

THE FAMILIES OF THE RHINOCEROTOIDEA
(MAMMALIA, PERISSODACTYLA)

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ABSTRACT: On the basis of molar cusp pattern, the family Hyrachyidae is transferred from the Rhinocerotoida to the Tapiroidea and is classified as a subfamily of the Helaletidae. The family Rhinocerotidae is restricted to forms with the unique chisel-shaped I^1 and procumbent, lanceolate I_2 shearing specialization seen in *Epiaceratherium* and *Trigonias* and, with modifications, their descendants. Non-amynodontid rhinocerotoids with other anterior dental specializations are placed in the Hyracodontidae.

INTRODUCTION

A study of the early evolutionary history of the order Perissodactyla shows that the currently accepted classification of the superfamily Rhinocerotoida is unnecessarily artificial and does not reflect present knowledge of rhinocerotoid phylogenies. Since the major revision of Wood (1927), most authors (e.g., Simpson, 1945; Viret, 1958) have recognized four families of rhinocerotoids: Hyrachyidae Wood, 1927 (= Hyrachyinae Osborn, 1892); Aynodontidae Scott and Osborn, 1883; Hyracodontidae Cope, 1879; and Rhinocerotidae Gray, 1821. Gromova (1962) treated the subfamily Indriotheriinae Borissiak, 1923, usually classified as a rhinocerotid, as a separate family. After consideration of all Eocene and Oligocene ceratomorph (= tapiroid and rhinocerotoid) perissodactyls, I have come to the following conclusions: 1) The Aynodontidae is a compact, distinct family, although oversplit on the generic level. 2) The Rhinocerotidae is a polyphyletic group and includes several genera which should be transferred to the Hyracodontidae. 3) The family Hyrachyidae is neither diverse enough nor distinct enough to be separated on the family level from the tapiroid family Helaletidae. Systematic revisions of hyrachiids, aynodontids and hyracodontids, on the specific and generic level, are being treated elsewhere (Radinsky, in press) and only such taxonomic details as are pertinent to the present discussion will be mentioned here.

STATUS OF THE HYRACHYIDAE

The family Hyrachyidae was revised by Wood (1934), who recognized four genera: *Hyrachyus* Leidy, 1871; *Colonoceras* Marsh, 1873; *Metahyrachyus* Troxell, 1922; and *Ephyrachyus* Wood, 1934. They form a compact, conservative group which exhibits no more morphological diversity than could be expected within a single genus (see Radinsky, in press). Superfamilial allocation of hyrachiids involves the question of how rhinocerotoids should be separated from tapiroids.

The oldest known representatives of the five superfamilies of perissodactyls are distinguished from each other primarily by differences in molar cusp pattern (Radinsky, 1964). The primitive ceratomorph molar pattern, as exempli-

fied by the early Eocene helaletid tapiroid *Heptodon*, is characterized by the presence of complete, unbroken transverse crests (protoconule and metaconule no longer distinct cuspules) in the upper molars, and anteriorly-directed metalophids in the lower molars. In common with molars of other primitive perissodactyls, the early ceratomorph molars had relatively distinct, approximately equal-sized paracone and metacone, good-sized parastyles, low paralophids and metalophids, and a hypoconulid, or third lobe, on M_3 .

In some tapiroid families (e.g., the Helaletidae and Deperetellidae) the molar metacone became lingually depressed and reduced in size, and paralophids and metalophids were reduced, resulting in a bilophodont cusp pattern. In other tapiroid groups (e.g., the Lophiodontidae and Isectolophidae), the primitive early Eocene molar pattern, with a full-sized metacone, was retained unchanged. In some genera of the family Lophialetidae, such as *Lophialetes*, the M^{1-2} metacones were lengthened and flattened, producing a long ectoloph, and M_{1-3} metalophids and paralophids were relatively high.

The M_3 hypoconulid was retained in its primitive form in the Isectolophidae, but was lost completely in the Deperetellidae. In the Lophiodontidae it was retained in *Lophiodon* but lost in *Chasmothorium*; in the Lophialetidae, retained in *Lophialetes* and *Breviodon* but lost in *Rhodopagus*; in the Helaletidae, retained in reduced form in *Heptodon*, *Helaletes* and some species of *Colodon* but lost in *Selenaletes*, *Dilophodon*, some species of *Colodon*, and the line leading to the tapirids. Thus the M_3 hypoconulid was reduced and lost independently several times in different tapiroid lineages and is not diagnostic even on a family level. (For references on tapiroids, see Radinsky, 1963, 1965 and 1966.)

The molar patterns of the rhinocerotoid families Amyndontidae, Hyracodontidae and Rhinocerotidae, in contrast to those of the tapiroid ceratomorphs, have in common the following features: long and flat M^{1-2} metacones, reduced parastyles, high paralophids and metalophids (the whole tooth is higher crowned), and no M_3 hypoconulid. That combination of features characterized the basic molar pattern of the Rhinocerozoidea and can be considered diagnostic of the superfamily. Within the Rhinocerozoidea, specializations of the anterior dentition (incisors and canines) and modifications of M^3 distinguish the families; those features will be discussed in the next section.

The molar pattern of the Hyrachyidae, as exemplified by that of *Hyrachyus* (Fig. 1), is basically that of a primitive ceratomorph, with large parastyles, unmodified molar metacones, and low metalophids and paralophids; it closely resembles molar patterns of such primitive tapiroids as *Heptodon* and *Lophiodon*. The only specialized feature in the hyrachyid molar pattern is the loss of the M_3 hypoconulid, an event which occurred several times in different tapiroid lineages. The basic hyrachyid molar pattern lacks the characteristic rhinocerotoid features of long M^{1-2} metacones, small parastyles and high metalophids and paralophids. Some advanced individuals of one species of *Hyrachyus* show the beginnings of those characters, and may be ancestral to

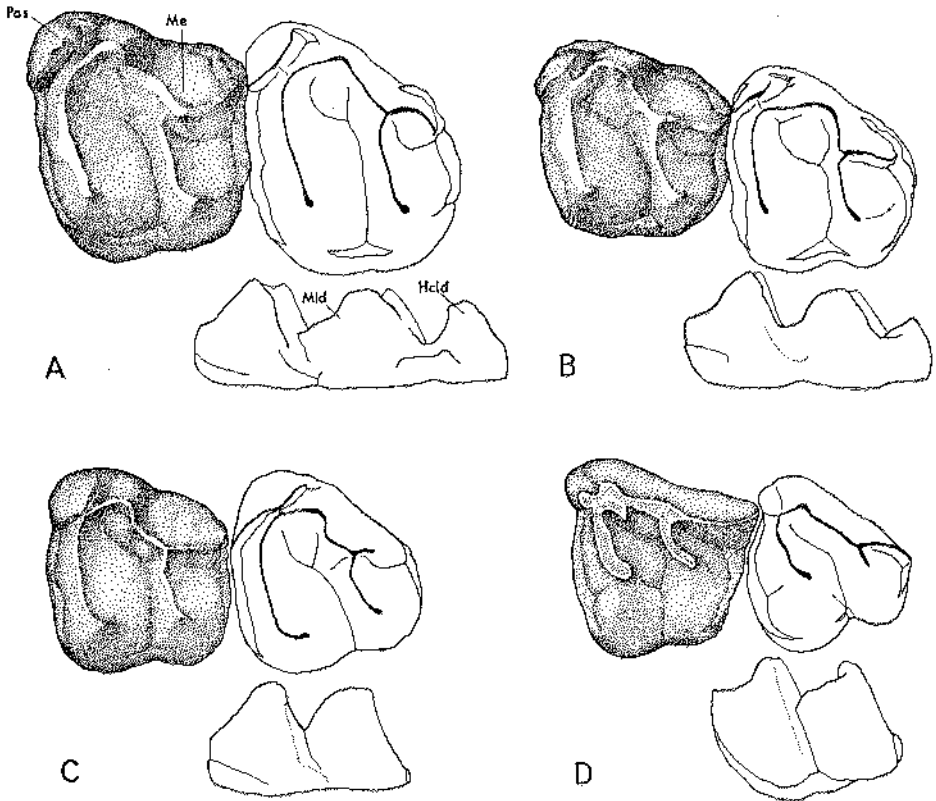


FIG. 1.— M_2-3 , crown view, and M_3 , lateral view, of A. *Heptodon caliculus*, Amer. Mus. Nat. Hist. nos. 4855 and 14874 (early Eocene); B. *Helaletes nanus*, A.M.N.H. nos. 11672 and 13124 (middle Eocene); C. *Hyrachyus modestus*, A.M.N.H. nos. 12671 and 19243 (middle Eocene); D. *Hyracodon nebraskensis*, A.M.N.H. no. 1166 (middle Oligocene). *Hyrachyus* is here classified with *Heptodon* and *Helaletes* as a helaletid tapiroid; *Hyracodon* is a hyracodontid rhinocerotoid. A and B, $\times 2.3$; C and D, $\times 1.16$. Abbreviations: Hcld, hypoconulid; Me, metacone; Mld, metalophid; Pas, parastyle.

the primitive hyracodontid rhinocerotoid *Triplopus*. However, in most hyrachyid specimens the molar pattern is that of a primitive ceratomorph, and the anterior dentition and skeleton are typical of primitive perissodactyls in general. Since, except for some advanced individuals, *Hyrachyus* lacks the features diagnostic of the Rhinocerotioidea, there is no reason to assign it to that superfamily. *Hyrachyus* is extremely similar to the helaletid tapiroid *Heptodon*, from which it differs mainly in being somewhat larger and in having lost the M_3 hypoconulid. Therefore I transfer *Hyrachyus* to the tapiroid family Helaletidae, which I divide into two subfamilies: Helaletinae Osborn, 1892, including the main *Heptodon-Helaletes-Colodon* line (with *Selenaletes* and *Dilophodon* offshoots), characterized by a trend towards increasing bilophodonty and development of a proboscis; and the Hyrachyinae Osborn, 1892,

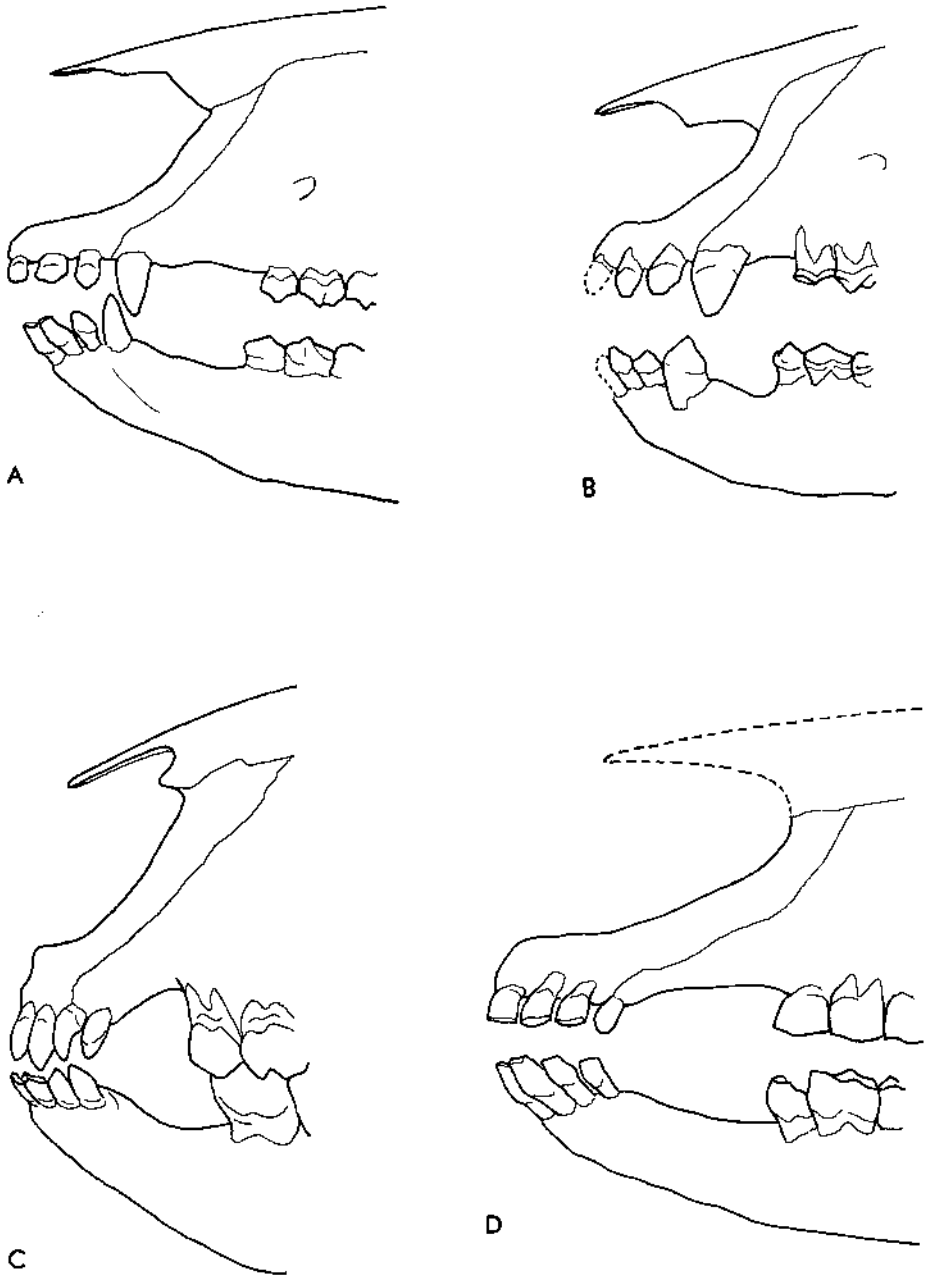


FIG. 2.—Anterior dentition of A. *Hyrachyus*, A.M.N.H. nos. 1645 and 12364; B. *Pappaceras*, A.M.N.H. no. 26660; C. *Hyracodon*, after Scott, 1941, pl. 89; D. *Ardynia*, A.M.N.H. nos. 26039 and 26183. Not to scale.

for the *Hyrachyus* group, including *Colonoceras*, *Metahyrachyus* and *Ephyrachyus*, a conservative group which persisted basically unchanged through the middle Eocene.

INCISOR SPECIALIZATIONS AND RHINOCEROTOID CLASSIFICATION

The primitive perissodactyl anterior dentition consisted of three pairs of approximately equal-sized, spatulate incisors above and below and moderate-sized canines. That is the condition seen in *Heptodon*, *Hyrachyus* and most other Eocene tapiroids. The oldest known rhinocerotoids, characterized by the molar pattern described above, first appeared at the beginning of the late Eocene, already differentiated into two families, the Amyndontidae and the Hyracodontidae. (These two families were probably derived from different groups of tapiroids, which would make the Rhinoceroidea a polyphyletic category.) In the amyndontids the canines are medium-sized to large erect tusks, and the incisors are small and pointed. The hyracodontids display greater variation in anterior dentition. In late Eocene hyracodontids such as *Triplopus* Cope, 1880, and related forms (*Prothyracodon* and *Eotrionias*), the primitive condition of approximately equal-sized, spatulate incisors is retained, although the canines may be only slightly larger than the third incisors. From this basic type of anterior dentition, several different specializations were developed in different rhinocerotoid lines (Fig. 2 and 3).

In the Asiatic Oligocene genus *Ardynia* Matthew and Granger, 1923, the incisors are spatulate and increase in size slightly anteriorly; the canines are reduced in size and slightly smaller than I_3^3 . In the North American Oligocene genus *Hyracodon* Leidy, 1856, incisors are equal-sized, small, slender and pointed, and the canines are the same size and shape as the incisors.

In the late Eocene Asiatic group represented by *Forstercooperia* Wood, 1939 (replacing *Cooperia* Wood, 1938), *Pappaceras* Wood, 1963, and *Juxia* Chow and Chiu, 1964, the incisors are pointed and, in some species, show a slight size increase anteriorly; the canines are stout but stubby. This group of rhinocerotoids appears to have given rise to the giant indricotheres of the Oligocene. A transitional form is represented by the early Oligocene genus *Urtinotherium* Chow and Chiu, 1963, in which I_1 is enlarged and procumbent, a stubby conical tusk, and the posterior incisors and canines are reduced in size. In the later indricotheres (*Paraceratherium* Cooper, 1911, and *Indricotherium* Borissiak, 1915) the second and third incisors and canines are lost, although a vestigial C^1 may be present, and only the hypertrophied, stubby, pointed I_1^1 tusks are present.

Another type of anterior dentition was developed in a group of European and Asiatic Oligocene rhinocerotoids for which the names *Praeaceratherium* Abel, 1910, *Eggysodon* Roman, 1911, and *Allacerops* Wood, 1932, were proposed. In this group the canines are moderate-sized, erect tusks, and the incisors are reduced in size and number; in the mandibles figured by Stehlin (1930) and Osborn (1900), only two pairs of incisor alveoli are present between the tusks.

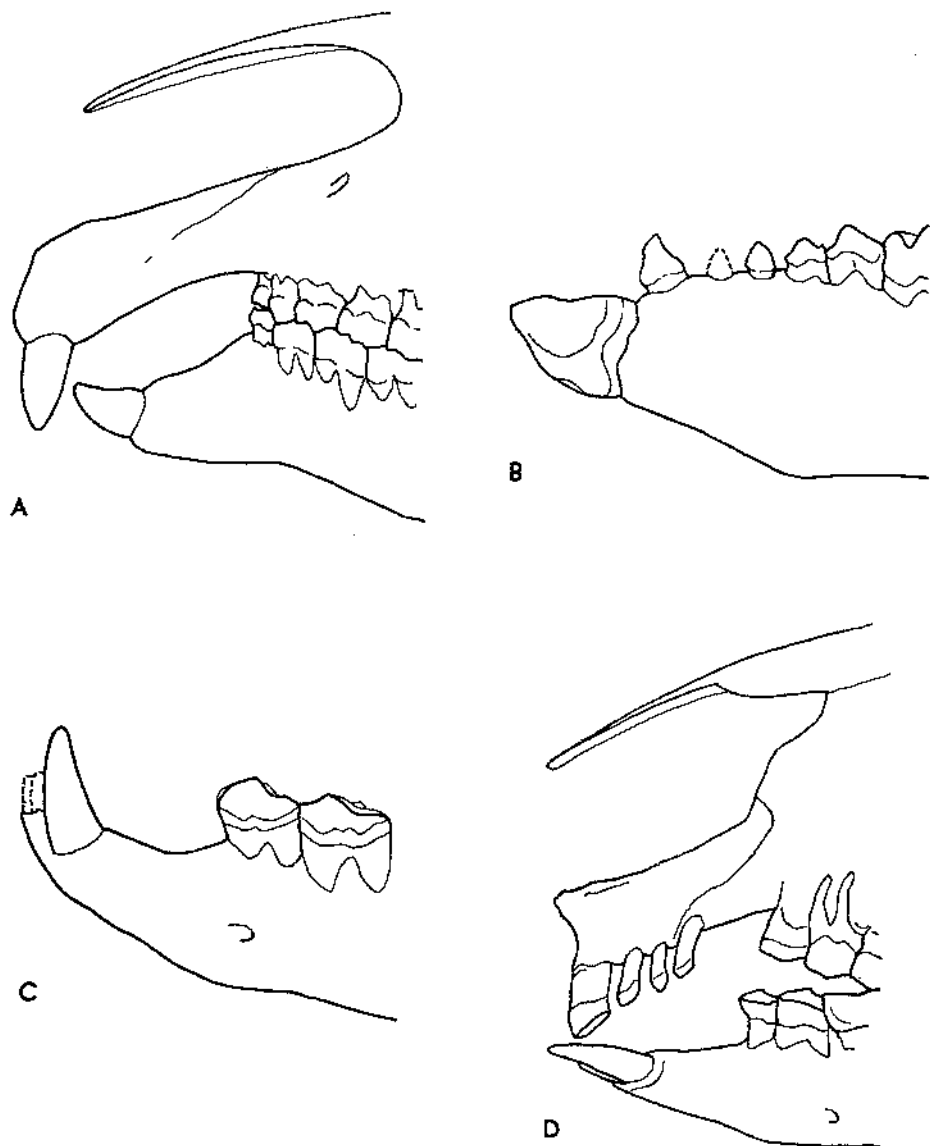


FIG. 3.—Anterior dentitions of A. *Indricotherium*, after Granger and Gregory, 1936, Fig. 1; B. *Urtinotherium*, after Chow and Chiu, 1963, Fig. 1; C. *Eggysodon*, after Stehlin, 1930, Fig. 3; D. *Trigonias*, after Scott, 1941, pl. 82. Not to scale.

The last major specialization of the rhinocerotoid anterior dentition first appeared at the beginning of the Oligocene in two closely related forms, one in Europe, *Epiaceratherium* Abel, 1910, and the other in North America, *Trigonias* Lucas, 1910. In these forms I^1 is elongated posteriorly into a chisel-like blade which shears against an enlarged, procumbent, pointed I_2 . The posterior upper

incisors and canine and the first pair of lower incisors are reduced in size; I_3 and C_1 are lost. From the *Epiaceratherium-Trigonias* stock, with its unique I^1/I_2 shearing specialization, a major evolutionary radiation occurred in the middle and late Tertiary. Some lines retained the basic incisor shearing mechanism much as it was in the early Oligocene, with only the loss of some or all of the teeth behind I^1 . This condition is seen today in *Rhinoceros*. In other lines, such as *Aphelops* or *Chilotherium*, all upper incisors, including I^1 , were reduced and lost, while large lower tusks were retained. In still other groups, including the living *Diceros* and *Ceratotherium*, all upper and lower anterior teeth were lost.

Amynodontids differ from other rhinocerotoids in having quadrate M^3 s, with a small metacone consistently retained, relatively long and narrow molars, and premolars that are reduced in both size and number. The remaining rhinocerotoids, however, cannot be grouped into families on the basis of the cheek teeth. Premolar patterns are variable, and premolar molarization occurred independently in different lines during the late Eocene and Oligocene. The M^3 s are basically triangular in all non-amynodontid rhinocerotoids, with a small, lingually-deflected, variable vestige of the metacone present in the earliest hyracodontid species. The metacone vestige was lost independently during the late Eocene in advanced species of the *Triplopus* group, the *Forstercooperia* group, in *Epitriplopus* Wood, 1927, and in *Prohyracodon* Koch, 1897. It was retained in only one Oligocene non-amynodontid rhinocerotoid, the North American genus *Hyracodon*.

The family Hyracodontidae traditionally included *Hyracodon* and the *Triplopus* group, and was characterized by the presence of equal-sized incisors, small canines and a persistent vestige of the M^3 metacone. *Epitriplopus* and *Ardynia* were later added to the Hyracodontidae on the basis of their relatively unspecialized anterior teeth, although both lack the M^3 metacone. Thus the Hyracodontidae has come to include all early rhinocerotoids without tusks, while all non-amynodontid rhinocerotoids with tusks of any sort have been placed in the Rhinocerotidae.

From this discussion it is evident that the family Rhinocerotidae, as presently constituted, is a polyphyletic group, comprising forms with large, erect C^1/C_1 tusks (the *Allacerops* group), stubby, conical I^1/I_1 tusks (the *Paraceratherium* group), and chisel-shaped I^1 /hypertrophied, lanceolate I_2 tusks (the *Epiaceratherium-Trigonias* group and its descendants). This last group was the only really successful one of the lot, and it includes virtually all post-Oligocene rhinocerotoids. To accurately reflect rhinocerotoid evolutionary history in classification, I suggest restricting the family Rhinocerotidae to the last group only, that is, to those forms with the I^1/I_2 incisor specialization and their descendants. The *Forstercooperia*, *Allacerops* and *Paraceratherium* groups and those few late Eocene forms for which the incisors are unknown, such as *Prohyracodon*, should be placed in the Hyracodontidae. Under this

arrangement the Hyracodontidae includes the primitive late Eocene non-amynodontid rhinocerotoids and the (relatively) unsuccessful lines of the late Eocene and Oligocene radiation which arose from those forms. The Rhinocerotidae, here monophyletic, represents the one really successful experiment (in terms of diversity and longevity) of the Oligocene rhinocerotoid radiation—the *Epiaceratherium-Trigonias* group and its numerous descendants.

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