New Rhinocerotoids from the Oligocene of Nebraska

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Abstract

The rhinocerotoid *Penetrigonias hudsoni* gen. et sp. nov. differs from previously described rhinocerotoids in the unusual crown pattern developed on upper premolars two and three (P^2–P^3). The hypocones of these teeth are joined to the protocone by a narrow mure while the metaloph is more closely associated to the protocone than to the hypocone. A new species of *Hyracodon* is also described.

Introduction

The Chadronian deposits of North America have produced a varied rhinocerotoid fauna, which was reduced by Orellan times. *Toxotherium* and *Triplopides* are rare and appear to be exclusively Chadronian forms, while the remains of hyracodontids are relatively numerous and compose an important part of the Oligocene rhinocerotoid population. Study of the rhinocerotoid remains from the Oligocene of northwestern Nebraska has produced evidence that a new genus and two new species occur in these deposits.

Four species of *Hyracodon* have been described from Chadronian sediments: *Hyracodon priscidens, H. selenidens, H. petersoni* and *H. browni.* The holotype of *Hyracodon selenidens* Troxell has usually been assigned to the middle Oligocene

(Troxell, 1921). However, there is a titanothere tooth which should have been collected in association with the holotype since they carry the same number and associated data (YPM 1173, Fig. 1). There is also a maxilla of an old individual of *Hyracodon* and several rami in the University of Nebraska State Museum Study Collections which are from the Chadron Formation and are closely similar to *H. selenidens*. We are not aware of any definite post-Chadronian records of titanotheres and regard the associated titanothere tooth as evidence that *H. selenidens* is a Chadronian form. It has been placed in synonomy with *H. arcidens* by Sinclair (1922) and Wood (1927). Scott (1942) and Radinsky (1967, p. 30) regarded all described species of *Hyracodon* as synonyms of *H. nebraskensis* Leidy. The published descriptions indicate that both *H. arcidens* and *H. nebraskensis* are about 20 per cent larger than *H. selenidens* and both are geologically younger (Orellan?). In our opinion, *H. selenidens* is a valid species. We have not examined the type material of *H. browni*. This form was not illustrated and the complete absence of a metaloph as listed in the diagnosis is not approached by any hyracodontid with which we are familiar. *Hyracodon petersoni* is probably a synonym of *H. priscidens*, but it is about 15 per cent smaller and the name might be retained at the subspecific level. *H. selenidens* seems ancestral to the larger *H. arcidens minimus* Troxell of the middle Oligocene. Examination of several hundred jaws of early to late Oligocene *Hyracodon* in the University of Nebraska State Museum suggests that later species of *Hyracodon* tend to be larger than Chadronian forms and no examples as small as *H. selenidens* were found from Orellan or later sediments.

A new species of Chadronian hyracodontid is described here in which P^4 is molariform, and is similar in that respect to *Epitriplopus*. The new species differs from that genus in having the protocone on the molars constricted. However, it is not impossible that *Epitriplopus* may have given rise to the Chadronian species through an advanced form such as *E. medius*. The constriction of the protocone found in *Hyracodon* (Radinsky, 1967) seems to be a progressive feature which may have occurred independently in several lineages.

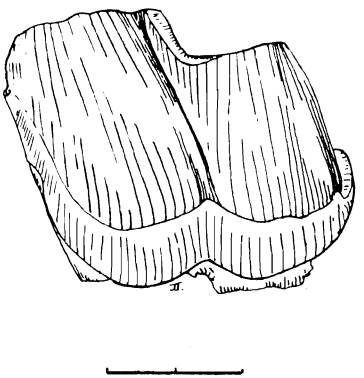

Fig. 1 Titanothere left lower molar, buccal view, YPM 1173. Scale = 20 mm.

Systematics

Class Mammalia
Order Perissodactyla
Superfamily Rhinocerotoidea
Family *Incertae sedis*

Penetrigonias, gen. nov.

Etymology
From Latin *paene* ("near") *Trigonias* (a genus of Oligocene rhinocerotoid with a P^4 similar to that of *Penetrigonias*).

Type Species
Penetrigonias hudsoni sp. nov.

Generic Diagnosis
About 12 per cent larger than *Hyracodon priscidens petersoni* Wood; premolars brachydont; external cingula absent; internal cingula very heavy; metaloph attached to protocone on P^{2-4}; hypocone attached to protocone by a thin spur, and closely adpressed to the internal cingulum on each tooth.

Discussion
The familial affiliations of *Penetrigonias* are at the present uncertain. It is similar to the Hyracodontidae in its small size and general overall resemblance to the Hyrachyidae which we regard as the ancestral stock of the hyracodontids. *Penetrigonias* can be separated from *Hyracodon* by its more brachydont teeth; lack of distinct external cingula on P^{2-4}; heavy internal cingula on these teeth; association of the metaloph with the protocone rather than the hypocone; and the small tear-shaped hypocones which are closely adpressed to the internal cingula. The crown pattern of P^4 resembles that of some species of *Subhyracodon*, while the P^3 of *Trigonias gregoryi* shows similarity to that of *Penetrigonias*. However, none of the Oligocene Rhinocerotidae known to the writers approaches the very small size and combination of tooth characters in *Penetrigonias*; thus close relationship with that family seems unlikely.

In comparison to other Oligocene rhinocerotoids, *Penetrigonias* has retained a very primitive premolar pattern. It is only a more hypsodont state of the pattern found in some species of *Hyrachyus* (Fig. 2c). This pattern is approached in some Eocene amynodonts and, together with the very heavy internal cingulum, might tend to support a tentative assignment to that family. However, P^2 in *Penetrigonias* is less reduced than P^2 of even the Eocene amynodonts and has a prominent mesial interstitial wear facet so that P^1 must have been well-developed. *Penetrigonias* may also be separated from the described species of *Metamynodon, Megalamynodon, Amynodontopsis* and *Amynodon* by its small size and tear-shaped hypocones. The Asiatic Eocene amynodont *Caenolophus* differs from *Penetrigonias* in that: cingula are not as well developed on the premolars; hypo-

cones are not developed on P^{3-4}; and the medial valley of P_4 is open. It is apparently part of a middle to late Eocene radiation that led to a group of miniature rhinocerotoids with tooth characters resembling those of the amynodonts. *Toxotherium*, which is known from the lower Oligocene of Wyoming, Texas, and Saskatchewan, may be a related genus. The upper dentition of *Toxotherium* is presently unknown. *Penetrigonias hudsoni* is larger than any of the described species of *Toxotherium*, but additional specimens are required to establish the degree of relationship between the two forms. Skinner and Gooris (1966, p. 10) point out that the lower dentitions of *Toxotherium* lack well-developed cingula and that it is unlikely that they would go with an upper dentition that has strong cingula. This might also serve to exclude *Penetrigonias* from *Toxotherium*.

Penetrigonias hudsoni sp. nov.

Fig. 2A, B

Etymology

Named in honour of the late William F. Hudson of Crawford, Nebraska.

Holotype

Left P^{2-4}, UNSM. 62049 (Fig. 2, A-B).

Hypodigm

Type only.

Type Locality

UNSM. Coll. Loc. SX–41 (Sec. 5, T. 33 N., R. 53 W.), located in the central portion of the Chadron Flats north of Toadstool State Park, approximately 26 mi (= 41 km) northwest of Crawford, Sioux County, Nebraska.

Stratigraphic Occurrence

Oligocene, White River Group, upper part of the Chadron Formation.

Specific Diagnosis

Same as for genus.

Description

A small rhinocerotoid with brachydont teeth; P^{2-4} lacking external cingula, but with strong internal cingula; P^2 square with protoloph confluent with a large protocone; protocone with a thin connection to the hypocone; hypocone isolated when unworn and abutting on internal cingulum in P^{2-4}; P^3 squared; metaloph connected to protocone by a thin mure; hypocone joined to protocone by a narrow connection; P^4 subtriangular; metaloph confluent with protocone; hypocone present as a small spur from protocone; parastyles and postfossettes present on P^{2-4}; ectolophs of teeth with "tartar" deposits.

Discussion

The two hyracodontids closest both geographically and temporally to *P. hudsoni* are *Hyracodon priscidens petersoni* and *H. selenidens*. Comparison of the holotypes of these two forms (CM 3572 and YPM 1173 respectively) indicate that they both differ from *Penetrigonias hudsoni* in that: they are smaller; they are more hypsodont; their metalophs are more closely associated with the hypocone than with the protocone; their protocones are not isolated cusps before wear; and they have external cingula and lighter internal cingula.

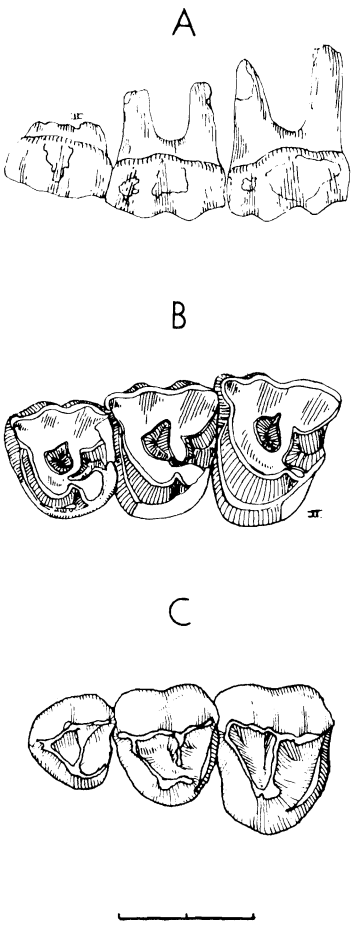

Fig. 2 A–B *Penetrigonias hudsoni*, gen. et sp. nov., holotype, UNSM 62049, left P^{2-4}. Scale = 20 mm.
A. Buccal view.
B. Crown view.
C. *Hyrachyus* sp., UNSM 62099, left P^{2-4}, crown view.

Family Hyracodontidae

***Hyracodon doddi*, sp. nov.**
Fig. 3

Etymology
Named in honour of the late Howard Dodd of Crawford, Nebraska.

Holotype
A right maxilla with P^4-M^2, UNSM. 11066 (Fig. 3A, B).

Hypodigm
Type and one referred specimen, UNSM. 62072 (Fig. 3C).

Type Locality
UNSM Coll. Loc. sx-29, Twin Buttes, 7¾ mi (= 12.5 km) north, 5½ mi (= 9 km) west of Crawford, Sioux County, Nebraska.

Stratigraphic Occurrence
Oligocene, White River Group, Chadron Formation, 18 ft (5.5 m) below the Upper Purplish White Layer (Schultz and Stout, 1955).

Specific Diagnosis
About 13 per cent larger than *Hyracodon priscidens petersoni* Wood and *H. selenidens* Troxell; external cingula on P^4-M^2 restricted to posterior parts of teeth; P^4 molariform with medial valley opening medially (not posteriorly as in *H. priscidens*).

Description
Maxilla slightly smaller than in most *Hyracodon nebraskensis* Leidy; P^4 with metaloph and protoloph straight as in molars, leaving the medial valley open; small antecrochet on protoloph; internal cingulum about as in *H. priscidens petersoni*; protoloph longer than metaloph on P^4 making tooth subtriangular; protocones on P^4-M^2 constricted; cristae, parastyles, postfossettes and antecrochets present on P^4-M^2.

Discussion
Hyracodon doddi is unusual for a Chadronian hyracodontid in having a molariform P^4, a condition that is absent in about 50 maxillae of other species of *Hyracodon* from late Orellan or older deposits examined by us. *Hyracodon doddi* was compapred with referred material of *H. apertus* Sinclair and the holotype of *H. leidyanus* Troxell (YPM 11169) both of which have molariform P^4's. However the younger species are about 20 per cent larger than *H. doddi*. The holotype of *H. arcidens minimus* Troxell (YPM 1174) and *H. selenidens* Troxell have the medial valley of P^4 closed by the protoloph and *H. arcidens minimus* is larger than *H. doddi*. The holotype of *H. priscidens petersoni* Wood (CM 3572) differs from *H. doddi* in having the medial valley opening to the rear on P^4, the metaloph shorter and the protoloph confluent with the hypocone. *Hyracodon doddi* resem-

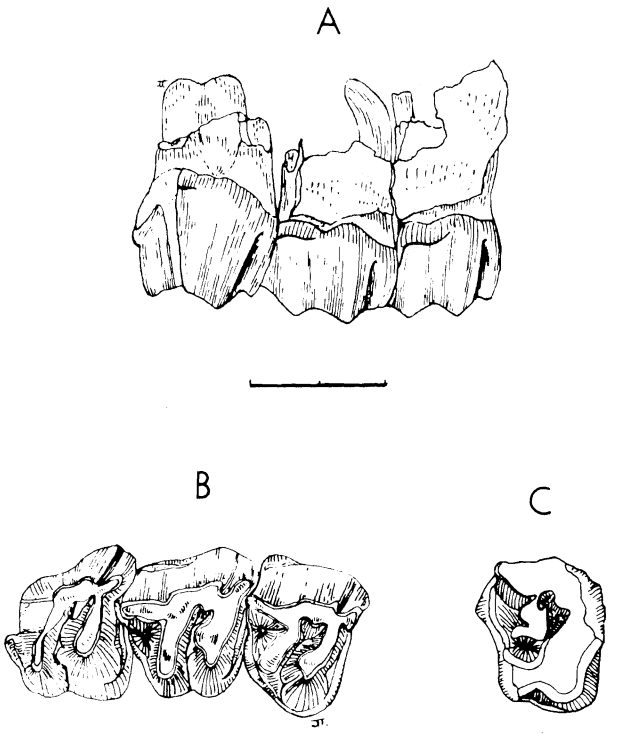

Fig. 3 *Hyracodon doddi*, sp. nov., holotype, UNSM 11066, right P^4–M^2.
A. Buccal view.
B. Crown view. Scale = 20 mm.
C. Referred specimen, UNSM 62072, crown view slightly enlarged.

bles closely the late Eocene *Epitriplopus medius* Peterson from the Duchesne Formation of Montana. It differs in having a constricted protocone on the molars. *Epitriplopus medius* also lacks the prominent external cingulum on P^4 and is much smaller.

In 1964, a specimen was collected from the Chadron Formation at UNSM Coll. Loc. DW-107 a few miles east of the type locality of *H. doddi*. The size and proportions of this tooth, UNSM 62072 (Fig. 3C), suggest that it may be a P^3 of *H. doddi*. The ectoloph is broken off the tooth, as is a portion of the hypocone. The protoloph is large and continuous with the hypocone. The protocone and hypocone are connected by a thick mure. The metaloph is short so that the medial valley opens posteriorly to the rear, but additional wear would seal off the medial valley and isolate a lake just posterior and lingual to the medial valley. The metaloph is posteriorly directed and slightly folded on itself; it bears a labially directed crochet which isolates a small lake posterior and labial to the medial valley. A postfossette

and internal cingulum are present. The tooth is brachydont, and from a mature but not old individual.

This tooth is smaller and more complicated than that of any of the caenopine rhinocerotoids known to the writers, but it does resemble P^3's of a few species, notably *Trigonias hypostylus*, although that species is much larger.

For tooth measurements of *Penetrigonias hudsoni* and *Hyracodon doddi*, see Table 1.

Table 1. Maximum measurements of tooth diameters (mm) in *Penetrigonias hudsoni* and *Hyracodon doddi*.

Species	Width	Length
Penetrigonias		
P^2	17.4	13.2
P^3	18.8	16.0
P^4	22.5	15.2
Hyracodon		
M^1	22.1	15.3
M^2	20.5	16.4
M^3	22.6	broken

Summary and Conclusions

The taxonomic position of *Penetrigonias* is uncertain and the placement of *Hyracodon doddi* in *Hyracodon* is largely a matter of convenience and may not correctly reflect its relationships. The hyracodonts seem to be a primitive stem-group of rhinocerotoids which have become a depository for primitive forms or, as in the present case, forms known from fragmentary materials. One possible interpretation of the phylogenetic relationships of these forms is shown in Figure 4. If this arrangement is correct, *Penetrigonias* and *Toxotherium* should be placed in a separate family, and *Hyracodon doddi* may belong in *Epitriplopus*. However, until better materials are available it seems useful to retain the more conservative classification in the text of this paper.

Penetrigonias, Toxotherium, Triplopides and *Hyracodon* represent a continuance of a middle and late Eocene radiation of diminutive browsing rhinocerotoids, which were in competition with the early horses. This competition continued unsuccessfully for *Hyracodon* during the Oligocene.

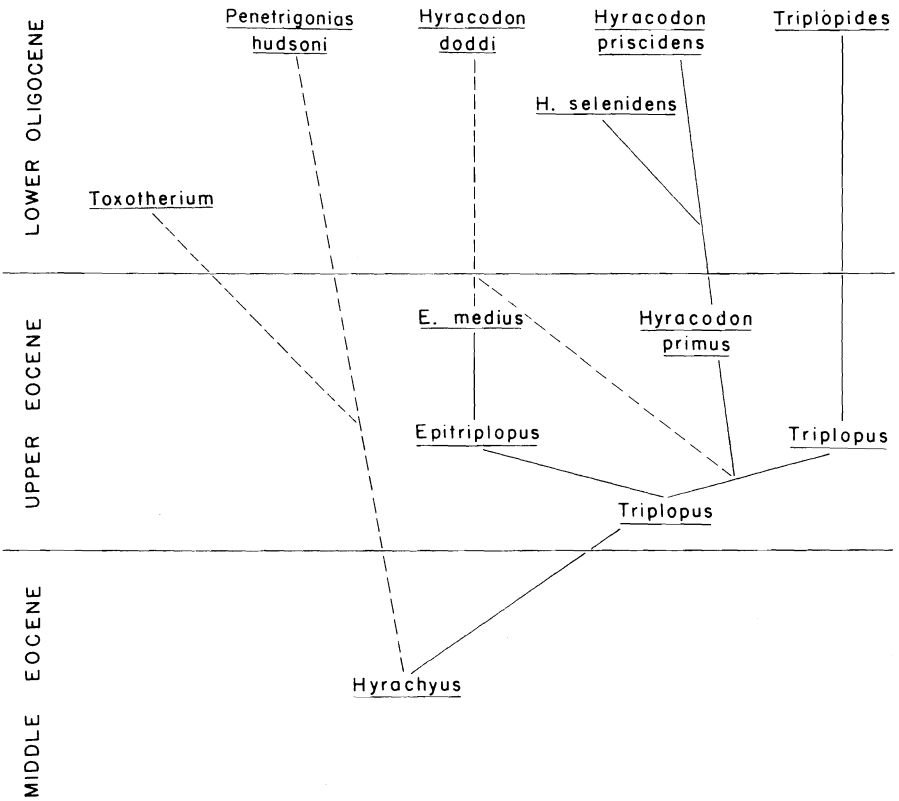

Fig. 4 Chart showing phylogenetic relationships of the Upper Eocene and Lower Oligocene small rhinocerotoids in North America (partly modified after Radinsky, 1967).

Acknowledgments

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