moved back to level of P^3-M^1; enlarged, oblique supraorbital processes; bilateral symphyseal ridges lost; convex inferior border of mandible; ascending ramus of mandible slopes backward; foreleg longer than hindleg; occipital crest angle above 100°.

Homogalax, Isectolophus or *Heptodon*. Thus, in the discussion of the character states below, *Hyrachyus, Homogalax, Isectolophus* and *Heptodon* serve as the out-groups for comparison.

Skull characters

Primitive ceratomorphs (like *Hyrachyus*) have a skull that is characterized by the following features (Fig. 5): long distinct sagittal crest; narrow lambdoid crest; narrow posterior portion of skull; small braincase; posteriorly inclined occiput; convex dorsal skull profile; short, narrow nasals with no rugosities or horns; basicranial axis longer than palatal area; long posterior portion of premaxilla excluding maxilla from nasal incision; nasal incision above dp^1; slender unflared zygomatic arches; small paroccipital and mastoid processes; postglenoid processes narrow and facing anterolaterally; short diastema between dp^1 and canines. This primitive condition is also true of *Hyracodon*. Most of the indricotheres retain these features on a large scale, except that they deepen the nasal incision and develop hypertrophied paroccipital processes, upturned zygomatic arches and posteriorly shifted mastoid processes. Some of these features may be related to the larger size and heavy head of indricotheres.

Some amynodonts (e.g. *Metamynodon*) modify the skull in a different way. They develop a very brachycephalic skull, which has wide zygomatic arches, a short broad snout and heavy lambdoid crests. Amynodonts frequently develop a
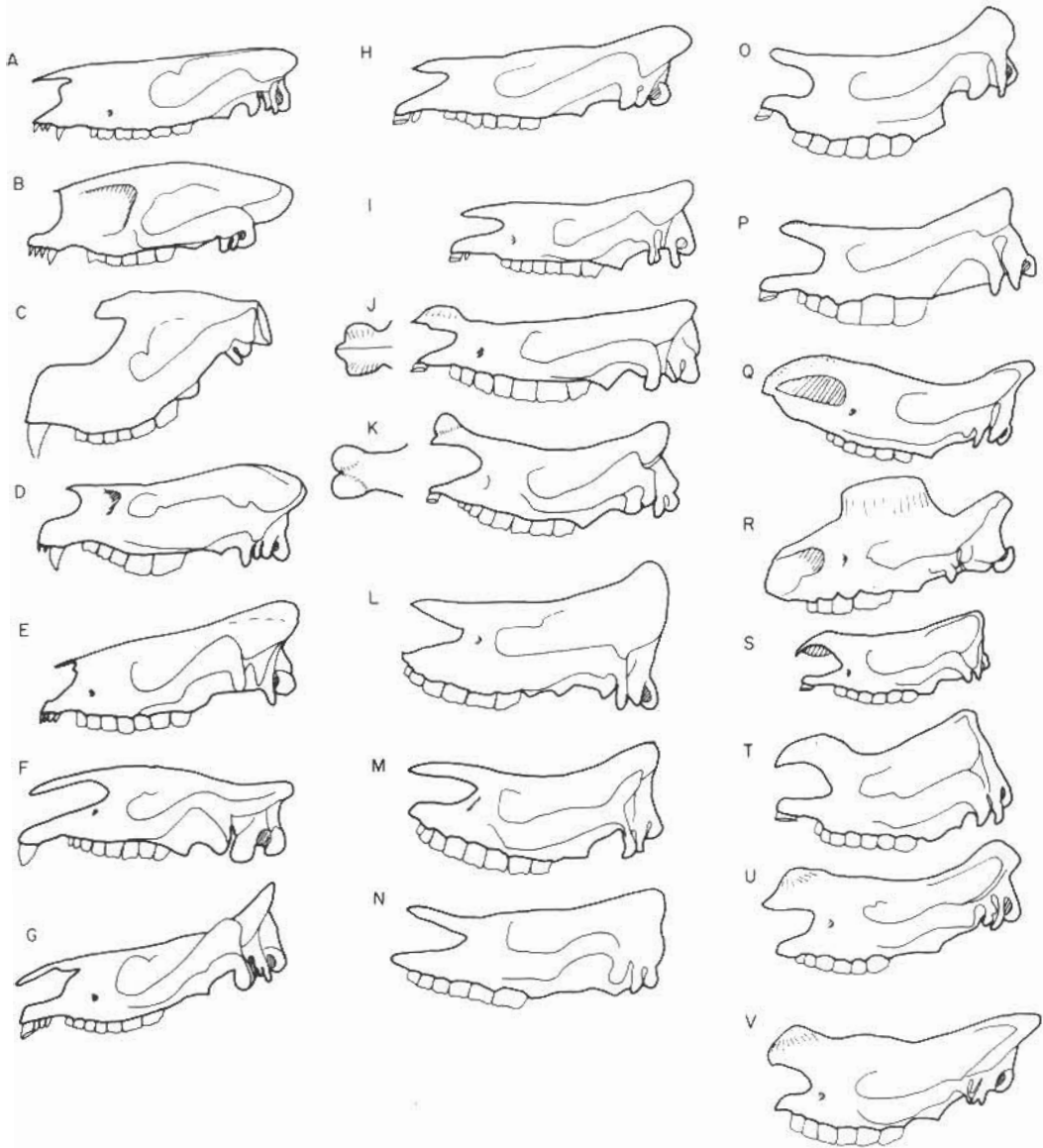
Figure 5. Left lateral views of rhinocerotoid skulls (not to scale). A, *Hyrachyus*. B, *Sharamynodon*. C, *Cadurcodon*. D, *Metamynodon*. E, *Hyracodon*. F, *Indricotherium*. G, *Trigonias*. H, *Amphicaenopus*. I, *Subhyracodon*. J, *Diceratherium* (showing dorsal view of nasal ridges). K, *Menoceras* (showing dorsal view of nasal knobs). L, *Aceratherium*. M, *Aphelops*. N, *Chilotherium*. O, *Brachypotherium*. P, *Teleoceras*. Q, *Coelodonta*. R, *Elasmotherium*. S, *Dicerorhinus*. T, *Rhinoceros*. U, *Diceros*. V, *Ceratotherium*.

broad facial region with a shallow facial fossa. *Cadurcodon* and *Metamynodon* have retracted the nasal incision and *Cadurcodon* apparently had a well-developed proboscis (Wall, 1980).

Rhinocerotid skulls are also distinctive and divergent from the *Hyrachyus–Hyracodon* type. Primitive forms like the Clarno rhinoceros (C. B. Hanson, unpubl. obs.) and *Penetrigonias* (incorrectly referred by Russell, 1982,

to '*Subhyracodon*' *sagittatus*) still show most of the primitive features seen in *Hyrachyus*. But *Trigonias*, *Amphicaenopus* and *Subhyracodon* all have an unmistakably rhinocerotid skull, characterized by a flat or concave dorsal skull profile with a wider, flaring lambdoid crest and a low broad sagittal crest. The sagittal crest is even further reduced in *Menoceras* and the higher rhinoceroses. Rhinocerotids develop a deep nasal incision (very deep in aceratherines), resulting in elongate free nasals that are arched in cross-section. As the anterior dentition is reduced, rhinocerotids also reduce the premaxilla. The posterodorsal extension of the premaxilla eventually loses contact with the nasals and allows the maxilla to form part of the margin of the nasal incision. *Menoceras* and the higher rhinoceroses also begin to change the proportions of the skull, which becomes broader, deeper and larger brained. In these forms, the basicranial axis is shortened relative to the palatal region since many higher rhinoceroses develop massive, often hypsodont teeth.

Two genera (*Teleoceras*, *Chilotherium*) independently develop grazing, hippopotamus-like species. This results in some convergence of characters related to the mode of life, such as the broad lambdoid crests and zygomatic arches. These features can be clearly shown to be convergent by the distribution of other characters not related to the common habitus and by the condition seen in the more primitive members of each of these genera.

In a number of rhinoceroses, the occiput has become posteriorly elongated, producing a dolichocephalic skull. As a result, the orbit shifts posteriorly relative to the tooth row. This happens independently in some of the Rhinocerotina and in *Ceratotherium*. In *Rhinoceros*, on the other hand, the skull is brachycephalic and the orbit shifts forward so that the anterior rim of the orbit is over the middle of P^4.

In primitive rhinocerotids, there is a thick bony bridge separating the foramen lacerum medium from the foramen ovale. In teleoceratines and rhinocerotines this bony bridge becomes very thin and is frequently broken or absent.

Horns

The horns of rhinoceroses are made of closely packed agglutinated fibres and have no bony cores like the true horns of some artiodactyls. Rhinoceros horns are only loosely attached to the skull, usually at rugose areas in the nasal or frontal region of the skull, occasionally with distinct 'bosses' or raised horn bases. Primitively, rhinoceroses were hornless and this is true of the majority of the genera. Horns occur only in certain groups of the Rhinocerotidae and not in the other two families.

The earliest horn combination (late Oligocene–early Miocene) was shown by the 'paired horned' rhinos, *Diceratherium* and *Menoceras*, in North America and *Pleuroceros* in Europe. Except for Wood (1927), all authors have considered paired horns as a good character uniting the 'Diceratheriinae'. Indeed, the type species of *Menoceras* was originally (1906) named as a species of *Diceratherium*. It was recognized as a separate genus by Troxell (1921), but later authors generally considered it a subgenus of *Diceratherium* (e.g. Wood, 1964). Tanner (1969) finally showed how different *Menoceras* and *Diceratherium* really are.

A close examination of the paired horn condition shows that the horns of *Diceratherium* and *Menoceras* are not strictly homologous. As Tanner (1969) showed, in *Diceratherium* (Fig. 5J), the horns are formed by subterminal elongate narrow ridges along the lateral edges of the nasals of males. More derived species of *Diceratherium* eventually develop a central boss or swelling, but the lateral ridge is still present. In *Menoceras* (Fig. 5K), on the other hand, the paired horn bosses are completely different in morphology. They are spherical knobs at the very tips of the nasals, with no trace of a ridge leading up to them. The bosses in *Pleuroceros* are subterminal, but as in *Menoceras* they are round, with no ridges. Thus, the 'paired horn' condition is not homologous in detail, and does not unite the 'Diceratheriinae'. *Menoceras* and *Pleuroceros* share many features (Table 1, Fig. 4) with higher rhinoceroses not found in *Diceratherium*. These characters support the hypothesis that *Menoceras* and *Pleuroceras* are sister-taxa and refute the monophyly of 'paired horn' rhinoceroses. Indeed, without the paired horns, *Menoceras* would never have been mistaken for a true dicerathere.

A terminal nasal horn occurs in some aceratherines (*Peraceras*) and in most of the teleoceratines and rhinocerotines except *Elasmotherium*, which has substituted an enormous frontal horn. Except for the genus *Rhinoceros*, all the rhinocerotines have a smaller frontal horn, which becomes larger in the dicerotines. Tandem horns are the rule among late Neogene rhinoceroses.

Upper cheek teeth

Since most fossil mammals (particularly those from the Paleogene) are known primarily from their teeth, it is no surprise that dental morphology has been one of the key features in earlier phylogenies. Some workers (e.g. Wood) have used subtle differences in crown pattern to the point of frustration (e.g. Wood, 1941); others have used teeth only in a limited way (Matthew, 1931). We have found that teeth, especially upper premolars, can occasionally be misleading. During the process of molarization of premolars in rhinoceroses, there was apparently a high degree of intraspecific variability in this character. In the early part of this century many species were recognized primarily by subtle differences of premolar pattern. This resulted in such absurdities as seven species and two genera for a single, uniform-sized quarry sample of *Trigonias* (Gregory & Cook, 1928). Upper premolar variability is also responsible for much of the confusion in Wood's (1927) phylogeny. We have avoided using premolar pattern when the quarry samples or morphologic continuity have shown it to be unreliable. In most taxa which are not undergoing molarization of the premolars, or have already completed it, the premolar pattern is no more or less reliable than any other part of the anatomy.

There are so many variations in upper tooth crown pattern that we cannot review them all here—nearly every node in Fig. 4 has a character from the upper cheek teeth. The key change that distinguishes the three major families is shown in Figs 6–8. Primitively, M^3 has a strong parastyle and metaloph with a subquadrate shape. Amynodonts modify this by elongating the tooth anteroposteriorly, resulting in a quadrate shape. In hyracodonts and rhinocerotids, on the other hand, the metastyle is shortened and inflected
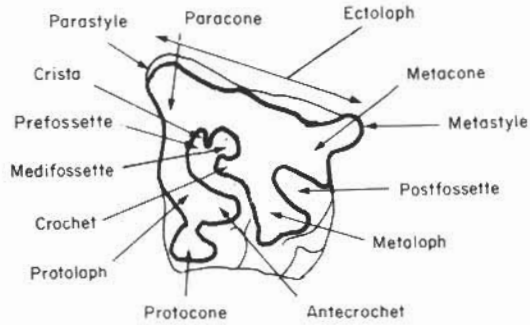
Figure 6. Dental nomenclature of a typical left upper first or second molar of a rhinocerotoid.

lingually. In true rhinocerotids and some hyracodonts the metastyle (metacone) is lost completely, resulting in a triangular tooth.

Once molarization of premolars was completed in the rhinocerotids, the teeth began to add features that improved their shearing ability, increased their crown area, and improved their durability. Several genera of rhinoceroses became hypsodont, nearly always in response to a grazing mode of life. A few genera also developed cement on their teeth and *Coelodonta* and *Elasmotherium* even have corrugated enamel. *Menoceras* and all the higher rhinoceroses developed additional extensions on their cross-lophs, called crochets, antecrochets and cristae (Figs 6, 9). Eventually these fused to form fossettes, or lakes in the enamel, as the teeth became more hypsodont. Incipient crochets and cristae can be seen in some *Diceratherium*, but the well-developed crochets in *Menoceras* are one of the many advanced features of this genus that unite it with higher rhinoceroses.

Lower cheek teeth

In contrast to the many useful characters found in rhinoceros upper dentitions, the lower cheek teeth are stereotyped in pattern from the very beginning. Lower cheek teeth are primitively strongly bilophodont (a dental morphology characteristic of browsers) in *Hyrachyus*. Amynodonts, hyracodonts and rhinocerotids have strengthened the paraconid and hypoconid, resulting in two obliquely orientated crescents which are concave anterolingually and not as
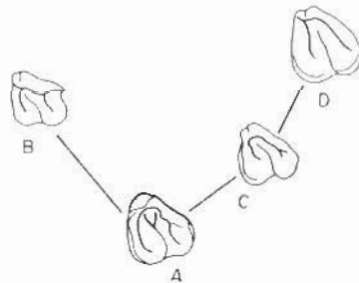

Figure 7. Evolution of M³. A, *Hyrachyus*. B, *Amynodon*. C, *Hyracodon*. D, *Aceratherium*. After Wall (1982: fig. 1).
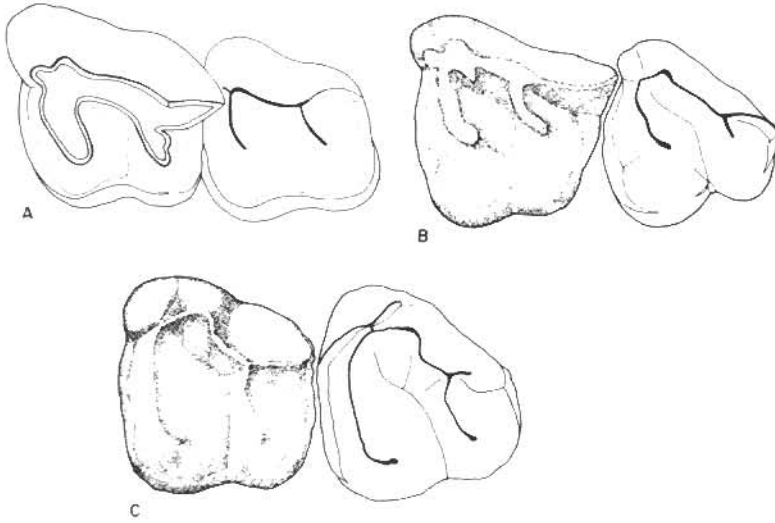
Figure 8. Second and third left upper molars of: A, *Amynodon*; B, *Hyracodon*; C, *Hyrachyus*. From Radinsky (1966).

lophodont. The other major change in the lower teeth is the loss of the hypoconulid on the M_3, which is one of the key synapomorphies for the Rhinocerotoidea. Some other significant changes are: increased hypsodonty; loss of dp^1/l (the first deciduous premolar is retained in nearly all perissodactyls;

Figure 9. Crown view of right upper cheek teeth of representative rhinocerotoids (not to scale). A, *Hyrachyus*. B, *Sharamynodon*. C, *Cadurcodon*. D, *Metamynodon*. E, *Hyracodon*. F, *Indricotherium*. G, *Trigonias*. H, *Amphicaenopus*. I, *Subhyracodon*. J, *Diceratherium*. K, *Menoceras*. L, *Aceratherium*. M, *Aphelops*. N, *Chilotherium*. O, *Brachypotherium*. P, *Teleoceras*. Q, *Coelodonta*. R, *Elasmotherium*.

permanent dp¹/l never erupts, except in *Hyracodon*); reduction of the premolars relative to the molars; occasional loss of P_2.

Anterior dentition

The major changes in the canines and incisors are crucial to rhinoceros phylogeny. Radinsky (1966) has discussed these changes in detail (Fig. 10). Primitively, all perissodactyls had three pairs of approximately equal-sized spatulate incisors above and below, with slightly larger canines (as seen in *Hyrachyus*, Fig. 10A). This condition is modified differently by each of the rhinocerotoid families.

Most hyracodonts (e.g. *Hyracodon*) develop conical incisors and equal-sized canines (Fig. 10C). The indricotheriine hyracodonts lose most of their anterior dentition except for hypertrophied I_1^1 tusks (Fig. 10D).

The more derived amynodonts also reduce the anterior dentition, and canine tusks develop in males (Fig. 10E). Amynodont tusks are not chisel-like or conical, but triangular in cross-section with a well-developed thegosis facet.

Primitive rhinocerotids retain their full anterior dentitions (Fig. 10B). *Trigonias* and higher rhinoceroses show a specialization unique to the Rhinocerotidae. The I^1 develops into a chisel-shaped tusk shearing against a lanceolate I_2 (Fig. 10F). Rhinocerotids gradually reduce the rest of the anterior
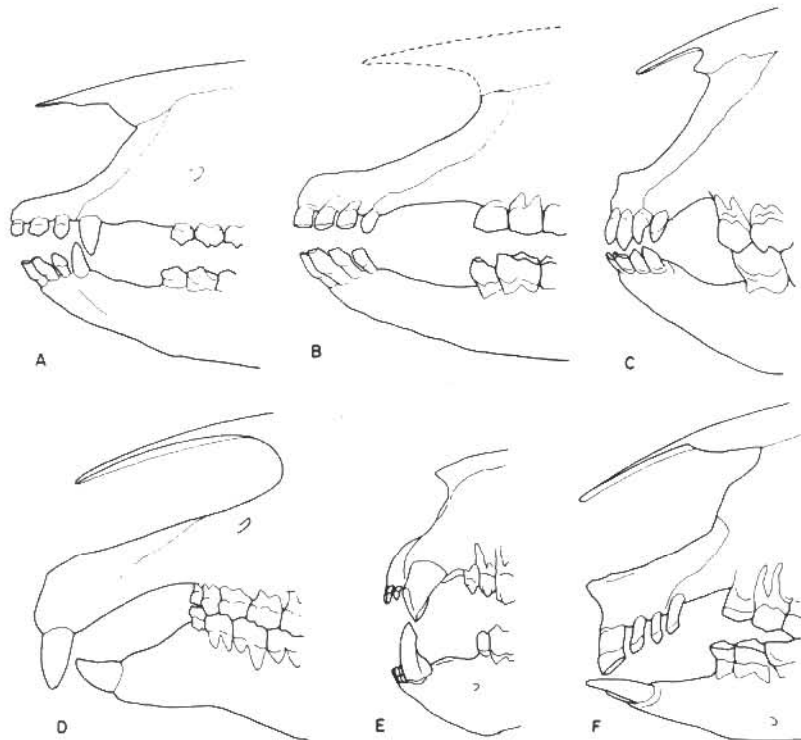

Figure 10. Anterior dentitions of rhinocerotoids. A, *Hyrachyus*. B, *Ardynia*. C, *Hyracodon*. D, *Indricotherium*. E, *Metamynodon*. F, *Trigonias*. From Radinsky (1966).

dentition. The loss of the upper canine appears to be highly variable, since some *Subhyracodon* skulls have it on one side and lack it on the other.

Advanced rhinoceroses have further modified the incisor chisel-tusk combination in several ways. Most aceratherines lose the I^1 but not the I_2, so their edentulous premaxillae are usually very reduced. Several of the rhinocerotines lose I^1_1 and the African rhinoceroses (*Diceros*, *Ceratotherium*) have no anterior teeth at all. In place of these teeth, they browse or graze with horny pads.

Mandible characters

A number of useful synapomorphies occur in the shape of the jaw. In *Hyrachyus* and most other primitive ceratomorphs, the ramus is shallow, with a shallow sloping symphysis and no 'chin'. The short coronoid process has a nearly vertical anterior border and a concave, anteriorly sloping posterior border. The condyles are rounded and tilted medially. This condition is also true of the hyracodonts: *Hyracodon* and most amynodonts develop a peculiar lateral constriction in the diastema.

Trigonias and all higher rhinocerotids have a very distinct mandible. The anterior and posterior borders of the coronoid process are generally straight and a distinctive oblique posterior crest (postcotyloid process) occurs behind the condyle. This latter feature is unique to the Rhinocerotidae. *Subhyracodon*, *Diceratherium* and higher rhinoceroses have further modified the condyle so that the trochlea is flat-surfaced and oriented horizontally, rather than convex and medially tilted. Naturally, the postglenoid process on the skull shows a corresponding change from an anterolaterally oriented articular surface, to one that is more anteriorly oriented.

Atlas–axis complex
(Fig. 11)

Hyrachyus and other rhinocerotoids have a number of features in the atlas–axis complex which do not occur in tapiroids or other perissodactyls. All rhinocerotoids have fused the intervertebral canal in the atlas. The nerves pass instead through the alar notch that cuts into the anteromedial margin of the transverse processes of the atlas. This condition is not seen in advanced tapiroids or horses. Only a shallow notch occurs in chalicotheres, primitive tapiroids, and titanotheres. In *Hyrachyus* (Fig. 11F) the notch is rather shallow, but in all amynodonts, hyracodonts and rhinocerotids it is very deep, giving the transverse processes a 'wing-like' appearance (Fig. 11G, I, K). The dorsal and ventral notches between the anterior articulations on the atlas are normally deep in rhinocerotids. *Menoceras* and higher rhinos have secondarily developed a shallow anteroventral notch in the atlas (Fig. 11L). *Hyrachyus* and all other rhinocerotoids also have an odontoid process on the axis that is circular in cross-section. In tapirs, horses, and chalicotheres it is dorsally flattened. Only titanotheres converge on the rhinocerotoid condition.
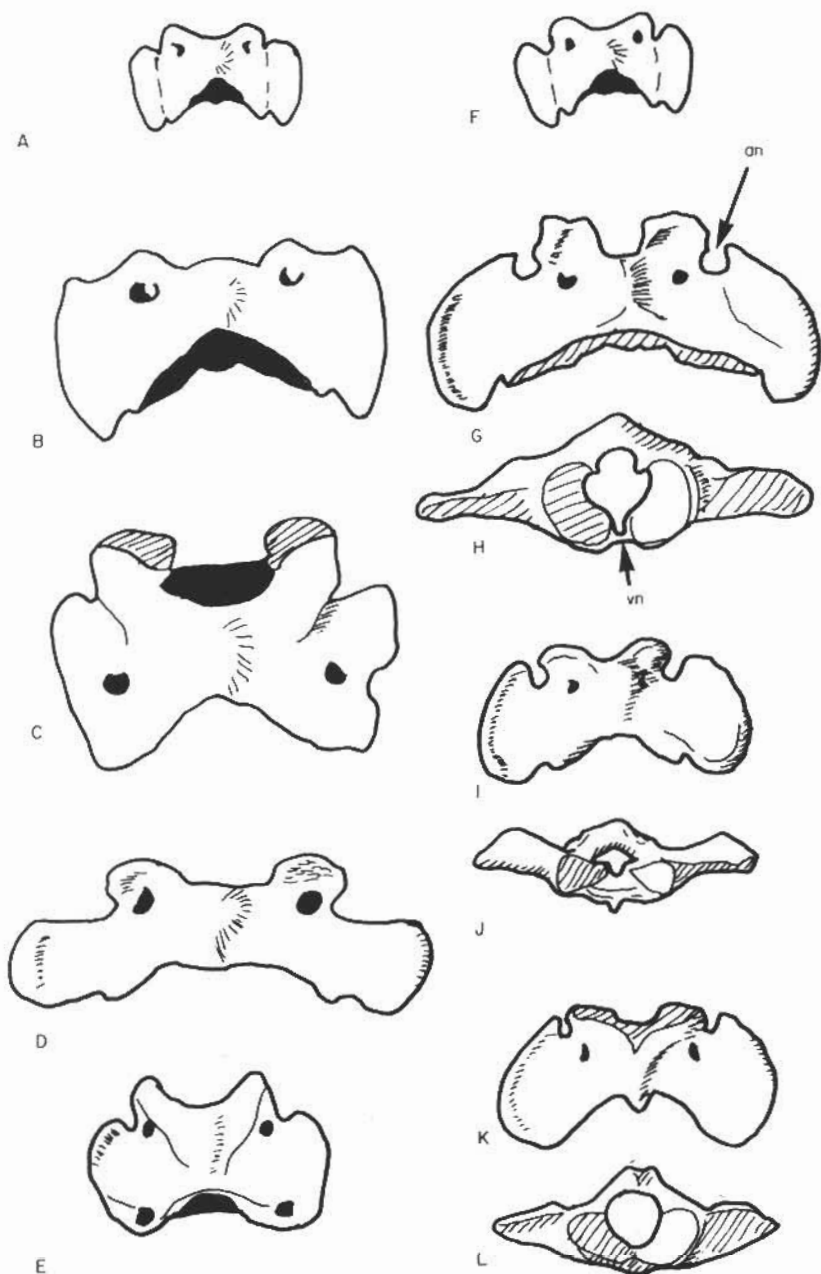
Figure 11. Atlases of representative perissodactyls. All atlases are shown in dorsal view, except H, J and L, which are shown in anterior view. Abbreviations: an = alar (atlantodiapophyseal) notch; vn = ventral notch. A, *Heptodon*, a primitive tapiroid. B, *Tapirus*, an advanced tapiroid. C, *Moropus*, a chalicothere. D, *Palaeosyops*, a titanothere. E, *Mesohippus*, a horse. F, *Hyrachyus*, a primitive rhinocerotoid. G, H, *Metamynodon*, an amynodont. I, J, *Trigonias*, a primitive rhinocerotoid. K, L, *Menoceras*, an advanced rhinocerotoid, showing a shallow ventral notch.

Limbs

Most of the changes in rhinoceros limbs are related to the mode of life of the particular species. Thus, many features that are related to graviportality appear several times in rhinoceroses. Some features are consistent regardless of body size or habitus. Thus, all hyracodonts have long limbs and metapodials related to an originally cursorial mode of life, even though the gigantic indricotheriine hyracodonts could not have been very swift runners. Some amynodonts and some rhinocerotids are relatively graviportal, and show very robust and stocky limbs. Teleoceratines have carried graviportality to an extreme. Their limbs are abnormally short for their body size, and their carpals and tarsals are extremely compressed proximodistally (Harrison & Manning, 1983).

Ceratomorphs primitively have four functioning digits in the manus and three in the pes. The first metacarpal is lost in all perissodactyls. The fifth metacarpal is very reduced in all higher rhinos above *Trigonias*, except for the aceratherines. Contrary to Wood (1964), *Floridaceras* is not the only post-Oligocene rhinoceros with a functioning fifth metacarpal. Small but significant fifth metacarpals are now known from large quarry samples of most of the aceratherines (*Peraceras*, *Aphelops* and '*Aceratherium*' *tetradactylum*). The fifth metacarpal just happens to be rarely preserved, since it is so highly reduced and is usually only detected in large quarry samples or in rare articulated feet. The peculiar reappearance of the functional fifth metacarpal in the aceratherines suggests that it has been epigenetically repressed, but is still coded for in the genome and can reappear fully formed. Similar instances of polydactyly in horses suggests that the reappearance of 'lost' side toes is not unusual in perissodactyls (N. Shubin & D. R. Prothero, unpubl. obs.).

Another significant carpal character is the posterior articulation of the scaphoid and the lunar. This feature is one of several that unites teleoceratines and rhinocerotines.

The humerus also shows several derived features unrelated to its robustness or degree of graviportality. In *Trigonias* and all higher rhinoceroses, the medial process of the proximolateral tuberosity is much longer, narrower and more posteromedially inflected than in any other perissodactyl. This is true of all rhinocerotids, no matter how cursorial or graviportal their limbs are. In addition, the distal trochlea of the humerus in *Subhyracodon* and all higher rhinoceroses is highly asymmetrical, with the medial condyle much stronger than the lateral condyle. A similar asymmetry occurs in the distal trochlea of the femur. In all rhinocerotoids except *Hyrachyus*, the medial rim of the trochlea on the femur is much stronger than the lateral rim. The implications of this feature for rhinoceros locomotion would be interesting to investigate.

DISCUSSION

The Rhinocerotoidea is a good natural group which can be distinguished from the Tapiroidea on the following derived characters: P^4 protocone 'creased' lingually; M_3 hypoconulid lost; cylindrical odontoid process. The M_3 hypoconulid is also lost in some tapiroids (Radinsky, 1966), but no rhinocerotoid has an M_3 hypoconulid. Radinsky (1966) argued that *Hyrachyus*

was a tapiroid because it lacked the characters of *Triplopus* and higher rhinocerotoids. Although *Hyrachyus* shares primitive similarities with tapiroids, it still possesses the derived characters given above.

The first rhinocerotoid family, the Amynodontidae, is so aberrant that its distinctness was appreciated very early. The most primitive forms, *Caenolophus* and *Teilhardina*, from the late Eocene of Mongolia, were originally placed in the Hyracodontidae based on shared primitive characters (Matthew & Granger, 1925, 1926; Simpson, 1945). Radinsky (1967: 10) showed that the quadrate M^3, anteroposterior lengthening of the molars, posteriorly directed metaloph of P^4, and the long ectolophs and metalophs on the molars clearly indicate that these taxa are very primitive amynodonts.

The Amynodontidae include some primitive Eocene forms (*Amynynodon* and another form currently being described by W. Wall) which are sister-taxa of two distinctive subfamilies, the Paramynodontinae (metamynodonts) and Cadurcodontinae. These two groups were discussed by Wall (1982), who used the term 'Metamynodontini'. However, Paramynodontinae was proposed by Kretzoi (1942), and therefore has priority. Metamynodonts are united by their broad zygomatic arches, large tusks in males, and shortened metapodials. *Cadurcotherium* and *Metamynodon* are characterized by their very hypsodont teeth, with reduced M^3 metacones and broad ectolophs.

Various authors have placed the enigmatic forms *Toxotherium* and *Schizotheroides* in the Tapiroidea (Radinsky, 1964; Schiebout, 1977; Schoch & Prins, 1984), in the hyracodonts (Wilson & Schiebout, 1984), or in the amynodonts (Emry, 1979), but their affinities are still very controversial. We suggest that they may not be rhinocerotoids at all, but members of the predominantly European family Lophiodontidae, which Schoch & Prins (1984) consider tapiroids. As indicated by its reduced premolars and relatively deep posterior ramus, *Toxotherium* had a very brachycephalic face, like some amynodonts. But Wilson & Schiebout (1984) showed that the ossified external auditory meatus in *Toxotherium* ruled out amynodont affinities and more closely resembled the condition seen in *Triplopus*. They did not examine the basicranium of more primitive perissodactyls. We suggest that this feature may be primitive for ceratomorphs, rather than unique to hyracodonts, and thus does not place *Toxotherium* in the rhinocerotoids. In addition, the upper teeth of *Toxotherium* and *Schizotheroides* are definitely not rhinocerotoid. The upper molar parastyles are far stronger than those in any rhinocerotoid or any more primitive perissodactyl. In addition, the shape of M^3 does not agree with amynodonts or any other rhinocerotoid. The cross crests are strongly oblique (posteriorly deflected) and the ectoloph is posterolingually deflected and almost continuous with the metaloph. The short metastyle is perpendicular to the continuous ectoloph—metaloph on M^3. This differs from the primitive condition for all perissodactyls and is also derived relative to the primitive condition for ceratomorphs (as seen in *Homogalax*). This derived M^3 shape, however, is seen in the Lophiodontidae. In addition, the obliqueness of the other molar cross lophs and the development of a lower tusk in *Toxotherium* rule out affinities with most tapiroids or chalicotheres. Fischer (1977) has recently shown that the Lophiodontidae is a good monophyletic group which includes not only *Lophiodon* and *Lophiaspis* but also the North American form *Paleomoropus*, which was previously considered a chalicothere. We know of no lophiodonts that are as

brachycephalic as *Toxotherium* but lophiodonts do have a lower tusk. It will be interesting to see if lophiodonts also have an ossified external auditory meatus, like *Toxotherium*. At present, *Toxotherium* and *Schizotheroides* are too incomplete to make a conclusive case for their affinities but we feel that the characters of their upper teeth makes their inclusion in the Rhinocerotoidea doubtful on the present evidence.

A number of characters (Table 1, node 2) seem to suggest that the amynodonts are rhinocerotoids. This idea dates back at least to Scott & Osborn (1898). However, one of us (C.B.H.) is not completely convinced of this relationship and feels that amynodonts may be more closely related to lophialetid tapiroids. The two remaining rhinocerotoid families (Hyracodontidae, Rhinocerotidae) clearly form a monophyletic group. Several authors (e.g. Scott, 1941) placed the hyracodonts and amynodonts together based on shared primitive characters, or for lack of a better place. The evolution of the M^3 (Fig. 7), however, clearly indicates that the hyracodonts are more closely related to rhinocerotids than they are to amynodonts.

The Hyracodontidae includes two subfamilies, the Triplopodinae (mostly small, primitive forms such as *Triplopus* and *Hyracodon*) and the giant indricotheres (Subfamily Paraceratheriinae). All hyracodonts are united in having long, laterally compressed metapodials, despite the enormous range in body size.

Rhodopagus and *Pataecops* are tiny ceratomorphs described by Radinsky (1965) from the late Eocene of China. Radinsky (1965: 214) tentatively assigned them to the lophialetid tapiroids. Lucas & Schoch (1981) assigned these taxa to the Hyracodontidae, as defined by Radinsky (1967). Since we have restricted the definition of the Hyracodontidae to make the group monophyletic, the affinities of *Rhodopagus* and *Pataecops* require further discussion.

Lucas & Schoch (1981: 50) cited eight characters which placed *Rhodopagus* and *Pataecops* within the Hyracodontidae *sensu* Radinsky. Characters 1, 2, 3, 4 and 7 of Lucas & Schoch (1981) show the condition seen in *Triplopus*, and are more derived than the condition seen in *Hyrachyus*. Character 8 (loss of M_3 hypoconulid) is primitive for rhinocerotoids. Lucas & Schoch (1981) noted that there was a strong similarity with the dentition of *Triplopus*. Character 6 (confluence of the metaloph with ectoloph) and the restriction of the P^{3-4} postprotocrista are, however, features more derived than the condition in *Triplopus*, but are found in amynodonts, hyracodonts and rhinocerotids. But *Rhodopagus* and *Pataecops* also have an M^3 metacone that is more reduced than any *Triplopus* or amynodont. This suggests that these two taxa might be primitive rhinocerotids or hyracodonts *sensu stricto*. In addition, the lower canine (based on the size of its alveolus in American Museum of Natural History 26112) is reduced, a hyracodont feature. This same specimen, however, has the primitive spatulate lower incisors, rather than the conical incisors of hyracodonts. The postcranial skeleton of *Rhodopagus* and *Pataecops* is virtually unknown, so the relative length of their metapodials (a key hyracodont synapomorphy) cannot be determined. Thus, *Rhodopagus* and *Pataecops* are probably primitive sister-taxa of either hyracodonts (based on the reduction of the canine), or possibly the sister-group of the rhinocerotids plus hyracodonts. For the present, we tentatively place them in an unresolved trichotomy with the hyracodonts and rhinocerotids (Fig. 4). When more complete material of these

enigmatic taxa is found, it will be possible to determine to which group they belong.

Hyracodon itself is a very primitive but long-lived form, surviving with very little change (except for molarization of premolars and increased size) for nearly 10 million years in North America. The indricotheres (Subfamily Paraceratheriinae) were once considered rhinocerotids by Matthew (1931) since they have enlarged incisor tusks. However, Radinsky (1967) correctly placed them with the hyracodonts, since their incisor enlargement is totally different from the condition seen in the Rhinocerotidae. Lucas, Schoch & Manning (1981) expanded the indricotheres to include their smaller sister-taxa, *Forstercooperia* and *Juxia*.

The Rhinocerotidae were a very diverse group in the early Oligocene. Many poorly understood European forms (e.g. *Eggysodon, Meninatherium, Epiaceratherium*) will eventually have to be placed within the framework of this hypothesis. Unfortunately, the validity of many of these taxa is hard to determine, and a complete revision of the European forms is necessary before we can evaluate them. In many cases, we suspect that the names may be indeterminate. Except for *Ronzotherium*, most of the primitive European rhinocerotids are based on very poor material, lacking key features of the anterior dentition and skull. Molarization of premolars is virtually useless as a supraspecific character in primitive rhinocerotids, so genera that differ from others based on slight premolar differences are probably invalid. In other cases, the name may never be determinate because the material is lost. Kollman (pers. comm.) tells us that the type and only specimen of *Meninatherium* (Abel, 1910) was apparently destroyed during the Second World War. In our cladogram we have used only the better known or more complete Asian and North American taxa, which sort out along a fairly clear morphocline. It will be interesting to see which European taxa are sufficiently complete and well-known that their affinities can be established.

The more advanced rhinocerotids diversify into two distinct lines in the middle and late Oligocene. In North America, the dominant rhinoceros is *Diceratherium sensu stricto*, which is the end of a lineage lasting over 20 million years. But in the Chattian and Aquitanian (Arvernian and Agenian) of Europe the earliest members of the menoceratines, aceratherines, teleoceratines and rhinocerotines occur. These four groups are united by a large suite of derived characters: a short basicranium (relative to the tooth row); reduced sagittal crests; premaxillary further reduced from the *Diceratherium* condition; nasal incision over the posterior part of P^2; I^2 lost; upper molar lingual cingula weak or absent; strong crochets on molars; and a shallow anteroventral notch on the atlas. This assemblage of higher rhinoceroses has never been recognized before, yet it is one of the most clear-cut and best-defined groups in this study.

Perhaps the reason that this group has never been previously recognized is that *Menoceras* and *Pleuroceras* have until now been considered diceratheres. In the discussion above, we showed that the knoblike paired horns of *Menoceras* are not strictly homologous with the broad lateral ridges of *Diceratherium sensu stricto*. In addition, *Menoceras* and *Pleuroceros* possess all the higher rhinoceros synapomorphies listed above, clearly distinguishing them from more primitive *Diceratherium sensu stricto* and uniting them with the remaining higher rhinoceroses. The 'paired horn' parallelism confused many early workers, since

abundant *Menoceras arikarense* ('*Diceratherium cooki*') occurs with the extremely rare *Diceratherium niobrarense* in Agate Springs Quarry. But the Menoceratinae (new taxon) are both cladistically and geographically distinct from true diceratheres. The two groups are sympatric in North America for only a very brief period (latest Arikareean–medial Hemingfordian).

The remaining higher rhinoceroses can be broken down into three good monophyletic groups: the true aceratherines, the teleoceratines and the rhinocerotines. The aceratherines have traditionally been another wastebasket group for all hornless fossil rhinoceroses. Most specimens referred to '*Aceratherium*' do not belong in this genus but are simply unallocated primitive rhinoceroses. A full revision of European Neogene rhinoceroses should clear up which taxa are actually referable to *Aceratherium sensu stricto*.

Aphelops, *Peraceras*, *Chilotherium*, *Floridaceras*, *Aceratherium sensu stricto* and an undescribed genus (Prothero, in review) form a well-defined monophyletic group, the Subfamily Aceratheriinae. Aceratherines are united by a lower tusk with a reduced medial flange and a long diastema posterior to it, and by a secondarily functional fifth metacarpal. Most aceratherines are easily recognized by their greatly reduced premaxillae lacking I^1, and their highly retracted nasal incision (to the level of P^4). *Floridaceras* appears to have a retracted nasal incision, although the skulls are so badly crushed that this is difficult to ascertain. Unlike other aceratherines, however, *Floridaceras* has a thegosis facet on the lower tusk, indicating the presence of an I^1. As the name implies, most aceratherines are hornless. However, the nasals of male *Peraceras* skulls clearly have a terminal horn rugosity which is very similar to the condition seen in the rhinocerotines (Prothero, in review). Two members of the Aceratheriinae (*Peraceras*, *Chilotherium*) start out with primitive skull proportions (like in *Aphelops*) but develop derived species which mimic *Teleoceras* in having broad zygomatic arches, flaring lambdoid crests and high-crowned teeth. As a result, *Chilotherium* is nearly always erroneously considered a teleoceratine (see Ringström, 1924; Heissig, 1973). Both *Chilotherium* and *Peraceras* have the characteristic aceratherine nasal retraction and reduced premaxilla lacking I^1. *Chilotherium* also lacks many of the distinctive teleoceratine synapomorphies that are unrelated to its similarities in mode of life.

The teleoceratines and the rhinocerotines have both been recognized as natural groups since the turn of the century. However, Heissig (1973) has suggested that the teleoceratines are more closely related to the aceratherines than they are to the rhinocerotines. We have already discussed our reasons for rejecting this hypothesis. We consider the teleoceratines more closely related to the rhinocerotines on the basis of the following synapomorphies: terminal nasal horn; fused nasals; reduced bony bar between the foramen ovale and foramen lacerum medium; posterior articulation between the scaphoid and lunar; and laterally expanded lambdoid crests. To express this relationship, we expand Dollo's (1885) Rhinocerotinae to include the teleoceratines and place it at subfamilial rank equivalent with the Aceratheriinae.

A *Teleoceras–Brachypotherium* group was first recognized by Osborn (1900), who called it the Subfamily Brachypodinae. Since subfamily names must be based on a genus, this name is invalid. Hay (1902) called it the Teleoceratinae, and this is apparently the correct name. Teleoceratines are very distinctive. Their most unusual features are the short, stumpy legs and feet (hence the

'Brachypodinae'), with short, flattened metapodials and flattened carpals and tarsals. Other synapomorphies include: brachycephalic skull with broad zygomatic arches and flaring lambdoids (mimicked by *Chilotherium* and *Peraceras*); nasal incision retracted to anterior P^3 (but not as far as in *Chilotherium* or *Peraceras*); nasals shaped like an inverted U in cross-section, with lateral edges downturned and thinned; strong antecrochet on molars; elongate calcaneal tuber. *Teleoceras* is further characterized by very hypsodont teeth and reduction of the premolar row (P_2 very reduced or lost).

The phylogeny of the Tribe Rhinocerotini (including the five living rhinoceroses) follows Groves (1983). We find his character analysis to be the most complete and convincing of any hypothesis so far proposed for this group .

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