Cladistic Analysis of the Family Rhinocerotidae (Perissodactyla)

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ABSTRACT

A cladistic analysis of the family Rhinocerotidae encompassing 45 taxa and 72 characters (referred to craniomandibular [20], dental [26], and postcranial [26] features), and using *Hyrachyus* and two subfamilies of Hyracodontidae as outgroups, discovered 104 equally parsimonious cladograms. When the analysis was run with *Hyrachyus* as the only outgroup (removing the hyracodontid subfamilies), only six equally parsimonious trees were discovered. The discovered trees of the two analyses are compared, which suggests a reinterpretation of the phylogenetic relationships within the Rhinocerotidae. The subfamilies Diceratheriinae and Menoceratinae are not supported, as the genera included within them appear as a paraphyletic group. Phylogenies of the subfamilies Rhinocer-

otinae and Aceratheriinae are questioned. Within the former, the elasmotheriines are separated into two groups: a new subtribe, Iranotheriina, is proposed, while *Elasmotherium* and *Ninxiatherium* appear more closely related to *Stephanorhinus* and *Coelodonta*. The content of the subtribe Rhinocerotina is revised. The tribe Teleoceratini is removed from the Rhinocerotinae and included within the subfamily Aceratheriinae. A new aceratherine tribe, Alicornopini, is proposed for *Alicornops, Peraceras,* and *Chilotheridium*. The analysis indirectly supports some synonymies previously suggested, such as "*Begertherium*" = *Hispanotherium,* and "*Dicerorhinus*" *schleiermacheri* = *Lartetotherium schleiermacheri.*

INTRODUCTION

The investigation of fossil rhinocerotids has long been considered a difficult task because of their great intraspecific variation, as well as the general homogeneity of the group at a higher taxonomic level. Unlike the body of data on other groups of perissodactyls (e.g., horses), investigations of fossil rhinoceroses are relatively scarce, at least at the family level. Some of the most recent monographic works on rhinos are those of Guérin (1980),

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TABLE 1
Genera and species of Hyracodontidae and Rhinocerotidae Studied, Geographical Distribution
AF = Africa; AS = Asia; EU = Europe; NA = North America.

HYRACODONTIDAE		*S. kirchbergensis*	EU
Hyracodon Leidy, 1856		*Coelodonta* Bronn, 1831	
H. nebraskensis	NA	*C. antiquitatis*	EU/AS
H. leydianus	NA	*Hispanotherium* Crusafont & Villalta, 1947	
Ardynia Matthew & Granger, 1923		*H. matritense*	EU/AS
A. praecox	AS	"*Begertherium*" Beliajeva, 1971	
A. kazachstanensis	AS	"*B.*" *grimmi*	AS
Prohyracodon Koch, 1897		"*Beliajevina*" Heissig, 1974	
P. meridionale	AS	"*B.*" *tekkayai*	AS
P. orientale	EU	*Iranotherium* Ringstrom, 1924	
Eggysodon Roman, 1911		*I. mongoliense*	AS
E. osborni	EU	*I.* cf. *longirhinus*	AS
		Elasmotherium Fischer, 1808	
RHINOCEROTIDAE		*E. shansiense*	AS
Ronzotherium Aymard, 1886		*E. lagreli*	AS
R. filholi	EU	*Gaindatherium* Colbert, 1934	
Protaceratherium Abel, 1910		*G. browni*	AS
P. albigense	EU	*G. vidali*	AS
P. minutum	EU	*Ceratotherium* Gray, 1867	
P. platyodon	EU	*C. neumayri*	EU
P. fahlbuschi	EU	*C. simun*	AF
P. mirallesi	EU	*Subhyracodon* Brandt, 1878	
Pleuroceros Roger, 1898		*S. occidentalis*	NA
P. pleuroceros	EU	*S. mitis*	NA
Diaceratherium Dietrich, 1931		*S. tridactylum*	NA
D. lemanense	EU	*Diceratherium* Marsh, 1875	
D. aurelianense	EU	*D. armatum*	NA
Brachypotherium Roger, 1904		*D. niobrarense*	NA
B. brachypus	EU	*D. annectens*	NA
Prosantorhinus Heissig, 1974		*Penetrigonias* Tanner & Martin, 1976	
P. germanicus	EU	*P. hudsoni*	NA
P. douvillei	EU	*P. dakotensis*	NA
Alicornops Ginsburg & Guérin, 1979		*Trigonias* Lucas, 1900	
A. simorrense	EU	*T. osborni*	NA
A. alfambrense	EU	*T. wellsi*	NA
Hoploaceratherium Ginsburg & Heissig, 1989		*Amphycaenopus* Wood, 1927	
H. tetradactylum	EU	*A. platycephalus*	NA
Aceratherium Kaup, 1932		*Menoceras* Troxell, 1921	
A. incisivum	EU	*M. arikarense*	NA
"*Mesaceratherium*" Heissig, 1969		*Floridaceras* Wood, 1966	
"*M.*" *gaimersheimensis*	EU	*F. whitei*	NA
Lartetotherium Ginsburg, 1974		"F:AM 95544" Prothero (in press)	NA
L. sansaniensis	EU	*Peraceras* Cope, 1880	
Dicerorhinus Gloger, 1841		*P. superciliosum*	NA
"*D.*" *schleiermacheri*	EU	*P. profectum*	NA
"*D.*" *pikermiensis*	EU/AS	*P. hesei*	NA
Stephanorhinus Kretzoi, 1942		*Aphelops* Cope, 1873	
S. miguelcrusafonti	EU	*A. megalodus*	NA
S. megarhinus	EU	*A. malacorhinus*	NA
S. etruscus	EU	*A. mutilus*	NA
S. hemitoechus	EU		

TABLE 1—(*Continued*)

Teleoceras Hatcher, 1894		*Rhinoceros* Linnaeus, 1758	
T. medicornutum	NA	R. unicornis	AS
T. meridianum	NA	R. sondaicus	AS
T. major	NA	*Diceros* Gray, 1821	
T. fossiger	NA	D. bicornis	AF
T. proterum	NA		
T. hicksi	NA		

Cerdeño (1989, 1992), Heissig (1989), Fortelius et al. (1993), and Prothero (in press). During the last decade, several cladistic phylogenetic analyses of rhinoceroses (sensu lato) have provided new hypotheses on their relationships (Heissig, 1981, 1989; Groves, 1983; Prothero et al., 1986). The work of Prothero et al. (1986) is the most ambitious attempt; it includes the whole superfamily Rhinocerotoidea and provides a good compilation of previous phylogenies of rhinos. However, duplication of these results is not possible because published data matrices are not available in the three cladistic analyses noted above. The phylogenetic hypotheses proposed by these authors are reflected in the current classification of rhinoceroses (Prothero and Schoch, 1989). The research reported here is an attempt at a more rigorous phylogenetic analysis of the family Rhinocerotidae.

MATERIAL AND METHODS

Specimens of most genera were studied directly by the author for more than 10 years. The material is housed in the following institutions:

Spain: Museo Nacional de Ciencias Naturales (MNCN), Museo del ITGE, Departamento de Paleontología de la Universidad Complutense, and Museo Arqueológico Nacional (Madrid); Instituto de Paleontología M. Crusafont (Sabadell), Museo Paleontológico (Valencia), Sociedad de Ciencias Aranzadi (San Sebastián).

Portugal: Departamento de Estratigrafia e Paleobiologia, Universidade Nova de Lisboa.

France: Institut de Paléontologie, MNHN (Paris; Département des Sciences de la Terre de l'Université Claude Bernard (Lyon).

Netherlands: Instituut voor aardwetenschappen, Rijksuniversiteit (Utrecht).

Germany: Universitäts–Institute für Paläontologie und historische Geologie (Munich), Senckenberg Museum (Frankfurt).

Italy: Museo di Geologia e Paleontologia (Florence).

USA: American Museum of Natural History (AMNH) (New York); Museum of Comparative Zoology (MCZ) (Harvard University, Cambridge); National Museum of Natural History–Smithsonian Institution (Washington).

Extant species were reviewed from the collection in the Department of Mammalogy, AMNH. Table 1 summarizes the species of the genus reviewed by the author and indicates their geographical distribution.

Taxa in quotation marks correspond to those forms previously considered or suggested to be synonymous, although a general consensus has not been reached: *Hispanotherium* = "*Begertherium*" and "*Beliajevina,*" Antunes and Ginsburg (1983)–Cerdeño (1989)–Fortelius and Heissig (1989). "*Dicerorhinus*" *schleiermacheri* = ?*Lartetotherium schleiermacheri*–Cerdeño (1992). "*Mesaceratherium gaimersheimensis*" = *Aceratherium paulhiacensus*–Bonis (1973), "*Mesaceratherium gaimersheimensis*" = *Protaceratherium gaimersheimensis*, author's opinion. One specimen in particular ("F:AM 95544," a skull in the Frick collection, AMNH) has not been formally defined taxonomically, although Prothero et al. (1986) and Prothero (in press) consider it to be a new genus. For "*Begertherium*" I have considered the type species *B. borrissiaki* as well as *B. grimmi,*

following the suggestion of Fortelius and Heissig (1989). "*Dicerorhinus*" *pikermiensis* (Geraads, 1988) seems to be a species very close to "*Dicerorhinus*" *schleiermacheri,* but it is not included in the analysis because I have examined just a few of its remains, and Geraads (1988) did not establish clear skeletal characteristics for it. Groves (1983) discussed the affinities of several Miocene species assigned to the genus *Dicerorhinus.* Species such as *D. leakeyi* (Hooijer, 1966), *D. orientalis* (Ringström, 1924), or *D. pikermiensis* (Geraads, 1988) are closely similar to *Lartetotherium sansaniensis* and "*Dicerorhinus*" *schleiermacheri,* and their detailed study would probably show their closer relationship with the genus *Lartetotherium,* as already suggested (Groves, 1983; Cerdeño, 1992).

Some poorly defined genera such as *Kenyatherium* (Aguirre and Guérin, 1974), *Shennongtherium* (Huang and Yan, 1983), and *Tesselodon* (Yan, 1979), based solely on dental material, were excluded from the study.

This analysis was executed using Hennig86, version 1.5 (Farris, 1988). The evolution of characters has been examined with the CLADOS program (Nixon, 1992). The close phylogenetic relationships between the families Rhinocerotidae and Hyracodontidae (Prothero et al., 1986, 1989) led to the choice of the latter as the outgroup, represented by the subfamilies Eggysodontinae (= Allaceropinae) and Hyracodontinae (Heissig, 1989). Heissig (1989) considered the subfamilial name Allaceropinae to be valid for the Eggysodontinae even though *Allacerops* Wood, 1932, was synonymized *Eggysodon* Roman, 1911. Nevertheless Eggysodontinae was first established in 1923 (Breuning, 1923), thus having priority. With respect to the family Hyracodontidae, I follow Heissig (1989) in considering *Hyracodon* and *Ardynia* within the Hyracodontinae, and *Eggysodon* and *Prohyracodon* within Eggysodontinae (see Dashzeveg [1991] for another perspective).

The primitive Rhinocerotoidea *Hyrachyus* has also been added as a third outgroup in order to clarify the polarity of some characters that appear with different character states or with missing data among the hyracodontid subfamilies. The matrix has also been run with *Hyrachyus* as the only outgroup, and the respective results are compared.

CHARACTER ANALYSIS

Dental morphology has been classically used as the basis for taxonomical studies, while postcranial characters have often been neglected. This analysis is mostly based on craniodental features, although a number of postcranial elements are also considered (table 2) in order to achieve a more complete anatomical characterization. All segments of the limbs were considered; many characters refer to the general shape of the bones, but some elements, like the astragalus, the calcaneum, or the scaphoid, provide good features in the articular facets that can be considered separate characters. Detailed explanation of commonly used terminology in rhinoceros anatomy, as well as the general shape of teeth and bones, and the position of the different articular surfaces, can be obtained in Heissig (1972), Guérin (1980), and Cerdeño (1989). Some characters are present with different character states within species of the same genus (sometimes they even vary within a species), which is reflected by question marks in the matrix (table 3). The amount of missing data is also increased by the lack of knowledge of some characters of certain taxa. Data are missing for several postcranial features of some genera because published descriptions are not sufficiently detailed, even when the bones are known, and I have not observed them. Detailed characters and character states can be obtained in table 2, and their distribution among the 45 taxa is given in table 3. Most characters are ordered (38 are binary); only 6 of the 34 multistate characters were left unordered (1, 2, 11, 47, 50, and 60), as directionality could not be established. The polarity of characters was established following the outgroup comparison methodology (Watrous and Wheeler, 1981; Nixon and Carpenter, 1993).

With respect to the evolution of characters, the present cladistic analysis makes it evident that many of them are quite homoplastic. Despite this behavior that diminishes some global value of these characters, they are valuable in defining some lesser groups within the whole ingroup. As a matter of fact, the removal of some characters only leads to more unresolved cladograms. Taking into account the high number of taxa considered, I have tried to use as many characters as possible, without judging them a priori. This first attempt at a rigorous cladistic analysis of the whole family Rhinocerotidae provides a basis for a reevaluation of the usefulness of the characters, the ingroup size, and the generic/specific level considered.

Some characters used by other authors have been ignored in this analysis mainly because they are not known (at least to me) for most of the considered taxa (e.g., position of the lacrymal bone, articulation tibia-fibula–Groves, 1983; the dorsal notch of the atlas–Prothero et al., 1986; the direction of the premaxillae, the articulation femur-fibula, or the median lower crest of the mandibular symphysis–Heissig, 1989). I consider others—such as shape and depth of the postfossete of upper premolars or the divergence of the parastyle of the upper teeth (Fortelius and Heissig, 1989)—not useful, at least at a generic level.

The following characters are used in this study (table 2):

1–3. Presence of horns. Nasal and frontal horns are considered separately, since they arise from different bones, and they are not homologous. Nasal horns have been treated as two characters depending on whether they are single or paired, to avoid a character with many different states which apparently evolved independently.

The analysis shows that the development of a nasal horn evolved independently to the apomorphic states (on the tip of the nasals or well developed in the middle of the nasals), and there are reversals from both to the plesiomorphic state (absence). The development of paired nasal horns also evolved independently to the apomorphic states, only once to rounded bosses, and twice to lateral ridges. The development of the frontal horn constitutes a synapomorphy of the rhinocerotine group, with independent reversals in *Rhi-*

noceros and three "elasmotherine" forms; the derived state 2 is an autapomorphy of *Elasmotherium.*

4. The ossification of the nasal septum is a synapomorphy at node 20 (fig. 1), and the most derived state (septum totally ossified) is reached independently in *Coelodonta* and *Elasmotherium.*

5. The dorsal profile of the skull is predominantly present with character state 1, but several changes occur. There are reversals to the plesiomorphic state in the *Subhyracodon* clade (fig. 1, node 05), excepting *Menoceras,* and independently in *Chilotherium* and *Dicerorhinus.* The apomorphic state 2 is achieved independently in *Pleuroceros, Teleoceras, Diaceratherium, Diceros,* and the *Rhinoceros* clade (fig. 1, node 17).

6. The deep nasal opening is a derived character of most Aceratheriinae, with a reversal for the *Teleoceras* group (fig. 1, node 31). The derived state is also a synapomorphy at node 20 (*Coelodonta* and *Elasmotherium* subclades).

7. The retraction of the anterior border of the orbit occurs independently in *Floridaceras, Iranotherium, Elasmotherium,* and gets its maximal degree in *Ninxiatherium* (autapomorphy).

8. The relative projection of the orbit happens in *Iranotherium* and the *Coelodonta* and *Elasmotherium* subclades, less markedly in *Coelodonta* and *Stephanorhinus* than in the other genera.

9. The sagittal crest (fig. 1, node 04) has been lost by most of the Rhinocerotidae, but several reversals to the pleisomorphic state occur independently, as well as the achievement of the apomorphic state 2 from the state 1.

10. The relative position of the postglenoid and posttympanic apophyses appears to be a rather homoplastic character. The character state 1 is a synapomorphy at node 06 (fig. 1; table 4), but both reversals and changes to the state 2 occur. The change from character state 0 to 2 seems to happen in *Menoceras.* Variation of this character among the species of a genus is known for *Subhyracodon, Ronzotherium, Teleoceras,* and *Diaceratherium.* Heissig (1989) established that no reversals occur in the evolution of this character, which disagrees with the present results.

11. The inclination of the occipital face is

TABLE 2
Characters and Character States Considered for the Cladistic Analysis
Plesiomorphic state = (0) unless otherwise noted. See comments in the text about the polarity
of certain characters (*).

A. Skull-mandible

1. Unique nasal horn: absent (0), small, on the tip of nasals (males) (1), well developed in the middle of the nasals (2). Unordered.
2. Paired nasal horns: absent (0), rounded bosses on the tip (1), lateral ridges (2). Unordered.
3. Frontal horn: absent (0), well developed (1), hugely developed (2).
4. Nasal septum: not ossified (0), partially ossified (1), totally ossified (2).
5. Cranial dorsal profile: flattened (0), slight occipital elevation (1), great occipital elevation (2).
6. Nasal opening: short (posterior edge between P1P3) (0), deep (posterior edge above P4M1) (1).
7. Anterior border of the orbit: P4M2 level (0), M3 level (1), behind M3 level (2).
8. Border of the orbit: continuous with the zygomatic arch, not projected laterally (0), projected laterally (1).
9. Sagittal crest: present (0), parietal crests very little separated (1), parietal crest clearly separated (2).
10. Postglenoid and posttympanic apophyses: separated (0), in contact (1), fused (2).
11. Occipital face: vertical (0), inclined backward (1), inclined forward (2). Unordered.
12. Occipital outline: high and narrow (0), roughly squared (1), low and broad (2).
13. Zygomatic width: normal (0), very broad (1).
14. Skull: dolicocephalic (0), brachycephalic (1).
15. Nasal length: very short, retracted (0), long (1).
16. Apophysis on the lateral border of the nasal bone: present (0), absent (1).
17. Mandibular symphysis: narrow (0), broad (1), very broad (2).
18. Mandibular ventral profile: straight (0), with upraised symphysis (1), clearly convex (2).
19. Posterior edge of the symphysis: short (p1p2 level) (0), long (p3p4 level) (1).
20. Ascending ramus: inclined forward (0), vertical (1), inclined backward (2).

B. Dentition

21. Upper I3-C: present (0), absent (1).
22. Lower i3: present (0), absent (1).
23. Lower C: present (0), absent (1).
24. Upper I2: present (0), absent (1).
25. Lower i1: present (0), absent or minimum development (1).
26. Upper I1, shape: incisorlike (0), small chisel-shaped, laterally compressed (1), large chisel-shaped (2), absent (3).
27. Lower i2, shape: incisorlike (0), small tusk (1), large tusk (2), absent (3).
28. Lower p1: present (0), absent (1).
29. Lower p2: present (0), absent (1).
30. Cheek teeth: brachydont (0), subhypsodont (1), hypsodont (2).
31. Upper M3: quadrangular (metacone developed) (0), triangular (metacone lost) (1).
32. Posterior cingulum on upper M3: long, somewhat projecting, lengthening the base of the tooth (0), short, little developed (1).
33. Metacone rib on upper premolars: well developed (0), slight or absent (1).
34. Hypocone on upper P2: united to the protocone, not to the metaloph (0), united to the metaloph and with a "bridge" to the protocone (1), hypocone and protocone separated (molarized premolars) (2). (*).
35. Hypocone on upper P3-P4: united to the protocone, not to the metaloph (0), united to the metaloph and with a "bridge" to the protocone (1), hypocone and protocone separated (molarized premolars) (2).
36. Protocone on upper premolars: not constricted (0), slightly constricted (1), very constricted (2).
37. Protocone on upper molars: not constricted (0), slightly constricted (1), very constricted (2).
38. Secondary folds on upper premolars: absent (0), simple (1), multiple (2).
39. Enamel of cheek teeth: little folded (0), quite folded (1), very much folded (2).
40. Lingual cingula on upper premolars: strong (0), weak (1), absent (2).
41. Lingual cingula on upper premolars: strong (0), weak (1), absent (2). Plesiomorphic state = (1).
42. Lingual cingula on lower premolars: strong (0), weak (1), absent (2). Plesiomorphic state = (1).
43. Labial cingula on lower premolars: strong (0), weak (1), absent (2).
44. Metaconid of lower p2: very prolonged backward (0), normal (1).
45. Labial groove on lower cheek teeth: deep (0), shallow, faded (1).
46. Cement on cheek teeth: absent (0), moderate (1), abundant (2).

TABLE 2—(*Continued*)

C. Postcranial skeleton

47. Metapodials: long and narrow (0), long and broad (1), short but not massive (2), short and massive (3). Unordered.
48. Metacarpal V: functional (0), reduced (1).
49. Metacarpal IV, proximal facet: trapezoidal outlined (0), triangular outlined (1).
50. Metacarpal II, lateral facet for the McIII: anteriorly and posteriorly developed, with or without medial union (0), continuous, without marked medial narrowing (1), only anteriorly developed (2), very reduced or absent (3). Unordered. Plesiomorphic state = (2).
51. Metacarpal II, trapezium-facet: present (0), absent (1).
52. Scaphoid and semilunate: with short proximolateral and without a posterolateral facet (0), with long proximolateral and without posterolateral facet (1), with posterolateral facet (2).
53. Semilunate: with proximal facet for the ulna (0), without it (1). (*).
54. Pyramidal, medial distal facet: simple (0), bilobed or L-shaped (1).
55. Astragalus: high and narrow (0), short, squared (1), low and broad (2).
56. Astragalus, anteroposterior diameter (APD): normal (0), large, with facet 2 outstanding from posterior face (1).
57. Astragalus, trochlea: very oblique to the distal articular zone (0), slightly or not oblique (1).
58. Astragalus, facet 1 (proximoexternal): without distal prolongation (0), with narrow prolongation (1), with wide prolongation (2). Plesiomorphic state = (1).
59. Astragalus, facet 1: very concave (0), more or less flattened (1).
60. Astragalus, facet 2: isolated (0), united to facet 3 (1), elongated to proximal border (2). Unordered. Plesiomorphic state = (1).
61. Astragalus, facet 2: high and narrow (0), roughly rounded or oval (1), transversely elongated (2).
62. Calcaneum, tibial facet: present (0), absent (1).
63. Calcaneum, fibular facet: present (0), absent (1). (*).
64. Calcaneum, tuber: short (0), long (1).
65. Calcaneum, tuber: smooth unevenness (0), strong unevenness (1). (*).
66. Calcaneum, sustentaculum: at obtuse angle (0), at right angle (1).
67. Humerus, laterodistal epicondyle: short (0), high (1).
68. Humerus, laterodistal epicondyle: slightly laterally projected (0), well projected (1).
69. Femur, third trochanter: little developed (0), very developed (1).
70. Radius, posterior articular facets: united (0), separated (1). (*).
71. Tibia, anterior groove: wide (0), narrow (1).
72. Long bone epiphyses: narrow (0), wide (1).

rather homoplastic, with independent reversals to the plesiomorphic state (vertical face) from the apomorphic state 1. The character state 2 is achieved independently from the states 0 and 1.

12. The occipital outline also shows a homoplastic behavior in its evolution. Changes occur from the plesiomorphic state to the character state 1, and from state 1 to state 2, with several reversals from state 1 to state 0.

13, 14. Broad zygomatic width and brachycephaly. The derived state of these characters is achieved independently by different taxa. Both derived states co-occur in *Peraceras* and most teleoceratines. Therefore, these characters are not necessarily related, as previously claimed by Heissig (1989).

15. The nasal length appears as a derived character (long) in the family, with some independent reversals in *Subhyracodon, Amphicaenopus, Aceratherium, Peraceras,* and *Chilotherium.* Nasal shortening also occurs in some species of *Teleoceras* and *Aphelops.*

16. The lateral apophysis of the nasal bone appears as a derived character (absent) for most of the family, with retention of the plesiomorphic character state in *Teletaceras, Penetrigonias,* and *Subhyracodon.*

17. The width of the symphysis is present with the derived state 1 in most aceratheriines, related to the development of the i2, reaching the most derived state 2 in *Chilotherium*; there are reversals to the plesiomorphic state in *Prosantorhinus* and *Chilotheridium.* Most of the rhinocerotines are also plesiomorphic for this character, except *Gaindatherium* and *Rhinoceros.*

18. The mandibular ventral profile has var-

TABLE 3

Data Matrix Including Three Outgroups (*Hyrachyus*, Eggysodontinae, and Hyracodontinae), 43 Rhinocerotid Taxa, and 72 Characters

Characters

Taxa		11111	11111	22222	22222	33333	33333	44444	44444	55555	55555	66666	66666	777
	1234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	012
Hyrachyus	0000	00000	00000	00000	00000	00000	00000	11210	00000	20100	00010	10000	00000	00000	000
Eggysodontinae	0000	?0??0	0????	??000	01?0?	00000	0100?	01121	0001?	?1010	000?0	00110	11001	1?0
Hyracodontinae	0000	00000	00010	00000	00011	?1210	00000	00011	0?010	0?010	00010	10110	10000	?00
Teletaceras	0000	00000	00000	10000	00000	01190	0000?	00000	01000	010??	?0?0?	0?0??	?1???	?00
Penetrigonias	0000	000?0	0?000	10010	00110	0?00?	?00?0	02110	00?1?	?0101	0?010	0?010	10010	1???
Amphicaenopus	0000	10001	11110	01110	01200	01002	01002	00100	0222?	001??	20???	?????	??00?	0?0
Trigonias	0000	10000	01000	11000	00110	0100?	0100?	00100	02??0	01000	20120	10010	?00?0	0?0
Subhyracodon	0000	?000?	?0000	00000	01110	01112	?0100	0?000	0?010	21?10	00010	?0010	11000	100
Diceratherium	0200	0000?	01000	11000	01110	01112	200?0	00000	01010	21010	00010	?1000	01000	010
Menoceras	0100	10002	22000	11001	11111	01112	20120	01100	01011	30010	00010	11000	11000	110
Floridaceras	0000	?01?0	??0?0	11100	01111	11200	01012	20010	00100	00110	10101	00100	01100	101
"F:AM 95544"	0000	01000	11???	?111?	?????	13210	01012	20120	01???	?0???	?????	?????	?????	???
Peraceras	0000	11000	0?011	01?11	01111	13210	11012	21?90	01001	11200	10?10	10111	?1??1	10?
Aphelops	0000	1100?	12101	?1101	11111	11011	11011	11290	00101	10100	10000	11021	01000	?1011	101
Teleoceras	1000	2000?	?2111	?1111	11111	02211	21111	11290	02221	02310	10210	21121	?2000	11110	101
Ronzotherium	0000	10001	?1100	11?0?	01110	11100	01011	10000	01?90	0000?	?1210	000?0	11?11	??00?	1?1
Mesaceratherium	????	?????	?????	?1010	?1111	01110	01001	10200	01101	0000?	20000	00???	??11?	?????	???
Protaceratherium	0000	0100?	00000	11010	11111	01100	01112	11120	01???	00000	31010	00110	11?90	0????	?10
Pleuroceras	0200	20001	10100	11000	?1111	01100	01?11	10?10	??011	00010	0?0?0	10000	?1101	0????	??0
Diaceratherium	1000	20002	?0211	11101	01111	02200	01012	22210	00???	11300	?0210	211?1	0210?	11101	001
Brachypotherium	1000	10002	10211	01111	01111	02200	11012	22210	00?21	11310	?0200	211?1	????1	11101	001
Prosantorhinus	1000	10000	1??0?	11011	01111	01210	01112	22220	0011?	00300	?0210	211?1	01000	11101	001
Alicornops	0000	11000	10100	11111	11111	01210	01012	20210	01101	01200	?0010	211?1	00110	11000	101

TABLE 3—(Continued)

Characters

Taxa			11111	11111	22222	22222	33333	33333	44444	44444	55555	55555	66666	66666	7777
	1234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	01234	56789	012
Hoploaceratherium	1000	11000	10000	11110	11111	13200	01012	20210	01111	00100	11010	10120	01021	0100?	000
Aceratherium	0000	11002	20000	01110	11111	?2200	01011	10210	02221	00100	1?010	101?0	01021	0100?	?00
Lartetotherium	2010	10000	10100	11001	1111?	01100	01102	21110	22221	00111	20211	10100	11010	00??1	?00
L. schleiermacheri	2010	10001	22000	11010	?1110	01110	01102	201?0	22221	00111	20201	10100	11010	1?001	101
Stephanorhinus	2011	21?12	21100	11000	11111	13310	?1102	21120	22??1	0?111	20?01	10100	1100?	1?001	?0?
Coelodonta	2012	11?12	21100	1102?	21111	13310	20012	21120	22221	12111	20201	10100	11??1	00001	001
Hispanotherium	00?0	?????	?1000	?111?	01110	01110	11101	11221	02011	02011	20000	101?0	11011	01??0	?10
"Begertherium"	?000	?00??	?????	11000	1111?	0?110	11001	11221	?22?1	02011	20000	10110	11111	01100	1?0
"Beliajevina"	2000	?00??	?????	11000	1111?	03110	11?01	11221	22221	0201?	20000	10120	21071	11000	110
Iranotherium	2000	10112	01000	11000	01111	0???0	11?01	12221	2222?	021??	00000	101??	?????	?????	???
Elasmotherium	0022	11112	00200	1102?	21111	1331?	21101	12222	2222?	02110	?????	101??	?????	?????	?01
Ninxiatherium	2001	11212	00100	?1???	?1111	?3???	11?0?	11221	2222?	?2???	?????	?????	?????	?????	???
Acerorhinus	?000	11001	00?00	11111	11111	03210	11011	10210	02001	001??	1??10	?1111	0?000	01000	?00
Chilotherium	0000	01002	10211	01211	11111	13210	21111	?1210	22221	0?310	??010	11121	?10??	??111	?01
Chilotheridium	2000	11002	01000	1100?	?1111	13210	21?12	20210	10??1	00100	??010	1?1??	0111?	1???0	?01
Aprotodon	0000	?????	2110?	112??	?1111	?12?0	1111?	10210	02??0	012??	20200	20010	11000	10??1	?01
Gaindatherium	2000	10002	20000	11110	01110	11200	01102	20000	22220	0011?	?????	?????	?????	?????	???
Punjabitherium	2010	20002	22100	1100?	?1110	01110	21?2	21120	22???	?21??	?????	?????	?????	?????	???
Rhinoceros	2000	20002	22101	1110?	01111	01110	?1112	21110	?2221	02111	00101	10101	10001	01111	001
Dicerorhinus	2010	00002	00100	11000	11111	?1110	01102	20010	22221	01111	0?101	001?0	?0000	10111	1?1
Diceros	2010	20002	01200	11021	21111	13310	01112	20010	02221	01111	11101	10101	00000	10111	?01
Ceratotherium	2010	10002	01100	1102?	21111	13310	21112	20010	22221	12111	11101	10101	10000	01111	001
Paradiceros	2010	10002	00100	11021	?1111	13310	01112	21110	12??1	0???1	?????	071??	?????	??10?	??0

ied several times within the group, with independent reversals from the upraised symphysis condition to the straight one; the derived state 2 (very convex) characterizes the group of rhinocerotines at node 18 (fig. 1), with a reversal to the plesiomorphic state in *Stephanorhinus*.

19. Length of symphysis. A long symphysis is present in *Menoceras* and all the Aceratheriinae, while it remains short in most Rhinocerotinae except *Lartetotherium sansaniense* (it is short in *L. schleiermacheri*, so it varies within this genus) and the dicerotine group (also variable within *Ceratotherium*).

20. The ascending ramus appears with the derived state 1 (vertical) in *Protaceratherium* and most of the Aceratheriinae, with reversals in *Peraceras* and some teleoceratines. This reversal also occurs within rhinocerotines in *Iranotherium* and *Rhinoceros*, while the derived state 2 (inclined backwards) is a synapomorphy of the clade at node 18 (fig. 1), with reversal to the state 1 in *Stephanorhinus*.

21–23. Third incisor and canine. These characters have been assumed as character-state 1 (absence of third incisor and canine) for some forms whose anterior dentition is actually unknown, based on the fact that these teeth are only documented among the most ancient species of Rhinocerotidae (*Teletaceras, Penetrigonias,* and *Trigonias*; table 3). *Teletaceras* is, in fact, the only one with complete dental formula, while the other two taxa have already lost the i3 and lower canine. Character 21 gathers I3 and upper canine since both teeth behave in the same way.

24, 25. I2 and i1. The absence of I2 and i1 is a common derived feature among the Rhinocerotidae; however a secondary development of I2 occurs in *Gaindatherium, L. schleiermacheri,* and *Punjabitherium,* and the presence of i1 is more common in the acerathines as well as in the rhinocerotines.

26, 27. The complex chisel-shaped I1/tusk-like i2 is a characteristic of the whole family. The large i2 (27^2) is present in all Aceratheriinae, while most Rhinocerotinae present the character state 1 for both teeth. The loss of I1/i2 (state 3) is characteristic of the Dicerotina and the *Coelodonta* and *Elasmotherium* clades (fig. 1, node 18). The loss of the upper I1 is also documented among the aceratheres (table 4, node 24), with reversals

to the state 1 in *Alicornops,* and to the state 2 in some teleoceratines.

28. The presence or absence of a lower p1 is rather variable even among the outgroups (absent in Hyracodontinae). It is absent in most aceratheres (derived state), while it is present in the Rhinocerotinae except *Gaindatherium* and *Lartetotherium sansaniense* (it is absent in *L. schleiermacheri*).

29. The absence of p2 happens in *Teleoceras* (although the p2 is actually present in *T. proterus*), and it is variable in *Elasmotherium*.

30. Tooth hypsodonty. Most rhinoceroses have brachyodont teeth, although the development of a certain hypsodonty (state 1) occurs several times as a response to a more siliceous diet, and some taxa reach a higher degree of hypsodonty (state 2) like *Chilotherium* or *Teleoceras,* and mainly *Elasmotherium*.

31. Shape of the M3. The triangular shape is a derived character of the family, excluding *Teletaceras,* which retains the plesiomorphic quadrangular shape with the metacone rib developed. Only one reversal happens in *Coelodonta*.

32. Shape of posterior cingulum on M3. The considered character states (table 2) reflect the main observed patterns, although variation within these patterns occurs even intraspecifically. The well-developed posterior cingulum of the M3 is reduced several times in the *Subhyracodon* group, some aceratheres, and all rhinocerotines except *Coelodonta* (reversal).

33–38. Morphology of the upper premolars. As in the previous case, the character states reflect the main observed patterns, which include a greater variation that can occur mainly at specific level.

The fading or loss of the metacone rib on the ectoloph (character 33) occurs in the *Subhyracodon* group and the aceratheres, while it is present in most Rhinocerotinae, being lost in Dicerotina, *Rhinoceros,* and *Coelodonta*.

Molarization of the premolars is achieved (34, 35^2) several times independently (*Subhyracodon* group, some aceratheres and most rhinocerotines). Some genera present a molarized P2, while the P3-P4 remain pre- or submolariform (character states 0, 1). Heissig (1989: fig. 21.1) considered five different de-

grees of molarization with which I do not agree. The premolariform and submolariform stages established by Heissig seem to reflect minor variations within a premolariform stage equivalent to the state 0 considered herein, and the paramolariform stage would be included in the molariform state (state 2).

The greatest constriction of the protocone (36, 37^2) is developed among the aceratheres (more on molars than on premolars) and in the elasmotheriine (sensu lato) group.

Concerning the development of secondary folds on upper premolars (character 38), a certain variation occurs mainly referred to multiple folds (state 2); I consider this state only when most of the premolars present multiple folds (crochets and/or cristae), even if some teeth with simple ones are documented within a same sample. There is an independent evolution from character state 0 to both apomorphic states. State 2 is present at node 05 (fig. 1), except *Subhyracodon*. State 1 appears as a synapomorphy at node 08 (fig. 1; table 4), changing to character state 2 in *Prosantorhinus, Punjabitherium,* the *Iranotherium* clade, and the *Elasmotherium* and *Coelodonta* subclades.

39. Folding of dental enamel is a derived state characteristic of the *Iranotherium* and *Elasmotherium* clades, reaching its maximum degree in *Elasmotherium.*

40–43. Development of lingual and labial cingula is very variable, even among the outgroups. The derived condition (state 2: absence) is constant in Rhinocerotinae; only the lingual cingulum on upper premolars appears in *Paradiceros* and *Diceros.* It can also be present in *Stephanorhinus.* For characters 41 and 42 the plesiomorphic state seems to be state 1 (weak development), conditioned by variation among the outgroups.

44. The metaconid of p2 is not prolonged backward in most members of the family (except the oldest ones) or in Eggysodontinae. Reversals happen in *Floridaceras, Aprotodon,* and *Gaindatherium.*

45. The shallow labial groove on lower cheek teeth is independently reached in some taxa (*Peraceras, Aphelops, Diaceratherium, Brachypotherium, Ceratotherium,* and *Coelodonta*).

46. Presence of a certain quantity of cement on the teeth occurs in different taxa independently, but the most derived state (2) characterizes the Rhinocerotinae, except *Gaindatherium* and *Lartetotherium.*

47. Type of metapodials. The apomorphic states 2 and 3 are achieved independently from state 1 (long and broad); state 2 (short but not massive) is present in *Alicornops, Peraceras, and Aprotodon.* The short and massive metapodials are characteristic of the teleoceratine group, except *Aphelops* (47^1). In some cases the difference between states 0 and 1 can be somewhat subjective, conditioned by the size of the bones, and a possibility for further analysis might be the quantification of the character based on the gracility index.

48. The McV is functional in *Hyrachyus* while it is reduced in the hyracodontid subfamilies. The plesiomorphic condition remains in most aceratheres, becoming reduced in *Chilotherium, Teleoceras,* and *Brachypotherium.* The derived state is also present in all Rhinocerotinae.

49. The outline of the proximal facet of the McIV is unknown for many taxa, including the basal ones. The derived state (triangular) is present in one of the outgroups (Hyracodontinae), in *Menoceras,* and in the Rhinocerotinae, except *Elasmotherium* in which the trapezoidal outline appears as a reversal.

50. The lateral McIII facet of the McII shows an independent evolution from the plesiomorphic state (2: anteriorly developed) to the different apomorphic states, with reversal from state 1 (continuous facet). The reduction of the facet (state 3) occurs in *Menoceras* and *Protaceratherium.* State 1 appears in some aceratheres and the Dicerotina, while most Rhinocerotinae present the plesiomorphic state as reversal from the state 1.

51. The loss of the trapezium facet on the McII appears as derived state in one outgroup (Eggysodontinae), and independently in the *Subhyracodon* group (except *Menoceras*), in *Hoploaceratherium,* and the Dicerotina.

52. Articulation scaphoid-semilunate. The evolution of this character shows that possession of a posterolateral articular facet between the scaphoid and the semilunate (state 2) is achieved independently from the plesiomorphic state 0 (only one short proximolateral facet) or from state 1, which implies a previous elongation of the proximo-

lateral facet. The posterolateral facet is present in *Ronzotherium,* most teleoceratines (fig. 1, node 31), and some rhinocerotines (*Lartetotherium* and *Coelodonta*; it varies in *Stephanorhinus*).

53. Ulnar facet. The polarity of this character is conditioned by the different state of the outgroups. Taking both analyses into account, the plesiomorphic state is considered to be the presence of an ulnar facet (0). Both hyracodontid subfamilies, some basal rhinoceroses and all aceratheres present state 1. Reversals to state 0 occur in *Mesaceratherium, Aphelops, Brachypotherium,* and the Rhinocerotinae, changing in *Lartetotherium sansaniense.*

54. Presence of a bilobed or L-shaped inferomedial facet on the pyramidal is the derived condition present in all Rhinocerotinae, with reversal to the plesiomorphic state in the *Hispanotherium* group. However, a certain posterolateral extension of that facet has been observed on one specimen of *Hispanotherium matritense* (Cerdeño, 1992).

55. General shape of the astragalus. Most of the family presents the apomorphic states. The roughly squared shape is present in *Trigonias,* and as a synapomorphy at node 06 (fig. 1). The broadening of the astragalus (state 2) occurs independently within the Aceratheriinae, in *Alicornops,* and in most teleoceratines (node 31); *Aprotodon* also has this state. The rhinocerotines are derived with character state 1, with two reversals in *Dicerorhinus* and *Paradiceros.*

56. Astragalus development. The special anteroposterior development, with outstanding facet 2, is a derived condition achieved by most aceratheriines (fig. 1 node 25), with a reversal in *Peraceras.*

57. Obliquity of trochlea. The loss of obliquity with respect to the distal articulation is a derived feature for Aceratheriinae and Rhinocerotinae, with reversals in *Aphelops* and *Aprotodon,* in which the obliquity is quite marked.

58. Shape of astragalar facet 1 is a relatively variable character, which is reflected by missing data for different character states in a genus. From the plesiomorphic state (1: with narrow prolongation), this character evolves to both apomorphic states. The state 0, without prolongation, appears in *Pleuro-*

ceros, Floridaceras, and many rhinocerotines, with reversals from state 0 to 1 in *Aprotodon* and *Hispanotherium.* The apomorphic state 2 is present in "*Beliajevina,*" *Hoploaceratherium,* and the teleoceratine group, although the character varies in some genera of the latter.

59. Flattening of astragalar facet 1 occurs several times from the primitive concave condition. Within aceratheres it happens in *Floridaceras* and the clade at node 25 (fig. 1), while within the rhinocerotines it appears in *Rhinoceros* and the dicerotine clade.

60. Astragalar facet 2 is primitively united to facet 3 (state 1), although one of the outgroups, Eggysodontinae, presents the apomorphic state 0 (isolated facet). At node 06 (fig. 1) there is a change within rhinocerotids to this same condition, but there is a reversal in the rhinocerotine group (node 10), within which only *Diceros* reaches the isolated condition. "*Beliajevina*" is the only taxon with character state 2 (proximal elongation of the facet), although this condition can also appear (maybe less markedly) in some taxa such as *Diceratherium,* where other states are also present and are predominant. From the description of Borissiak (1938) it can be assumed that the four known astragali of *Beliajevina caucasica* present the same characteristic of facet 2, without variation. This species also presents character state 1, since facets 2 and 3 are united. A possibility could be the division of character 60 into two, one with the character states 0 and 1 established here (table 2), and the other considering the presence or absence of a proximal elongation. However, the results would be similar since such elongation in other taxa does not seem to be constant, and this would be reflected by missing data. Therefore the presence of this feature would still be an autapomorphy of "*Beliajevina*".

61. Shape of astragalar facet 2. Most of the family Rhinocerotidae is derived for this character with the state 1 (rounded or oval astragalar facet-2) (fig. 1, node 04), although several reversals occur in *Subhyracodon, Floridaceras, Alicornops, Rhinoceros* and the dicerotine group. The evolution to character state 2 (transversely elongated) takes place within the teleoceratine clade (*Teleoceras, Diaceratherium* and *Brachypotherium*).

62, 63. Tibial and fibular facets on calcaneum. In both cases *Hyrachyus* presents the state 0 (presence), and the hyracodontid subfamilies the state 1 (absence) (table 3). The loss of the tibial facet occurs several times within Rhinocerotidae, in *Mesaceratherium, Pleuroceros, Chilotheridium, Diaceratherium* and *"Begertherium."* Here the latter taxon is definitely considered a synonym of *Hispanotherium,* in which the tibial facet is present, what would reflect a variation of the character within the genus.

With respect to the fibular facet, its absence occurs in the *Alicornops* group, in *Lartetotherium, Hispanotherium,* and *"Begertherium."* Many taxa present missing data for this character.

64. Development of a long tuber calcis occurs in *Ronzotherium* and as a synapomorphy of the clade at node 06 (fig. 1). Within the Aceratheriinae there is a reversal at node 25, with a new change to the apomorphic state in *Brachypotherium.* Within the Rhinocerotinae the reversal takes place in the *Iranotherium* clade (node 16), *Rhinoceros* (node 17, but unknown in *Punjabitherium*), and the *Elasmotherium* and *Coelodonta* subclades (node 20).

65. The unevenness of the tuber calcis is a more variable character. The derived state (strong) appears in *Diceratherium* and as synapomorphy at node 06 (fig. 1 ; table 4). Within the aceratheres, there is a reversal at node 26 (Alicornopini and Teleoceratini). Among the rhinocerotines several independent changes occur.

66. The angle of the sustentaculum of the calcaneum is present with the derived state (at right angle) in one of the outgroups (Eggysodontinae) and most rhinocerotids, with a reversal for the rhinocerotine group at node 10 (fig. 1), within which the derived state is reached independently in the *Hispanotherium* group (node 16), *Ceratotherium,* and *Rhinoceros.*

67, 68. The laterodistal epicondyle of the humerus becomes high and well projected (derived states) in the teleoceratine clade, with reversals for character 67 in *Aphelops,* and for character 68 at node 33 (fig. 1). There are several independent changes within the rhinocerotines.

69. The development of the third trochanter of the femur takes place in the outgroup Eggysodontinae, in *Peraceras,* the teleoceratines (except *Teleoceras*), and all rhinocerotines except the *Hispanotherium* group.

70. Posterior facets of the radius. The polarity of this character depends on the different state present on the outgroups. The derived character state (posterior facets of the radius united) is present in Eggysodontinae and some basal taxa; data are missing for Hyracodontinae and *Teletaceras.* The character appears to be very homoplastic; it varies within a number of genera.

71. The anterior tibial groove is present with the apomorphic state (narrow) in the clade at node 05 (fig. 1) except in *Subhyracodon,* and in the *Hispanotherium* group.

72. The acquisition of wide long bone epiphyses happens independently in *Floridaceras, Alicornops,* and the teleoceratines within the acerathere group, and in most rhinocerotines except the *Hispanotherium* group, *Lartetotherium sansaniense,* and *Paradiceros,* which present reversals to the plesiomorphic state.

RESULTS AND DISCUSSION

One hundred and four equally parsimonious trees with a length of 497 (consistency index 22, and retention index 59) were discovered in the first analysis including three outgroups. Figure 1 shows the strict consensus tree of these 104 trees, from which several interesting reinterpretations of rhinocerotid phylogeny are proposed. The different cladograms correspond to alternative topologies for the polytomies of the consensus tree. Figure 2 presents the consensus tree corresponding to the second analysis of the data matrix including just *Hyrachyus* as outgroup. This second analysis provided six equally parsimonious trees with a length of 473 (ci = 23; ri = 59). Comparison of the two analyses reveals the stability of some of the obtained groups, while relationships of other taxa, mainly the geologically oldest ones, vary from one analysis to the other. The following discussion will focus on the first analysis (fig. 1).

The basal node presents a trichotomy for *Hyrachyus,* the two hyracodontid subfamilies as a monophyletic group, and the family Rhinocerotidae as another monophyletic
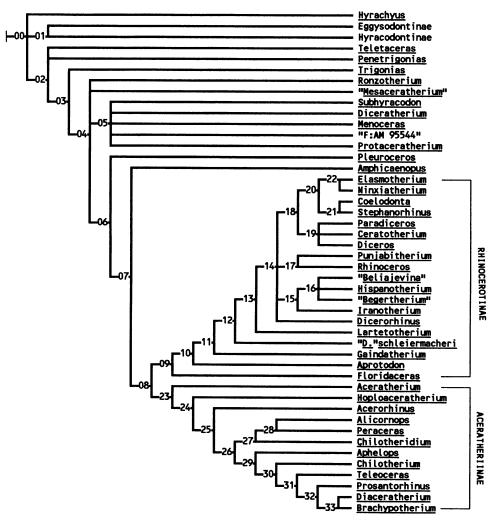
Fig. 1. Strict consensus tree of the 104 obtained cladograms for the family Rhinocerotidae, with *Hyrachyus* and the hyracodontid subfamilies Eggysodontinae and Hyracodontinae as outgroups. Characters at each node in table 4. "F:AM 95544" = new genus in Prothero (in press).

group (fig. 1, nodes 00–03). Due to this basal trichotomy and to the fact that the outgroups sometimes present different character states, the polarity of certain characters (34, 53, 63, 65, and 70) differs from the first analysis to the second. In the first one, these characters appear to be derived for *Hyrachyus* (with character state 0), but the second analysis shows these five characters as derived with character state 1 for all Rhinocerotidae except *Teletaceras* (fig. 2; table 5, node 01). Thus considering both analyses, the plesiomorphic

state is considered to be state 0 (hypocone united to the protocone on P2; presence of ulnar facet on the semilunate; presence of fibular facet on the calcaneum; smooth unevenness of the tuber calcis; posterior facets of the radius united).

The clade of the hyracodontid subfamilies is supported by three synapomorphies (48^1, 50^0, 62^1): McV reduced, McII with lateral McIII facet anteriorly and posteriorly developed (missing data for Eggysodontinae), and the absence of tibial facet on the calcaneum.
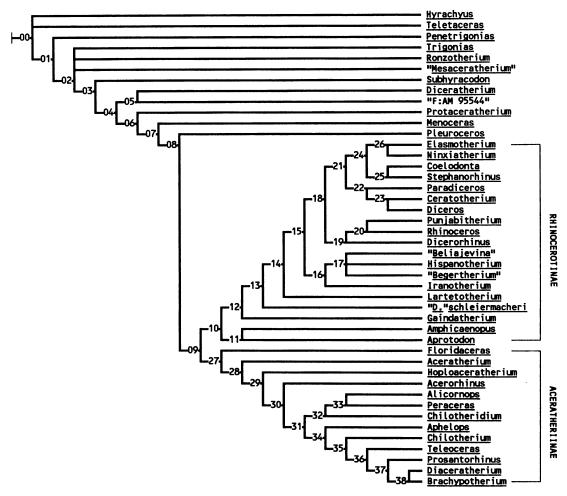
Fig. 2. Strict consensus tree of the six obtained cladograms for the family Rhinocerotidae, with *Hyrachyus* as the only outgroup. Characters at each node in table 5. "F:AM 95544" = new genus in Prothero (in press).

The monophyly of Rhinocerotidae is supported by four synapomorphies: 15^1, 26^1, 27^1, and 66^1: nasal long, chisel-shaped I1, i2 developed as a tusk, and sustentaculum of the calcaneum at a right angle. However, this monophyly is not totally supported in the second analysis (fig. 2), which shows the primitive condition of *Teletaceras,* and its closer relationship with the Hyracodontinae.

Teletaceras retains the plesiomorphic states for characters 21^0, 22^0, and 23^0 (presence of I3/i3 and canines) while all other rhinocerotids exhibit the apomorphic state at least for

characters 22 and 23 (see below). This result agrees with Hanson (1989: 379), who already discussed the primitive condition retained in *Teletaceras,* and regarded its phylogenetic position to be between *Hyrachyus* and all other rhinocerotids. On the other hand, characters 26^1 (chisel-shaped I1) and 27^1 (tusklike i2) unit *Teletaceras* with the rhinocerotids.

Penetrigonias is also a primitive taxon which has already lost the lower i3 and canine (22^1, 23^1), but retains the upper I3-C (21^0) like *Teletaceras* and *Trigonias.*

The derived state is shared by most of the

TABLE 4
Distribution of Character States at Each Node of the Consensus Tree in Figure 1
Synapomorphy = S; parallelism = P; parallel reversal = PR; reversal = R.

Node 01: 48^1, 50^0, 62^1 = P
Node 02: 15^1 = S; 26^1, 17^1, 66^1 = P.
Node 03: 16^1 = S; 5^1, 11^1, 22^1, 23^1, 31^1, 37^1 = P.
Node 04: 9^1 = S; 21^1, 33^1, 35^1, 61^1 = P.
Node 05: 5^0, 42^0, 63^0 = PR; 32^1, 34^2, 35^2, 38^2, 48^1, 51^1, 71^1 = P.
Node 06: 58^0 = S; 63^0, 65^0 = PR; 10^1, 12^1, 24^1, 43^1, 50^1, 55^1, 60^0, 64^1 = P.
Node 07: 27^2, 47^1 = S; 17^1, 18^1, 41^2, 43^2 = P.
Node 08: 12^0 = PR; 25^1, 38^1, 57^1 = P.
Node 09: 64^0 = PR; 10^2, 34^2, 52^1, 72^1 = P.
Node 10: 60^1 = R; 53^0, 50^2, 66^0 = PR; 32^1, 42^2, 52^2, 69^1 = P.
Node 11: 24^0, 33^0 = PR; 1^2, 35^2, 40^2, 48^1, 49^1 = P.
Node 12: 3^1, 54^1 = S; 17^0, 25^0, 27^1 = PR; 44^1, 63^1 = P.
Node 13: 10^1, 18^0 = PR; 12^1, 20^1, 24^1, 36^1, 67^1 = P.
Node 14: 10^0, 52^1, 61^0, 63^0 = PR; 9^2, 28^1, 46^1, 50^1, 68^1 = P.
Node 15: 3^0, 12^0, 34^1, 35^1, 50^2, 52^0, 54^0, 68^0, 69^0, 72^0 = PR; 30^1, 37^2, 38^2, 39^1, 61^1, 64^1 = P.
Node 16: 47^0, 58^1 = PR; 63^1, 66^1, 71^1 = P.
Node 17: 20^0, 70^0 = PR; 5^2, 10^2, 11^2, 30^1, 64^1 = P.
Node 18: 18^2, 20^2, 27^3 = S; 70^0 = PR; 25^1, 26^3 = P.
Node 19: 36^0, 37^0, 40^1 = PR; 19^1, 33^1, 51^1, 59^1 = P.
Node 20: 4^1 = S; 50^2, 67^0, 68^0 = PR; 6^1, 8^1, 30^1, 38^2, 61^1, 64^1 = P.
Node 21: 10^2, 30^2, 52^2 = P.
Node 22: 11^0, 34^1, 35^1, 49^0 = PR; 7^1, 37^2, 39^1 = P.
Node 23: 11^0, 58^1 = PR; 6^1, 20^1, 26^2, 37^2, 44^1 = P.
Node 24: 41^1, 43^1 = PR; 26^3 = P.
Node 25: 56^1 = S; 10^0, 43^0, 64^0 = PR; 19^1, 28^1, 30^1, 59^1 = P.
Node 26: 65^1, 72^1 = P.
Node 27: 34^2, 35^2, 62^1, 63^1 = P.
Node 28: 9^0 = PR; 46^1, 47^2 = P.
Node 29: 9^2, 10^1, 12^1, 14^1, 36^1, 58^2, 68^1, 69^1 = P.
Node 30: 47^3 = S; 13^1, 32^1, 42^2, 43^1, 67^1 = P.
Node 31: 6^0, 25^0, 26^2 = PR; 1^1, 46^1, 52^2, 55^2 = P.
Node 32: 20^0, 41^0, 68^0, 70^0 = PR; 12^2, 34^2, 35^2, 36^2 = P.
Node 33: 28^0, 32^0 = PR; 45^1, 61^2 = P.

family Rhinocerotidae and one of the out-groups for character 31, the shape of M3, which appears as state 1 (triangular) in Eggysodontinae and all Rhinocerotidae except *Teletaceras* and *Coelodonta* (reversal).

The polytomy at node 04 in figure 1 in-cludes the genus "*Mesaceratherium*," whose position varies in the alternative topologies owing to the large amount of missing data. This is also true for "F:AM 95544," which appears in the polytomy at node 05 (fig. 1), although in the second analysis it constitutes the sister group of *Diceratherium* (fig. 2, node 05). "*Mesaceratherium*" seemed to be closer to *Protaceratherium* as supported by a num-ber of similarities between the species *Mes-*

aceratherium gaimersheimensis (Heissig, 1969) and *Protaceratherium minutum* (Cer-deño, 1989). However, the cladograms (figs. 1, 2) do not support this view, but relate it more closely to *Ronzotherium*.

Node 05 of figure 1 gathers most of the genera included in the subfamilies Diceratheriinae and Menoceratinae of the current classification (Prothero and Schoch, 1989), except *Pleuroceros*. The main feature used to define these subfamilies is the presence of paired nasal horns (character 2), but the apo-morphic states of this character appear as an independent acquisition in the genera *Men-oceras* (2^1), *Diceratherium* (2^2), and *Pleuro-ceros* (2^2). On the other hand, the synapo-

TABLE 5

Distribution of Character States at Each Node of the Consensus Tree in Figure 2

Synapomorphy = S; parallelism = P; parallel reversal = PR; reversal = R.

Node 01: 22^1, 23^1 = S; 28^1, 34^1, 53^1, 63^1, 65^1, 70^1 = P.

Node 02: 16^1, 21^1, 31^1 = S; 11^1, 35^1, 37^1 = P.

Node 03: 11^0, 42^0 = PR; 32^1, 33^1, 34^2, 48^1, 51^1 = P.

Node 04: 63^0 = PR; 38^2, 61^1, 71^1 = P.

Node 05: 65^0, 70^0 = PR; 11^1, 35^2 = P.

Node 06: 28^0 = PR; 24^1, 42^1 = P.

Node 07: 51^0 = PR; 5^1, 9^1, 10^1 = P.

Node 08: 58^0 = S; 38^1 = R; 65^0, 71^0 = PR; 43^1, 55^1 = P.

Node 09: 27^2, 47^1 = S; 10^2, 17^1, 41^2, 43^2 = P.

Node 10: 33^0, 53^0, 66^0 = PR; 18^1, 42^2, 52^2, 65^1, 69^1 = P.

Node 11: 58^1, 70^0 = PR; 11^1, 12^1 = P.

Node 12: 24^0 = PR; 1^2, 35^2, 40^2, 49^1, 57^1 = P.

Node 13: 3^1, 54^1 = S; 17^0, 27^1 = PR; 11^1, 44^1, 63^1 = P.

Node 14: 10^1, 18^0, 65^0 = PR; 20^1, 24^1, 36^1 = P.

Node 15: 10^0, 52^1 = PR; 9^2, 28^1, 46^2, 67^1 = P.

Node 16: 3^0, 34^1, 35^1, 52^0, 54^0, 69^0 = PR; 30^1, 37^2, 38^2, 39^1, 64^1 = P.

Node 17: 47^0, 58^1 = PR; 66^1, 71^1 = P.

Node 18: 61^0, 63^0, 70^0 = PR; 12^1, 50^1, 72^1 = P.

Node 19: 50^0, 68^1 = P.

Node 20: 20^0 = PR; 5^2, 10^2, 11^2, 30^1, 64^1 = P.

Node 21: 18^2, 20^2, 27^3 = S; 25^1, 26^3 = P.

Node 22: 40^1 = PR; 19^1, 33^1 = P.

Node 23: 36^0, 37^0 = PR; 51^1, 59^1, 68^1 = P.

Node 24: 4^1 = S; 50^2 = R; 67^0 = PR; 6^1, 8^1, 30^1, 38^2, 61^1, 64^1 = P.

Node 25: 10^2, 30^2, 52^2 = P.

Node 26: 11^0, 34^1, 35^1, 49^0 = PR; 7^1, 37^2, 39^1 = P.

Node 27: 32^0, 48^0 = PR; 25^1, 50^1, 57^1, 60^0 = P.

Node 28: 34^1, 58^1 = PR; 6^1, 18^1, 20^1, 26^2, 37^2, 44^1 = P.

Node 29: 10^1, 41^1, 43^1 = PR; 26^3 = P.

Node 30: 56^1 = R; 10^0, 43^0 = PR; 19^1, 28^1, 30^1, 59^1 = P.

Node 31: 65^1, 72^1 = P.

Node 32: 34^2, 35^2, 62^1, 63^1 = P.

Node 33: 9^0 = PR; 46^1, 47^2 = P.

Node 34: 9^2, 10^1, 12^1, 14^1, 36^1, 58^2, 68^1, 69^1 = P.

Node 35: 47^3 = S; 13^1, 32^1, 42^2, 43^1, 67^1 = P.

Node 36: 6^0, 25^0, 26^2 = PR; 1^1, 46^1, 52^2, 55^2 = P.

Node 37: 20^0, 41^0, 68^0, 70^0 = PR; 12^2, 34^2, 35^2, 36^2 = P.

Node 38: 28^0, 32^0 = PR; 45^1, 61^2 = P.

morphy used by Prothero et al. (1986) to define the subfamily Menoceratinae (terminal nasal horn bosses) would not include *Protaceratherium*, as later stated by Prothero and Schoch (1989). Heissig (1989: 405–406) considered the tribe Trigoniadini within the subfamily Diceratheriinae for the genera *Trigonias, Ronzotherium,* and *Amphicaenopus* (Prothero and Schoch, 1989, in the same volume, did not follow Heissig). Looking now at the cladograms (figs. 1, 2), neither the tribe nor the subfamilies Diceratheriinae and Menoceratinae are supported, since their genera appear as a paraphyletic group. Therefore, it is better to maintain all these genera as primitive Rhinocerotidae without gathering them at any other taxonomic level. "F: AM 95544" is added to them, closer to *Diceratherium* (fig. 2), and thus is removed from the aceratheres (Prothero et al., 1986; Prothero, in press).

At node 06 of figure 1, *Pleuroceros* is the

sister group of the remaining rhinocerotids, sharing eight synapomorphies and three parallel reversals (table 4).

All other taxa comprise a monophyletic group (fig. 1, node 08), which comprises in turn two monophyletic clades, which to some degree support the subfamilies Rhinocerotinae and Aceratheriinae of the current classification, although there are exceptions. The second analysis (fig. 2) also shows two main clades, with two main differences: (1) in the first analysis (fig. 1, node 07), *Amphicaenopus* is the sister group of the great monophyletic group while it is included in the clade of the Rhinocerotinae in the second one (fig. 2) related to *Aprotodon*; (2) *Floridaceras* is included in the rhinocerotine clade in the first case, while it is within the aceratheres in the second one.

Amphicaenopus is considered a primitive rhinocerotid by Prothero and Schoch (1989), although the present analysis suggests that it is more derived than previously thought, sharing the synapomorphies of the node 07 (fig. 1; table 4). Within the clade, it presents characters 15^0, 33^0, 35^0, 50^2, and 70^0 as reversals to the plesiomorphic state, and 13^1, 34^2, and 42^2 as apomorphic.

With respect to *Aprotodon,* it is evident that its current ascription to the teleoceratines (Prothero and Schoch, 1989) is questioned. As can be seen in the matrix (table 3), a number of characters are unknown for this genus (14 of them corresponding to the skull, mandible, and dentition), but they do not affect its position in the cladogram. *Aprotodon* shares all the synapomorphies of the rhinocerotine clade (fig. 1; table 4; nodes 09, 10), without missing the corresponding characters, except for characters 34 and 42. With regard to the eight synapomorphies shared by the teleoceratine clade (fig. 1; table 4; node 29), *Aprotodon* shares with them characters 12^1 and 69^1 only, with missing data for characters 9, 14, and 68. Similarly, with respect to the seven synapomorphies shared by the Aceratheriinae (fig. 1; table 4; node 23), *Aprotodon* is missing two characters, and only shares the characters 37^2 (protocone of the upper molars very constricted) and 58^1 (facet 1 of the astragalus with narrow prolongation), which are apomorphies for *Aprotodon* within the clade united at node 10.

Floridaceras appears at node 9 in the first analysis (fig. 1) with six apomorphies and four reversals (7^1, 9^0, 18^0, 35^2, 37^0, 50^0, 59^1, 61^0, 62^1, 67^1). In the second analysis, where it appears related to the aceratheres, it shows one more apomorphy (72^1) within the clade (fig. 2, node 27). In this case, the character states shared at node 27 are 25^1 (presence of i1), 32^0 (long posterior cingulum of M3), 48^0 (functional McV), 57^1 (astragalus trochlea not oblique), and 60^0 (astragalus facet 2 isolated), while those shared at the node 9 of the first cladogram (fig. 1, table 4, node 9) are 10^2 (fused posttympanic and postglenoid apophyses), 34^2 (molarized premolars), 52^1 (scaphoid with long proximolateral facet), 64^0 (short calcaneum tuber), and 72^1 (narrow long bone epiphyses). These latter character states (except for 52^1) are also present in some acerathere taxa. On the other hand, among the character states shared with the aceratheres at node 27 (fig. 2), characters 32^0, 48^0, and 60^0 are not present within the rhinocerotines (only 32^0, posterior cingulum of the M3 long, is a reversal in *Coelodonta*). Therefore it can be said that a close relationship of *Floridaceras* is better supported to the aceratheres (fig. 2) than to the rhinocerotines (fig. 1), even when the most parsimonious option in the first analysis relates it to the latter group at the base of the clade.

The rest of the Rhinocerotinae, apart from *Amphicaenopus, Floridaceras,* and *Aprotodon,* is roughly equivalent to the tribe Rhinocerotini of Prothero and Schoch (1989), but it differs in the internal relationships of its genera, except for the subtribe Dicerotina. In both cladograms (figs. 1, 2) *Gaindatherium* appears to be closer to *Lartetotherium* than to *Rhinoceros,* to which it was supposed to be directly related (Colbert, 1934; Prothero et al., 1986; Prothero and Schoch, 1989). Out of the four characteristics (9^2, 11^0, 37^0, and 38^0) of *Gaindatherium* within the clade at node 11 (fig. 1), only one (9^2: parietal crests clearly separated) is shared with *Rhinoceros.* Characters 11, 37, and 38 in *Gaindatherium* are reversals to the plesiomorphic state (vertical occipital face; protocone of the upper molars not constricted; absence of secondary folds on upper premolars).

A close relationship that is also supported by both analyses is that of the species "*Di-*

cerorhinus" schleiermacheri with the genus Lartetotherium (L. sansaniense) (figs. 1, 2; table 4, node 12; table 5, node 13), as suggested in a previous paper (Cerdeño, 1992). Therefore, I propose to formally include "D." schleiermacheri as a second species of Lartetotherium, together with L. sansaniense. This species presents several plesiomorphic states with respect to L. schleiermacheri such as characters 9^0 (presence of sagittal crest), 10^1 (postglenoid and posttympanic apophyses in contact), 11^0 (vertical occipital face), 18^0 (straight mandibular ventral profile), and 72^0 (narrow long bone epiphyses). In turn, L. schleiermacheri retains the plesiomorphic condition for characters 19 (short posterior edge of the symphysis), 36 (protocone of the upper premolars not constricted), and 53 (semilunate with ulnar facet), also plesiomorphic in Dicerorhinus. Both Lartetotherium species appear close to the extant Dicerorhinus (D. sumatrensis) in the first analysis (fig. 1, node 14), and to a lesser degree in the second one (fig. 2, node 19); in both cases Dicerorhinus appears characterized within the respective clades by reversals to the plesiomorphic states 5^0, 11^0, 36^0, 37^0, and 55^0.

The genus Punjabitherium is here considered the sister group of Rhinoceros, supported by both analyses (figs. 1, 2; tables 4, 5; nodes 17 and 20, respectively), contrary to Prothero and Schoch (1989: 536) who placed the former within the Rhinocerotoidea as incertae sedis. However, their relationship with respect to other rhinocerotines is still not well supported. In the first analysis (fig. 1, node 14), they appear as part of a polytomy together with two other subclades and the genus Dicerorhinus, while in the second analysis both are the sister group of Dicerorhinus, forming a monophyletic clade at node 19 (fig. 2). The current subtribe Rhinocerotina (Prothero and Schoch, 1989) is not supported by these analyses, since it gathers the genera Rhinoceros and Gaindatherium.

A group well supported by both analyses within Rhinocerotinae is that formed by the genera Paradiceros, Diceros, and Ceratotherium, the subtribe Dicerotina (Prothero and Schoch, 1989). In figure 1 (node 19) they constitute a trichotomy, while in figure 2 (nodes 22, 23), Diceros and Ceratotherium appear more closely related, sharing five syn-

apomorphies (fig. 2, node 23), concerning the constriction of the protocone (not constricted, plesiomorphic), the absence of trapezium facet on the McII, the flatness of the astragalar facet 1, and the strongly projected lateral epicondyle of the humerus.

Paradiceros shows characters 11^0, 55^0, 68^0, and 72^0 as plesiomorphic with respect to the two other dicerotines, and it is derived for characters 36^1 and 37^1 (protocone of upper teeth slightly constricted). The monophyly of these three genera is supported in any case, and the subtribe Dicerotina is thus maintained. The close relationship between Diceros and Ceratotherium is considered well supported, as shown in figure 2.

Other monophyletic clades can be established within the rhinocerotine group. In both analyses, a monophyletic clade gathers two smaller groups as a sister group of the subtribe Dicerotina. One of them (fig. 1, node 21) joins the genera Stephanorhinus and Coelodonta, and the other one (fig. 1, node 22) unites Ninxiatherium and Elasmotherium. This implies the separation of the elasmotheriine genera as currently considered. These four genera were previously placed in two different subtribes, Dicerorhinina and Elasmotheriina (Prothero and Schoch, 1989). Ninxiatherium was considered by these authors within Rhinocerotoidea as incertae sedis, although since its original description its relationships with the elasmotheriines were clearly established (Chen, 1977). Present results lead to a modification of both subtribes Elasmotheriina and Dicerorhinina. The group (Elasmotherium plus Ninxiatherium) appears to be much closer to other Rhinocerotini than to the Iranotherium group, which appears as a well-defined monophyletic group in both analyses (figs. 1, node 15; fig. 2, node 16). Elasmotherium and Ninxiatherium share five synapomorphies (11^0 and 49^0 as plesiomorphic, and 34^1, 35^1, and 37^2 as apomorphic). Character 7 (anterior border of the orbit) is apomorphic in both genera, but with state 1 in Elasmotherium (border over M3), and state 2 in Ninxiatherium (border behind M3). Similarly, character 39 appears with character state 1 in Ninxiatherium (enamel of the cheek teeth quite folded), and with character state 2 in Elasmotherium (very much folded). In this later feature Ninxiathe-

rium is coincident with the whole *Iranotherium* group. The separation of *Elasmotherium* from the other Miocene "elasmotheriines" is not so surprising, taking into account several features, such as the huge frontal horn or the extremely hypsodont teeth, that render this genus a very peculiar rhino. But it is not the same for *Ninxiatherium*, whose dental characteristics and the presence of a nasal horn are much closer to *Iranotherium*.

The main synapomorphy shared by (*Ninxiatherium* plus *Elasmotherium*) and (*Stephanorhinus* plus *Coelodonta*) refers to character 4 (nasal septum partially or totally ossified), while many of the other synapomorphies (table 4, node 20; table 5, node 24) are also shared by the *Iranotherium* group (table 4, node 15; table 5, node 16; 30^1, 38^2, 50^2, 61^1, 64^1), out of which *Ninxiatherium* has missing values for characters 50, 61, and 64.

There are also three other synapomorphies to be considered, which gather the subclades (*Ninxiatherium* plus *Elasmotherium*) and (*Stephanorhinus* plus *Coelodonta*) with the Dicerotina: 18^2 (convex ventral mandibular profile), 20^2 (ascending mandibular ramus inclined backwards), and 27^3 (absence of i2), although *Stephanorhinus* presents reversals for characters 18^0 and 20^1, and *Ninxiatherium* has missing values for the three characters. So the inclusion of *Ninxiatherium* in this group is really supported by the presence of nasal septum (4^1) as well as the derived state of character 6 (deep nasal opening) in contrast to the *Iranotherium* group. In summary, the closer relationship of *Ninxiatherium* to (*Coelodonta* plus *Stephanorhinus*) is more weakly supported than that of *Elasmotherium*. Further studies on this "elasmotheriine" group, especially on some Miocene remains from China and Spain (Cerdeño, in progress), will likely provide new data to establish more accurate relationships. The Miocene age of *Ninxiatherium* (Chen, 1977) implies an early acquisition of the nasal septum with respect to the other three Plio-Pleistocene genera. The development of the nasal septum may be an independent acquisition within two different evolutionary lineages if *Ninxiatherium* is proven to belong to the *Iranotherium* group.

At present the best known "elasmother-

iine" species is *Hispanotherium matritense* from Spain. Recent discoveries (Iñigo and Cerdeño, in prep.; unpubl. data) have greatly increased knowledge of this species, including the morphometrical variation within a large single population. Nevertheless, an important character is not yet clear, the presence of nasal or nasofrontal horn, that was established as a synapomorphy of the elasmotheriine group by Fortelius and Heissig (1989). Personal observation of the nasal fragments of *H. matritense* (unpubl. data) and "*Begertherium*" *grimmi* from Sofça (Turkey; Heissig, 1976: 29) did not reveal any rugosity that could demonstrate the existence of a horn, although Heissig (1976) included its presence as a diagnostic character of "*B.*" *grimmi*. The polytomy of the *Hispanotherium* clade (fig. 1, node 16; fig. 2, node 17) renders evident the very close relationships among them. It appears that "*Begertherium*" is characterized only by the apomorphic character 62^1 (calcaneum without tibial facet), which indirectly supports the suggested synonymy with *Hispanotherium* not only at the generic level (Antunes and Ginsburg, 1983; Cerdeño, 1989; and contrary to Fortelius and Heissig, 1989), but also at the specific level as stated by Iñigo and Cerdeño (in prep.). This synonymy would imply a possible sexual dimorphism regarding the presence of a horn, since *B. borissiaki* does have a well-developed nasal horn boss.

"*Beliajevina*" presents six apomorphies within the group at node 16 (fig. 1): absence of I1 (26^3), lateral facet of McII anteriorly and posteriorly developed (50^0), facet 1 of the astragalus with wide prolongation (58^2), facet 2 elongated to the proximal border (60^2), strong unevenness of the tuber calcis (65^1), and short laterodistal humeral epicondyle (67^0). These features support its separation from *Hispanotherium* and "*Begertherium*" (with character states 26^1, 50^2, 58^1, 60^1, 65^0, and 67^1), in agreement with Fortelius and Heissig (1989), although Iñigo and Cerdeño (in prep.) establish it just as a different species of *Hispanotherium*, keeping their synonymy at generic level. All these characters as well as most of the synapomorphies at node 16 (fig. 1, table 4) are missing data in *Iranotherium*.

The phylogenetic analysis of Fortelius and Heissig (1989) only dealt with the elasmo-

theriine (sensu lato) species. The synonymy of *Caementodon oettingenae* and *Hispanotherium matritense* was already justified (Cerdeño, 1989; Iñigo and Cerdeño, in prep.). Fortelius and Heissig (op. cit.: 227) identified two monophyletic clades of elasmotheriines, recognizable at a suprageneric level, but concluded that "to do so formally serves no useful purpose." Looking now at the global analysis of the family, this recognition seems to be useful, since the *Elasmotherium-Ninxiatherium* group appears quite well differentiated from the *Iranotherium* clade. So, the subtribe Elasmotheriina of Prothero and Schoch (1989) could be transformed into two. This view would really correlate with the old concept of the subfamilies Iranotheriinae and Elasmotheriinae (Kretzoi, 1943; Viret, 1958) being placed at a lower taxonomic level. However, this would not be real, since *Elasmotherium* and *Ninxiatherium* gather with other quite different genera in the present cladograms (figs. 1, 2). Trying to fit these results into a systematic classification, I propose the subtribe Iranotheriina (new rank) for the clade including *Iranotherium, Hispanotherium* (= *Begertherium*), and "*Beliajevina.*" *Elasmotherium* and *Ninxiatherium*, in turn, remain in the subtribe Elasmotheriina that also includes *Coelodonta* and *Stephanorhinus* as two different genus groups, but caution must be used with respect to *Ninxiatherium* as explained before.

The second large clade previously referred to (fig. 1, node 23; fig. 2, node 27) includes most taxa assigned to the subfamily Aceratheriinae. The basal node of this clade varies from one analysis to another and, as commented above, the inclusion of *Floridaceras* within the Aceratheriinae is considered better supported than within the Rhinocerotinae. The remaining aceratheres share six synapomorphies and two reversals (fig. 1; table 4, node 23): short nasal opening, upraised mandibular symphysis, ascending ramus inclined forward, large chisel-shaped I1, protocone of upper molars slightly constricted, metaconid of p2 not prolonged backward, vertical occipital face and astragalar facet 1 with narrow prolongation. The following node 24 (fig. 1; table 4) presents an apomorphy in character 26^3 (absence of I1) with respect to node 23, and it is also characterized by two reversals,

41^1 and 43^1 (weak labial cingulum on upper and lower premolars). *Hoploaceratherium,* in turn, presents six apomorphies for characters 1^1, 34^2, 35^2, 51^1, 58^2, and 64^1. Node 30 (fig. 1) unites the remaining genera, sharing five apomorphies and two reversals (table 4). *Acerorhinus* is apomorphic for character 41^2 (absence of labial cingulum on upper premolars), and presents reversals for 25^0 (presence of i1) and 42^0 (strong lingual cingulum on lower premolars).

The remaining aceratheres form a monophyletic group with two clades in the same way in both analyses (fig. 1, node 26; fig. 2, node 31). These two clades share two synapomorphies: strong unevenness of the tuber calcis (65^1) and wide long-bone epiphyses (72^1). The first clade (fig. 1, table 4, node 27) gathers *Chilotheridium* with *Alicornops* plus *Peraceras,* sharing the following synapomorphies: molarized premolars (34^2–35^2), and absence of tibial and fibular facets on the calcaneum (62^1–63^1). Within this clade, *Chilotheridium* has characters 1^2, 9^2, 11^1, 30^2 and 40^1 apomorphic, and characters 17^0, 18^0, and 41^0 as reversals. *Alicornops* and *Peraceras* share the moderate presence of cement on the cheek teeth (46^1) and the short but not massive metapodials (47^2), as well as the presence of a sagittal crest as a reversal (9^0). This monophyletic clade of three genera is proposed as the new tribe Alicornopini.

The other monophyletic clade (fig. 1, node 29; fig. 2, node 34), with *Aphelops, Chilotherium, Teleoceras, Prosantorhinus, Diaceratherium,* and *Brachypotherium,* includes most teleoceratines of the current classification (Prothero and Schoch, 1989) and two other aceratheriine genera, sharing the following synapomorphies: parietal crests clearly separated (9^2), postglenoid and posttympanic apophyses in contact (10^1), occipital outline roughly squared (12^1), brachycephalic skull (14^1), protocone of the upper premolars not constricted (36^1), facet 1 of the astragalus with wide prolongation (58^2), laterodistal epicondyle of the humerus well projected (68^1), and third trochanter of the femur very developed (69^1). Excluding *Aphelops,* the remaining teleoceratines are gathered at node 30 (fig. 1) with six synapomorphies among which the acquisition of short and massive metapodials (47^3) is unique within the Rhin-

ocerotidae. The others refer to: the great zygomatic width (13[1]), also present in *Peraceras*; the short posterior cingulum of M3 (32[1]) with reversal to the plesiomorphic state in *Diaceratherium* and *Brachypotherium*; the absence of lingual cingulum on lower premolars (42[2]) with reversal to state 1 (weak cingulum) in *Prosantorhinus*; the presence of a weak labial cingulum on lower premolars (43[1]) with two changes to apomorphic state 2 (absence) in *Chilotherium* and *Teleoceras*; and finally the high laterodistal epicondyle of the humerus (67[1]).

At node 31 (fig. 1; Table 4) the group shares the presence of a little horn on the tip of the nasals (1[1]), the presence of a third posterolateral facet on the scaphoid (52[2]), and a low and broad astragalus (55[2]). The presence of cement on the teeth is moderate (46[1]), as in *Peraceras* and *Alicornops,* and becomes abundant in *Teleoceras* (46[2]). *Prosantorhinus* is plesiomorphic for this character (46[0]). The group (fig. 1 , node 31) is also characterized by two additional reversals: the short nasal opening (6[0]) and the presence of i1 (25[0]).

The tribe Teleoceratini was included within the subfamily Rhinocerotinae by Prothero and Schoch (1989: 535), but not Heissig (1989: 406), who, in the same volume, grouped the teleoceratines with the aceratheres. The first authors clearly followed the previous opinion of Prothero et al. (1986) when they discussed Heissig's viewpoint. The present cladograms support the inclusion of the teleoceratines within the Aceratheriinae, and implies an extension of the tribe Teleoceratini to include *Aphelops* and *Chilotherium*.

Qiu et al. (1988) established a new tribe, Chilotherini, within Aceratheriinae, including *Acerorhinus* and *Chilotherium*. This view was not followed by Prothero and Schoch (1989), nor is it supported by the present analysis.

CONCLUSIONS

The cladistic analyses of the family Rhinocerotidae, using two subfamilies of Hyracodontinae and/or *Hyrachyus* as outgroups, show a basal polytomy which differs from one analysis to the other in the inclusion of *Te-*

letaceras together with the other Rhinocerotidae; *Teletaceras* is included when the three outgroups are considered, while it remains separated from the rest when only *Hyrachyus* is the outgroup.

The previous recognized subfamilies Diceratheriinae and Menoceratinae are not supported by the analyses, since their genera form paraphyletic groups.

The cladograms exhibit two main clades which roughly correspond to previous concepts of the subfamilies Rhinocerotinae and Aceratheriinae, with several exceptions. Within the former, the tribe Rhincerotini is modified: the new subtribe Iranotheriina is proposed, including some of the "elasmotheriine" taxa of previous classifications; the subtribes Elasmotheriina and Rhinocerotina are reconstituted; and the subtribe Dicerorhinina is not supported. *Punjabitherium* and *Ninxiatherium,* previously considered as Rhinocerotoidea incertae sedis, are included in the Rhinocerotini: the former as sister taxon to *Rhinoceros*, the latter as sister taxon to *Elasmotherium*. The subtribe Dicerotina is well supported in both analyses.

The suggested synonymy between "*Begertherium*" and *Hispanotherium* is supported, as well as the close relationship of the species "*Dicerorhinus*" *schleiermacheri* with the type species of the genus *Lartetotherium*, becoming *Lartetotherium schleiermacheri*. Other Miocene species usually ascribed to *Dicerorhinus* might belong to *Lartetotherium* as well.

The second main clade unites the acerathere and teleoceratine genera; so that the tribe Teleoceratini (with additional number of genera) is removed from the subfamily Rhinocerotinae, and included in the Aceratheriinae. A new tribe of aceratheres, Alicornopini, is proposed.

The phylogenetic relationships of the Rhinocerotidae lead to the classification listed below if the following conditions are met: (1) differences between the two analyses performed here, and (2) evident homoplasy of certain characters, as well as the incomplete knowledge of many taxa.

Family Rhinocerotidae Owen, 1845
    Teletaceras Hanson, 1989
    Trigonias Lucas, 1900

Penetrigonias Tanner and Martin, 1976
Ronzotherium Aymard, 1886
Mesaceratherium Heissig, 1969
Subhyracodon Brandt, 1878
Diceratherium Marsh, 1875
Pleuroceros Roger, 1898
Protaceratherium Abel, 1910
   (=*Plesiaceratherium*)
Menoceras Troxell, 1921
"F:AM 95544," new genus
   in Prothero (in press)
Subfamily Aceratheriinae Dollo, 1885
   Floridaceras Wood, 1966
   Aceratherium Kaup, 1932
   Hoploaceratherium
      Ginsburg and Heissig, 1989
   Acerorhinus Kretzoi, 1942
Tribe Alicornopini NEW
   Alicornops Ginsburg and Guérin, 1979
   Peraceras Cope, 1880
   Chilotheridium Hooijer, 1971
Tribe Teleoceratini Hay, 1902
   Prosantorhinus Heissig, 1974
   Diaceratherium Dietrich, 1931
   Brachypotherium Roger, 1904
   Teleoceras Hatcher, 1894
   Aphelops Cope, 1873
   Chilotherium Ringström, 1924

Subfamily Rhinocerotinae Owen, 1845
   Amphicaenopus Wood, 1927
   Aprotodon Forster Cooper, 1915
   Gaindatherium Colbert, 1934
   Lartetotherium Ginsburg, 1974
Tribe Rhinocerotini Owen, 1845
   Dicerorhinus Gloger, 1841
Subtribe Rhinocerotina Owen, 1845
   Punjabitherium Khan, 1971
   Rhinoceros Linnaeus, 1758
Subtribe Dicerotina Ringström, 1924
   Paradiceros Hooijer, 1968
   Diceros Gray, 1821
   Ceratotherium Gray, 1867
Subtribe Iranotheriina Kretzoi, 1943 (new
   rank)
   Hispanotherium Crusafont and Villalta,
   1947
   (= *Begertherium*; *Caementodon*)
   Beliajevina Heissig, 1974
   Iranotherium Ringström, 1924
Subtribe Elasmotheriina Bonaparte, 1845
   Group *Elasmotherium-Ninxiatherium*
   Ninxiatherium Chen, 1977
   Elasmotherium Fischer, 1808
   Group *Coelodonta-Stephanorhinus*
   Stephanorhinus Kretzoi, 1842
   Coelodonta Bronn, 1831

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