

# The Phylogeny and Classification of Tapiromorph Perissodactyls (Mammalia)

Luke T. Holbrook<sup>1</sup>

Department of Anatomy, New York College of Osteopathic Medicine, Old Westbury, New York 11568

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Despite an excellent fossil record, the phylogeny of Perissodactyla is not well understood, in terms of both the relationships within Perissodactyla and the position of the Perissodactyla among the orders of mammals. This paper provides a phylogenetic analysis of one major perissodactyl lineage, the Tapiromorpha. This analysis combines a more comprehensive sampling of characters and taxa with rigorous tree-searching methods to create a new hypothesis of tapiromorph relationships. The phylogeny of tapiromorph perissodactyls is analyzed using 45 characters of the skull, postcranial skeleton, and dentition scored for 29 taxa, including three nontapiromorph outgroups. Phylogenetic taxonomic definitions are constructed for suprageneric taxa. According to the results of this analysis, the Chalicotherioidea cannot be unequivocally assigned to the Tapiromorpha, nor can *Homogalax* or *Cardiolphus*. *Isectolophus*, Tapiroidea, and Rhinoceroidea are unequivocal members of the Tapiromorpha. Heptodon is included in a monophyletic Tapiroidea. Amynodontid rhinocerotoids come out as the sister group to rhinocerotids, and indricotheres do not fall within the Hyracodontidae. The results of this study provide further arguments that tapiromorphs (and putative tapiromorphs) may be important for understanding

the ancestral morphology of Perissodactyla. © 1999 The Willi

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## INTRODUCTION

This paper attempts to clarify the relationships among the members of Tapiromorpha, one of the major lineages of the mammalian order Perissodactyla. Understanding the phylogeny of Tapiromorpha is important for understanding the relationships among major perissodactyl lineages, because the basal members of this lineage may preserve important information about ancestral character states for the entire order. This study combines a greater emphasis on cranial and postcranial osteological data with computer algorithms for finding shortest trees, a methodological combination that previously has not been applied to this group of organisms.

The order Perissodactyla includes the extant horses, rhinoceroses, and tapirs. There is a large literature on the evolution and rich fossil record of this order. Only relatively recently have cladistic analyses taken a rigorous look at the phylogeny of perissodactyls, and higher level studies have represented the Perissodactyla either with extant forms or with a small number of early

<sup>1</sup>Present address: Dept. of Biological Sciences, Rowan University, 201 Mullica Hill Rd., Glassboro, NJ 08028-1701.

fossil taxa, particularly *Hyracotherium*, the earliest well-known perissodactyl. Lower level studies of perissodactyl relationships are therefore needed to provide greater confidence in our representation of the ancestral morphology of perissodactyls.

This study analyzes the osteological characters of tapiromorph perissodactyls, the lineage including (as defined by Hooker, 1989) the traditional superfamilies Tapiroidea, Rhinoceroidea, and Chalicotherioidea.

## PREVIOUS PHYLOGENETIC WORK

The order Perissodactyla includes the “odd-toed” hoofed mammals, and perissodactyls are usually grouped with other hoofed mammals in the Ungulata (e.g., McKenna, 1975; Novacek, 1986). Radinsky (1966b) postulated that perissodactyls evolved from an archaic group of ungulates called phenacodontids, and most cladistic studies have placed phenacodontids relatively close to perissodactyls (McKenna, 1975; MacFadden, 1976; Prothero *et al.*, 1988; Thewissen and Domning, 1992; Fischer and Tassy, 1993). Among living mammals, there is a controversy over whether hyracoids are the sister group to perissodactyls (McKenna, 1975; Fischer, 1986, 1989; Prothero *et al.*, 1988, Fischer and Tassy, 1993) or whether proboscideans and sirenians should be included with hyracoids in the perissodactyl sister group (Novacek, 1986; Novacek and Wyss, 1986; Novacek *et al.*, 1988; Shoshani, 1993).

Perissodactyla is traditionally divided into five superfamilies: the Equoidea (horses and kin), Brontotherioidea (brontotheres), Chalicotherioidea (chalicotheres), Tapiroidea (tapirs), and Rhinoceroidea (rhinoceroses). Few workers have dealt with the interrelationships of these superfamilies cladistically, and those who have generally treated this topic in broad terms.

Wood (1934, 1937) provided the basis for subsequent perissodactyl classifications when he divided the order into two suborders, the Hippomorpha (equoids, brontotherioids, and chalicotherioids) and the Ceratomorpha (tapiroids and rhinocerotoids). Wood based this division on lower molar morphology, namely whether the lophs of the lower molars were W-shaped (hippomorphs) or transverse (ceratomorphs). Interestingly,

neither of these lower molar morphologies may be a synapomorphy for either suborder.

Scott (1941) separated out a third taxon for chalicotheres, the Ancylopoda, a term originally established as an order by Cope (1889). Scott differentiated the suborder Ancylopoda from other perissodactyls by placing Ceratomorpha and Hippomorpha together as infraorders in the suborder Chelopoda.

Radinsky contributed more to the study of tapiromorphs than any other individual. He published comprehensive treatises on tapiroids (Radinsky, 1963, 1965a, 1965b, 1967b), rhinocerotoids (Radinsky, 1966a, 1967a), and early chalicotherioids (Radinsky, 1964). As an evolutionary systematist, Radinsky emphasized several points: (1) distinguishing intraspecific variation from interspecific variation; (2) recognizing discrete, homogeneous populations and species through statistical analysis; (3) describing ancestor-descendant relationships among genera; and (4) identifying diagnostic features that signified evolutionary transitions between taxa. Radinsky (1964) modified Scott's (1941) classification by treating Ceratomorpha, Hippomorpha, and Ancylopoda as suborders and therefore as being of equal rank. Savage *et al.* (1965) essentially followed Radinsky for their phylogeny of the Perissodactyla, and Radinsky's work remains influential to this day.

Radinsky's work is extremely valuable for providing an objective basis for evaluating alpha taxonomy, but cladistic studies have sometimes failed to appreciate his noncladistic perspective and ideas. Radinsky, like other evolutionary systematists, did not constrain named taxa to be holophyletic; thus, he deliberately recognized paraphyletic and polyphyletic groups as taxa. For instance, Radinsky's Tapiroidea has a single common ancestor, but excludes some of the descendants of that ancestor, namely the Rhinoceroidea (Radinsky, 1963). Thus, his Tapiroidea is a paraphyletic group. Radinsky considered the Rhinoceroidea, on the other hand, possibly to be a polyphyletic group, since he suggested that (1) Asian tapiroids might be ancestral to amynodontid rhinocerotoids (Radinsky, 1966a) and (2) two different lineages of hyracodontid rhinocerotoids might have been independently derived from different species of *Hyrachyus* (Radinsky, 1967b).

Whereas Radinsky's practices would be seen by cladists as invalid taxonomy, they were perfectly consistent

with the taxonomic principles of evolutionary systematists. [For another example, see Simpson's (1928, 1929) polyphyletic Mammalia.] Subsequent cladistic workers, however, sometimes mistakenly interpreted Radinsky's taxonomic concepts to always designate monophyletic groups. As a result, some holophyletic groups were recognized on the basis of membership of Radinsky's nonmonophyletic taxa, and diagnoses for these new clades were proposed. Ironically, the cladograms inspired by Radinsky's taxonomy did not always reflect his phylogenetic ideas.

Since Radinsky's papers in the 1960s, only a handful of studies have examined perissodactyl relationships, but almost all of them have adopted a cladistic methodology. MacFadden (1976) first applied cladistic methods to the early evolution of equids but cladistic analyses of the relationships of tapiromorphs did not occur until the 1980s. The results of these cladistic studies of perissodactyls were summarized in a 1984 symposium that led to a published volume (Prothero and Schoch, 1989).

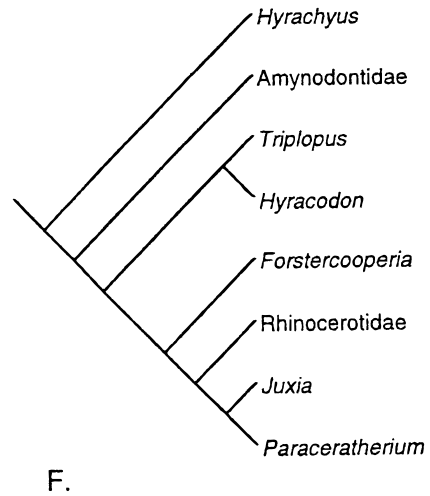
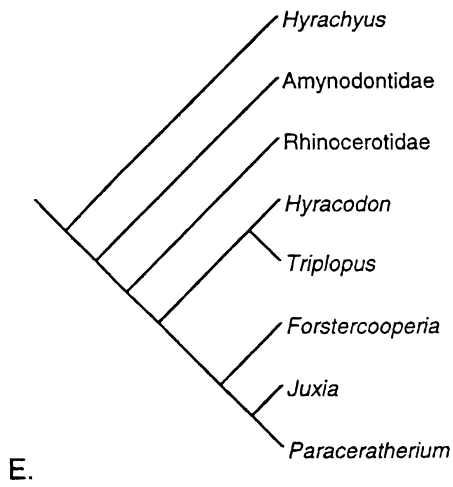
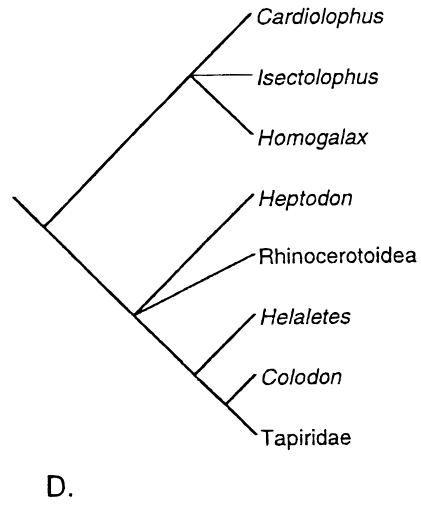
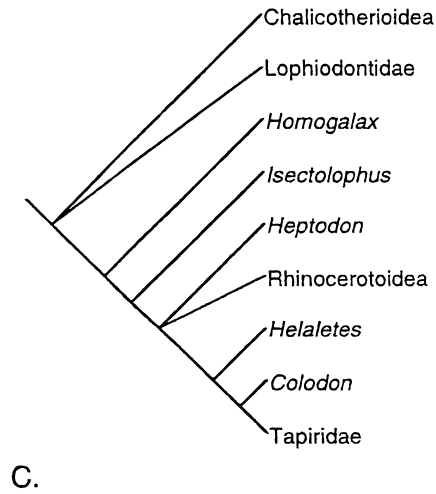
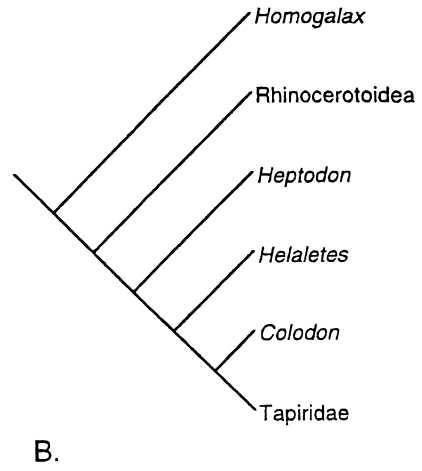
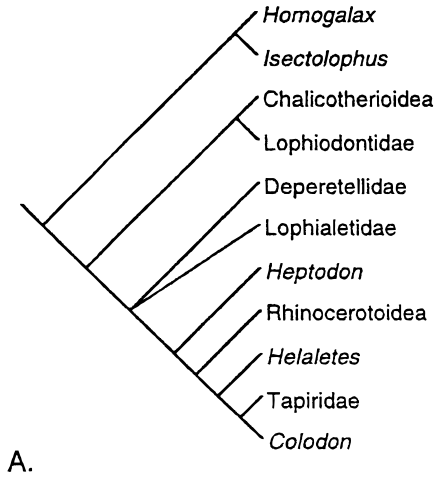
One paper from this volume was Hooker's (1989) study of perissodactyl interrelationships (Fig. 1A). This was the first cladistic study of perissodactyls to employ parsimony analysis by computer. Hooker examined numerous characters, mostly dental, in numerous perissodactyls. Hooker's phylogeny, however, was, by his own admission, not the shortest possible tree. In fact, he interpreted his initial results as a trichotomy of Titanotheriomorpha (brontotherioids), Hippomorpha (equoids), and Tapiromorpha (tapiroids, chalicotherioids, and rhinocerotoids). He then ran separate analyses of Hippomorpha and Tapiromorpha that were constrained to produce certain "traditional" groupings. Despite all of the assumptions in Hooker's analysis, his Tapiromorpha was accepted as independent confirmation of a close relationship between chalicotherioids and ceratomorphs, an idea that Schoch (1989) independently proposed. No one has tested Hooker's concept of Tapiromorpha since.

There are several interesting aspects of the internal structure of Hooker's (1989) Tapiromorpha. (1) Hooker constrained *Homogalax* and *Isectolophus* to form a monophyletic Isectolophidae, consistent with Radinsky's (1963) membership for that family. (2) Chalicotherioidea was united with Lophiodontidae (historically considered to be "tapiroids") in Ancylopoda. (3) Isectolophidae was the sister taxon to a clade including Ancylopoda and Ceratomorpha (i.e., other "tapiroids" and rhinocerotoids). (4) *Heptodon* was the sister taxon to a clade including Rhinoceroidea and a restricted, monophyletic Tapiroidea.

Three other studies from the 1989 volume deserve mention in this section, Schoch (1989), Prothero *et al.* (1989), and Heissig (1989), because they summarize the current ideas about tapiromorph interrelationships. Schoch (1989) produced a phylogeny of "tapiroids," recognizing that the traditional Tapiroidea (sensu Radinsky, 1963) was a paraphyletic group (Fig. 1C). Schoch's phylogeny was based mostly on dental characters, and he implied a close relationship between chalicotherioids and ceratomorphs. Instead of Tapiromorpha, Schoch used the term Moropomorpha for this group. Some of the points of interest in this phylogeny [in comparison to Hooker (1989)] are: (1) the placement of chalicotherioids as the sister group to other tapiromorphs; (2) the placement of *Isectolophus* as closer to other ceratomorphs than it is to *Homogalax*; (3) the placement of *Heptodon* in a trichotomy with Rhinoceroidea and a clade similar to Hooker's Tapiroidea; and (4) the establishment of *Plesiocolopirus* as a new tapiroid genus. In a subsequent paper (Colbert and Schoch, 1998), Schoch tentatively supported a monophyletic Isectolophidae (sensu Radinsky, 1963) (Fig. 1D). Emry (1989) supported a similar phylogeny (Fig. 1B).

Prothero *et al.* (1989) discussed the evolutionary history of rhinocerotoids. Their discussion was based on the phylogeny of Prothero *et al.* (1986) (Fig. 1E), which has the following interesting points. (1) *Hyrachyus* was placed as the sister taxon to other rhinocerotoids; (2)

FIG. 1. Previous cladistic phylogenies of tapiromorph perissodactyls. (A) Hooker's (1989) phylogeny of Tapiromorpha, including taxa relevant to this study. (B) Emry's (1989) phylogeny of North American "tapiroids" and rhinocerotoids. (C) Schoch's (1989) phylogeny of Moropomorpha (= Tapiromorpha), based on North American taxa. (D) Phylogeny of Moropomorpha (= Tapiromorpha) according to Colbert and Schoch (1998), based on North American taxa. Only taxa relevant to this study are indicated; *Plesiocolopirus*, *Protapirus*, and *Tapirus* are placed by these authors in Tapiridae. (E) Phylogeny of Rhinoceroidea according to Prothero *et al.* (1986), including taxa relevant to this study. (F) Phylogeny of Rhinoceroidea according to Heissig (1989), including taxa relevant to this study.



Amynodontidae was the sister group to a hyracodontid–rhinocerotid clade; (3) Indricotheres, Asian rhinocerotoids including one of the largest land mammals known (*Paraceratherium*), were placed within a monophyletic Hyracodontidae, following Lucas *et al.* (1981; see also Lucas and Sobus, 1989). Radinsky (1966a, 1967a) originally placed the indricotheres in the family Hyracodontidae, although it is doubtful that he actually considered hyracodontids as a monophyletic group. In fact, Radinsky defined Hyracodontidae as all rhinocerotoids lacking the specialized anterior dentitions of Amynodontidae and Rhinocerotidae. Heissig (1989) produced a phylogeny of rhinocerotoids expressing an alternate view, i.e., that the indricotheres are more closely related to rhinocerotids than to any other rhinocerotoid (Fig. 1F).

The most recent classification of tapiromorphs (and mammals in general) is that of McKenna and Bell (1997). Interestingly, they do not follow Hooker's scheme of relationships, but place chalicotherioids and brontotherioids in a new infraorder, Selenida. McKenna and Bell place Selenida, Tapiroidea, and Rhinoceroidea (the latter two groups comprising their Tapiromorpha) in a more inclusive Ceratomorpha. Apart from the taxonomic differences, the main difference between the phylogeny of McKenna and Bell and that of Hooker (1989) is the inclusion of brontotherioids in Tapiromorpha (*sensu* Hooker). Unfortunately, McKenna and Bell provide no character support for this arrangement.

## MATERIALS AND METHODS

### Phylogenetic Analysis

Characters from the dentition, cranium, and postcranial skeleton were scored for ingroup and outgroup taxa (Tables 1 and 3), and the scores were entered into MacClade 3.05 (Maddison and Maddison, 1992). Most parsimonious trees were determined using the Branch and Bound option of PAUP 3.1 (Swofford, 1991). Trees were rooted and character polarity was determined using the outgroup method of Nixon and Carpenter (1993). In this method, both the outgroup and the ingroup taxa are included in the search for the shortest network, and the root of the tree is placed between the outgroups and the ingroup.

TABLE 1  
Ingroup and Outgroup Taxa

Family	Genus
Phenacodontidae	<i>Phenacodus</i>
Brontotheriidae	<i>Eotitanops</i>
Equidae	<i>Hyracotherium</i>
Isectolophidae	<i>Homogalax</i>
	<i>Cardiolphus</i>
	<i>Isectolophus</i>
	<i>Eomoropus</i>
Eomoropidae	<i>Moropus</i>
Chalicotheriidae	<i>Heptodon</i>
	<i>Heleletes</i>
	<i>Plesiocolopirus</i>
	<i>Colodon</i>
Tapiridae	<i>Protapirus</i>
	<i>Tapirus</i>
Lophialetidae	<i>Lophialetes</i>
	<i>Schlosseria</i>
	<i>Deperetella</i>
Deperetellidae	<i>Deperetella</i>
Hyrachyidae	<i>Hyrachyus</i>
Amynodontidae	<i>Amynodon</i>
	<i>Rostriamynodon</i>
	<i>Hyracodon</i>
	<i>Triplopus</i>
Hyracodontidae	<i>Forstercooperia</i>
	<i>Juxia</i>
	<i>Paraceratherium</i>
	<i>Teletaceras</i>
Rhinocerotidae	<i>Trigonias</i>
	<i>Subhyracodon</i>
	<i>Uintaceras</i>
<i>Incertae sedis</i>	

Note. Traditional familial assignments are given for each genus.

*Phenacodus* was designated as an outgroup for purposes of rooting the tree, but *Hyracotherium* and *Eotitanops*, two representative nontapiromorphs, were not designated as outgroups. The positions of *Hyracotherium* and *Eotitanops* provide a reference for determining which taxa are unequivocal members of the Tapiromorpha. In other words, any taxon that is more closely related to *Tapirus* than to *Hyracotherium* and/or *Eotitanops* is an unequivocal tapiromorph. Hooker (1984, 1989, 1994) has demonstrated that species previously assigned to *Hyracotherium* may not constitute a monophyletic group. In fact, the type species of *Hyracotherium*, *H. leporinum*, may be a palaeotheriid, not a basal equid. While they may not be monophyletic, all of the species of "*Hyracotherium*" [with the possible exception of *Cymbalophus cuniculus* (Hooker, 1994)] are considered to be hippomorphs, i.e., they are more closely related to *Equus* than to *Tapirus*. Most of the scores

for *Hyracotherium* in this study were drawn from *H. venticolum*, whose skeleton was described by Kitts (1956).

The ingroup includes a broad sampling of tapiromorph taxa. Any diverse clade whose monophyly is well-supported was represented by two or more “basal” genera. For instance, the monophyly of the Rhinocerotidae is well-supported (Cerdeno, 1995), so three genera (*Teletaceras*, *Trigoniias*, and *Subhyracodon*) were scored to represent this diverse family. Taxa known only from teeth were excluded, since the missing data consequently would greatly impede the analysis. Thus, all of the taxa included in this analysis are known from at least some cranial or postcranial material. Only taxa that had been examined firsthand were included.

Table 2 lists all of the characters used in this study and their various primitive and derived states. The data matrix for the analysis is given in Tables 3, 4, and 5. A more detailed explanation of each character is given below. Unless otherwise stated, multistate characters were treated as unordered. Two characters (C8 and P13) were ordered, because their respective derived states have a hierarchical relationship, i.e., state 2 is a special case of state 1. Cranial and postcranial characters were drawn from Holbrook (1997). A full description of tapiromorph osteology will be published elsewhere.

### Cranial Characters

**C1. Nasals short (1).** The nasals of perissodactyls primitively extend to the point above the anterior tip of the premaxilla or further, as in *Hyracotherium*. Possession of significantly shorter nasals is a derived condition.

**C2. Nasals posteriorly broad (1).** The nasals of most mammals are split- or diamond-shaped, and the posterior portion of the nasals intrudes between the frontals. This is probably the primitive condition for eutherians. The nasals of perissodactyls are unique in having a triangular shape, where the base of the triangle is a suture with the frontal that does not intrude but, instead, runs transversely.

**C3. Lacrimal small and not contacting nasal (1) or large and not contacting nasal (2).** Nasolacrimal contact is

primitive for perissodactyls, as demonstrated by presence of this contact in many tapiromorph and nontapiromorph perissodactyls. This contact is the consequence of the broad posterior portion of the nasals and the prominent facial exposure of the lacrimal. Reduction of the facial exposure of the lacrimal results in loss of nasolacrimal contact, a derived state. The absence of nasolacrimal contact in *Phenacodus* is a fundamentally different condition from that seen in some tapiromorphs, such as *Heptodon*. *Phenacodus* possesses a prominent facial exposure of the lacrimal, but its nasals are very narrow and do not spread posteriorly (as in perissodactyls) to reach the lacrimals. To reflect this fundamental difference, *Phenacodus* is scored as “2” for this character. While the condition in *Phenacodus* may not actually be derived, this score reflects the fact that the condition in this genus is different from that in the other taxa.

**C4. Premaxilla robust and not contacting nasal (1) or small and not contacting nasal (2).** The primitive condition of the premaxilla, seen in many tapiromorphs, nontapiromorph perissodactyls, and nonperissodactyl outgroups, is a relatively small bone with a prominent ascending process that contacts the nasals. In some tapiromorphs, such as tapirids, the premaxilla is robust and does not contact the nasals. Despite the fact that its only contact is with the maxilla, the premaxilla is still a well-developed element in condition “1.” In rhinocerotids, the ascending process of the premaxilla is reduced and does not contact the nasals; the premaxilla of rhinocerotids is generally not well-developed.

**C5. Incisive foramen single and median (1).** The contact between the premaxilla and maxilla on the palate is pierced by one or two incisive foramina. Primitively, a bilateral pair of foramina are present, as in *Hyracotherium*. In some tapiromorphs, a single, median foramen is present.

**C6. Maxillary (preorbital) fossa well-developed pocket (1) or vertical groove (2).** The facial portion of the maxilla primitively possesses a shallow or no fossa of any note, as in *Hyracotherium*. In some rhinocerotoids, a prominent fossa is present. It is difficult to say what actually occupied this fossa in life [although Gregory (1920) argued that it housed a nasal diverticulum], and it is possible that these fossae are not homologous in different rhinocerotoids. In the absence of evidence to

**TABLE 2**  
 Characters Used in This Analysis

Character	Primitive state	Derived state(s)
C1. nasal length	Long	Short (1)
C2. nasal shape	Posteriorly narrow	Posteriorly broad (1)
C3. nasolacrimal contact	Present	Absent (1); absent with large lacrimal (2)
C4. premaxilla	Small, contacts nasals	Robust, no nasal contact (1); small, no nasal contact (2)
C5. incisive foramen	Paired	Single, median (1)
C6. maxillary fossa	Shallow or absent	Well-developed pocket (1); vertical groove (2)
C7. infraorbital foramen	Over premolars	Over molars (1)
C8. narial incision	Over canine or P1	Over P4 or molars (1); retracted and "stepped" (2)
C9. supraorbital foramen	Absent	Present (1)
C10. postglenoid foramen	Present	Absent (1)
C11. postglenoid process	Facing anterior	Facing anterolateral (1)
C12. ant. face of postglen. proc.	Flat or concave and undivided	Convex with median ridge (1)
C13. posttympanic process	Long	Short (1)
C14. postcotyloid process	Absent	Present (1)
P1. acromion process	Present	Absent (1)
P2. deltopectoral crest	Absent or low ridge	Present, hooks laterally (1)
P3. entepicondylar foramen	Present	Absent (1)
P4. capitulum of humerus	Unkeeled	Keeled (1)
P5. lateral process of prox. radius	Present	Weak or absent (1)
P6. scaphoid radial facet	Short lunar contact	Emarginated contact (1); long, straight contact (2)
P7. iliac crest	Convex	Concave (1)
P8. lesser trochanter	Prominent	Weak or absent (1)
P9. femur: med. trochlear ridge	Small, same as lateral	Enlarged (1)
P10. gastrocnemius fossa	Absent	Present (1)
P11. patella	Unflattened	Broad and flattened (1); elongate and flattened (2)
P12. astragalar trochlea	Lined up above neck	Laterally offset (1); overlapping short neck (2)
P13. sustent./dist. calc. facets	Separate	Confluent (1); confluent with ridge (2)
P14. distal ectocuneiform	Posterior process absent	Posterior process present (1)
P15. astragalar head	Not saddle-shaped	Saddle-shaped (1)
P16. pes	Pentadactyl	Tridactyl (1)
D1. upper incisors	Spatulate	Conical (1); buccolingually compressed (2); absent (3)
D2. I1	Present, not chisel-shaped	Chisel-shaped (1)
D3. i2	Present, not lanceolate	Lanceolate (1); absent (2)
D4. postcanine diastema	Short or absent	Long (1)
D5. P1	Present, diastema behind	Present, no diastema behind (1); absent (2)
D6. p1	Present, diastema behind	Present, no diastema behind (1); absent (2)
D7. P cross lophs	Unconnected	Connected into "U"-shape (1)
D8. M parastyles	Large	Small and narrow (1)
D9. M paraconules	Distinct	Indistinct or absent (1)
D10. M metaconules	Distinct	Indistinct or absent (1)
D11. M3 metastyle	Strong, undeflected	Strong, labially deflected (1); lingually deflected (2); absent (3)
D12. m cristid obliqua	Mestolingually directed	Labially positioned
D13. m metastylids	Present	Absent (1)
D14. m3 hypoconulid	Present, large	Small, narrow (1); absent (2)
D15. premetaconule crista	Present	Absent (1)

the contrary, these fossae are considered to be homologous for this study. Some tapiroids possess another type of fossa, a vertical groove anterior to the orbit. In *Tapirus*, these grooves accommodate cartilaginous nasal diverticula.

*C7. Infraorbital foramen positioned over molars (1).* The

infraorbital foramen of most mammals is positioned over the upper premolars, usually P2 or P3, and this position is found in most perissodactyls. The infraorbital foramen of amynodontids is positioned more posteriorly, over the molars and often within the posterior part of the maxillary fossa.

TABLE 3  
Data Matrix for Cranial Characters

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14
<i>Homogalax</i>	0	1	?	?	?	0	?	0	0	?	0	0	?	?
<i>Cardiophus</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	?
<i>Isectolophus</i>	?	1	?	?	?	0	0	?	0	0	1	0	0	?
<i>Eomoropus</i>	?	1	?	?	?	0	0	?	1	?	0	0	1	0
<i>Moropus</i>	0	1	0	?	0	0	0	1	1	?	0	0	1	0
<i>Heptodon</i>	0	1	i	0	0	0	0	0	0	0	1	0	0	0
<i>Heleletes</i>	0	1	1	1	0	2	0	2	0	0	1	0	0	0
<i>Colodon</i>	1	1	1	1	?	2	0	2	0	?	1	0	?	0
<i>Plesiocolopirus</i>	1	1	?	1	1	2	0	2	0	?	1	0	?	0
<i>Protapirus</i>	1	1	1	1	1	2	0	1	0	?	1	0	0	?
<i>Tapirus</i>	1	1	1	1	1	2	0	1	0	1	1	0	0	0
<i>Lophialetes</i>	1	1	?	?	0	?	0	1	0	?	?	?	?	0
<i>Schlosseria</i>	?	1	?	?	?	?	0	?	0	?	?	?	?	0
<i>Deperetella</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Hyrachyus</i>	0	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Rostriamynodon</i>	0	1	0	0	?	1	1	0	0	?	1	1	0	0
<i>Amynodon</i>	0	1	0	0	1	1	1	0	0	1	1	1	0	0
<i>Triplopus</i>	0	1	?	0	0	0	0	0	0	0	1	?	?	0
<i>Hyracodon</i>	0	1	0	0	0	0	0	0	0	0	1	0	0	0
<i>Forstercooperia</i>	0	1	?	0	?	1	0	0	0	?	1	0	0	0
<i>Juxia</i>	0	1	?	0	?	1	0	0	0	?	1	0	0	0
<i>Paraceratherium</i>	0	1	0	1	1	1	0	1	0	1	1	1	0	0
<i>Teletaceras</i>	0	1	0	2	1	0	0	0	0	1	1	1	0	1
<i>Trigonias</i>	0	1	0	2	1	0	0	0	0	1	1	1	0	1
<i>Subhyracodon</i>	0	1	0	2	1	0	0	0	0	1	1	1	0	1
<i>Uintaceras</i>	0	1	0	0	?	0	0	0	0	1	1	1	0	1
<i>Hyracotherium</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eotitanops</i>	0	1	0	0	?	0	0	0	0	0	0	0	0	0
<i>Phenacodus</i>	0	0	2	0	0	0	0	0	0	0	0	0	0	0

Note. The scores for each character assigned to various taxa are listed. Missing entries are indicated by a question mark ("?").

**C8. Posterior edge of narial incision retracted to point over P4 or molars (1) or retracted as in state 1 and postero-ventrally excavated (2).** The narial incision primitively has its posterior border over the first premolar or more anterior. A number of tapiromorphs have a border positioned much more posteriorly. In *Heleletes*, *Colodon*, and *Plesiocolopirus*, the ventral aspect of the posterior border is deep and rounded, giving the impression of a "keyhole" shape. This character was treated as ordered.

**C9. Supraorbital foramen present (1).** The postorbital process of the frontal is primitively unpierced, as in *Hyracotherium* and *Phenacodus*. In *Eomoropus* and *Moropus*, a foramen pierces this process.

**C10. Postglenoid foramen absent (1).** This foramen is present in *Phenacodus*, *Hyracotherium*, and a number of tapiromorphs, and its presence is therefore primitive for perissodactyls.

**C11. Postglenoid process facing anterolateral (1).** The

postglenoid process of the squamosal of *Hyracotherium* and *Phenacodus* is small, peg-like, and faces anteriorly; this is the primitive condition. In a number of tapiromorphs, this process is large, flattened, and obliquely oriented.

**C12. Anterior face of postglenoid process convex with median ridge (1).** The anterior face of the postglenoid process is primitively flat or concave. In some rhinocerotoids, this face has become convex and divided into medial and lateral portions by a ridge.

**C13. Posttympanic process short (1).** In *Hyracotherium* and many tapiromorphs, the posttympanic process of the squamosal is about as long as the postglenoid process. The posttympanic process is significantly shorter in *Eomoropus* and *Moropus*.

**C14. Postcotyloid process of dentary present (1).** Present in rhinocerotids and *Uintaceras*, this process is a buttress on the posterior edge of the ascending ramus



TABLE 4  
Data Matrix for Postcranial Characters

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	P13	P14	P15	P16
<i>Homogalax</i>	?	0	1	1	0	0	1	0	0	?	?	0	0	0	1	1
<i>Cardiolophus</i>	?	?	?	?	?	?	?	?	?	?	?	0	0	?	1	?
<i>Isectolophus</i>	?	?	?	?	0	0	1	0	?	?	?	?	?	?	?	1
<i>Eomoropus</i>	?	?	?	?	?	0	?	0	?	?	?	0	0	0	1	1
<i>Moropus</i>	1	0	1	1	0	0	1	0	0	0	0	2	0	0	1	1
<i>Heptodon</i>	?	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1
<i>Helaletes</i>	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	1
<i>Colodon</i>	?	0	1	1	0	0	1	0	0	1	?	0	0	0	1	1
<i>Plesiocolopirus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Protapirus</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
<i>Tapirus</i>	1	0	1	1	0	1	1	0	0	1	0	0	1	0	1	1
<i>Lophialetes</i>	0	0	1	1	0	0	1	?	0	1	2	0	0	0	1	1
<i>Schlosseria</i>	?	?	1	?	?	0	?	?	?	?	2	0	0	0	1	1
<i>Deperetella</i>	?	?	1	1	1	0	?	?	0	?	2	0	0	0	1	1
<i>Hyrachyus</i>	1	0	1	1	0	0	1	0	0	1	0	1	1	0	1	1
<i>Rostriamynodon</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Amynodon</i>	?	?	1	1	1	2	1	0	0	?	0	1	1	1	1	1
<i>Triplopus</i>	?	0	1	1	0	0	?	0	0	?	0	1	2	0	1	1
<i>Hyracodon</i>	1	0	1	1	0	0	1	0	0	1	0	1	2	0	1	1
<i>Forstercooperia</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Juxia</i>	?	?	?	?	1	0	1	?	?	?	?	0	0	0	1	1
<i>Paraceratherium</i>	1	0	1	1	1	0	1	1	1	0	1	1	?	0	1	1
<i>Teletaceras</i>	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1
<i>Trigonias</i>	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1
<i>Subhyracodon</i>	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1
<i>Uintaceras</i>	1	1	1	1	1	2	?	1	0	?	0	1	1	1	1	1
<i>Hyracotherium</i>	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1
<i>Eotitanops</i>	?	0	1	1	1	0	?	?	0	0	?	0	0	0	1	1
<i>Phenacodus</i>	?	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0

Note. The scores for each character assigned to various taxa are listed. Missing entries are indicated by a question mark ("?").

of the mandible, just below the mandibular condyle. This process is absent in other perissodactyls and non-perissodactyls.

### Postcranial Characters

**P1. Acromion process of scapula absent (1).** A distinct acromion process is present on the scapula of *Hyracotherium* and many nonperissodactyls, including *Phenacodus*, and its presence is considered to be primitive.

**P2. Deltopectoral crest of humerus prominent and hooking laterally (1).** The deltopectoral crest of nontapiromorph perissodactyls and nonperissodactyls is either absent or a low ridge. Both of these conditions are scored as primitive here.

**P3. Entepicondylar foramen of humerus absent (1).** The presence of this foramen is considered to be primitive

for eutherians (Thewissen and Domning, 1992), and it is present in *Phenacodus*.

**P4. Capitulum of humerus keeled (1).** The capitulum is primitively a rounded surface articulating with the radius, as in *Phenacodus*. In perissodactyls, the capitulum is trochleate due to a median ridge or keel.

**P5. Lateral process of proximal radius weak or absent (1).** The radius of *Hyracotherium* shows the primitive condition, where the lateral articular facet for the humerus extends beyond the shaft laterally on a prominent process or tuberosity.

**P6. Radial facet of scaphoid with emarginated lunar contact (1) or long, straight lunar contact (2).** The border of the radial facet of the scaphoid is relatively short in *Hyracotherium* and brontotheres, and this condition is considered to be primitive.

**P7. Anterior iliac crest concave (1).** The anterior crest

TABLE 5  
Data Matrix for Dental Characters.

	D1	D2	D3	D4	D5	D6	D7	D8	D9	D10	D11	D12	D13	D14	D15
<i>Homogalax</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Cardiolophus</i>	0	?	?	0	0	0	0	0	0	0	0	1	0	0	0
<i>Isectolophus</i>	?	?	?	0	1	1	0	0	1	1	0	1	1	0	1
<i>Eomoropus</i>	?	?	?	1	?	2	0	0	0	1	0	0	0	0	1
<i>Moropus</i>	3	0	0	1	2	2	0	0	0	1	0	0	0	2	1
<i>Heptodon</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1
<i>Helaletes</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1
<i>Colodon</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	1	1
<i>Plesiocolopirus</i>	?	?	?	1	1	1	0	0	1	1	0	1	1	1	1
<i>Protapirus</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	2	1
<i>Tapirus</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	2	1
<i>Lophialetes</i>	?	0	0	1	1	1	1	0	1	1	0	1	1	0	1
<i>Schlosseria</i>	?	0	0	1	1	1	1	0	1	1	0	1	1	0	1
<i>Deperetella</i>	?	?	?	1	1	1	0	0	1	1	0	1	1	2	1
<i>Hyrachyus</i>	0	0	0	1	1	1	0	0	1	1	0	1	1	2	1
<i>Rostriamynodon</i>	0	0	0	1	2	2	0	1	1	1	1	1	1	2	1
<i>Amynodon</i>	0	0	0	1	2	2	0	1	1	1	1	1	1	2	1
<i>Triplopus</i>	?	0	0	1	1	1	0	1	1	1	0	1	1	2	1
<i>Hyracodon</i>	1	0	0	1	1	1	0	1	1	1	2	1	1	2	1
<i>Forstercooperia</i>	0	0	0	1	1	1	0	1	1	1	0	1	1	2	1
<i>Juxia</i>	0	0	0	1	1	1	0	1	1	1	3	1	1	2	1
<i>Paraceratherium</i>	1	0	2	1	1	1	0	1	1	1	3	1	1	2	1
<i>Teletaceras</i>	2	1	1	1	1	1	0	1	1	1	0	1	1	2	1
<i>Trigonias</i>	2	1	1	1	1	1	0	1	1	1	3	1	1	2	1
<i>Subhyracodon</i>	2	1	1	1	1	1	0	1	1	1	3	1	1	2	1
<i>Uintaceras</i>	2	?	?	1	1	1	0	1	1	1	0	1	1	2	1
<i>Hyracotherium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Eotitanops</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
<i>Phenacodus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Note. The scores for each character assigned to various taxa are listed. Missing entries are indicated by a question mark ("?").

of the ilium is primitively convex, as in *Phenacodus* and many other eutherians.

P8. Lesser trochanter of femur weak or absent (1). The lesser trochanter of *Phenacodus* and *Hyracotherium* is present as a prominent flange.

P9. Medial trochlear ridge of femur expanded into tuberosity (1). The medial and lateral trochlear ridges are primitively about equal in size, as in *Phenacodus* and *Hyracotherium*.

P10. Gastrocnemius (supracondylar) fossa of femur present (1). A distinct fossa for attachment of the gastrocnemius is not present above the lateral condyle on the posterior side of the femur in *Phenacodus*, *Hyracotherium*, and brontotheres.

P11. Patella broad and flattened (1) or elongate and flattened (2). Primitively, the patella is teardrop-shaped and anteroposteriorly thick, as in *Hyracotherium* and *Phenacodus*.

P12. Trochlea of astragalus laterally offset from neck (1) or overlapping onto short neck (2). The trochlea of equids and primitive brontotheres like *Eotitanops* lies more or less directly above a distinct neck of the astragalus.

P13. Sustentacular and distal calcaneal facets of astragalus confluent (1) or confluent with a ridge formed at their junction (2). These facets are separate in nontapiromorph perissodactyls. Since state 2 is simply a special case of state 1, this character was treated as ordered.

P14. Process on posterodistal aspect of ectocuneiform present (1). The distal facet of the ectocuneiform in nontapiromorph perissodactyls is flat with no processes.

P15. Navicular facet of astragalus saddle-shaped (1). The astragalar head (navicular facet) of non perissodactyls is not saddle-shaped. In *Phenacodus*, this facet is rounded for a ball-and-socket joint.

*P16. Pes tridactyl (1).* Five digits on the pes is primitive for eutherians and is seen in *Phenacodus*.

### Dental Characters

The terminology used for dental morphology here is described by Hooker (1989, 1994). Selection of dental characters was based on a critical evaluation of characters used by previous studies, in particular those of Hooker (1984, 1989, 1994). The following dental characters are included in this analysis, with the derived condition(s) described first:

*D1. Upper incisors conical (1), buccolingually compressed (2), or absent (3).* Spatulate upper and lower incisors are found in all outgroup taxa and many tapiromorphs, and this condition is scored as (0). The presence of conical incisors has been used as a synapomorphy of hyracodontids (sensu Radinsky, 1966a, 1967a; Lucas *et al.*, 1981; Prothero *et al.*, 1986), although the primitive condition is seen in some hyracodontid taxa, and the lower incisors of *Uintaceras* may be conical. *Uintaceras* and rhinocerotids both possess buccolingually compressed upper incisors.

*D2 and D3. I1 chisel-shaped (1) (char. D2); i2 lanceolate (1) or absent (2) (char. D3).* State 1 for both of these characters is characteristic of rhinocerotids (Radinsky, 1966a). The primitive condition is both incisors spatulate or conical. Conical incisors are actually derived, but that fact is accounted for in character D1.

*D4. Postcanine diastema long (1).* Primitively, the diastema between the canine and first premolar is short, as in *Phenacodus* and *Hyracotherium*, or absent, as in *Eotitanops* and *Isectolophus*. In a number of derived tapiromorphs, the diastema is clearly elongated and not just because of the repositioning or loss of the first premolar (see characters 4 and 5).

*D5 and D6. P1 (char. D4) and p1 (char. D5) abutting P2/p2 (1) or absent (2).* In *Phenacodus* and *Hyracotherium*, there is a short diastema between the first and the second premolars. In many tapiromorphs, this diastema has become closed, so that there are no spaces between the seven cheek teeth or, in others, one or both of the first premolars may be lost.

*D7. Upper premolar cross lophs connected into "U"-shape (1).* This feature is characteristic of lophialetids (Radinsky, 1965b). Primitively, the cross lophs of the upper premolars are separate or else connect at the protocone in a "V"-shape.

*D8. Upper molar parastyles small and narrow (1).* Primitively, the parastyle is large and shaped like a lozenge. Radinsky (1967b) used the derived condition of this character to distinguish rhinocerotoids from other ceratomorphs, including *Hyrachyus*.

*D9 and D10. Upper molar paraconules (char. D8) and metaconules (char. D9) indistinct or absent (1).* The "loss" of the paraconules and metaconules is one of the last steps in the acquisition of bilophodont upper molars. These cusps are present as bumps or swellings on the protoloph and metaloph of less lophodont (and therefore primitive) forms.

*D11. M3 metastyle labially deflected (1), lingually deflected (2), or absent (3).* The morphology of the M3 metastyle has been used to distinguish different families of rhinocerotoids (Wood, 1927), although there may be considerable variation of this character within genera (e.g., Hanson, 1989). It is, however, possible to characterize all of the taxa in this analysis according to the conditions described here. The first two derived states can be ascertained by referring to the primitive condition, which is seen in many tapiromorphs, including *Hyrachyus*.

*D12. Lower molar cristid obliqua (metalophid) labially positioned (1).* In all nonperissodactyl outgroups, as well as all brontotheres and equoids, the metalophid is an oblique, mesiolingually directed crest. This condition is primitive and has been used by Wood (1934) to characterize the Hippomorpha. Wood characterized the Ceratomorpha as having a labially positioned metalophid, running longitudinally.

*D13. Lower molar metastylid absent (1).* A lower molar metastylid [or "twinning metaconid" of Hooker (1994)] is found in nonperissodactyl outgroups, as well as many nontapiromorph perissodactyls; thus, the presence of this cusp is considered to be primitive.

*D14. m3 hypoconulid small and narrow (1) or absent (2).* A prominent hypoconulid is present on the m3 of *Hyracotherium* and other nontapiromorphs.

*D15. Upper molar premetaconule crista/lower molar lingual postcristid absent (1).* This complex was treated by Hooker as two derived characters: (1) upper molar premetaconule crista and lower molar postcristid lingual branch absent and (2) upper molar metaloph and lower molar hypolophid present (Hooker, 1989, Table 6.1, characters 44 and 45). According to Hooker, these two changes represent a fundamental reorientation of

the metaloph. These characters were described as unequivocal synapomorphies of the Tapiromorpha, but Hooker's data matrix lists a number of nontapiromorph taxa as possessing the derived condition of both of these characters, including all of the members of the Palaeotheriidae. Four species assigned to *Hyracotherium*, including the type of the genus, *H. leporinum*, are listed by Hooker as having lost the premetaconule crista. In my own investigations, the only aspect of this character complex that can be reliably scored is the presence or absence of the premetaconule crista. The molars of *Cardiolphus* appear to possess a premetaconule crista and possibly a lingual postcrisid branch (Gingerich, 1991, Figs. 9A and 11B). Interestingly, Hooker (1994), in his analysis of early equoid interrelationships, treated presence of the premetaconule crista as derived and scored it as present in *Cardiolphus*, the only putative tapiromorph included in that analysis. This character was scored according to Hooker (1989, 1994).

## RESULTS

The analysis yielded 576 most parsimonious trees each with a length of 85 steps, a consistency index (CI) of 0.65, and a retention index (RI) of 0.84, excluding uninformative characters. If the six characters uniting perissodactyls are included in the calculation, the length is 91 and the CI is 0.67. Majority Rule and Adams consensus are given in Fig. 3 for heuristic purposes, but the strict consensus (Fig. 2) is used here for the main phylogenetic conclusions. The strict consensus (Fig. 2) shows a basal polytomy of *Eotitanops*, *Hyracotherium*, *Homogalax*, *Cardiolphus*, a chalicothere clade, and a clade including *Isectolophus*, a monophyletic grouping of tapiroids, and Rhinoceroidea. This is not a result that supports Hooker's concept of Tapiromorpha, because chalicotherioids, *Homogalax*, and *Cardiolphus* are not demonstrated to be more closely related to *Tapirus* than to *Hyracotherium*. This result also does not support Hooker's (1994) representation of Tapiromorpha with *Cardiolphus*. Majority rule (50%) and Adams consensus trees (Fig. 3) give results similar to those of the strict consensus, the main differences being the resolution of the relationships of certain rhinocerotoids.

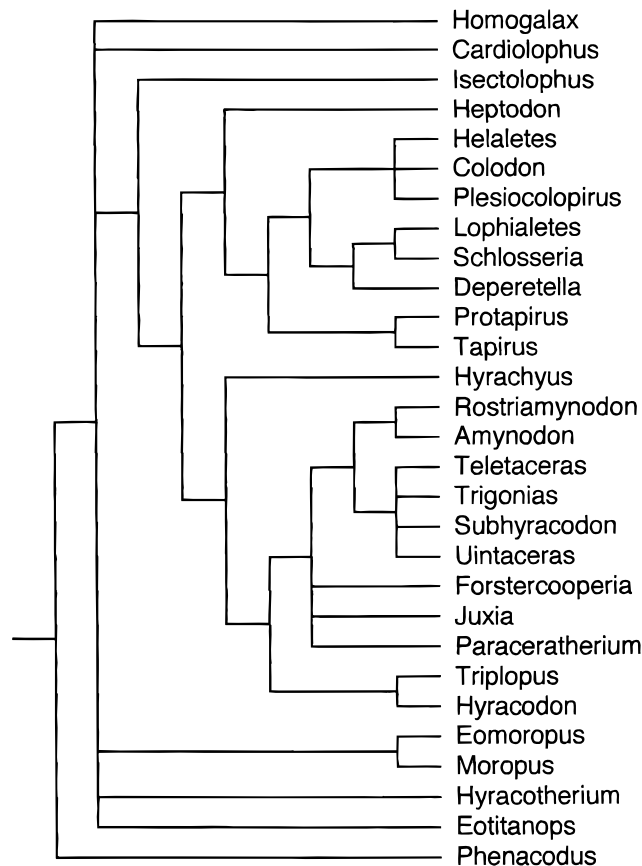


FIG. 2. Strict consensus cladogram of 576 trees generated by PAUP. Shared derived characters for each node are discussed in the text.

The monophyly of Chalicotherioidea is indicated by the presence of a clade including *Eomoropus* and *Moropus*.

The paraphyly of the "Isectolophidae" is indicated here, since *Isectolophus*, *Cardiolphus*, and *Homogalax* do not form a monophyletic group. This result supports the hypothesis of Schoch (1989) and provides evidence that Hooker (1989) was not justified in constraining his own results so that *Homogalax* and *Isectolophus* would form a monophyletic group.

This result also supports the monophyly of each of the clades that can be termed Tapiroidea and Rhinoceroidea. The main difference between this result and other hypotheses is that *Heptodon* is a basal tapiroid. Most other hypotheses (e.g., Hooker, 1989; Schoch, 1989) placed *Heptodon* outside of a monophyletic tapiroid clade. One recent analysis of new perissodactyls from Mongolia (Dasheveg and Hooker, 1997) also places *Heptodon* within Tapiroidea (sensu stricto).

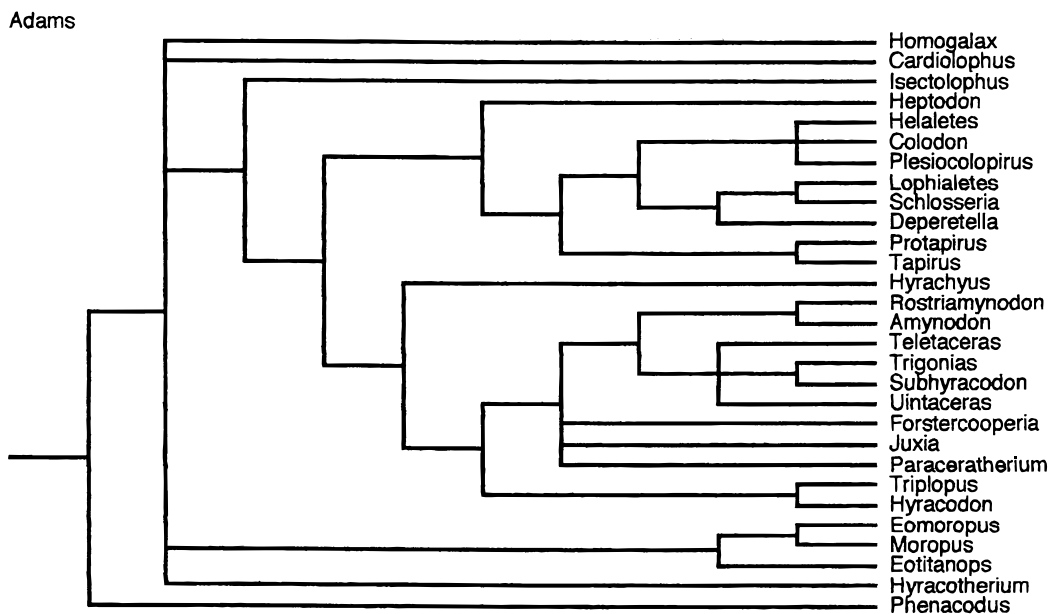
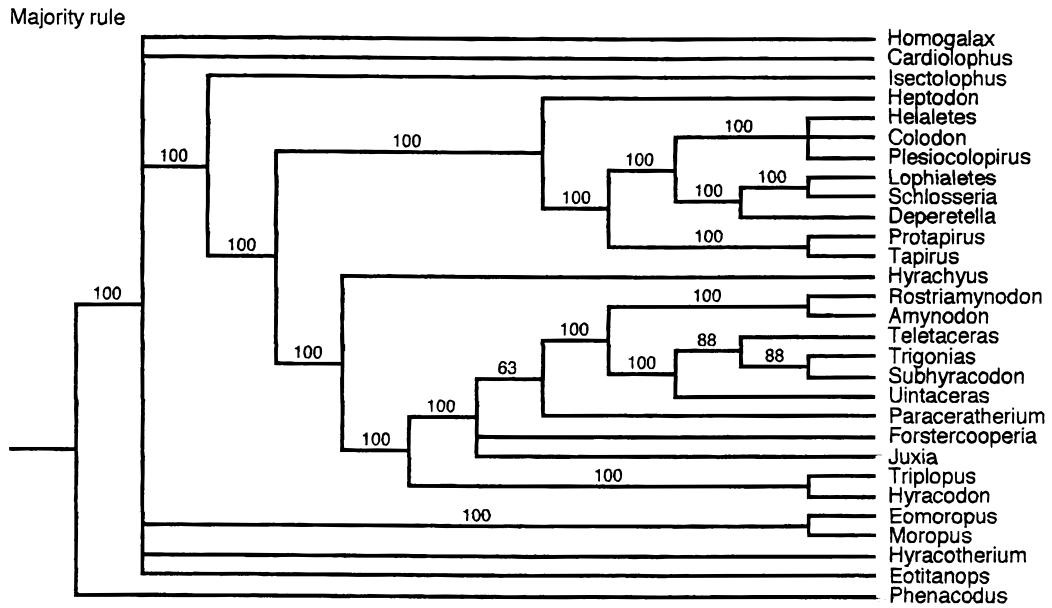


FIG. 3. (a) Majority rule (50%) and (b) Adams' consensus cladogram of 576 trees generated by PAUP.

The interrelationships of rhinocerotoids suggested by these results are different from those hypothesized by others (e.g., Lucas *et al.*, 1981; Lucas and Sobus, 1989;

Prothero *et al.*, 1986). Previous studies (e.g., Prothero *et al.*, 1986) claimed that hyracodontids are more closely related to rhinocerotids than are amynodontids.

These studies also placed indricotheres (*Forstercooperia*, *Juxia*, and *Paraceratherium* in this analysis) within the Hyracodontidae. The results of this analysis place amynodontids as the sister group to rhinocerotids. The results provide no support for indricothere monophyly, but they do place all three indricothere genera outside of the hyracodontid clade and closer to the amynodontid/rhinocerotid clade. *Uintaceras*, as suggested by Holbrook and Lucas (1997), is united with rhinocerotids.

## DISCUSSION

The relatively low ratio of characters to taxa means that most nodes are supported by no more than a few unequivocal synapomorphies. The high retention index (0.84), however, indicates that even homoplastic characters are providing support for many nodes. In this section, the unequivocal synapomorphies for different groups will be discussed, and in some cases characters supporting a node but showing some homoplasy will also be discussed. Character state changes were examined on each of the shortest trees to ensure that unequivocal support for a given node was present in all shortest trees. The “show all most parsimonious reconstructions” resolving option for MacClade was used to identify unequivocal and equivocal character state reconstructions for different nodes.

This study was unable to come up with an unequivocal synapomorphy for the Tapiromorpha sensu Hooker. The lack of resolution at the base of the consensus tree does not preclude the existence of such a clade; the data simply could not provide any more support for that topology than it could for others. Using a phylogenetic definition (discussed later), we can, however, identify a clade of unequivocal tapiromorphs, including *Isectolophus* and Ceratomorpha (Tapiroidea and Rhinoceroidea). Tapiromorpha can be diagnosed by the following unequivocal synapomorphies: oblique orientation of the postglenoid process (C11[1]), loss of the diastema posterior to the upper first premolar (D5[1]), submerging of the paraconule into the proto-loph (D9[1]), and the loss of the metastylid (D13[1]). Ceratomorpha is diagnosed by the loss or reduction of the m3 hypoconulid (D14[1/2]). The m3 hypoconulid reduction is not an unequivocal synapomorphy for

Ceratomorpha here, because it is also lost in *Moropus*, but it is likely that this loss occurred within the Chalicotheriidae (Coombs, 1989).

The chalicotherioid clade (*Eomoropus* and *Moropus*) is supported unequivocally by a cranial character, the presence of a supraorbital foramen (C13[1]). This character may not prove to be a good synapomorphy, since this foramen is absent in some chalicotherioids [e.g., *Chalicotherium* (Zapfe, 1979)]. Another character, the short posttympanic process (C9[1]), also supports chalicotherioid monophyly, but the uncertainty of the condition of this character for *Homogalax* makes this support equivocal.

The tapiroid clade is supported by one unequivocal synapomorphy, the loss of nasolacrimal contact (C3[1]). Exclusive of *Heptodon*, other tapiroids form a clade supported unequivocally by a maxillary fossa forming a vertical groove (C6[2]), and a robust premaxilla not contacting the nasals (C4[1]) is an equivocal synapomorphy of this group paralleled only in *Paraceratherium*. Within this clade, the Tapiridae is supported unequivocally by the “embracing” contact between the scaphoid and lunar (P6[1]), and two characters that also appear in other clades, loss of the hypoconulid of m3 (D14[2]) and presence of a single incisive foramen (C5[1]). The sister group of the Tapiridae is another pair of tapiroid clades, one representing the endemic Asian tapiroids (Lophialetidae and Deperetellidae) and a monophyletic Helaletidae. The helaletids, *Helaletes*, *Colodon*, and *Plesiocolopirus*, are united by their posteroventrally expanded narial incision (C8[2]).

The lophialetids are united by the U-shaped loop formed by the premolar cross lophs (D7[1]), and they are united to the Deperetellidae by an elongated, flattened patella (P11[2]). Because other lophialetid and deperetellid taxa are so poorly known, the apparent relationship between the Asian tapiroids and the North American tapiroids is tenuous. The Asian tapiroids are united to the helaletids by a reversal to the primitive state, namely the reacquisition of an acromion process (P1[0]). *Lophialetes*, the best known of the Asian genera, is the only endemic Asian genus for whom this character has been scored. Until more data are available for *Schlosseria* and *Deperetella*, the position of the endemic Asian tapiroids should be taken as provisional.

One character supports Rhinoceroidea without parallelism, the “offset” position of the trochlea of the

astragalus (P12[1]). The presence of the primitive condition in *Juxia* weakens this support slightly, but in all shortest trees *Juxia* is nested within Rhinoceroidea, and *Juxia*'s condition is reconstructed as a reversal. Two other characters equivocally support Rhinoceroidea: confluence of the sustentacular and distal calcaneal facets of the astragalus (P13[1]) and the absence of the m3 hypoconulid (D14[2]). Other rhinocerotoids are distinguished from *Hyrachyus* by the presence of narrow parastyles on the upper molars (D8[1]). *Hyracodon* and *Triplopus* are united by the presence of a ridge at the confluence of the sustentacular and distal calcaneal facets of the astragalus (P13[2]). Amynodontids (*Rostriamynodon* and *Amynodon*) are united by the placement of the infraorbital foramen over the molars (C7[1]) and a labially displaced M3 metastyle (D11[1]).

No unequivocal synapomorphy supports the close relationship of amynodontids, indricotheres, *Uintaceras*, and rhinocerotids. This clade is supported by one character also seen in other clades, the reduction of the lateral tuberosity of the proximal radius (P5[1]) (also seen in *Eotitanops* and *Deperetella*). The presence or absence of the postglenoid foramen (C10) is not known for *Juxia* and *Forstercooperia*, but the absence of this foramen in these taxa would provide additional (though not unequivocal) support for uniting indricotheres, amynodontids, *Uintaceras*, and rhinocerotids. Amynodontids are united to rhinocerotids by one unequivocal synapomorphy, the elongated lunar contact on the radial facet of the scaphoid (P6[2]). The presence of a posterodistal process on the ectocuneiform (P14[1]) may also be a synapomorphy for this clade, or it could unite this clade with *Forstercooperia*, depending on the condition of this character present in the latter.

The failure of this analysis to find support for indricothere monophyly is not too surprising, because the one synapomorphy that had been used previously to unite these taxa, the presence of a deep preorbital fossa (C6[1]), was scored as present in amynodontids. It is possible that the morphologies observed in the skulls of indricotheres and amynodontids are distinct and should be scored differently, but an anatomical argument for or against this idea is beyond the scope of this paper.

*Uintaceras* is united to rhinocerotids unequivocally by the presence of a postcotyloid process of the mandible (C14[1]) and buccolingually compressed upper incisors (D1[2]). A prominent deltopectoral crest (P2[1]) is

an equivocal synapomorphy for this group, because of the uncertainty of the condition in amynodontids included in this analysis. Other amynodontids possess the primitive condition, so it is likely that this character will turn out to be an unequivocal synapomorphy for rhinocerotids and *Uintaceras*.

### ***Tapiromorph Classification***

A revised classification of Hooker's (1984, 1989) Tapiromorpha is given in Table 6, in terms of the taxa analyzed here, and as interpreted from the analysis described above. In general, the classification is the most conservative interpretation of the strict consensus cladogram.

In the past decade or so, a number of papers have dealt with the topic of phylogenetic taxonomy (e.g., Rowe, 1987; de Queiroz and Gauthier, 1990; Lucas, 1992). The most controversial idea from this discussion is the emphasis on relationship-based definitions of groups over trait-based definitions (de Queiroz and Gauthier, 1990). A lengthy discussion of this controversy is beyond the scope of this paper, but relationship-based definitions (including node-based and stem-based definitions) are useful for discussing perissodactyl classification. Most of the suprafamilial taxon names for perissodactyls were established to represent relationship to a particular family or subfamilial taxon. For instance, Rhinoceroidea is a group of organisms related to the genus *Rhinoceros* that is more inclusive than Rhinocerotidae. Relationship-based definitions can be applied to such groups with little difficulty and help to eliminate ambiguity about what is and what is not part of a particular taxon. For the purposes of explicitly outlining the basis for the classification given in Table 6, I have detailed the definitions of various groups below.

Some of these definitions mention Lophiodontidae, a group not included in this study. Lophiodontid material was not available for analysis, but future studies will include this group and provide a test of the phylogenetic hypotheses presented here.

**All families.** Because each family is based on a type genus, each family can be provided a stem-based definition, i.e., the type genus and all genera which are more closely related to it than to any other type genus. *Heptodon* is clearly not allied with any type genus and should be given its own family, which is established

**TABLE 6**  
Classification of Perissodactyls Included in This Analysis (Based on Fig. 2)

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Order Perissodactyla
Suborder Tapiromorpha
Infraorder Ceratomorpha
Superfamily Tapiroidea
Family Heptodontidae
<i>Heptodon</i>
Unnamed taxon
Family Helaletidae
<i>Helaletes</i>
<i>Colodon</i>
<i>Plesiocolopirus</i>
Family Tapiridae
<i>Protapirus</i>
<i>Tapirus</i>
Family Lophialetidae
<i>Lophialetes</i>
<i>Schlosseria</i>
Family Deperetellidae
<i>Deperetella</i>
Superfamily Rhinoceroidea
Family Hyrachyidae
<i>Hyrachyus</i>
Unnamed taxon
Family Hyracodontidae
<i>Hyracodon</i>
<i>Triplopus</i>
Unnamed taxon
Family Indricotheriidae
<i>Paraceratherium</i>
Family Amynodontidae
<i>Rostriamynodon</i>
<i>Amynodon</i>
Family Rhinocerotidae
<i>Uintaceras</i>
<i>Teletaceras</i>
<i>Trigonias</i>
<i>Subhyracodon</i>
Family uncertain
<i>Forstercooperia</i>
<i>Juxia</i>
Unnamed infraorder
Family Isectolophidae
<i>Isectolophus</i>
Suborder uncertain
Family uncertain
<i>Homogalax</i>
<i>Cardiolphus</i>
Superfamily Chalicotherioidea
Family Eomoropidae
<i>Eomoropus</i>
Family Chalicotheriidae
<i>Moropus</i>

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below. The relationships among nontapiromorphs need to be examined more fully before *Homogalax* and *Cardiolphus* can be assigned to a family. Isectolophidae is restricted here to *Isectolophus*. The lack of resolution for indricothere relationships makes their placement in a family uncertain. *Uintaceras* should be included in Rhinocerotidae. Other family assignments suggested by the results are consistent with previous taxonomic ideas.

**Tapiroidea.** Gill (1872) first erected this superfamily, but Radinsky (1963) is generally credited with providing the definition that was used until recently. Tapiroidea, sensu Radinsky, was a paraphyletic taxon that included the ancestors of both the living tapirs and the Rhinoceroidea. Hooker (1989) restricted Tapiroidea to a monophyletic group including the Tapiridae and some "helaletids." Colbert and Schoch (1998) followed a similar approach. The essence of this usage of the term is that the Tapiroidea is the lineage that split off from the common ancestor of tapirs and rhinoceroses and gave rise to the Tapiridae. For the purposes of this study, the Tapiroidea is defined as including the family Tapiridae and all taxa more closely related to the Tapiridae than to the Rhinocerotidae and Chalicotheriidae. Helaletidae, Lophialetidae, Deperetellidae, and Tapiridae are included in the Tapiroidea.

**Rhinoceroidea.** This term comes from Owen (1845). Radinsky (1966a, 1967b) considered this group to be possibly polyphyletic, but recent studies (Prothero *et al.*, 1986; Emry, 1989) have proposed a monophyletic Rhinoceroidea. In this study, Rhinoceroidea is defined as the taxon including the Rhinocerotidae and all taxa more closely related to Rhinocerotidae than to the Tapiridae, Chalicotheriidae, and Lophiodontidae. Hyrachyidae, Hyracodontidae, Amynodontidae, Rhinocerotidae, and the indricotheres are included in Rhinoceroidea.

**Chalicotherioidea.** This is another Gill (1872) superfamily. It is defined here as including the Chalicotheriidae and those taxa more closely related to the Chalicotheriidae than to the Lophiodontidae, Tapiridae, and Rhinocerotidae.

**Ceratomorpha.** The term Ceratomorpha (Wood, 1937) has generally been used to describe a close relationship between tapirs and rhinoceroses and has been used by recent workers (e.g., Hooker, 1989; Colbert and Schoch, 1998) in a somewhat restricted sense, which is followed here. Ceratomorpha is defined here as the



taxon including the most recent common ancestor of Rhinoceroidea and Tapiroidea and all of its descendants. McKenna and Bell (1997) define Ceratomorpha in a much more inclusive way, essentially similar to Tapiromorpha (sensu Hooker; see below), which is not adopted here.

**Ancylopoda.** This taxon was originally proposed by Cope (1889) as a separate order for the chalicotheres. Scott (1941) made this taxon a suborder of perissodactyls, and Radinsky (1964) treated the Hippomorpha, Ceratomorpha, and Ancylopoda as the basic tripartite division of Perissodactyla. Hooker (1989) emended Radinsky's definition of Ancylopoda to include Chalicotherioidea and Lophiodontidae. This last usage is essentially followed here: Ancylopoda is defined as the most recent common ancestor of Chalicotherioidea and Lophiodontidae and all of its descendants, but excluding Tapiridae and Rhinocerotidae. Since lophiodontids were not available for inclusion in this study, Ancylopoda will not be discussed beyond providing its definition.

**Tapiromorpha and Moropomorpha.** The term Tapiromorpha was first coined by Haeckel (1873) and has recently been resurrected by Hooker (1984, 1989, 1994) to describe a clade including Rhinoceroidea, Tapiroidea (in a restricted, monophyletic sense), Ancylopoda (Chalicotherioidea and Lophiodontidae), and Isectolophidae. A similar concept has been termed Moropomorpha by Schoch (1989), essentially to describe a special relationship between chalicotheres and ceratomorphs. Schoch (1989) argued that his new term was preferable, because it would not be confused with the various uses of Tapiromorpha, by Haeckel himself and by others (e.g., Simpson, 1945).

Tapiromorpha is used in this study rather than Moropomorpha. The reason has to do with its definition in this study, which is subtly different from that of Hooker (1989). Hooker, like Schoch (1989), was attempting to show the close relationship between chalicotheres and traditional ceratomorphs (i.e., Lophiodontidae, Rhinoceroidea, Tapiroidea, and Isectolophidae). Hooker's cladogram describes a fundamental trichotomy in perissodactyl phylogeny between the Hippomorpha (equids and their relations), Titanotheriomorpha (brontotheres, including *Lambdaotherium*), and Tapiromorpha.

If we think of this arrangement in terms of the living taxa (only because they are most familiar), we can

distinguish between horse-like and tapir-like (or rhinoceros-like) taxa. This study analyzes the relationships of the tapir-like taxa. Thus, Tapiromorpha is defined here as including the Tapiroidea and all taxa more closely related to the Tapiroidea than to the Equoidea (horses, etc.) or Titanotheriomorpha (i.e., brontotheres). Note that this definition does not require that chalicotheres are tapiromorphs; indeed, one aim of this study is to test the evidence for chalicotheres/ceratomorph affinities.

McKenna and Bell (1997) use the term Tapiromorpha in a way that is more similar to the definition of Ceratomorpha in this paper. For the sake of consistency with other work on this group (Hooker, 1989; Colbert and Schoch, 1998), the terminology of McKenna and Bell (1997) will not be adopted here.

Because chalicotheres cannot be included in the Tapiromorpha as defined here, Schoch's (1989) Moropomorpha is not a sensible alternative as a name. Using the definition of Tapiromorpha given above, the results support the inclusion of *Isectolophus* and Ceratomorpha in Tapiromorpha.

#### Systematic Paleontology

Order Perissodactyla Owen, 1848  
 Suborder Ceratomorpha Wood, 1937  
 Superfamily Tapiroidea Gill, 1872  
 Family Heptodontidae nov.

Type genus: *Heptodon*.

Included genera: type only.

Diagnosis: Tapiroids with primitive skull, narial incision unretracted, nasolacrimal contact absent, postglenoid process obliquely oriented, dental formula I 3/3, C 1/1, P 4/4, M 3/3, postcanine diastema present, no diastema between first and second premolars, premolars not molariform, upper molars lophodont without visible conules, lower molars with transverse lophs, hypoconulid of third lower molar present but narrow, manus tetradactyl.

#### *Tapiromorpha and Perissodactyl Phylogeny and Evolution*

This study is part of an ongoing program of investigations into perissodactyl phylogeny. The focus of much of the previous work on perissodactyl origins has been on horses, particularly the putative ancestral

equid (or ancestral perissodactyl for some) *Hyracotherium*, the oldest well-known perissodactyl. Recent discoveries have suggested that the ancestral perissodactyl may have been more like a tapiromorph. Gingerich (1991) described *Cardiolphus* from the early Wasatchian of North America, and Ting (1993) described *Orientalophus* from the early Eocene of China, both of which are more lophodont (and hence more tapiromorph-like) than *Hyracotherium* yet about as old. Rose (1996) has described features in the skeleton of *Homogalax* (long thought to be a basal tapiroid) that are more primitive than those found in the skeleton of *Hyracotherium*.

These finds are consistent with Hooker's (1989) assertion that a more lophodont dentition than that characteristic of *Hyracotherium* may be primitive for perissodactyls. They also suggest that putative tapiromorphs may hold important clues about perissodactyl origins. The results of this study suggest that the evidence for allying *Homogalax* and *Cardiolphus* with the tapiromorph lineage is lacking and that these primitive perissodactyls should be given due consideration, along with other early forms like *Hyracotherium*, when discussing perissodactyl ancestry.

Although the results do not unequivocally ally *Homogalax* and *Cardiolphus* with a major lineage, they do suggest that at least one of the two extant tapiromorph lineages can be traced back to the Wasatchian. The Wasatchian genus *Heptodon* is the earliest known member of the Tapiroidea, indicating that the ancestry of *Tapirus* can be traced back to the early Eocene before it shares an ancestor with another extant lineage. Because, according to the results, the tapiroid and rhinocerotoid lineages split before the occurrence of *Heptodon*, the unique ancestry of rhinocerotoids should also extend into the Wasatchian. Thus, the results suggest that perissodactyls had radiated into a number of lineages, including the extant lineages, by the late Wasatchian (early Eocene). This differs somewhat from Radinsky's (1969) hypothesis of three early Wasatchian lineages (equoid, tapiroid, and chalicotherioid) giving rise to radiations occurring later in the Eocene than is suggested here.

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