A REVIEW OF THE RHINOCEROTOID FAMILY HYRACODONTIDAE (PERISSODACTYLA)

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CONTENTS

INTRODUCTION

DURING THE EARLY and Middle Eocene in North America and Asia, ceratomorph perissodactyls underwent an extensive evolutionary radiation, based primarily, as far as the available evidence indicates, on differences in molar cusp patterns and in body size. Two groups emerged from this radiation at the beginning of the Late Eocene with the complex of tooth characters diagnostic of the superfamily Rhinocerotoidea: long molar metacones, small parastyles, high paralophids and metalophids, and no M_3 hypoconulid. One group, the family Amynodontidae, consisted mainly of large, heavy-bodied forms with canine tusks and short facial regions. The second group, the family Hyracodontidae, consisted of small to large, basically cursorial animals, one of the earliest of which (*Triplopus*) had a tridactyl manus.

Cheek tooth morphology was fairly stable in the Hyracodontidae (as well as in other ceratomorph families), and the main evolutionary changes in this area consisted of the molarization of the premolars, the loss of the M^3 metacone, and an increase in tooth height. These changes took place independently and sporadically in different hyracodontid lines. Greater experimentation, as far as the dentition is concerned, occurred in the incisors and canines, and by the Oligocene several different types of anterior dentition were present in non-amynodontid rhinocerotoids. One specialization consisted of an enlarged, chisel-like I^1 which sheared against a lanceolate, procumbent I_2. The rhinocerotoids with this adaptation gave rise to an extensive Middle and Late Tertiary radiation which comprises the family Rhinocerotidae. Some Oligocene rhinocerotoids with different anterior dental specializations were classified in the Rhinocerotidae. However, to provide a more natural rhinocerotoid classification, I have recently (Radinsky, 1966) restricted the family Rhinocerotidae to those forms with the above-mentioned incisor specialization, and have transferred the genera with other anterior dental specializations to the Hyracodontidae. This arrangement leaves the Rhinocerotidae as a monophyletic group. The Hyracodontidae, as herein delimited, includes several relatively short-lived lines, all of which were extinct by the end of the Oligocene.

The classification of the Hyracodontidae that I encountered at the beginning of this study was badly over-split on specific and generic levels. The basic reason for this situation is the typological attitude, or lack of appreciation of intraspecific variation, apparent in the taxonomy of most of the previous workers in this area. In addition, the scarcity and incomplete nature of the remains of many hyracodontid genera have led to unnecessary proliferation of names. In this review, I have followed, where applicable, the rule of Ockam's razor; that is, I recognize separate taxa only when they can be shown to be distinct. Thus I believe that the burden of proof should rest with those who would separate taxa. The disadvantage of this approach in the Hyracodontidae is that the cheek teeth are relatively conservative, and, in the absence of information about the anterior dentition, some distinct groups may be lumped. However, I believe that the advantage gained, which is, on the whole, a more realistic picture of the evolutionary history of the group, outweighs the possible obscuring of some phylogenetic branchings.

DEFINITIONS

The term "non-molariform" is used here to refer to upper premolars lacking two lingual cusps; "submolariform," to premolars with two lingual cusps but in which those cusps (protocone and hypocone) are close together; and finally, "molariform," to premolars in which the protocone and hypocone are separated and the medial valley is open lingually.

The M^3 ectoloph extends posteriorly past the metaloph in primitive hyracodontids, whereas in several advanced genera the M^3 ectoloph is confluent with the metaloph. To simplify descriptions I have referred to the posterior extension of the ectoloph of M^3 as the metacone.

I have described hyracodontids with molar series from about 30 mm. to 60 mm. in length as small; those with molar series of 60 mm. to 100 mm. as medium-sized; those with molar series of 100 mm. to 150 mm. as large; and

those with molar series of more than 150 mm. in length as gigantic. For comparisons of relative tooth height, I have used an index of unworn M^3 paracone height (measured from the base of the enamel) divided by M^3 width; this is referred to as the crown height index.

ACKNOWLEDGMENTS

ABBREVIATIONS

A.M.N.H., the American Museum of Natural History

C.M., Carnegie Museum

C.N.H.M., Field Museum of Natural History (formerly Chicago National History Museum)

M.S.U., Montana State University, Missoula

P.I.N., Paleontological Institute, Moscow

P.U., Princeton University

U.C.M.P., University of California Museum of Paleontology, Berkeley

U.F.H., Utah Field House of Natural History, Vernal

U.S.N.M., United States National Museum, Smithsonian Institution

U.W., University of Wyoming, Laramie

Y.P.M., Peabody Museum of Natural History, Yale University

L, anteroposterior length

W, labiolingual width

mm., millimeters (all measurements are given in millimeters)

N, number of specimens included in sample

O.R., observed range

M, mean and its standard error

s, standard deviation

V, coefficient of variation

FAMILY HYRACODONTIDAE COPE, 1879

TYPE GENUS: *Hyracodon* Leidy, 1856.

INCLUDED GENERA: Type genus and *Triplopus* Cope, 1880 (including *Prothyracodon, Eotrigonias,* and *Ephyrachyus*); *Forstercooperia* Wood, 1939 (including *Pappaceras* and *Juxia*); *Prohyracodon* Koch, 1897; *Epitriplopus* Wood, 1927; *Triplopides,* new genus; *Ardynia* Matthew and Granger, 1923 (including *Ergilia* and *Parahyracodon*); *Allacerops* Wood, 1932 (? = *Ronzotherium* Aymard, 1854; ? = *Eggysodon* Roman, 1911); *Urtinotherium* Chow and Chiu, 1963; *Paraceratherium* Cooper, 1911 (including *Baluchitherium, Aralotherium,* and *Benaratherium*); and (or including) *Indricotherium* Borissiak, 1915.

RANGE: Late Eocene to Late Oligocene of North America, Asia, and Europe.

DIAGNOSIS: Small to gigantic, basically cursorial rhinocerotoids. $I\frac{3-1}{3-1}$, $C\frac{1-0}{1-0}$, $P\frac{4-3}{4-3}$, $M\frac{3}{3}$. Hornless. Incisors spatulate or pointed, approximately equal-sized or increasing in size anteriorly. Premolars non-molariform to molariform. M^3 roughly triangular, with or without a small, lingually deflected vestige of the metacone.

DISCUSSION: *Triplopus cubitalis,* one of the oldest known hyracodontids, has a tridactyl manus, as do the other, later, hyracodontid genera in which the manus is known. However, that condition of the manus should not be considered diagnostic of the family, for some Late Eocene, non-amynodontid rhinocerotoid must have retained a tetradactyl manus, since that is the condition in *Trigonias* and *Epiaceratherium,* the oldest (Early Oligocene) rhinocerotids. Because the characteristic rhinocerotid incisor specialization is so primitive in *Epiaceratherium,* we may assume that its Late Eocene ancestor lacked that specialization, and therefore would be considered a hyracodontid. Also, the manus is unknown and may have been tetradactyl in the oldest species of *Forstercooperia.* It is possible that the Hyracodontidae, as here conceived, is a polyphyletic group, including two or more lines which independently achieved the rhinocerotoid condition.

TRIPLOPUS COPE, 1880

Hyrachyus: COPE, 1873 (not Leidy, 1871).
Hyrachyus: SCOTT AND OSBORN, 1887 (not Leidy, 1871).
Prothyracodon SCOTT AND OSBORN, 1887.
Caenolophus: MATTHEW AND GRANGER, 1925 (part).
Eotrigonias WOOD, 1927.
Ephyrachyus WOOD, 1934.

TYPE SPECIES: *Triplopus cubitalis* (Cope, 1880).

INCLUDED SPECIES: Type and *T. obliquidens* (Scott and Osborn, 1887); *T. implicatus* (Cope, 1873), new combination; *T. rhinocerinus* (Wood, 1927), new combination; *T.? proficiens* (Matthew and Granger, 1925), new combination; and *T.? progressus* (Matthew and Granger, 1925), new combination.

RANGE: Late Eocene of North America and ?Asia.

REVISED DIAGNOSIS: Small hyracodontids: length of M^{1-3}, in various species, ranging from about 30 mm. to 50 mm. Crown height index averaging 0.61. Dentition unreduced. Incisors approximately equal-sized and spatulate. Premolars non-molariform to submolariform. M^3 with small metacone. Manus tridactyl.

DISCUSSION: Cope (1880, p. 383) named the genus *Triplopus* for a small rhinocerotoid from the Washakie Basin, Wyoming. As the name implies, the feature that Cope considered diagnostic of the genus is the presence of only three toes on the front foot.

Seventeen years later Scott and Osborn (1887, p. 260) erected the genus *Prothyracodon* for a maxillary fragment with P^4-M^2 from the Uinta Basin, Utah, which they considered to be intermediate between *Hyrachyus* and *Hyracodon.* In that paper Scott and Osborn made no mention of *Triplopus.* Two years later, Osborn (1889, p. 525) compared the Uinta Basin species with Washakie Basin *Triplopus* and concluded that *Prothyracodon* was a synonym of *Triplopus.* Osborn (*ibid.,* p. 528) considered *Triplopus* to be transitional in both foot structure and dentition between Middle Eocene *Hyrachyus* and Oligocene *Hyracodon.*

7

In 1919, Peterson (p. 131) resurrected the genus *Prothyracodon*, distinguishing it from *Triplopus* mainly on the basis of dental characters possessed by a new species of Uinta Basin rhinocerotoid which Peterson assigned to *Prothyracodon* under the name *P. uintense*. However, Peterson did distinguish the type species of *Prothyracodon*, *P. obliquidens*, from the type species of *Triplopus*, *T. cubitalis*, by its larger size and relatively shorter forelimb. Peterson considered *Prothyracodon obliquidens* to be ancestral to *Hyracodon*, and *P. uintense* and *Triplopus cubitalis* to represent independent side lineages.

In 1927, in a major work on Early Tertiary rhinocerotoids, Wood placed *Prothyracodon uintense* Peterson in a new genus, *Epitriplopus*, but retained the name *Prothyracodon* for *P. obliquidens*. Wood distinguished *Prothyracodon* from *Triplopus* by the following characters: ". . . the ratios in the front leg, the presence of internal cingula on the molar protocones, the absence of an ossified auditory bulla, the absence of cristae, the much greater progressiveness of P², the greater progressiveness of P⁴, the greater reduction of the posterior buttress of M³" (Wood, 1927, p. 185).

Wood's (*ibid.*) paper was the last work that compared *Prothyracodon* with *Triplopus*. The classification of Simpson (1945, p. 141) and the comprehensive surveys of Viret (1958, p. 432) and Gromova (1962, p. 317) all listed *Prothyracodon* as a distinct genus. After examining all known specimens of *Triplopus cubitalis* and *Prothyracodon obliquidens*, I have come to the conclusion that Osborn was right in 1889 in placing *Prothyracodon* in synonymy with *Triplopus*. Most of the characters cited by previous authors as diagnostic of *Prothyracodon* are invalid, and the remaining ones I consider indicative of specific separation only.

Prothyracodon obliquidens is *not* distinguished from *Triplopus cubitalis* by the following characters: (1) The presence of cingula internal to molar protocones. The development of lingual cingula on molar protocones is extremely variable in *P. obliquidens*. Only one specimen, A.M.N.H. No. 1917, possesses them on all three molars; in most specimens lingual cingula are absent from the molar protocones. (2) The absence of an ossified auditory bulla. An ossified auditory bulla is known in only one specimen of *Triplopus cubitalis*,

A.M.N.H. No. 5095. It is a thin sheet of bone that covers only half of the petrosal as seen in ventral view, and apparently it is only loosely attached to the skull. It would be preserved only under the most favorable conditions of burial and fossilization. In the two specimens of *Prothyracodon obliquidens* that include the ear region, no tympanic bone is preserved in one, C.M. No. 3201, and in the other, C.M. No. 11957, on one side only fragments of an ossified tympanic bulla appear to be present. (3) The absence of cristae. In the one specimen of *Triplopus cubitalis* with upper molars, A.M.N.H. No. 5095, a crista can be seen on M¹ but appears to be absent from M² and M³. The presence or absence of an M¹ crista can be ascertained definitely in only two specimens of *Prothyracodon obliquidens*: it is present in C.M. No. 11957 and absent from U.F.H. No. 138. (4) The greater reduction of the posterior buttress (= metacone) of M³. The degree to which the M³ metacone is reduced in *Prothyracodon obliquidens* is variable; in most specimens it is *not* more reduced than in *Triplopus cubitalis*.

Prothyracodon obliquidens does differ from *Triplopus cubitalis* in having a relatively shorter forearm. In A.M.N.H. No. 5095, the only specimen of *T. cubitalis* that preserves the radius and humerus, the radiohumeral index is about 1.35. It should be noted that A.M.N.H. No. 5095 is a juvenile individual; the radiohumeral index would probably average lower in adults of the species. The radius and humerus are preserved in only one specimen that can be assigned definitely to *Prothyracodon obliquidens*, P.U. No. 11224. In this individual the radiohumeral index is 1.09. C.M. No. 2942, a specimen referred by Peterson (1919, p. 132) and Wood (1927, table 7) to *Prothyracodon obliquidens*, has a radiohumeral index of 1.04. This specimen may represent *P. obliquidens*, but, since it lacks dentition, its assignment cannot at present be verified. On the basis of this evidence it appears that the forearm of *Prothyracodon obliquidens* was not so elongate relative to the humerus as it is in *Triplopus cubitalis*. However, the degree of difference does not justify, in my opinion, generic separation of the two species.

The only other features in which *Prothyracodon obliquidens* is known to differ from *Triplopus cubitalis* are its slightly larger size and

more advanced premolars. In *T. cubitalis*, P² is very narrow, with hardly more than cristae representing protoloph and metaloph, whereas in *P. obliquidens* both lingual lophs are well developed on P². In *T. cubitalis* P³⁻⁴ protoloph and metaloph (preserved only in A.M.N.H. No. 5095) are equally prominent and fused into a U-shaped loop, but in six of nine specimens of *P. obliquidens* the protoloph is more prominent than, and extends posteriorly past, the metaloph. However, since the *T. cubitalis* P³⁻⁴ condition is essentially duplicated in some of the *P. obliquidens* specimens (A.M.N.H. No. 1972, C.M. No. 2336, and P.U. No. 11224), and in view of the overwhelming similarities in molar pattern, I do not consider the differences in premolar structure indicative of generic separation. Therefore I here place *Prothyracodon* once again into synonymy with *Triplopus*.

In 1927, Wood (p. 188) erected the genus *Eotrigonias* for two new species of rhinocerotoids: the type, *E. rhinocerinus*, from the Uinta Basin, and a referred species, *E. petersoni*, from the Washakie Basin. The following characters are listed in Wood's generic diagnosis: P⁴ protoloph curves posteriorly past the metaloph and bears a lingual groove indicating incipient separation of a hypocone; M¹⁻³ with small parastyles, virtually no lingual cingula; M¹ metacone with an external cingulum; no crista on M³. Most of these differences do not distinguish *Eotrigonias rhinocerinus* from *Triplopus cubitalis*. The only differences that I note between the two species are the larger size, more advanced premolars, and more reduced M³ metacone in *E. rhinocerinus*. The difference in size is about 35 per cent; P³⁻⁴ of *E. rhinocerinus* are non-molariform and resemble those teeth in *T. obliquidens*, but P² is submolariform and only slightly more advanced than in the latter species; the M³ metacone is more reduced than in *T. cubitalis* and in most but not all specimens of *T. obliquidens*. *Eotrigonias petersoni* is even less different from *Triplopus cubitalis*, having a more prominent metacone on M³ and, presumably, a P² less advanced than that of *E. rhinocerinus*.

The differences that exist between *Eotrigonias rhinocerinus* and *E. petersoni*, on the one hand, and *Triplopus cubitalis* and *T. obliquidens*, on the other, do not, in my opinion, justify retention of a separate genus for the first two species. A similar conclusion was reached by Matthew (1932, p. 413) and Scott (1945, p. 248). Scott kept the two genera apart provisionally, pending further information. However, in the absence of adequate evidence that the two genera are distinct, I recognize only one. I therefore here transfer *E. rhinocerinus* and *E. petersoni* to the genus *Triplopus*, thus making *Eotrigonias* a synonym of *Triplopus*.

Wood (1934, p. 232) erected the genus *Ephyrachyus* for *Hyrachyus implicatus* Cope, 1873, from the Washakie Formation, and included in that genus *Ephyrachyus cristalophus* Wood, 1934, from the Bridger Formation. *Ephyrachyus cristalophus* falls within the range of variation of *Hyrachyus* (Radinsky, MS), but the type of *E. implicatus*, A.M.N.H. No. 5078, appears to represent a primitive variant of *Triplopus*. Had A.M.N.H. No. 5078 been found in the Bridger Formation it would have been considered an advanced variant of a small species of *Hyrachyus*, for it lacks the labial half of M³, which is critical for distinguishing advanced *Hyrachyus* specimens from primitive *Triplopus*. Since A.M.N.H. No. 5078 was found in the Washakie Formation, in which no *Hyrachyus* of that size occurs, and since it falls within the size range and, in known features, the range of dental variation of the large species of *Triplopus* in that formation (see p. 12), I hereby assign *E. implicatus* to *Triplopus*. *Ephyrachyus* thus becomes a synonym of *Triplopus*.

Two species of rhinocerotoids from the Late Eocene of Asia, currently assigned to the genus *Caenolophus*, closely resemble North American species of *Triplopus*. The genus *Caenolophus* was erected by Matthew and Granger (1925b, p. 6) to receive three species of small rhinocerotoids from the Late Eocene Shara Murun beds of Inner Mongolia: *C. promissus*, *C. obliquus*, *C. progressus* (named in that order). No type species was designated for *Caenolophus*, but the generic diagnosis includes cusp features of P⁴ that apply only to the first two species (P⁴ is not known for *C. progressus*). Thus, following what was apparently the intent of Matthew and Granger (and which agrees with page priority), I designate *C. promissus* as the type species of *Caenolophus*.

Matthew and Granger (1925b) considered

Caenolophus a hyracodontid rhinocerotoid, and this assignment was followed by all later authors. However, it is obvious from the characteristic quadratic pattern of M^3, long M^2, and the posterolingually directed metaloph of P^4 that *Caenolophus promissus* and *C. obliquus* are actually amynodontid rhinocerotoids. *Caenolophus progressus*, on the other hand, has a triangular M^3 which closely resembles that of *Triplopus*, indicating that it cannot be included in the genus *Caenolophus*.

Caenolophus progressus is known only from M^{1-3} and M_{2-3} which closely resemble those teeth in *Triplopus cubitalis* (see text fig. 7). The only evident differences are the more pinched paracone and more reduced metacone on M^3 and the apparently longer M^2 in *C. progressus*. (In these features *C. progressus* resembles some specimens of *T. obliquidens*.) Also, M^2 of *C. progressus* has a crochet, the presence or absence of which cannot be determined in *T. cubitalis*. All things considered, the similarities between these two species are great enough to suggest that they might be congeneric. However, in view of our scanty knowledge of *C. progressus*, I refer it only provisionally to *Triplopus*.

A fourth rhinocerotoid species, from the Late Eocene Irdin Manha beds of Inner Mongolia, was assigned by Matthew and Granger (1925c, p. 7) to *Caenolophus* under the name *C. proficiens*. At the Irdin Manha locality, *C. proficiens* is known mainly from the lower dentition, and only a fragment of M^3 is preserved. The lower premolars are unreduced in number and length, which suggests that *C. proficiens* is not an amynodontid rhinocerotoid. A form that is at least congeneric and possibly conspecific with *C. proficiens* occurs in the slightly older Ulan Shireh beds in the Shara Murun region of Inner Mongolia and provides knowledge of the upper dentition. The M^3 is triangular and resembles that of *Triplopus* (see text fig. 6), thus supporting the evidence of the lower dentition that *C. proficiens* should be removed from *Caenolophus*.

The upper cheek teeth of the Ulan Shireh form are slightly more primitive than those of most specimens of *Triplopus* in having a less reduced M^3 ectoloph, larger molar parastyles, and more convex P^{2-4} metacones. However, considerable variation exists in these features in even the few specimens that are known of the Asiatic species, and there is overlap with *Triplopus*, especially *T. implicatus*. In view of the general similarity between *C. proficiens* (including its Ulan Shireh relative) and *Triplopus* species, and in consideration of our ignorance of the range of dental variation and skeletal morphology of the Asiatic species, it seems best at present to assign *C. proficiens* provisionally to *Triplopus*.

Triplopus differs from the Middle Eocene helaletid tapiroid *Hyrachyus* (Radinsky, MS) in having smaller and more lingually deflected M^3 metacones, smaller molar parastyles and more pinched paracones, and, in general, slightly higher and narrower lophs. These features readily distinguish later species of *Triplopus*, such as *T. obliquidens* or *T. rhinocerinus*, from most specimens of *Hyrachyus*, but some small, Late Bridgerian specimens of *Hyrachyus* approach primitive variants of the early *Triplopus* species *T. implicatus* in those features, and a spectrum of intermediate forms exists which bridges the gap in dental morphology between primitive *Hyrachyus* and advanced *Triplopus* (see discussion p. 12). The manus of the dentally advanced *Hyrachyus* population is unknown; if those *Hyrachyus* specimens represent the group that evolved into *Triplopus*, as the dentition suggests, then we would expect to find in them concomitant reduction of the fifth digit of the forefoot.

NORTH AMERICAN SPECIES OF *Triplopus*

The type species of *Triplopus*, *T. cubitalis* Cope, 1880, is known from a juvenile skull, jaws, and forelimb, A.M.N.H. No. 5095 (the type specimen), and a few lower dentitions (A.M.N.H. Nos. 2344, 5090, and 13203; C.M. No. 9419). All known specimens of *Triplopus cubitalis* come from the Washakie Formation of the Washakie Basin, Wyoming, but the exact stratigraphic horizon is unknown for most specimens. Wood (1927, p. 173) stated that the type, A.M.N.H. No. 5095, came from Washakie A beds, but the only locality datum with that specimen is "South Bitter Creek, Washakie Basin," which includes both Washakie A and Washakie B beds. The only specimen with more precise stratigraphic data, C.M. No. 9414, comes from Washakie B beds, which are very early Late Eocene in age.

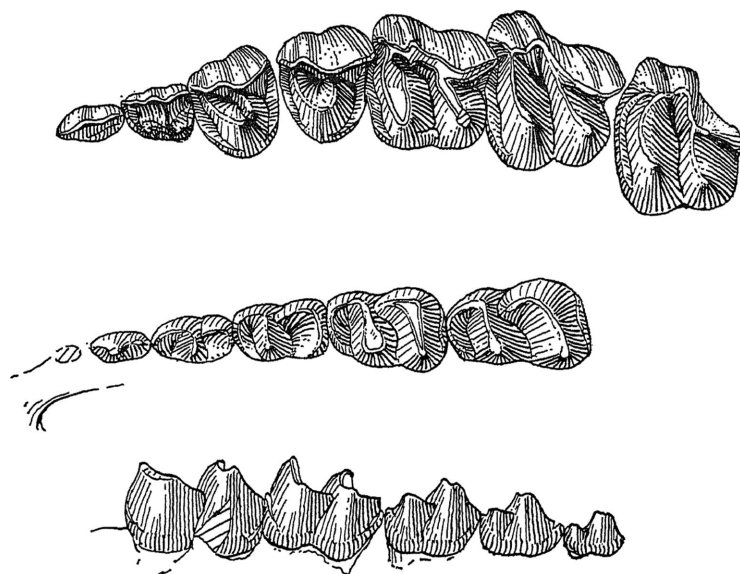*Triplopus cubitalis* is distinguished from

FIG. 1. *Triplopus cubitalis*, type, A.M.N.H. No. 5095. *Top:* P^1–M^3, M$^{2-3}$ reversed from opposite side. *Middle and bottom:* P$_2$–M$_2$ in occlusal and labial views, respectively. The premolars were unerupted but in this figure are restored to the adult position. All ×1.5.

other species of *Triplopus* mainly by its small size (mean length of M$_{1-3}$, 35 mm.), primitive P^2 (see text fig. 1), and, possibly, its high radiohumeral index. The primitive condition of P^2 is probably due to the small size of *T. cubitalis*. Weidenreich (1941, p. 346) has shown that in small breeds of domestic dogs the cusp patterns are altered by disproportionate reduction and loss of some cusps. Thus the primitive P^2 of *T. cubitalis* should not be considered indicative of a comparably primitive evolutionary stage for the species. The high protoloph-metaloph loop of P$^{3-4}$ may be characteristic of *T. cubitalis*, but the range of variation in premolar pattern is unknown for that species. A premolar protoloph-metaloph loop is characteristic of the tapiroid *Lophialetes* and the rhinocerotoid *Ardynia* and occurs as an occasional variant in other species of *Triplopus*, some species of *Forstercooperia*, and is even approached in some *Hyrachyus* specimens. This premolar pattern does not appear to have phylogenetic significance; it has occurred independently in different ceratomorph lines in which the metaloph has become as prominent as the protoloph before protocone and hypocone were separated. Ac-

TABLE 1

STATISTICAL DATA ON TEETH OF
Triplopus cubitalis

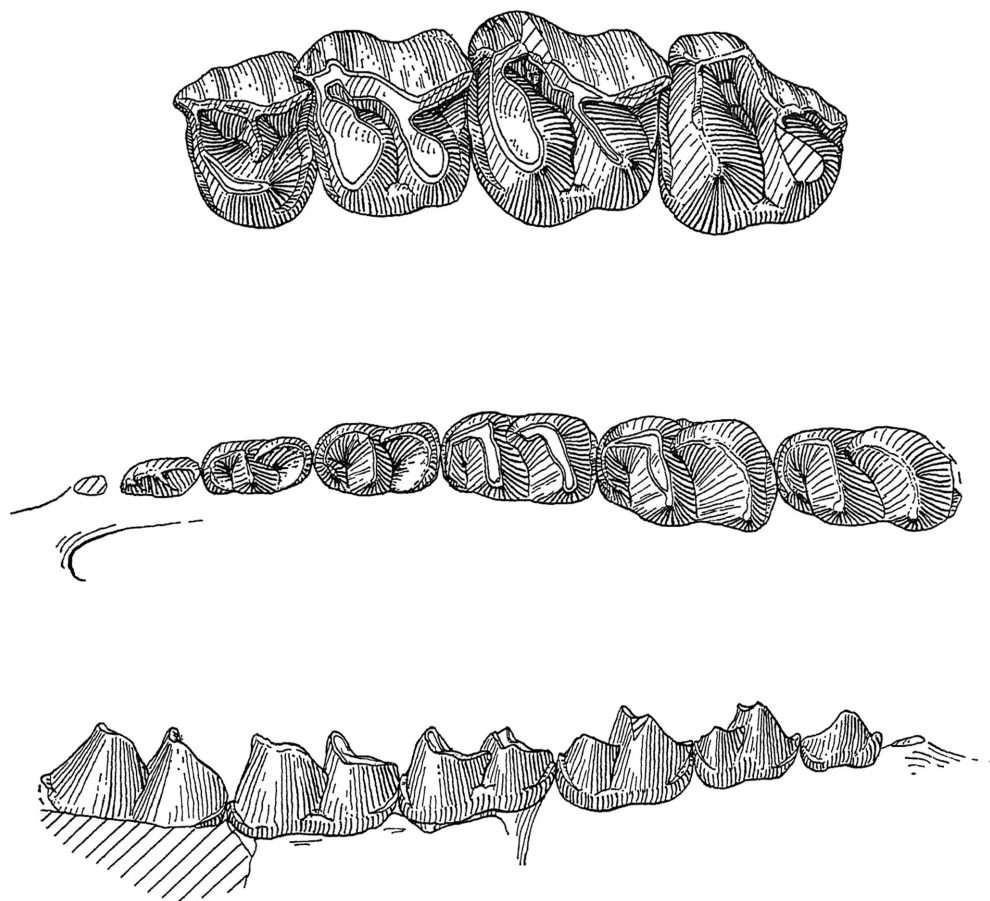|	N	O.R.	M
P$_1$			
L	2	4.8–5.3	5.05
W	2	2.5–2.8	2.65
P$_2$			
L	2	6.9–6.9	6.9
W	2	3.2–3.6	3.4
P$_3$			
L	1	—	8.0
W	1	—	4.5
P$_4$			
L	3	8.3–9.0	8.73
W	3	5.8–6.3	6.10
M$_1$			
L	5	9.8–11.5	10.60
W	5	6.5– 8.7	7.54
M$_2$			
L	3	11.9–12.0	11.93
W	3	7.8– 9.0	8.37
M$_3$			
L	3	12.8–14.1	13.63
W	3	8.0– 8.7	8.40
L M$_{1-3}$	3	34–37	35.33

FIG. 2. *Triplopus implicatus*, new combination. *Top:* A.M.N.H. No. 2341, P^4–M^3. *Middle and bottom:* A.M.N.H. No. 2342, P$_2$–M$_3$, in occlusal and labial views, respectively. In A.M.N.H. No. 2342 the premolars were unerupted but in this figure are restored to the adult position. All ×1.5.

tually, in A.M.N.H. No. 5095, a small notch marks an incipient separation of protocone and hypocone on P^3.

A second species of *Triplopus* occurs in the Washakie Formation with *T. cubitalis*, from which it is distinguished by its larger size (mean length of M$_{1-3}$, 46 mm., or about 25% larger than that of *T. cubitalis*) and more advanced P^2 (see table 2 and text fig. 2). In the three specimens of this larger species in which the upper premolars are preserved (A.M.N.H. Nos. 2341, 5078, and C.M. No. 18461), the protoloph extends posteriorly past the metaloph. The four specimens preserving upper molars (the above-mentioned three and C.M. No. 9384) display a considerable range of var-

iation in the size and orientation of the M^3 metacone. In C.M. No. 9384 it is almost as large and as perpendicular to the metaloph as in *Hyrachyus*; in A.M.N.H. No. 2341, it is large, but lingually oriented; in C.M. No. 18461, the M^3 metacone is small and lingually deflected, as in younger and more advanced *Triplopus* specimens. M$^{1-2}$ parastyles in A.M.N.H. No. 5078 are about as large as in advanced *Hyrachyus* variants; in A.M.N.H. No. 2341 they are smaller. Since these specimens occur in the same beds, are about the same size, and as a group display continuous variation in any given character, I consider them as belonging to a single species. The primitive variants (A.M.N.H. No. 5078 for

parastyle; C.M. No. 9384 for M³ metacone and parastyle) resemble advanced specimens of the small Late Bridgerian *Hyrachyus* species, whereas advanced variants (A.M.N.H. No. 2341 for parastyles, C.M. No. 18461 for M³ metacone) more closely resemble *T. cubitalis* and the younger (Uinta Formation) *Triplopus* specimens. Thus this small sample appears to bridge the gap in dental morphology between *Hyrachyus*, recently assigned to the Tapiroidea (Radinsky, 1966), and *Triplopus*, a primitive hyracodontid rhinocerotoid.

The oldest name given to the large Washakie Basin *Triplopus* species is *Hyrachyus implicatus* Cope, 1873. Cope (1873, p. 5), in his original species description, mentioned two specimens, A.M.N.H. Nos. 5072 and 5078, but no type was named. In a later work Cope (1884, pp. 675–676) transferred A.M.N.H. No. 5072 to *Hyrachyus agrarius* (= *H. modestus*) and restricted *H. implicatus* to A.M.N.H. No. 5078, which then became the lectotype. Wood (1934, p. 232) made *H. implicatus* the type of a new genus, *Ephyrachyus*, which I have synonymized with *Triplopus* (see above, p. 9). The second name applied to the large Washakie Basin species of *Triplopus* is *Eotrigonias petersoni* Wood, 1927 (type, A.M.N.H. No. 2341), which thus becomes a synonym of *Triplopus implicatus* (Cope, 1873).

The total known sample of *T. implicatus* includes the following specimens: A.M.N.H. Nos. 2341, 2342, 5074, 5075, 5078, 13194, and 13202; C.M. Nos. 9384, 18461–18464; U.C.-M.P. Nos. 69374–69376. All specimens for which the horizon is known came from Washakie B beds.

Triplopus is fairly common in the Uinta B beds of the Uinta Basin, Utah, where it is represented by a species that is similar to *T. implicatus*, although differing in a few features. Scott and Osborn (1887, pp. 259–260) originally recognized two species of Uinta B *Triplopus*, *Hyrachyus obliquidens*, and *Prothyracodon intermedium*, but soon realized (Osborn, 1889, p. 525) that only one species was represented, which Osborn transferred to *Triplopus* under the name *T. obliquidens*. The type is P.U. No. 10402. Wood (1927, p. 176) separated three of the *T. obliquidens* specimens as a new species, *Triplopus grangeri*, which he distinguished from *T. cubitalis* but did not compare with *T. obliquidens*. The specimens that

TABLE 2

STATISTICAL DATA ON TEETH OF
Triplopus implicatus

	N	O.R.	M
P¹	—	—	—
P²			
L	1	—	8.1
W	1	—	9.0
P³			
L	2	9.3– 9.6	9.45
W	2	12.0–12.5	12.25
P⁴			
L	3	10.0–11.7	10.97
W	3	14.0–17.2	15.53
M¹			
L	4	13.1–14.8	13.95
W	4	15.9–17.5	16.70
M²			
L	3	15.5–16.9	16.13
W	3	17.2–18.7	17.87
M³			
L	5	14.8–17.2	15.76
W	5	16.2–19.3	17.48
L M¹⁻³	3	44–49	46.33
P₁	—	—	—
P₂			
L	2	8.0–9.1	8.55
W	2	4.8–5.5	5.15
P₃			
L	3	9.8–11.2	10.37
W	3	6.4– 6.8	6.63
P₄			
L	6	10.3–12.8	11.70
W	6	7.4– 9.2	8.38
M₁			
L	7	12.7–14.0	13.56
W	7	8.4–10.0	9.21
M₂			
L	6	14.6–16.5	15.58
W	6	9.6–11.0	10.13
M₃			
L	3	16.5–18.0	17.20
W	3	10.3–11.5	10.80
L M₁₋₃	7	44–49	46.14

Wood referred to *T. grangeri*, A.M.N.H. No. 1972 and C.M. Nos. 2336 and 3110, differ from other Uinta B *Triplopus* specimens only in one feature: the P⁴ protoloph does not extend posteriorly past the metaloph. However, that is only one extreme of a broad spectrum of continuous variation (see text fig. 3) and is obviously not a valid specific character. There-
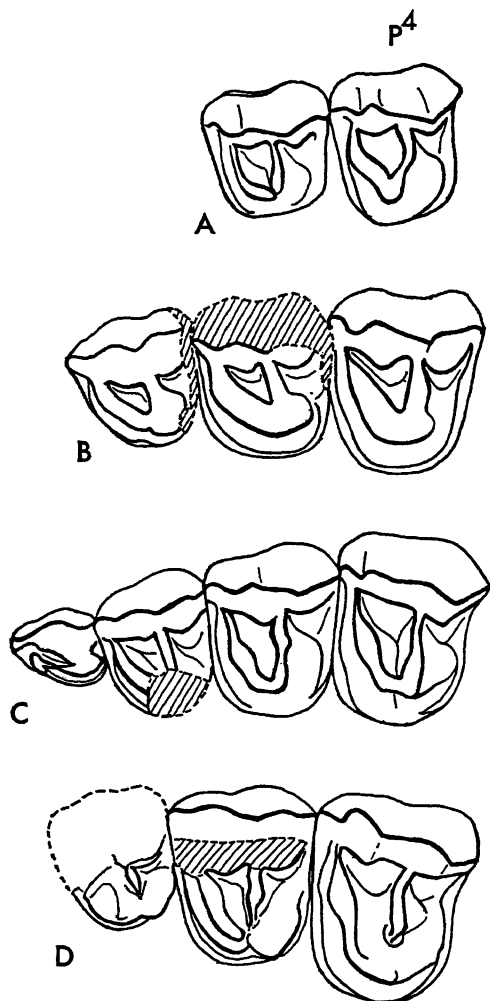
P⁴

A

B

C

D

FIG 3. Upper premolars of *Triplopus obliqui-dens*, showing variation in degree of molarization. A. C.M. No. 2336. B. A.M.N.H. No. 1971. C. P.U. No. 11224. D. Y.P.M. No. 16907. The right-hand tooth in all specimens is P⁴. All ×2.

fore I place *T. grangeri* in synonymy with *T. obliquidens*.

It is questionable whether *T. obliquidens* should be recognized as a separate species from the Washakie Basin *T. implicatus*. *Triplopus obliquidens* averages slightly smaller than *T. implicatus* (length of M_{1-3}, 42 mm.), displays none of the primitive molar variation seen in *T. implicatus* (relatively large parastyles and M^3 metacones), and in many specimens exhibits incipient separation of premolar hypocones and protocones (see text fig.

3). However, there is considerable overlap in these features between the two species, and, when larger samples will allow more accurate assessment of the range of intraspecific variation of *T. implicatus*, it may become desirable to place *T. obliquidens* in synonymy with *T. implicatus*.

Specimens assigned to *Triplopus obliquidens* include the following: A.M.N.H. Nos. 1968, 1971, 1972, 1973, 1975; C.M. Nos. 2336, 3110, 3201, 11957; C.N.H.M. No. P14596; P.U. Nos. 10397 (part), 10402, 10403, 11224; 11295; U.C.M.P. Nos. 31852, 31865, 31867, U.F.H. Nos. 137, 138; Y.P.M. Nos. 11186, 16907. All specimens for which the horizon is known come from the Uinta B beds. Dental measurements are summarized in table 3.

A few specimens of *Triplopus* from the Uinta Formation fall outside the size range of *T. obliquidens* and apparently come from beds younger than Uinta B. Y.P.M. No. 13331, made the type of *Eotrigonias rhinocerinus* by Wood (1927, p. 192; here transferred to *Triplopus*; see p. 9), includes the remains of two individuals: left and right maxillae and jaws of one individual which Wood (1927, figs. 17–19) figured as the type of *T. rhinocerinus*, and left and right lower molars of a second individual of the same species. Y.P.M. No. 13331 was collected near the mouth of Lake Fork, Uinta Basin, Utah, probably from Uinta C beds (see note in Wood, 1929a, p. 63). The only other specimen definitely referable to *T. rhinocerinus* is P.U. No. 11231, an isolated P⁴ from upper Uinta B or lower Uinta C beds.

Y.P.M. 13331 is about 20 per cent larger than the *T. obliquidens* mean (length of M_{1-3}, 50 mm.), and has a more reduced M^3 metacone (see text fig 4). However, since virtually nothing is known of the range of intraspecific variation in *T. rhinocerinus*, larger samples may show that it is closer to *T. obliquidens* than the present evidence indicates.

Triplopus rhinocerinus is about the same size as another hyracodontid rhinocerotoid from the same beds, *Epitriplopus uintensis* (Peterson, 1919) (see p. 27), but can be distinguished from that species by its slightly less molariform premolars, relatively shorter and wider M^{1-2}, and retention of a trace of the M^3 metacone. Several specimens from the Uinta C beds do not include these diagnostic teeth and therefore cannot be assigned with certainty to

TABLE 3

STATISTICAL DATA ON TEETH OF *Triplopus obliquidens*

	N	O.R.	M	S	V
P¹					
L	1	—	6.1	—	—
W	1	—	7.6	—	—
P²					
L	3	7.4– 7.9	7.70	—	—
W	3	8.9–10.2	9.40	—	—
P³					
L	6	8.2–10.2	8.90±0.31	0.75	8.41
W	6	9.3–12.8	11.17±0.46	1.13	10.09
P⁴					
L	7	8.8–10.8	9.87±0.25	0.65	4.34
W	7	11.2–14.7	13.00±0.42	1.12	8.60
M¹					
L	4	12.2–13.1	12.75	—	—
W	4	14.3–16.0	15.28	—	—
M²					
L	5	14.0–14.8	14.34±0.15	0.34	2.39
W	5	14.2–16.9	15.74±0.46	1.04	6.58
M³					
L	7	13.0–15.1	13.76±0.29	0.76	5.54
W	7	14.9–18.3	15.51±0.51	1.35	8.72
L M¹⁻³	7	39–41	40.14±0.34	0.90	2.25
P₁	—	—	—	—	—
P₂					
L	4	7.3– 8.3	7.85	—	—
W	4	4.7– 5.0	4.85	—	—
P₃					
L	4	9.3–10.2	9.73	—	—
W	4	6.4– 7.2	6.75	—	—
P₄					
L	7	9.6–10.8	10.44±0.18	0.47	4.54
W	7	6.9– 7.9	7.47±0.14	0.37	5.01
M₁					
L	11	11.1–13.1	12.45±0.17	0.57	4.57
W	11	7.7– 8.6	8.16±0.10	0.33	4.08
M₂					
L	9	13.0–14.6	13.94±0.17	0.51	3.63
W	9	8.8– 9.8	9.24±0.11	0.34	3.73
M₃					
L	9	14.2–16.5	15.40±0.24	0.71	4.64
W	9	8.9– 9.7	9.31±0.09	0.27	2.92
L M₁₋₃	12	39–44	41.58±0.42	1.44	3.47

either of the two species. These specimens are: A.M.N.H. No. 1928, C.M. Nos. 2990, 3242, and P.U. No. 14653b. U.S.N.M. No. 25-38 and Y.P.M. No. 10259, from Uinta B beds, also represent either *Triplopus rhinocerinus* or *Epitriplopus uintensis*.

P.U. No. 11240, from upper Uinta B or lower C beds, includes the postcranial remains of a small perissodactyl with a tridactyl manus. It may represent *Triplopus obliquidens*, *T. rhinocerinus*, or *Epitriplopus medius*. The lengths of the complete limb bones are: humerus, 150 mm.; radius, 158 mm.; metacarpal III, 80 mm.; femur, 200 mm.; tibia, 175 mm.
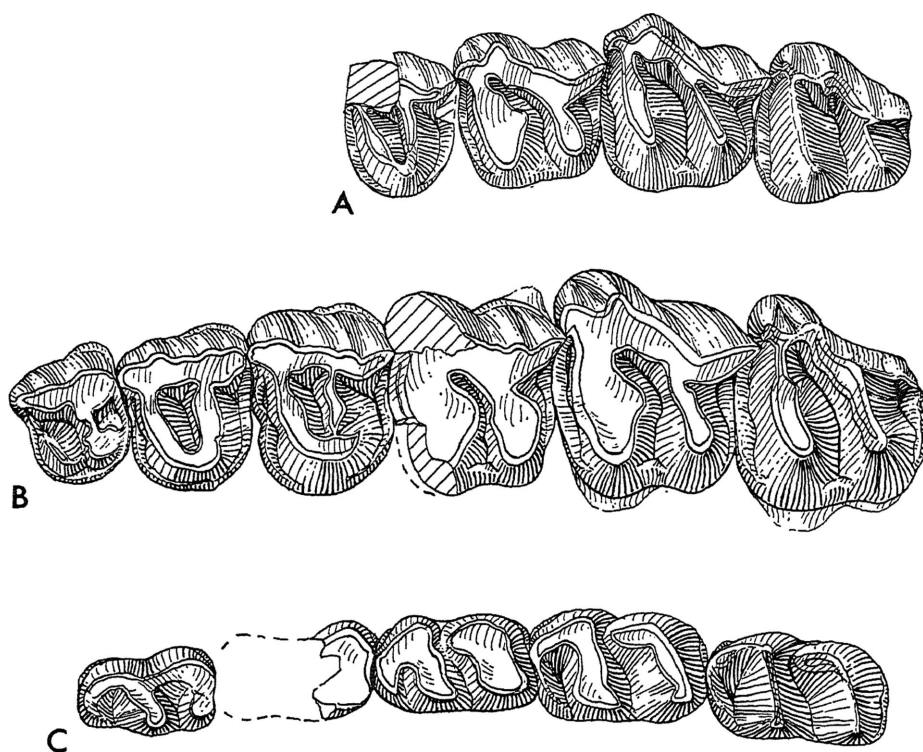
The skull of *Triplopus*, as interpreted from a

FIG. 4. *Triplopus* from the Uinta Basin. A. *T. obliquidens*, A.M.N.H. No. 1972, P^4-M^3. B, C. *T. rhinocerinus*, new combination, type, Y.P.M. No. 13331, P^2-M^3 and P_3-M_3. In C, P_3 is reversed from the opposite side. All ×1.5.

crushed adult specimen (C.M. No. 3201, *T. obliquidens*), is typical of primitive perissodactyls in general, and shows no special features. It resembles the skull of *Forstercooperia? grandis* (see text fig. 12), from which it differs in being smaller (length from occipital condyles to anterior tip of premaxilla is about 210 mm.), and in having a slightly less retracted nasal incision and a more widely open external auditory meatus.

ASIATIC SPECIES OF *Triplopus*

Small, primitive, hyracodontid rhinocerotoids in the early Late Eocene Irdin Manha fauna and later Late Eocene Shara Murun fauna, originally placed in the genus *Caenolophus* by Matthew and Granger (1925b, p. 6; 1925c, p. 7) are here provisionally assigned to *Triplopus* (see above, p. 10).

Triplopus? proficiens (Matthew and Granger, 1925), new combination, is known at the Irdin Manha locality, Inner Mongolia, from the type mandible, A.M.N.H. No. 20141

(including A.M.N.H. No. 20140, the right ramus of the same jaw), and a few miscellaneous teeth (A.M.N.H. Nos. 20239 and 20240). (See text fig. 5.) The length of M_{1-3} is 53 mm., or about the same size as the North American species *T. rhinocerinus*. A posterior fragment of an M^3 (A.M.N.H. No. 20240) indicates that a small metacone was retained. M_3 has a sharply convex posterior border. More complete knowledge of the upper and lower dentition is provided by several specimens from the slightly older Ulan Shireh beds, Shara Murun region, Inner Mongolia (see text fig. 6), which represent a species extremely similar to, and possibly conspecific with, *T.? proficiens*. The Ulan Shireh form is slightly smaller than the Irdin Manha *T.? proficiens* (mean length of M_{1-3}, 50 mm.) and has a straighter M_3 posterior border. The lower incisors are approximately equal-sized and spatulate. (A.M.N.H. No. 20167, a symphyseal fragment that Matthew and Granger, 1925c, p. 9, referred to *T.? proficiens* and interpreted as indicating an en-
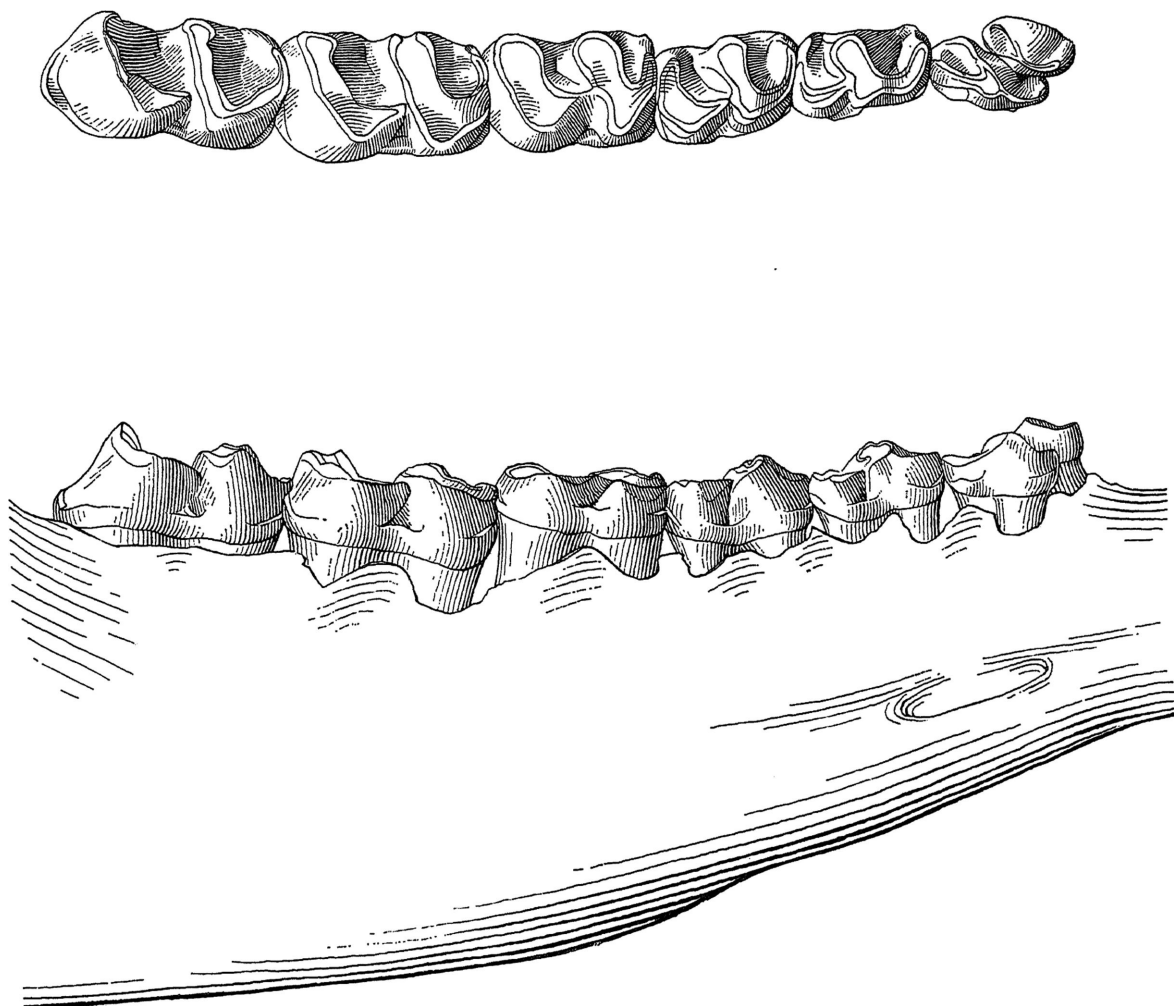
FIG. 5. *Triplopus? proficiens*, new combination, type, A.M.N.H. No. 20141, P_1–M_3.
From Matthew and Granger (1925c, fig. 9). ×1.5.

larged I_2 is not congeneric with *T.? proficiens*; it may belong to the tapiroid *Teleolophus medius*.) The upper premolars have a protoloph-metaloph loop, as do those of *Triplopus cubitalis*.

In the size of molar parastyles and degree of M^3 metacone reduction, *T.? proficiens* is about comparable to primitive variants of the North American *T. implicatus*, or, in other words, barely on the rhinocerotoid side of the tapiroid-rhinocerotoid boundary.

The Ulan Shireh *T.? proficiens* sample includes: A.M.N.H. Nos. 21552, 21561, 21562, 26123–26126, 81863–81867, and 81870. Dental measurements are summarized in table 4.

A.M.N.H. No. 26285, collected at the base of the Ulan Shireh beds 1 mile north of the main Ulan Shireh quarry at Chimney Butte, North Mesa, apparently represents the same species. It has a yellowish brown concretionary coating not seen on any of the North Mesa, Ulan Shireh specimens, but similar to that seen on specimens from the Tukhum beds at Ula Usu, Baron Sog Mesa. This evidence supports the argument that the Tukhum beds and Ulan Shireh beds are approximate stratigraphic correlatives.

A.M.N.H. Nos. 26674 and 26675, mandibles from "Irdin Manha" beds at Camp Margetts, Inner Mongolia, are very similar to the Irdin
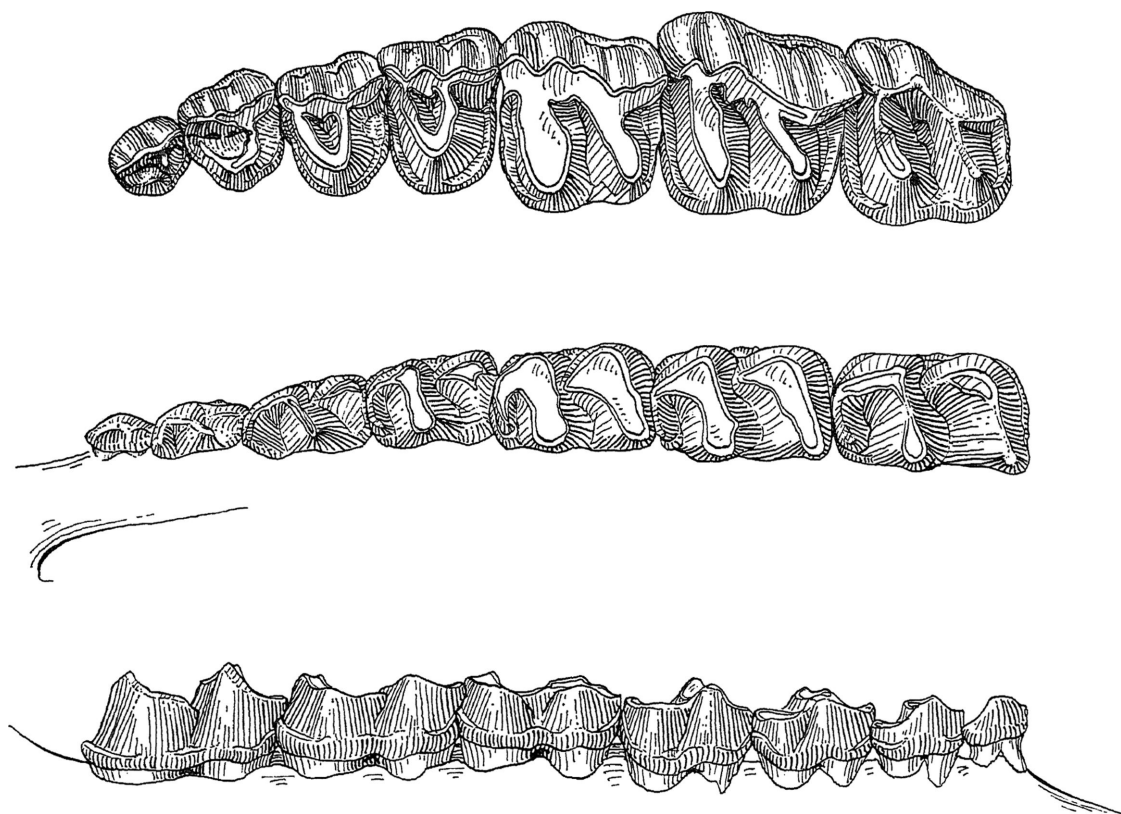
FIG. 6. *Triplopus? proficiens*, new combination, from the Ulan Shireh beds. *Top:* A.M.N.H. No. 21552, P^1–M^3. *Middle and bottom:* A.M.N.H. No. 26124, P_1–M_3, in occlusal and labial views, respectively. All ×1.5.

Manha *Triplopus? proficiens*, and have the same pointed posterior border on M_3. A.M.N.H. No. 26673, a maxilla with extremely worn P^1–M^2 from "Irdin Manha" beds 7 miles southwest of Camp Margetts probably also represents this species.

In the Shara Murun beds at Ula Usu, Shara Murun region, Inner Mongolia, a few specimens, A.M.N.H. Nos. 20298 (the type), 20309 (M_{2-3}), and 81872 (M^3), represent a small hyracodontid, *Triplopus? progressus* (Matthew and Granger, 1925), new combination. In A.M.N.H. No. 20298, the length of M^{1-3} is 35 mm.; the other two specimens represent somewhat smaller individuals. *Triplopus? progressus* is more advanced than *T.? proficiens* in the reduction of M^3 metacone and parastyle and is approximately comparable in these features to *T. obliquidens* (see text fig. 7).

FORSTERCOOPERIA Wood, 1939

Hyrachyus: PETERSON, 1919 (not Leidy, 1871).
Cooperia WOOD, 1938 (preoccupied).
Eotrigonias: BELIAJEVA, 1959 (not Wood, 1927).
Pappaceras WOOD, 1963.
Juxia CHOW AND CHIU, 1964.

TYPE SPECIES: *Forstercooperia totadentata* (Wood, 1938).

INCLUDED SPECIES: Type and *F. confluens* (Wood, 1963), new combination; *F. sharamurenense* (Chow and Chiu, 1964), new combination; *F. borissiaki* (Beliajeva, 1959), new combination; and *F.? grandis* (Peterson, 1919), new combination.

RANGE: Late Eocene of Asia and ?North America.

REVISED DIAGNOSIS: Medium-sized to large hyracodontids: length of M^{1-3} from about 70 mm. to 140 mm. Crown height index averaging

0.60. Dentition unreduced. Incisors approximately equal-sized and pointed. Canines medium-sized and stubby. Premolars non-molariform to submolariform. M^3 metacone small to absent.

DISCUSSION: Three generic names have been proposed for medium-sized to large non-amynodontid rhinocerotoids in the Late Eocene faunas of Asia. The first-named genus, *Forstercooperia*, was erected by Wood (1939; see Wood, 1938) for the rostral portion of a skull from the type Irdin Manha beds of Inner Mongolia. The dentition preserved in the type specimen includes only I^2 roots and I^3-P^4. Except for a few isolated, badly worn premolars, no other specimens of the type species of *Forstercooperia*, *F. totadentata*, are known. Salient features of the dentition include: I^2 slightly larger than I^3, C^1 large but stubby, and P^{1-4} non-molariform. The nasal incision extends back only to a point just behind the canine.

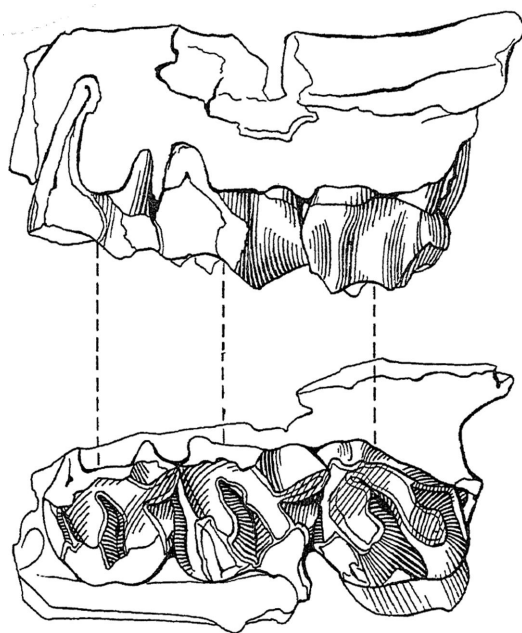Twenty-four years after describing *Forstercooperia*, Wood (1963) erected a second

FIG. 7. *Triplopus? progressus*, new combination, type, A.M.N.H. No. 20298, M^{1-3}. From Matthew and Granger (1925b, fig. 8). ×1.5.

TABLE 4

STATISTICAL DATA ON TEETH OF ULAN SHIREH
Triplopus? proficiens

	N	O.R.	M
P_1			
L	3	6.0– 6.1	6.07
W	3	2.7– 3.0	2.83
P_2			
L	3	8.6–10.0	9.20
W	3	4.5– 5.0	4.70
P_3			
L	3	11.1–12.7	11.93
W	3	6.6– 7.3	6.97
P_4			
L	5	12.0–13.8	12.68
W	5	8.0– 8.9	8.60
M_1			
L	4	14.3–15.4	14.78
W	4	8.5– 9.8	9.13
M_2			
L	4	16.4–17.3	16.88
W	4	9.7–10.8	10.30
M_3			
L	4	17.9–19.2	18.75
W	4	10.1–11.9	10.95
L M_{1-3}	4	48–52	50.25
L M^{1-3}	2	45–51	48.00

genus of large rhinocerotoid from Late Eocene beds in Inner Mongolia under the name *Pappaceras confluens*. Although he provided a detailed description of *Pappaceras confluens*, which is known from an incomplete skull and mandible, Wood failed to explain why he was separating it generically from *Forstercooperia*. In known features *Pappaceras confluens* is extremely similar to *Forstercooperia totadentata* (see text fig. 8). Both species have non-molariform premolars of a similar pattern, large stubby canines, pointed incisors, and similar rostral regions. As far as present knowledge indicates, *Pappaceras confluens* differs from *Forstercooperia totadentata* only in having equal-sized I^{2-3} (I^2 is slightly larger than I^3 in *F. totadentata*), more compressed C^1 roots, and in being about 35 per cent smaller. These differences are based on comparison between only two specimens, the types of each species. Nothing is known of the range of variation in either species. In my opinion, these differences warrant specific but not generic recognition. I therefore place *Pappaceras* in synonymy with *Forstercooperia*.

The third upper molar of *Forstercooperia confluens* resembles that of advanced species of
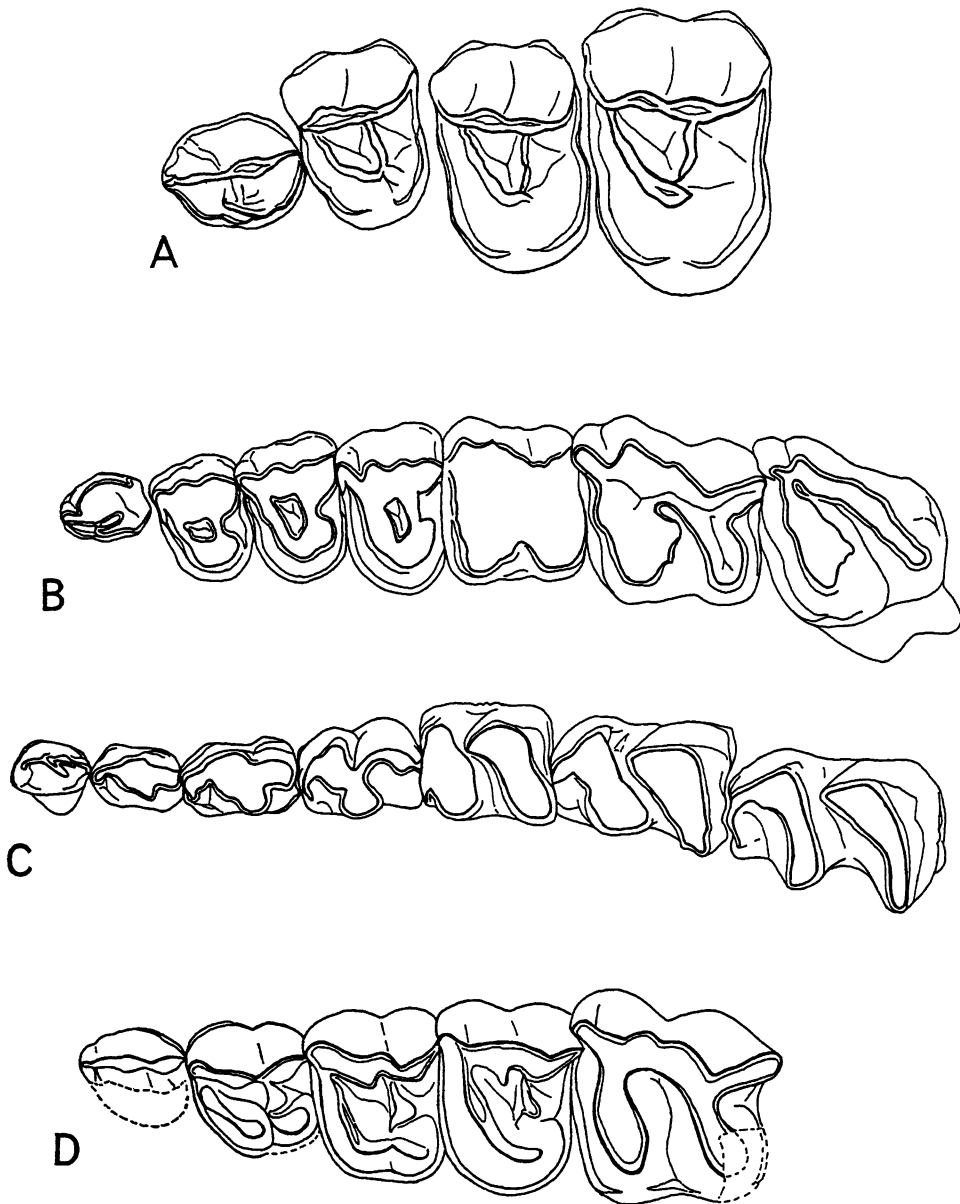
FIG. 8. Teeth of *Forstercooperia*. A. *F. totadentata*, type, A.M.N.H. No. 20116, P$^{1-4}$, from Wood (1938, fig. 5). B, C. *F. confluens*, new combination, type, A.M.N.H. No. 26660, P$^1_{\bar{1}}$–M$^3_{\bar{3}}$, reversed from Wood (1963, fig. 2). D. *F. sharamurenense*, new combination. P^1–M^1, drawn from a cast of No. SS4103 in the collections of the Paleontological Institute, Moscow. All ×3/4.

Triplopus (e.g., *T. rhinocerinus*) in being tri-angular, with only a low swelling on the posterior face of the confluent metaloph and ecto-loph representing the metacone. The remaining molars are typically rhinocerotoid and present no special features. The exact age of *Forstercooperia confluens* is uncertain. The type specimen was found 10 miles southwest of Camp Margetts, Inner Mongolia, in Late Eocene beds which may be slightly older than, contemporaneous with, or somewhat younger than the Irdin Manha beds in which *F. totadenta* occurs (see Radinsky, 1964, for a discussion of Late Eocene stratigraphy in Inner Mongolia).

The third-named genus of large, Late Eocene, non-amynodontid rhinocerotoid is *Juxia* Chow and Chiu, 1964. The type and sole named species of *Juxia*, *J. sharamurenense*, is about 15 per cent smaller in comparable dimensions than *Forstercooperia totadentata*, and is known from a few skulls, mandibles, and postcranial elements from the late Late Eocene Shara Murun beds of Inner Mongolia. Chow and Chiu compared *Juxia* mainly with *Indricotherium*, making only passing reference to *Pappaceras* and no mention of *Forster-cooperia*. However, the incisors of *Juxia* are approximately equal-sized (I^1 is slightly larger than the others) and are followed by a large,

stubby canine, as in *Pappaceras* (= *Forster-cooperia*) *confluens*, and unlike the condition in *Indricotherium*, in which I$^1_1$ are greatly enlarged and the posterior incisors and canines are atrophied or lost. *Juxia sharamurenense* displays the anatomy one would expect to find in the Eocene ancestor of the Oligocene in-dricotheres, which indeed it may be, but it more closely resembles the Eocene species of *Forstercooperia* than the most primitive known indricothere, *Urtinotherium incisivum* Chow and Chiu, 1963, and it is with the Eocene species that it should be compared.

Juxia sharamurenense differs from *Forster-cooperia totadentata* and *F. confluens* in having a more retracted nasal incision, which extends back to P^3 (see text fig. 9), and slightly more molariform, although still submolariform, pre-molars. The metacone swelling in the one M^3 that I have seen is confined to the base of the tooth, which may be a slightly more advanced condition than occurs in *F. confluens*. (The one M^3 known for that species is worn, so direct comparison cannot be made.) The question is whether these differences warrant generic separation of *J. sharamurenense*. The differences in dentition I consider indicative of specific-level differentiation only, but the difference in nasal incision retraction may be more significant. However, since nothing is
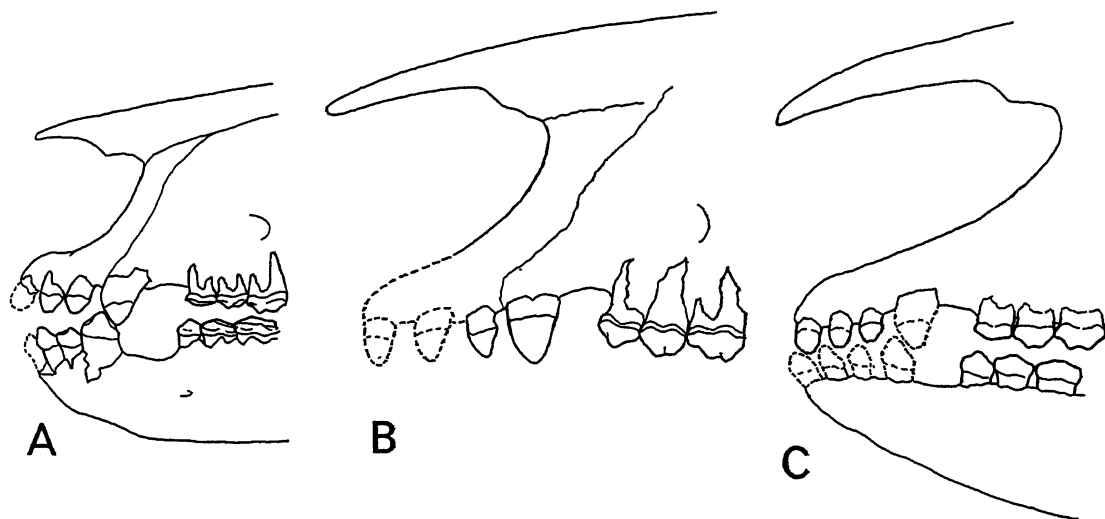

FIG. 9. Anterior portions of the skulls of species of *Forstercooperia*, to show differences in nasal incision enlargement. A. *F. confluens*, new combination, type, A.M.N.H. No. 26660. B. *F. totadentata*, type, A.M.N.H. No. 20116, C. *F. sharamurenense*, new combination, interpreted from Chow and Chiu (1964, fig. 3). All ×1/4.

known about the intraspecific range of variation of that feature, and since *Juxia* is otherwise so similar to *Forstercooperia*, I think that generic separation cannot be justified at this time. Therefore, I place *Juxia* in synonymy with *Forstercooperia* and transfer *J. sharamurenense* to the latter genus.

Beliajeva (1959, p. 83) described a new species of large rhinocerotoid from late Late Eocene or Early Oligocene coal beds of Artiom, near Vladivostok, U.S.S.R., under the name *Eotrigonias borissiaki*. Wood (1963, p. 10) transferred *E. borrisiaki* to *Pappaceras* (= *Forstercooperia*), a generic assignment with which I agree. Known only from M¹ and a few premolars (see Beliajeva, 1959, p. 84, figs. 1–4), *Forstercooperia borissiaki* is slightly smaller than, but otherwise very similar in comparable parts to, *Forstercooperia sharamurenense*. The premolars of both species are submolariform and of similar pattern and more advanced than the non-molariform premolars of *Forstercooperia totadentata* and *F. confluens*. Except for its slightly smaller size, *F. borissiaki* cannot be separated from *F. sharamurenense*, and, in view of our lack of knowledge of the intraspecific range of variation in size of either form, that difference may not be significant.

In review, four previously named species of *Forstercooperia*, probably all from the Late Eocene of Asia, have been recognized. A large and a medium-sized species, *F. totadentata* (length of M¹⁻³ estimated from premolar-molar indices in the other species at about 140 mm.) and *F. confluens* (M¹⁻³, 90 mm.) have non-molariform premolars. *Forstercooperia totadentata* is from the early Late Eocene Irdin Manha beds, and, judged from the non-molariform condition of its premolars, *F. confluens* is probably also of approximately Irdin Manha age. In the late Late Eocene Shara Murun beds we have a large species with submolariform premolars, *F. sharamurenense* (M¹⁻³, 125 mm.), which may be conspecific with *F. borissiaki* from beds of possibly the same age in eastern Siberia. Slight differences in relative size of different incisors and in canine-root cross section exist between the four named species but do not correlate with size or premolar differences.

Several undescribed specimens collected by the Central Asiatic Expeditions of the American Museum of Natural History indicate the presence of additional species of *Forstercooperia* in beds of Irdin Manha age and in those of Shara Murun age. However, since our knowledge of them and of the named species of *Forstercooperia* is so incomplete, I refrain from proposing new specific names at this time. The new material is described below; measurements allowing size comparisons are summarized in table 5.

IRDIN MANHA: At the type Irdin Manha locality, *Forstercooperia totadentata* is represented only by the type specimen, A.M.N.H. No. 20116, and a few worn isolated premolars (A.M.N.H. No. 20169). At least one and possibly two smaller species of *Forstercooperia* are also present at this locality. A.M.N.H. No. 20118, a heavily worn and damaged upper dentition with C¹ and P²–M³, is about 20 per cent smaller than *F. totadentata* and about 20 per cent larger than *F. confluens*. Except for size, A.M.N.H. No. 20118 appears very similar to *F. totadentata*. What is apparently a third size grade is represented by a few isolated molars (A.M.N.H. No. 20170) which are slightly smaller than those of *F. confluens*.

ULAN SHIREH: The Ulan Shireh beds in the Shara Murun region include a fauna that appears to be slightly older than the type Irdin Manha fauna. Two tapiroids, *Lophialetes expeditus* Matthew and Granger, 1925, and *Teleolophus medius* Matthew and Granger, 1925, and a rhinocerotoid, *Triplopus? proficiens* (Matthew and Granger, 1925), are represented by closely related forms in both the Irdin Manha and Ulan Shireh beds, and in all three cases the Ulan Shireh form averages slightly smaller than its Irdin Manha counterpart. Thus it is not surprising to find in the Ulan Shireh collection three specimens of *Forstercooperia* that average slightly smaller than the middle-sized form at Irdin Manha. These are: A.M.N.H. No. 21608, an almost complete skull (lacking only the tips of the nasals and the premaxillae) with P¹–M³; A.M.N.H. No. 22101, an incomplete mandible with P₃–M₃, and A.M.N.H. No. 22102, P₄–M₃. No features of cusp pattern distinguish the Ulan Shireh form (except on an individual basis) from the middle-sized Irdin Manha specimen (A.M.N.H. No. 20118) or from *F. confluens* and it is intermediate in size between the two.

CAMP MARGETTS REGION: "Irdin Manha"

TABLE 5
Measurements (in Millimeters) of Teeth of *Forstercooperia*

Specimen	Stratum	L M$^{1-3}$	L P$^{1-4}$	L M$_{1-3}$	L P$_{1-4}$
A.M.N.H. No. 20116[a]	Irdin Manha beds	140[b]	105	—	—
A.M.N.H. No. 20118	Irdin Manha beds	115[c]	85	—	—
A.M.N.H. No. 21608	Ulan Shireh beds	102	78	—	—
A.M.N.H. No. 22101	Ulan Shireh beds	—	—	110	—
A.M.N.H. No. 22102	Ulan Shireh beds	—	—	95	—
A.M.N.H. No. 26660[d]	"Irdin Manha" beds, 10 miles SW. of Camp Margetts	90	70	89	70
A.M.N.H. No. 26670	"Irdin Manha" beds, 10 miles SW. of Camp Margetts	—	55	—	—
A.M.N.H. No. 26672	"Irdin Manha" beds, 10 miles SW. of Camp Margetts	75	56[c]	79[c]	—
A.M.N.H. No. 26666	"Irdin Manha" beds, 7 miles W. of Camp Margetts	—	—	83	65[c]
A.M.N.H. No. 26643	"Irdin Manha" beds, 7 miles W. of Camp Margetts	73	55	—	—
A.M.N.H. No. 26669	"Irdin Manha" beds, 7 miles SW. of Camp Margetts	—	—	75[c]	—
A.M.N.H. No. 26668	"Irdin Manha" beds, 5 miles E. of Camp Margetts	—	—	75	55
A.M.N.H. No. 20286	—	—	—	112	87
SS4103[e]	—	110	90	110	85
V. 2891[f]	—	(L P^1–M^3, 215)		(L P$_1$–M$_3$, 200)	

[a] Type of *F. totadentata*.
[b] Length of molar series estimated from premolar/molar indices of other specimens.
[c] Approximate.
[d] Type of *F. confluens*.
[e] Skull and mandible at the Paleontological Institute, Moscow.
[f] Type of *F. sharamurenense*, in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Peking. Measurements taken from Chow and Chiu (1964, p. 265).

beds at several localities in the Camp Margetts region have yielded specimens similar to the type of *Forstercooperia confluens* but smaller. The type of *F. confluens* (A.M.N.H. No. 26660) was collected 10 miles southwest of Camp Margetts. The only other specimens of large rhinocerotoid found at that locality are A.M.N.H. Nos. 26670, the anterior half of a skull with battered P^2–M^1, and 26672, M$^{1-3}$, P$_2$–M$_3$. These dentitions average 20 per cent shorter than the dentition of the type of *F. confluens*. Two specimens of *Forstercooperia* were found 7 miles west of Camp Margetts: A.M.N.H. No. 26666, a mandible with P$_3$–M$_3$ (described by Wood, 1963), and A.M.N.H. No. 26643, an incomplete skull with very damaged teeth. The M^3 metacone in the latter specimen is less reduced than in the type of *F. confluens*, but is within what I would consider to be a possible range of infra-specific variation of that feature. A mandible (A.M.N.H. No. 26669), with DP$_{3-4}$, M$_{1-2}$, from 7 miles southwest of Camp Margetts, matches in size comparable teeth in a jaw with P$_1$–M$_3$ (A.M.N.H. No. 26668) found 5 miles east of Camp Margetts.

I have found no dental characters that help in determining specific relationships of the specimens described above, and the size range (see table 5) is such that no definite species allocations can be made. Two hypotheses are suggested: (1) The type of *F. confluens* may be a large representative of a small species that includes all the other Camp Margetts area specimens. In this case the intermediate-sized Irdin Manha maxilla and Ulan Shireh specimens would represent a new species, distinguished by its size. (2) The type of *F. confluens* represents a small member of a species of which the Ulan Shireh and Irdin Manha
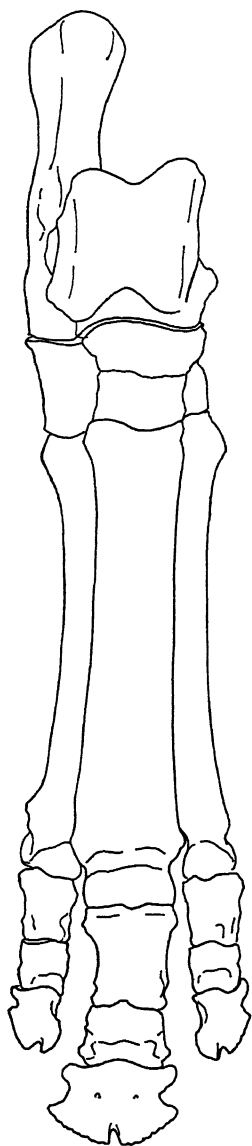
FIG. 10. Hind foot of *Forstercooperia shara-murenense*, new combination, A.M.N.H. No. 20288. ×1/2.

specimens are larger representatives. In this case the other Camp Margetts specimens would represent a new species, characterized by its small size and, possibly, by less reduced M³ metacones. Stratigraphic correlations between the "Irdin Manha" beds of the Camp Margetts area at various localities and the

type Irdin Manha and Ulan Shireh beds are uncertain; some of the size differences may reflect evolutionary size increase. The apparent presence of a hyracodontid of the size of *F. confluens* (A.M.N.H. No. 20170) in the Irdin Manha fauna suggests a slight preference for the first hypothesis.

SHARA MURUN: Chow and Chiu (1964) listed four specimens of *Forstercooperia shara-murenense* from the Shara Murun beds at Ula Usu in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Peking, but gave measurements for only one, the type (P^1–M^3, 215 mm.; P$_1$–M$_3$, 200 mm.). Two specimens of *F. sharamurenense* from the same locality are present in the collections of the American Museum of Natural History: A.M.N.H. No. 20286, a mandible with I$_2$–M$_3$ (M$_{1–3}$, 112 mm.; P$_{1–4}$, 87 mm.), and A.M.N.H. No. 20287, a juvenile skull and jaws, with deciduous premolars and the first molar (DP$^{1–4}$, 100 mm.; DP$_{1–4}$, 90 mm.). An isolated M³, A.M.N.H. No. 81806, from the same horizon and locality, was originally referred by me (Radinsky, 1965, p. 224) to the Deperetellidae, but it is actually a smaller duplicate of the M³ of *F. sharamurenense*. It is 25 per cent smaller than M³ of *F. sharamu-renense* and about the size of that of *F. confluens*, from which it differs in having a slightly more reduced metacone. In view of its later age, the species represented by A.M.N.H. No. 81806 may prove to have more advanced premolars than does *F. confluens*. However, since that evidence is lacking at present, and since the M³ alone does not present enough characters by which to distinguish a new species, I leave it unnamed. It indicates the presence of a medium-sized species of *Forstercooperia* in the Shara Murun fauna.

Two incomplete mandibles from beds probably equivalent to the Shara Murun Formation in the Shara Murun region, Inner Mongolia, are about the same size as *Forstercooperia sharamurenense* and similar in comparable morphology. They are A.M.N.H. No. 26750, P$_3$–M$_3$, from Twin Oboes, East Mesa, and A.M.N.H. No. 26753, P$_2$, P$_4$–M$_3$, from Urtyn Obo, East Mesa.

A hind foot found with teeth of *F. sharamu-renense* in Shara Murun beds is illustrated in text figure 10.
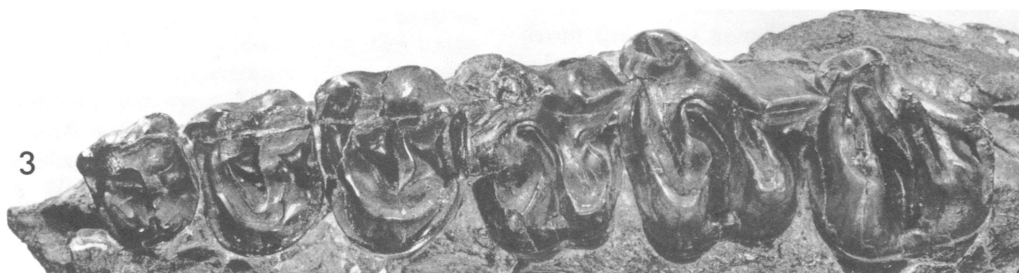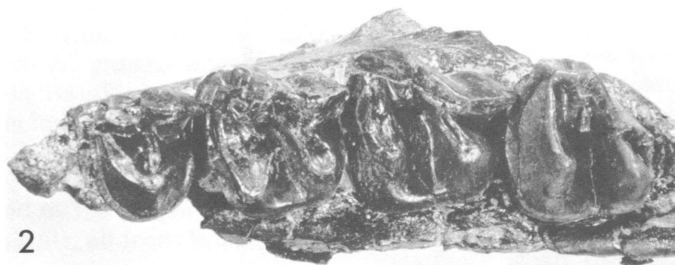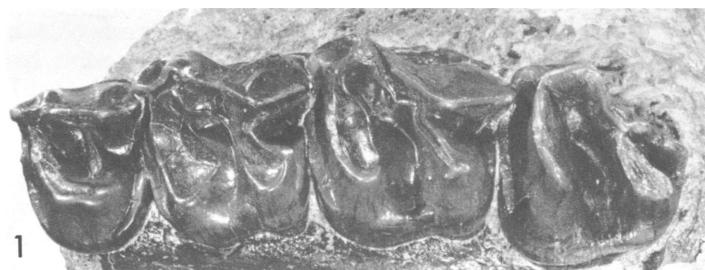
1. *Triplopus implicatus*, new combination, A.M.N.H. No. 2341.   ×1.5
2. *Triplopus obliquidens*, A.M.N.H. No. 1972.   ×1.5
3. *Triplopus rhinocerinus*, new combination, type, Y.P.M. No. 13331.   ×1.5
4. *Triplopus? proficiens*, new combination, from the Ulan Shireh beds, A.M.N.H. No. 21552. ×1.5
5. *Epitriplopus uintensis*, type, C.M. No. 3007a, P²-M³.   ×1.5

North American *Forstercooperia*

Peterson (1919, p. 129) described a new species of medium-sized rhinocerotoid from the early Late Eocene Uinta A beds, Uinta Basin, Utah, under the name *Hyrachyus grande* (corrected to *H. grandis* in Wood, 1934, p. 214). The type, C.M. No. 2908, consists of a mandible with incisor alveoli and C_1–M_3 and is the only specimen of the species known from the Uinta Basin. However, several previously undescribed specimens from the contemporaneous Washakie B beds, Washakie Basin, Wyoming, belong to *H. grandis* and provide new information on its affinities. The additional specimens include A.M.N.H. No. 5061 (M_2 or M_3); U.C.M.P. Nos. 69369 (M^{1-3}), 69370 (M_{1-3}), 69371 (P_4), 69722 (crushed skull and jaws), and 69373 (M_3 or M_2); U.W. No. 2410 (partial skull), all from Washakie B beds.

In *H. grandis* the M^3 metacone is smaller and more lingually directed, giving the tooth a more triangular appearance, than in most specimens of *Hyrachyus*. Also, the molar parastyles stand out less from the paracones, and the metalophids are higher, than is usually seen in *Hyrachyus*. These features indicate that *H. grandis* should be removed from the genus *Hyrachyus* and placed in the family Hyracodontidae.

Hyrachyus grandis is about the same size as *Forstercooperia confluens*, and the skull and dentition of the two species are very similar (see text figs. 11 and 12). The main differences are the smaller canine and less reduced M^3 metacone of *H. grandis*. The three M^3's available of *H. grandis* indicate that metacone reduction was variable, and, in any event, the degree of difference in this feature between the North American and Asiatic species is no more than occurs between species of *Triplopus*. The difference in canine size may be more significant, for all specimens of *Forstercooperia* in which the canine is preserved (six in all) have large, stubby canines. However, A.M.N.H. No. 26670, a small skull (M^{1-3} estimated at 75 mm.) from the Camp Margetts area, has a relatively small canine alveolus, about like that in *H. grandis*, but another small skull from the same area has a relatively large canine alveolus. Thus, perhaps in some species of *Forstercooperia* (at least the smallest one), there was sexual dimorphism in canine size. One final difference which should be mentioned is the presence of a small entoconid on P_{3-4} in U.C.M.P. No. 69722 and P_4 of U.C.M.P. No.
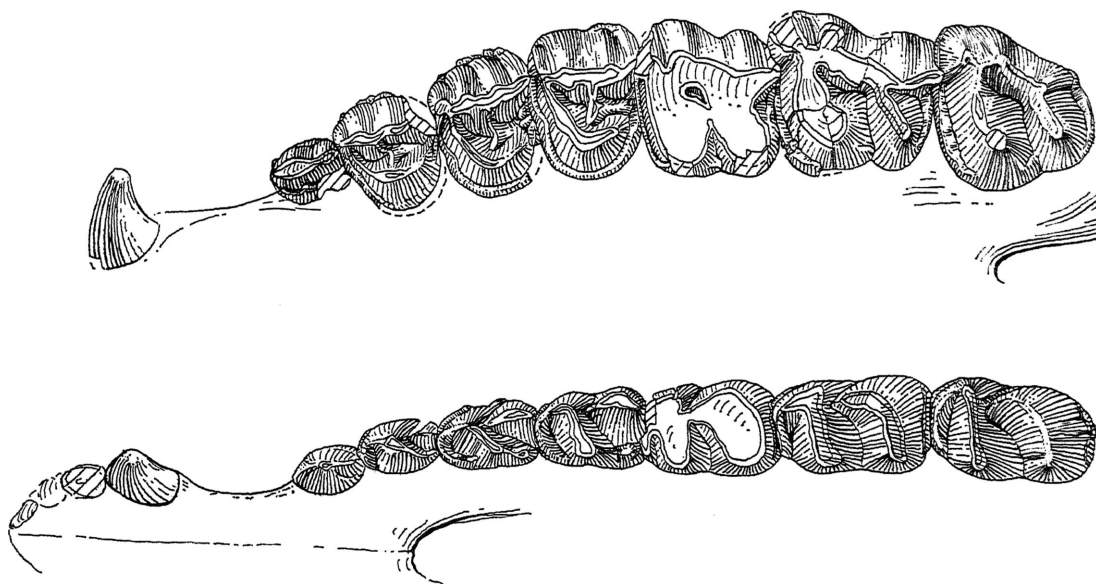

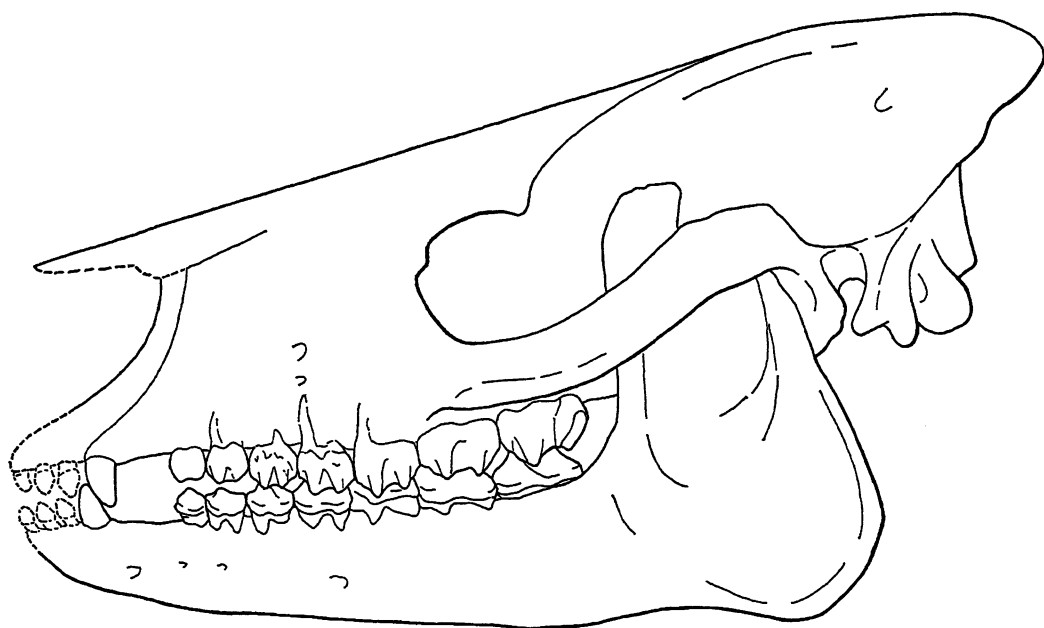FIG. 11. Upper and lower dentition of *Forstercooperia? grandis*, new combination, U.C.M.P. No. 69722. ×2/3.

FIG. 12. *Forstercooperia? grandis*, skull and mandible, drawn from U.C.M.P. No. 69722. ×1/3.

69371; *Forstercooperia confluens* and the other Camp Margetts area specimens lack this cusp. However, in the absence of knowledge of the range of variation of this feature in both species, such a difference is without significance and, in any case, of no more than specific taxonomic value.

The absence of a large stubby canine from *H. grandis* is the most significant difference now known between it and species of *Forstercooperia*, but I consider that character alone insufficient for generic separation. Therefore I transfer *H. grandis* to *Forstercooperia*.

PROHYRACODON Koch, 1897

TYPE SPECIES: *Prohyracodon orientale* Koch, 1897.

INCLUDED SPECIES: Type and *P. meridionale* Chow and Xu, 1961 (including *P. progressa* Chow and Xu, 1961).

RANGE: ?Middle and Late Eocene of Asia and eastern Europe.

REVISED DIAGNOSIS: Small hyracondontids: length of M^{1-3}, 53 mm. Crown height index, 0.63. Incisors and canines unknown. Premolars non-molariform to submolariform. M^{1-2} relatively longer and narrower than those of *Triplopus*, with less of an antecrochet. M^3 with no trace of a metacone.

DISCUSSION: *Prohyracodon* is more advanced than *Triplopus* in that the M^3 metaloph extends straight to the paracone, with no trace of the metacone remaining. This condition is approached but not attained in *Triplopus rhinocerinus* and advanced variants of *T. obliquidens*. Koch (1897) considered *Prohyracodon* to be closely related to *Hyracodon*, but Abel (1910, p. 24), Wood (1927, p. 36; 1929b), and later authors, presumably on the basis of its triangular M^3, have assigned *Prohyracodon* to the family Rhinocerotidae. Although the M^3 of *Prohyracodon* is as advanced as that of

TABLE 6

MEASUREMENTS (IN MILLIMETERS) OF TEETH OF
Forstercooperia? grandis

	L M^{1-3}	L P^{1-4}	L M_{1-3}	L P_{1-4}
C.M. No. 2908[a]	—	—	91	70
U.C.M.P. No. 69722	93	75[b]	93	70
U.C.M.P. No. 69369	97[b]	—	—	—
U.C.M.P. No. 69370	—	—	88	—
U.W. No. 2410	85[b]	68	—	—

[a] Type of *F.? grandis*.
[b] Approximate.

Oligocene and later rhinocerotids, having completely lost the metacone, the same condition occurs in M³'s of *Epitriplopus* and *Ardynia*, and in the latter two genera the incisors are approximately equal-sized, spatulate, and unreduced in number. In my opinion one of the critical adaptations responsible for the emergence of the family Rhinocerotidae was the specialization of the incisors (enlargement of I¹/I₂ and loss of the others), and this character should be considered diagnostic of the family (see p. 5). The loss of the M³ metacone, on the other hand, is of no adaptive significance (for mastication) once the M₃ hypoconulid has been lost, and therefore its absence should not be considered indicative of familial affinities. In the absence of knowledge of the incisors of *Prohyracodon*, and considering its early age and similarity to *Epitriplopus*, I include *Prohyracodon* in the Hyracodontidae.

The type species of *Prohyracodon*, *P. orientale*, was found with one other mammalian species, the brontothere *Brachydiastematherium transylvanicum*, in beds in Rumania considered to be of Middle Eocene age. This age assignment is based on the invertebrate fauna that occurs in strata overlying the *Prohyracodon* beds (Koch, 1894; Wood, 1929b, p. 2). The molar pattern of *Prohyracodon orientale* would be extremely precocious for a Middle Eocene rhinocerotoid. Although such a condition is not impossible (see, for example, the precociously molariform premolars of the Middle Eocene tapiroid *Chasmotherium cartieri*), I would not expect the dental morphology of *P. orientale* to be attained before the Late Eocene. A Late Eocene age is suggested by correlation with the Asiatic species of *Prohyracodon*.

Chow and Xu (1961) named two new species of *Prohyracodon*, *P. meridionale* and *P. progressa*, for two incomplete upper dentitions (see text fig. 13) from the Late Eocene (Shara Murun equivalent) Lower Lunan Series, Yunnan, China. They distinguished *P. progressa* from *P. meridionale* mainly on the basis of its more advanced premolars. However, the difference in premolar molarization between the two Asiatic species is encompassed by the range of variation seen in the premolar patterns of a single species of *Triplopus*, *T. obliquidens* (see text fig. 3) and thus, on the basis of only two specimens, is not a valid

criterion for distinguishing species. The M² of *P. progressa* is slightly relatively longer than that of *P. meridionale*, but again, the degree of difference is no greater than is seen in a single species, e.g., *T. obliquidens*. Since the single specimen known of *P. progressa* cannot be distinguished from *P. meridionale* on a basis adequate for specific diagnosis, I consider the former a synonym of the latter and recognize only one species of *Prohyracodon* from the Lunan beds.

Chow (1957, p. 206) erected the species *Caenolophus medius* for a juvenile maxilla with DP¹–M¹, from the Late Eocene Lunan beds. The length of the premolar series suggests that it does not belong in *Caenolophus*, which is an amynodontid rhinocerotoid (see p. 10). *Caenolophus medius* is about the same size as *Prohyracodon meridionale* and may represent the same species. If such proves to be the case, *P. medius* will be the valid name for the species.

The degree of variation exhibited by all known specimens of *Prohyracodon*, including both European and Asiatic forms, is no greater than would be expected in a single species, and no specific diagnosis can be drawn up that will adequately (i.e., on morphological grounds) distinguish two species. The absence of *Prohyracodon* from the well-known Middle and Late Eocene faunas of western and central Europe suggests that *P. orientale* may have been on the fringe of what was basically an Asiatic range for the genus.

EPITRIPLOPUS Wood, 1927

Prothyracodon: PETERSON, 1919 (not Scott and Osborn, 1887).

TYPE AND SOLE SPECIES: *Epitriplopus uintensis* (Peterson, 1919) (?including *E. medius* Peterson, 1934).

RANGE: Late Eocene of North America.

REVISED DIAGNOSIS: Small hyracodontids: length of M¹⁻³, 50 mm. Teeth higher-crowned than in other Late Eocene hyracodontids: crown height index, 0.78. Dentition unreduced. Incisors spatulate. Premolars submolariform to molariform. Upper molars with curved cross crests and paracones projecting labial to parastyles. M¹⁻² relatively longer and narrower than in *Prohyracodon*, and with a pronounced antecrochet. M³ with no trace of a metacone.
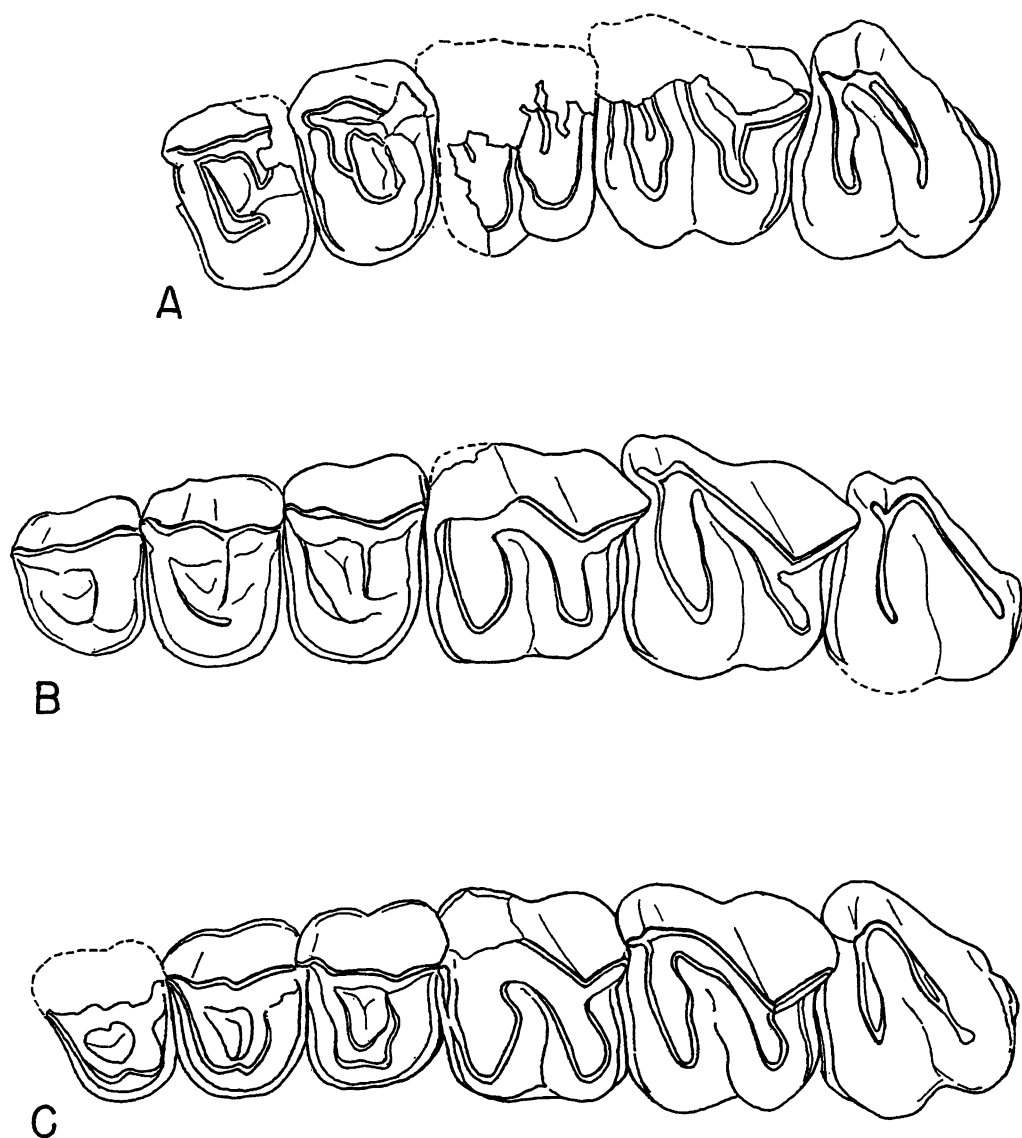
FIG. 13. Upper dentitions of *Prohyracodon*, taken from Chow and Xu (1961, fig. 2). A. *P. orientale*. B. *P. meridionale*, type. C. *P. progresssa*, type (= *P. meridionale*). All ×1.5.

DISCUSSION: Peterson (1919, p. 134) proposed the species *Prothyracodon uintense* for a juvenile rhinocerotoid skull, C.M. No. 3007a, from the Uinta C beds, Uinta Basin, Utah. He stated, however (p. 135), that, if the M³ of adult *P. uintense* should prove to lack a metacone, the species should be placed in a distinct genus. Matthew and Granger (1925a, p. 7) noted that *Prothyracodon uintense* resembled *Prohyracodon orientale* in lacking the M³

metacone, and therefore could not be congeneric with *Prothyracodon* (= *Triplopus*) *obliquidens*. Wood (1927, p. 179) proposed the new genus *Epitriplopus* to receive *P. uintense*, and listed as generic characters the relatively long M², loss of the M³ metacone, a peculiar cusp pattern on P², and a tridactyl manus. The first two characters are valid (see revised diagnosis above). However, what Wood interpreted as incompletely calcified crowns of P²⁻³
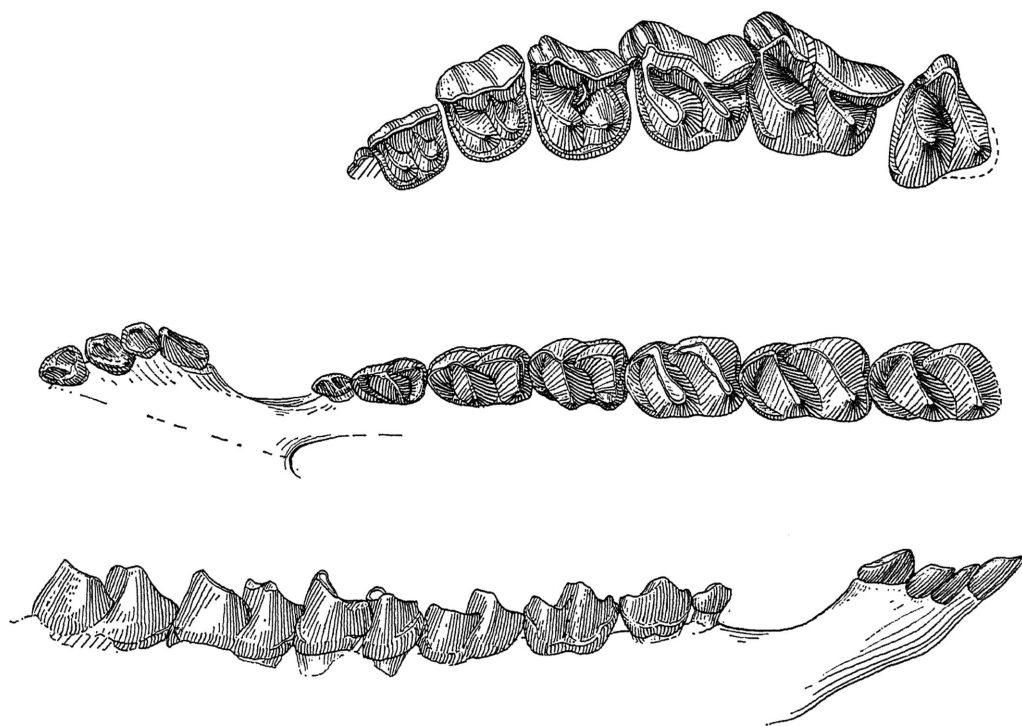
FIG. 14. *Epitriplopus uintensis*, type, C.M. No. 3007a. *Top:* P²–M³. *Middle and bottom:* Lower dentition in occlusal and labial views, respectively. The premolars were unerupted but in this figure are restored in adult position. All ×1.

were actually lumps of matrix covering those teeth. Further preparation has revealed precociously molariform, but otherwise unexceptional, unerupted premolars under the matrix (see text fig. 14). Wood stated in his diagnosis and again in the text (1927, p. 182) that *Epitriplopus uintensis* had a tridactyl manus, but neither Wood nor Peterson (1919) gave any reference to a specimen that demonstrates that condition. I have examined all known specimens of Late Eocene rhinocerotoids and have found no material definitely assignable to *E. uintensis* that indicates whether or not the manus was tridactyl. In consideration of the condition in *Triplopus*, *Epitriplopus* may well have had a tridactyl manus, but the evidence has not yet been found.

Peterson (1934, p. 387) erected the species *Epitriplopus medius* for a maxilla (C.M. No. 11915) with damaged P³–M² from the Duchesnean Randlett horizon, Uinta Basin, Utah (see text fig. 15). Scott (1945, pp. 247–249) recognized the species *E. medius* but in an apparent *lapsus* referred its type, C.M. No.

11915, to *Hyracodon primus*, another Duchesnean hyracodontid species. *Epitriplopus medius* differs from the type and sole specimen of *H. primus* (C.M. 11914, a maxillary fragment with P⁴–M²) in having a more molariform P⁴, relatively longer and narrower M¹, and no M² crista. The first difference may not be significant; the last two features suggest that *E. medius* belongs in the genus *Epitriplopus* and that *H. primus* does not. C.M. No. 11915 differs from C.M. No 3007a, the type of *Epitriplopus uintensis*, in having a more molariform P⁴, and slightly lower-crowned molars. Since only one specimen is known for each species, it is not possible to estimate the range of intraspecific variation in those features. *Epitriplopus medius* may be conspecific with *E. uintensis*.

Peterson (1931, p. 71) proposed, as a new genus and species, *Mesamynodon medius* for a mandibular fragment with P₃–M₂ (C.M. No. 11762) from the Duchesnean Lapoint horizon, Uinta Basin, Utah. It represents a slightly larger individual than does the type of
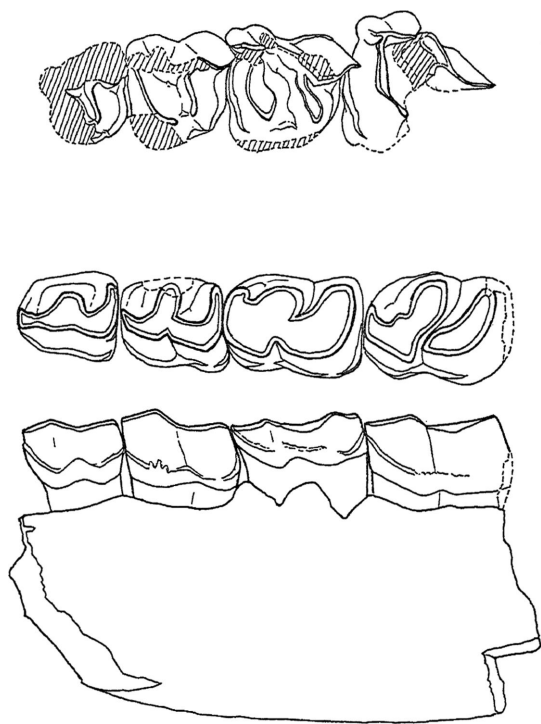
FIG. 15. Duchesnean *Epitriplopus*. *Top: E. medius*, type, C.M. No. 11915, P³–M². *Middle and bottom:* "*Mesamynodon medius*," type, C.M. No. 11762, P₃–M₂ in occlusal and labial views, respectively. All ×1.

Epitriplopus medius, but may belong to the same species. The P₃₋₄ of C.M. No. 11762 have prominent labial cingula, as do those teeth in *E. uintensis*.

Epitriplopus is most similar to species of *Prohyracodon*, from which it differs in having more molariform premolars (not a generic distinction), relatively longer and narrower M¹⁻² (the posterior half of these teeth is particularly narrow), less labially situated molar parastyles, and higher-crowned teeth. The long, narrow M¹⁻² of *Epitriplopus* resemble those teeth in the Asiatic Oligocene genus *Ardynia*, from which *Epitriplopus* differs in having more molariform P²⁻⁴, a less reduced premolar series (P¹ is lost and P₂ is single-rooted in *Ardynia*), more lingually situated molar parastyles, and less hypsodont teeth.

HYRACODON LEIDY, 1856

Rhinoceros: LEIDY, 1850 (not Linnaeus).

TYPE AND SOLE SPECIES: *Hyracodon nebraskensis* (Leidy, 1850).

RANGE: Early Oligocene to ?Early Miocene of North America.

REVISED DIAGNOSIS: Medium-sized hyracodontids: length of M¹⁻³ averaging 60 mm. Crown height index, 0.88. Incisors approximately equal-sized, small and slender, grading from spatulate at I¹₁ to pointed in I³₃. Canines approximately the same size and shape as I³₃. Premolars submolariform; P₁ lost. Premolar and molar paracones not delimited posteriorly from the ectolophs. M¹⁻² with large antecrochet and protocone set off by vertical grooves; these features less pronounced in M³. M³ with a persistent small metacone. Manus tridactyl.

DISCUSSION: Several species of *Hyracodon* have been erected, primarily on the basis of differences in upper premolar patterns. I agree with the last reviewer of the genus, Scott (1941, p. 841), that these represent individual variants of a single species, *H. nebraskensis*. *Hyracodon priscidens* Lambe, 1905, from the Cypress Hills Early Oligocene, Saskatchewan, Canada, which Scott retained pending further information, is not demonstrably different from *H. nebraskensis. Hyracodon primus* Peterson, 1934, does not belong in *Hyracodon* (see p. 38). Scott's work (1941, pp. 823–841) includes a detailed description of the osteology of *Hyracodon*. Illustrations of the dentition and skull are provided here for comparison with those of other hyracodontids (see text figs. 16 and 17).

Green (1958, p. 587) described a specimen of *Hyracodon* from the lower part of the Sharps Formation, South Dakota. This is the only record of *Hyracodon* from deposits younger than the Whitney Formation.

TRIPLOPIDES,[1] NEW GENUS

TYPE AND SOLE SPECIES: *Triplopides rieli*,[2] new species.

RANGE: Early Oligocene of North America.

DIAGNOSIS: Medium-sized hyracodontids: length of M¹⁻³, about 65 mm. Incisors slender and spatulate, increasing slightly in size anteriorly. Canines small and slender. P¹₁ lost; premolars submolariform. M³ without a trace of the metacone.

DISCUSSION: The ventral half of a skull with the lower jaws, C.M. No. 9370 (see text fig. 18), from Early Oligocene beds at

[1] *Triplopus*, plus Greek *-ides*, son of.
[2] Named after Mr. Stanley Riel, who first noticed the existence of this new species.
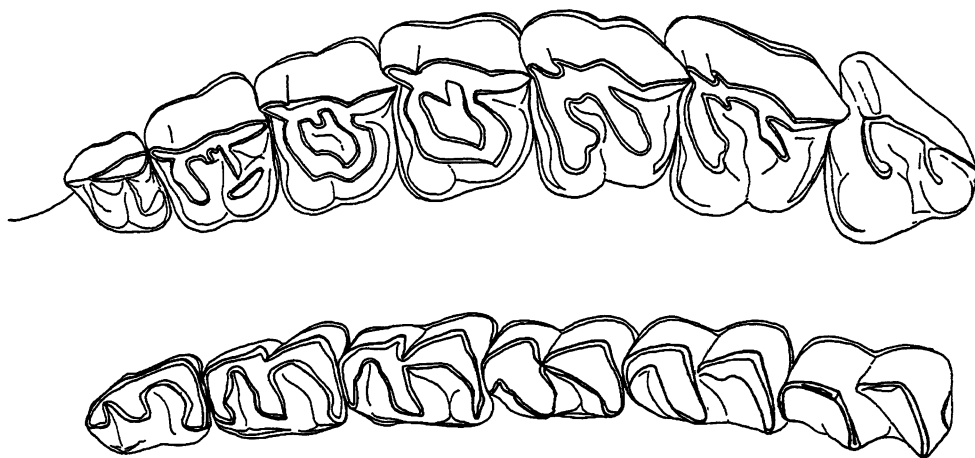
FIG. 16. Upper and lower dentition of *Hyracodon nebraskensis*, A.M.N.H. No. 11296.×1.

McCarty's Mountain, Montana, is here made the type of a new genus and species, *Triplopides rieli*, characterized by the unique combination of features listed in the diagnosis above. M.S.U. No. 0772, a maxilla with P^3–M^3, represents the same species. Of the anterior dentition only I^2–C^1 are known; the roots of I^1 suggest that it was slightly larger than I^2 and probably of similar shape. Roots of the lower anterior teeth indicate the presence of canines and three pairs of lower incisors. A short postcanine diastema is followed by P_2^2, with no trace of the first premolar above or below. Of the upper premolars, P^4 is the most molariform, with protoloph and metaloph connected only by a thin bridge at midlength; P^3 and P^2 are less molariform, with the protoloph and metaloph fused lingually. P_3 and P_4 are relatively short and wide and have complete hypolophids. The posterolingual
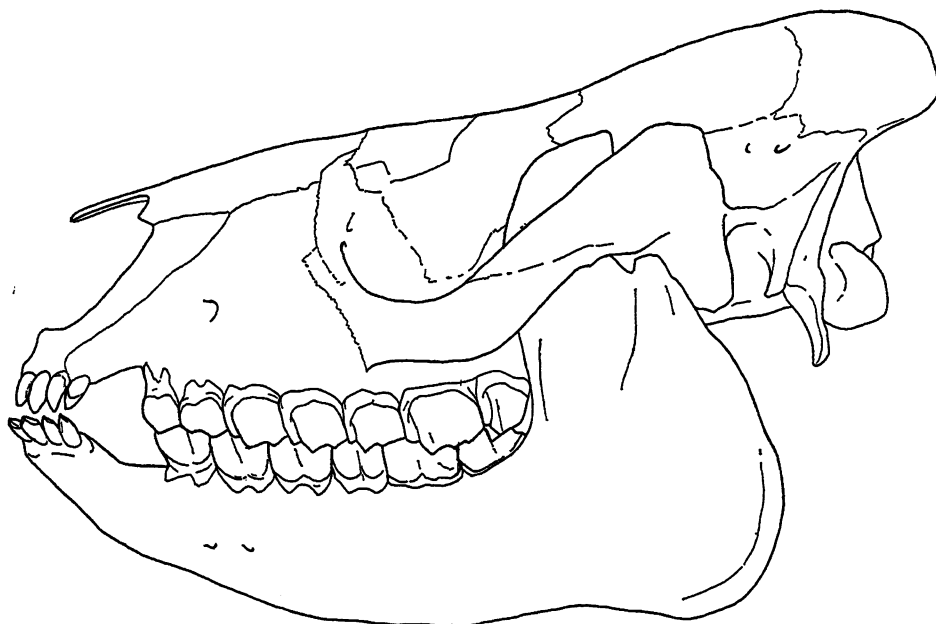

FIG. 17. Skull and mandible of *Hyracodon nebraskensis*, reversed from Scott (1941, pl. 89). ×1/2.
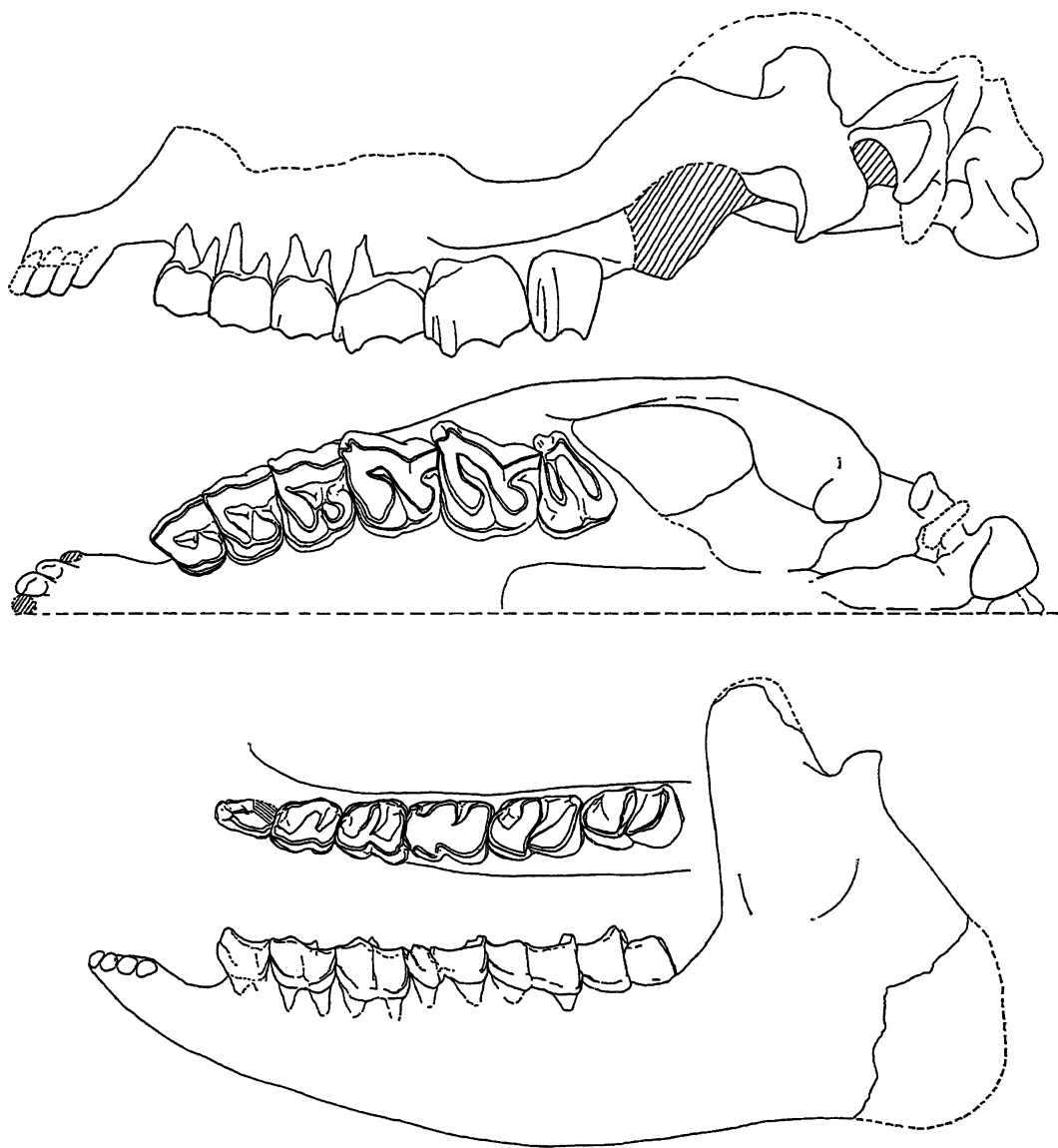
FIG. 18. *Triplopides rieli*, new genus and species, type, C.M. No. 9370. *Top and middle:* Incomplete skull and upper dentition in lateral and ventral views, respectively. *Bottom:* Mandible with lower dentition in occlusal and labial views. All ×1/2.

corner of P_2 is not preserved. M^3 has a smooth posterior wall, with no trace of the metacone.

Triplopides rieli is only slightly larger than the contemporaneous hyracodontid *Hyracodon nebraskensis*, from which it differs dentally in the following features: incisors spatulate, P^1 lost, premolars shorter relative to molars, upper premolars more molariform from back to front, M^{1-2} paracones projecting more labially and protocones not constricted, M^3 with no trace of the metacone. What is preserved of the skull of *Triplopides* suggests that it was similar in proportions to that of *Hyracodon*, with a short facial region and shallow nasal incision. The postglenoid process faces anteriorly in *Triplopides*, rather than anterolaterally as in *Hyracodon* and many other rhinocerotoids.

Triplopides rieli is about the same size as small species of the Oligocene rhinocerotid *Caenopus*, such as *C. dakotensis*, from which it differs dentally in incisor morphology and the loss of P^1. The cusp patterns of the cheek teeth are similar, and incomplete dentitions of *Caenopus* might be confused with those of *Triplopides*.

ARDYNIA Matthew and Granger, 1923

Ergilia Gromova, 1952.
Parahyracodon Beliajeva, 1952.

Type Species: *Ardynia praecox* Matthew and Granger, 1923.

Included Species: Type and *A. kazachstanesis* (Beliajeva, 1952), new combination.

Range: Early to Late Oligocene of Asia.

Revised Diagnosis: Medium-sized hyracodontids; length of M^{1-3}, approximately 60 mm. Teeth relatively high crowned: crown height index higher than 1.10. Incisors spatulate, increasing in size anteriorly; canines slightly smaller than I^3_3. Relatively long postcanine diastema. Premolar series shortened: P^1_1 lost, P^2_2 reduced in size. P_{3-4} molariform; P^{3-4} non-molariform, with protoloph-metaloph loop. M^{1-2} relatively long and narrow, with oblique cross crests; M^3 with or without a trace of the metacone. Manus tridactyl.

Discussion: Gromova (1952, p. 99) erected, as a new genus and species, *Ergilia pachypterna*, for a few foot bones and the proximal ends of a radius and ulna from the Early Oligocene Ardyn Obo beds of Inner Mongolia, the same formation in which *Ardynia praecox* occurs. Eight years later, Gromova (1960, p. 82) proposed a second species of *Ergilia*, *E. kazachstanica*, for a few foot bones from Middle Oligocene beds in central Kazakhstan. The foot bones on which Gromova based her two species are very similar to the foot bones of A.M.N.H. No. 26039, a specimen from the Early Oligocene Ulan Gochu beds at Urtyn Obo, Shara Murun region, Inner Mongolia, and A.M.N.H. No. 26039 includes, associated with the foot bones, a skull and mandible with dentition identical to that of *Ardynia praecox* (see text figs. 19 and 20). Such an association indicates that *Ergilia* and *Ardynia* are based on different parts of the same animal. *Ergilia pachypterna* thus becomes a synonym of *Ardynia praecox*. The association could have been anticipated by an application of Ockam's

razor, since the foot bones on which *Ergilia pachypterna* were based are the right size to belong with the teeth of *Ardynia praecox* and were found in the same fauna.

Beliajeva (1952, p. 122) created the genus *Parahyracodon* for two rhinocerotoid lower jaws; the type species, *P. mongoliensis*, is from the Ardyn Obo beds, and the second species, *P. kazachstanensis*, was found in the Middle Oligocene of Kazakhstan. In the diagnosis Beliajeva distinguished *Parahyracodon* from *Prothyracodon* (= *Triplopus*) and *Hyracodon*, but made no mention of *Ardynia*. Comparison of the jaw of *Parahyracodon mongoliensis* with that of *Arydnia praecox* from the same locality (A.M.N.H. No. 23058, figured in Matthew and Granger, 1925a, fig. 6, or P.I.N. No. 473-531, figured in Beliajeva, 1952, fig. 7) indicates that they represent the same species. The only difference is that the figured dentitions of *A. praecox* are more worn than is the type of *P. mongoliensis*, and the teeth are correspondingly shortened by interstitial wear. *Parahyracodon* thus becomes a synonym of *Ardynia*. The presence of P_2 is a variable feature in *Ardynia praecox;* a single-rooted alveolus is present in A.M.N.H. No. 23058 and absent from P.I.N. No. 473-531.

Parahyracodon kazachstanensis differs from *Ardynia praecox* in having relatively larger P_{3-4} (the length of P_{3-4} divided by the length of M_{1-3} is 0.53 in *P. kazachstanensis* and averages 0.43 in *A. praecox*). However, the P_2 of *P. kazachstanensis* is reduced almost as much as that of *A. praecox*, and the difference in size of P_{3-4} is not enough, in my opinion, to warrant separation on a generic level. Therefore I assign *P. kazachstanensis* to *Ardynia*. *Ergilia kazachstanica* Gromova, 1960, probably represents the feet of *A. kazachstanensis* (Beliajeva), since they both occur in the same fauna. Thus, of three genera and five species previously named, I recognize only two species belonging to one genus: *Ardynia praecox* Matthew and Granger, 1923 (including *Ergilia pachypterna* Gromova and *Parahyracodon mongoliensis* Beliajeva) and *Ardynia kazachstanensis* (Beliajeva, 1952) new combination (including *Ergilia kazachstanica* Gromova).

Gabunia (1964, p. 74) proposed the species *Ardynia plicidentata* for a DP^3 or DP^4 and an M^1 or M^2 from the Late Oligocene Benara
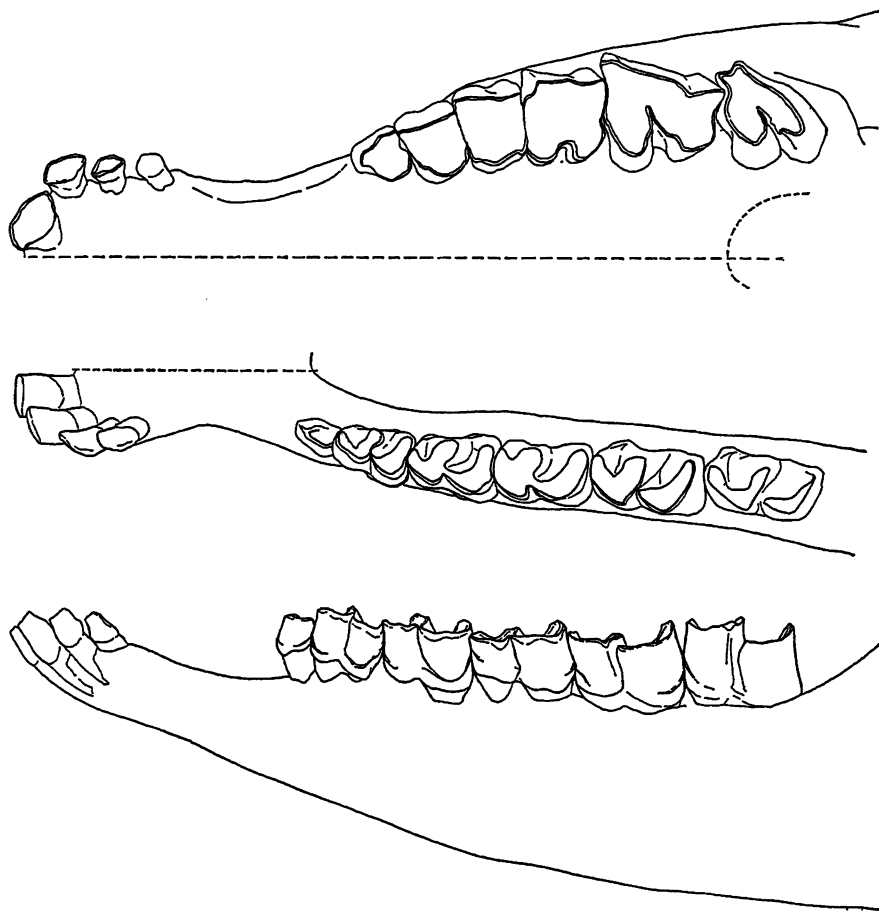
Fig. 19. *Ardynia. Top:* Upper dentition of *A. praecox,* A.M.N.H. No. 26039.
Middle and bottom: Lower dentition of *A. kazachstanensis,* new combination,
A.M.N.H. No. 26183, in occlusal and labial views, respectively. All ×2/3.

fauna of Georgia, U.S.S.R., which he distinguished from other species of *Ardynia* by the wrinkled enamel in the area of the crochet. This, in my opinion, is not an adequate basis for the recognition of a new species since that character is quite variable in *Ardynia praecox* specimens. *Ardynia plicidentata* falls within the size range of both *A. praecox* and *A. kazachstanensis,* and could belong to either species. It should be referred to as *Ardynia* sp.

Two upper premolars and two lower molars from the Benara fauna were referred to by Gabunia (1964, p. 70) as *Prothyracodon* sp. From Gabunia's illustrations (1964, p. 71, figs. 30–33) these appear to represent the same species as *Ardynia* sp. from the same fauna.

The anterior dentition of *Ardynia praecox* is known from A.M.N.H. No. 26039, the skull from the Ulan Gochu beds. The canine is very small, I^3 is slightly larger, and I^2 and I^1 are progressively larger. I^1, the largest incisor, is spatulate, unlike the much larger, elongate I^1 of the Rhinocerotidae. The anterior dentition of *Ardynia kazachstanensis,* known from A.M.N.H. No. 26183, a lower jaw from Middle Oligocene Baron Sog beds at Nom Khong Obo, Inner Mongolia, corresponds approximately to the upper dentition of *A. praecox,* except that the canine is slightly less reduced and the first incisor is slightly less

enlarged. These differences may not be significant, since the comparisons are based on only one specimen from each species. However, such a difference in incisor specialization would correlate with the lesser degree of P_{3-4} reduction seen in *A. kazachstanensis*, compared with the more advanced condition of *A. praecox*. This disparity is somewhat unexpected, since *A. praecox* is older than *A. kazachstanensis*.

An isolated M^3 from the Ardyn Obo beds, P.I.N. No. 473–800, was referred to by Beliajeva (1952, p. 127, see pl. 4, fig. 4) as "gen. et sp. indet." It is identical to the four M^3's known for *Ardynia praecox*, except that it has a small metacone. It probably represents an atavistic variant of the *Ardynia praecox* population.

All the known M^3's of *Ardynia* are worn, so it is not possible to determine accurately the crown height index. In the least worn M^3, A.M.N.H. No. 19156, the remaining height of the paracone divided by the width of the tooth is 1.09.

ALLACEROPS WOOD, 1932

During the Oligocene there existed in Europe and Asia a group of large rhinocerotoids (length of M^{1-3}, approximately 100 mm.) with erect canine tusks and M^3's lacking a metacone. This group had previously been assigned to the Rhinocerotidae, but recently (Radinsky, 1966) I restricted that family to forms stemming from the *Trigonias* group, with its unique I^1/I_2 incisor specialization. The *Allacerops* group, with cheek teeth typical of non-amynodontid rhinocerotoids and no particular anterior dental specialization, is most naturally included in the family Hyracodontidae.

The taxonomic nomenclature of the group under consideration has had a confusing history. Aymard (1854) proposed a new genus and species, *Ronzotherium velaunum*, for a mandible with $P_2–M_3$ (figured in Filhol, 1882, pl. 12, and in Osborn, 1900, fig. 3), from Early Oligocene beds in France. Abel (1910, p. 15) erected the genus *Praeaceratherium* based on teeth ($P_4–M_2$, DP^{1-4}, M_1, and DP^{2-3}) from the Quercy Phosphorites which had been described by Filhol (1884, p. 26) under the name "*Aceratherium minus* (Cuvier)." Cuvier
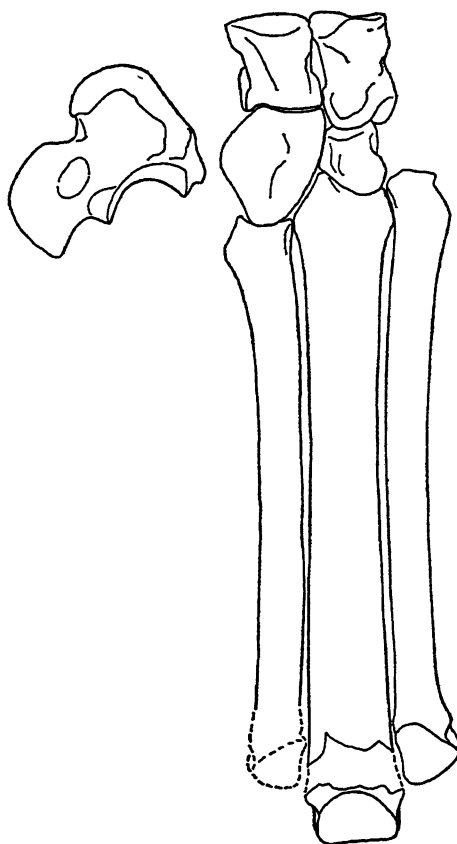

FIG. 20. Carpal bones of *Ardynia praecox*, A.M.N.H. No. 26039. The magnum is shown in lateral view also. ×3/4.

named a species not *A. minus*, but rather *A. minutus*. Thus Filhol's *A. minus* apparently is an incorrect subsequent spelling and has no nomenclatorial status (International Code, Art. 33b); consequently *Praeaceratherium* Abel, lacking its type species, has no valid status in nomenclature. Roman (1911, p. 7) created the genus *Eggysodon*, based on *Ronzotherium? osborni* Schlosser, 1902, the type of which is an isolated M^1 or M^2 (Schlosser, 1902, pl. 5, fig. 3) from the Oligocene of Germany. Stehlin (1930, p. 645) without justification emended Roman's *Eggysodon* to *Engyodon*.

Borissiak (1915b, p. 781) referred to the *Trigonias*-like rhinocerotid genus *Epiaceratherium* a maxillary from the Middle Oligocene of Kazakhstan, with a large C^1 alveolus
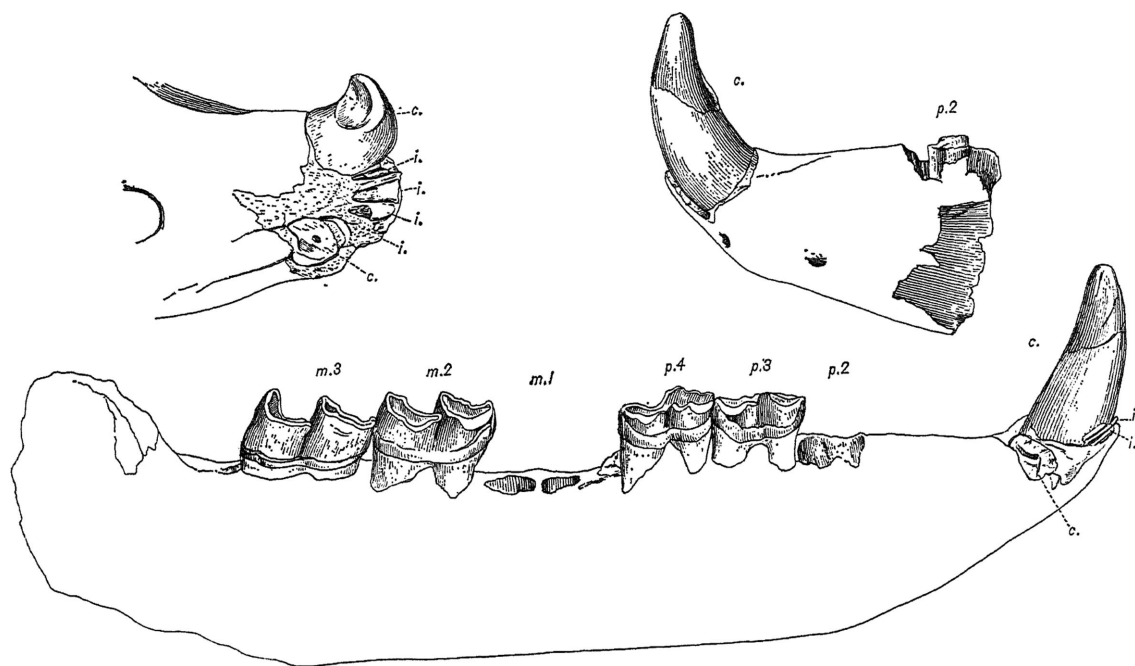
FIG. 21. Mandible of *Allacerops*. From Osborn (1900, fig. 2). ×1/2.

and P^1–M^3, under the name *Epiaceratherium turgaicum*. The mandible of *E. turgaicum* has a large erect canine. Wood (1932, p. 170) pointed out that *E. turgaicum* was not congeneric with the type of *Epiaceratherium*, *E. bolcense*, and erected for it a new genus, *Allacerops*. Wood considered *Allacerops* to include also the European rhinocerotoids with large, erect canines.

The cheek teeth of the *Allacerops* group are basically quite similar to those of contemporary rhinocerotids, such as *Aceratherium*, and it is primarily the anterior dentition that separates the two groups. When European Oligocene rhinocerotoids are revised on the species level, it may be possible to separate *Allacerops* from *Aceratherium* on the basis of size differences between species at a given locality. However, at present it is not possible to determine with certainty whether the types of *Ronzotherium* (*R. velaunum*) and *Eggysodon* (*E. schlosseri*) represent *Allacerops* or *Aceratherium*. That the *Allacerops* group was present in Europe is indicated by the mandible called *Aceratherium gaudryi* Rames (see text fig. 21), the maxillary referred to

Eggysodon osborni by Roman (1911, pl. 1, fig 1), and the mandible called *Engyodon* sp. by Stehlin (1930, fig. 1). The crown height index of the specimen figured by Roman (*ibid.*), estimated from the photograph, is 0.91.

The only known difference between the Asiatic *Allacerops turgaica* and the European forms is the presence of P$_1$ in the former and its absence from the latter. The European mandibles mentioned in the preceding paragraph have only two pairs of lower incisors; the incisor number is unknown in *Allacerops turgaica*. The manus of *A. turgaica* is tridactyl (see Borissiak, 1918, pl. 2, figs. 17, 25); it is unknown in the European species. If the European and Asiatic species are congeneric, and if *Ronzotherium velaunum* is shown to belong to this group, then the name *Ronzotherium* has priority. If *Ronzotherium* is invalid, or indeterminate, and the type of *Eggysodon* is proved to be congeneric with the referred maxillary mentioned above, then *Eggysodon* must take priority over *Allacerops*. However, if neither *Ronzotherium* nor *Eggysodon* can be shown to be valid, then the name *Allacerops* will stand. For the present, until the European

forms are revised, I provisionally use the name *Allacerops* for both European and Asiatic members of this group.

GIANT OLIGOCENE HYRACODONTIDS

There existed in Asia during the Oligocene a group of gigantic rhinocerotoids (length of M^{1-3}, 200–250 mm.), with enlarged nasal incisions and a unique incisor specialization—hypertrophied, conical first incisors, the upper one vertical and the lower procumbent. This group was formerly classified as a subfamily (Indricotherinae) of the Rhinocerotidae, but that family has recently been restricted to forms with the incisor specialization of chisel-shaped I^1 and lanceolate I_2, and the indricotheres have been assigned to the Hyracodontidae (Radinsky, 1966).

A mandible from the Ardyn Obo beds, Inner Mongolia, described under the name *Urtinotherium incisivum* by Chow and Chiu (1963, p. 230), indicates that by Early Oligocene time the giant size (length of M_{1-3}, 210 mm.) and the hypertrophied, conical, procumbent I_1 characteristic of the group had already been attained (*ibid.*, fig. 1, pls. 1, 2). *Urtinotherium incisivum* differs from the later giant hyracodontids in having I_2, I_3, C_1, and P_1 still present, although reduced in size.

Urtinotherium incisivum may be conspecific with the few isolated teeth from Early Oligocene beds in Lunan, China, named by Chow (1958, p. 264) *Indricotherium parvum*. A.M.N.H. No. 26032, an incomplete mandible from Early Oligocene beds at Jhama Obo, Shara Murun region, Inner Mongolia (for location, see Radinsky, 1964, fig. 2), probably also represents this species. In A.M.N.H. No. 26032, the length of M_{1-3} is 200 mm.

A few specimens in which the premaxillae and mandibular symphysis are preserved (A.M.N.H. Nos. 18650 and 26166) indicate that by Middle Oligocene time the second and third incisors, canines, and first lower premolar were lost. The cheek teeth of all the giant hyracodontids are very similar in pattern, and, on the basis of the teeth alone, not more than one genus is indicated (this conclusion was reached by Granger and Gregory, 1936, p. 62). However, the few skulls known are of two different types: one is small relative to the size of the dentition, has a flat dorsal profile, flat zygomatic arch, and a widely open external auditory meatus, whereas the other type is larger, with domed frontal bones, a curved zygomatic arch, and postglenoid and posttympanic processes almost touching (see text fig. 22). The small skulls include old individuals, so the differences are not merely onto-
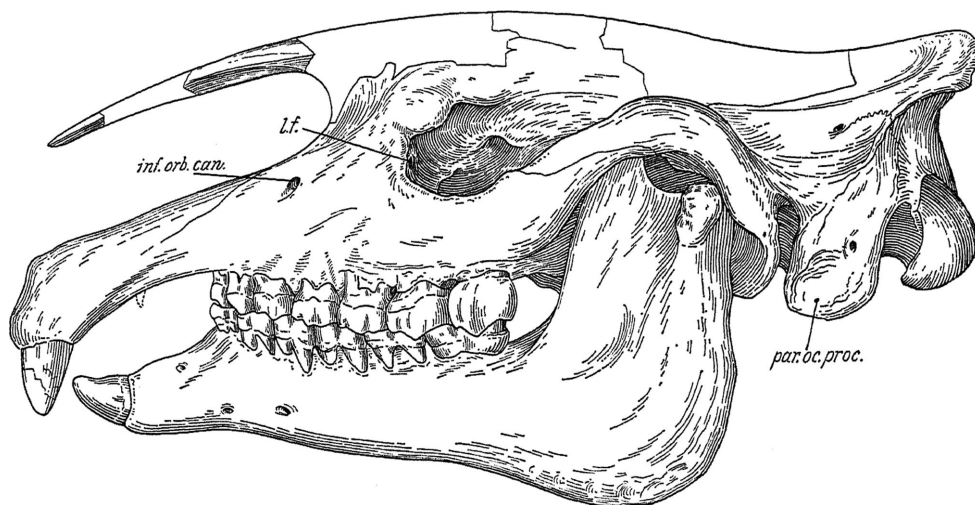

Fig. 22. Skull and mandible of *Indricotherium transouralicum*, from Granger and Gregory (1926, fig. 1). The skull, A.M.N.H. No. 18650, is the type of "*Baluchitherium grangeri.*" ×1/10.
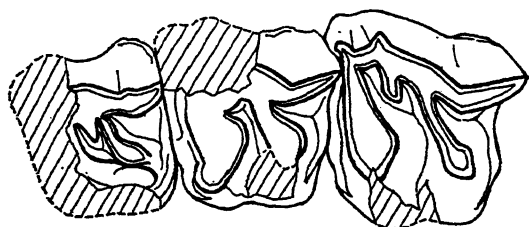
FIG. 23. "*Hyracodon primus*," type, C.M. No. 11914, P⁴–M². ×1.5.

genetic. In the most recent revision of this group, Gromova (1959, pp. 30, 38) placed the large-skulled forms in the genus *Indricotherium* Borissiak, 1915 (including *Baluchitherium grangeri* Osborn, 1923), and the small-skulled forms in the genus *Paraceratherium* Cooper, 1911 (including *Baluchitherium osborni* Cooper, 1913, and *Aralotherium* Borissiak, 1939). Since the available evidence on the range of variation in cranial morphology in this group is so limited, I hesitate at this time to evaluate the desirability of recognizing the cranial differences on the generic level. The crown height index for *Indricotherium* averages 0.70, which is low for an Oligocene hyracodontid.

Benaratherium callistrati Gabunia, 1955, is known primarily from a mandibular fragment with P₃–M₃ from the Late Oligocene Benara fauna of the Georgian S.S.R. It is smaller than known species of *Paraceratherium* and *Indricotherium* (length of M₁₋₃ of *B. callistrati*, 169 mm.), with less of a size increase from M₁ to M₃ but otherwise very similar to the previously named forms. In my opinion its generic distinctness has not been adequately demonstrated.

Isolated teeth of either *Paraceratherium* or *Indricotherium* have been found in Rumania (Gabunia and Iliescu, 1960, p. 425) and Yugoslavia (Petronijević and Thenius, 1957, p. 153). They mark the westernmost occurrence of this group of rhinocerotoids.

The giant Oligocene hyracodontids were probably derived from some Late Eocene species of *Forstercooperia*. *Forstercooperia sharamurenense* shows advances toward the indricotheres in such features as its large size, somewhat conical incisors, with the first pair slightly larger than the following ones, the beginnings of nasal incision enlargement, and its long, narrow, unguligrade metatarsus.

P²⁻³ of *F. sharamurenense* are slightly more molariform than those teeth in some Middle Oligocene specimens of *Indricotherium*, but the difference is not great enough in my opinion to disqualify *F. sharamurenense* as a possible ancestor of the Early Oligocene *Urtinotherium* and the later indricotheres.

TAXA OF UNCERTAIN SYSTEMATIC POSITION

NORTH AMERICA

The presence of a large-sized species of *Triplopus* (M₁₋₃, 60 mm.) in the Uinta B beds, Uinta Formation, Utah, is suggested by a few lower dentitions (C.M. Nos. 2940 and 3112; P.U. Nos. 11289 and 11292), and one deciduous upper dentition (A.M.N.H. No. 1929) referred by Wood (1934, p. 209) to *Hyrachyus douglassi*. The type of *H. douglassi* is C.M. No. 784, the anterior part of a skull with worn P¹⁻⁴ and P₂–M₃, from the Late Eocene Sage Creek beds, Montana. Unfortunately, without an M³ or unworn upper molars it is not possible to make a definite generic assignment of *H. douglassi*.

C.M. No. 11914, a maxillary fragment with damaged P⁴–M² (see text fig. 23) indicates the presence of a small hyracodontid in the late Late Eocene Duchesnean Lapoint beds, Uinta Basin, Utah. Peterson (1934, p. 388) named this specimen *Hyracodon primus*. It differs from *Hyracodon nebraskensis* in having a more projecting paracone and in lacking a constricted protocone on the molars, and in being smaller and having lower-crowned teeth. *Hyracodon primus* is about the same size as *Triplopus rhinocerinus*, from which it differs, in known features, in having prominent cristae on P⁴ and M², and a more posteriorly deflected P⁴ metaconule. It differs from *Epitriplopus uintensis* and *E. medius* in having a relatively shorter and wider M¹, a less molariform P⁴, and molar cristae. *Hyracodon primus* may be ancestral to *Hyracodon nebraskensis*, but the differences in molar pattern suggest that they should not be placed in the same genus. *Hyracodon primus* appears to be closest to *Triplopus* but may represent a different genus.

ASIA

A mandible with P₃–M₃ (A.M.N.H. No. 20299) from the Ulan-Shireh-equivalent Ar-

shanto beds at Ula Usu, Inner Mongolia, represents the only known specimen of *Teilhardia pretiosa* Matthew and Granger, 1926. This small rhinocerotoid was previously assigned to the Hyracodontidae, but the shortness of the premolars relative to the molar series suggests that it may represent an amynodontid. It may be ancestral to *Caenolophus promissus* Matthew and Granger (1925b) from the overlying Shara Murun beds. *Caenolophus promissus*, here transferred to the Amynodontidae (see p. 10), is slightly larger than *Teilhardia pretiosa* and has comparably short premolars.

Beliajeva (1954, p. 45) erected the species *Prothyracodon turgaiensis* for a jaw fragment with P_4–M_3 from Middle Oligocene beds in Kazakhstan. The length of the molar series is about 63 mm. Two incomplete mandibles in the collections of the American Museum of Natural History from the Shara Murun region, Inner Mongolia, are about the same size and probably represent the same species as *P. turgaiensis*. A.M.N.H. No. 26208, from Ulan-Gochu-equivalent beds at Twin Oboes, includes I_1, alveoli and roots of I_1, I_3, C_1, and P_1, and P_2–M_3. The length of M_{1-3} is 66 mm.;

the length of P_{1-4} is approximately 55 mm. The incisors were equal-sized and spatulate, and the canine was slightly larger than I_3. A.M.N.H. No. 81874, from "? Baron Sog" beds at Urtyn Obo, includes only M_{2-3}. On the basis of the known morphology, *P. turgaiensis* differs from species of *Triplopus* (of which *Prothyracodon* is a synonym) only in its larger size. However, the lower dentition is not so diagnostic as is the upper dentition, and, in view of the difference in size and stratigraphic horizon, it is quite possible that "*Prothyracodon*" *turgaiensis*, upon the discovery of its upper dentition, will prove to be generically distinct from *Triplopus*. Its main significance at present is that it indicates the survival into the Oligocene in Asia of a hyracodontid with unspecialized anterior teeth.

A.M.N.H. No. 26056, a mandible with C_1 and P_1–M_3, from "?Ulan Gochu" beds at East Mesa, Shara Murun region, Inner Mongolia, is similar in morphology to "*Prothyracodon*" *turgaiensis* but is about 20 per cent larger. The length of M_{1-3} is 77 mm.; the length of P_{1-4} is 60 mm.

HYRACODONTID RHINOCEROTOIDS first appear in the fossil record at the beginning of the Late Eocene, represented by the genera *Triplopus* and *Forstercooperia*. A suitable ancestor for these forms is the Middle Eocene helaletid tapiroid *Hyrachyus*. Known morphological changes involved in the transition from *Hyrachyus* to these primitive hyracodontids include some relatively minor dental changes (lengthening and flattening of the

tal morphology between *Hyrachyus* and *Triplopus*, but intermediates are not known between *Hyrachyus* and *Forstercooperia*; that transition may have occurred in the poorly known Middle Eocene of Asia. The primitive nature of the oldest species of *Triplopus* and *Forstercooperia* suggests that their most immediate common ancestor, presumably something like *Hyrachyus*, would probably be considered a tapiroid. Although the present
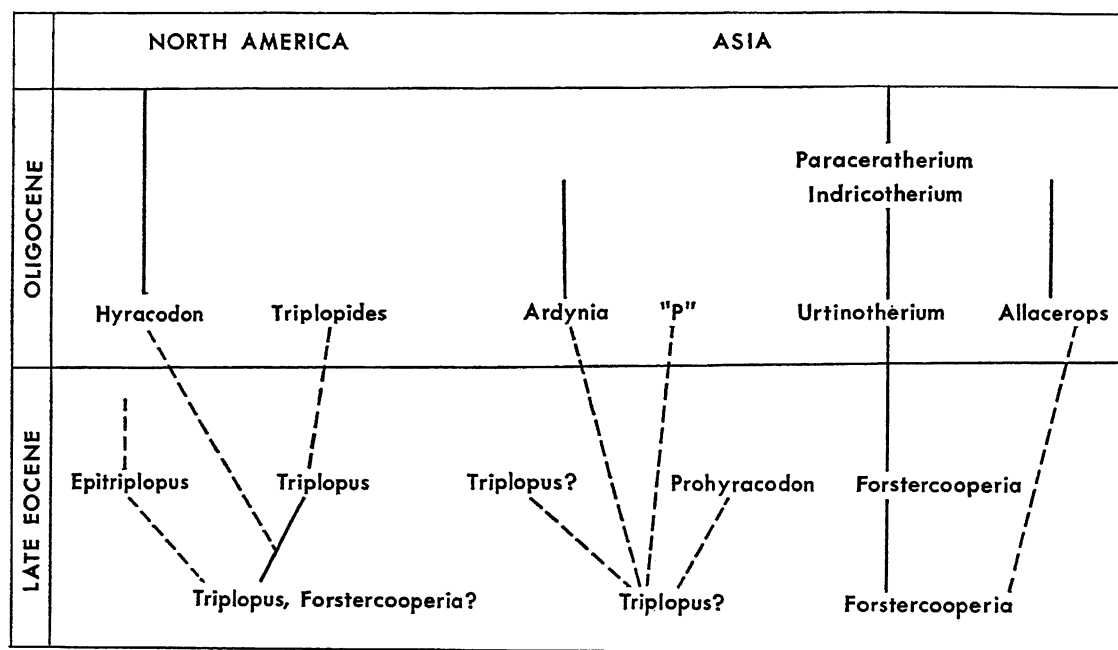

FIG. 24. Suggested phylogeny of the Hyracodontidae. "P" represents "*Prothyracodon*" *turgaiensis*. *Allacerops* occurs also in Europe.

M^{1-2} ectolophs and concomitant increase in height of lower molar paralophids and metalophids, suggesting increased emphasis on vertical shear along those labial ridges, reduction in size of parastyles, reduction in size and lingual deflection of the M^3 metacone, and a slight increase in crown height), loss of the fifth metacarpal (known definitely only for *Triplopus*), which indicates increased specialization for running, and, in the case of *Forstercooperia*, increase in size. A series of specimens from late Middle Eocene Bridger beds of North America bridges the gap in den-

taxonomic arrangement probably leaves the Hyracodontidae as a polyphyletic group, I find it preferable to the alternative of including *Hyrachyus* in the Hyracodontidae, which would make it impossible to diagnose the family within the bounds of the Rhinocerotoidea.

During the Late Eocene in North America and Asia, *Triplopus* and *Forstercooperia* underwent a moderate evolutionary radiation, with most of the diverging lineages represented by a single genus each (see text fig. 24). Within the genus *Triplopus*, evolutionary trends include increase in molarization of the premo-

lars and reduction of the M³ metacone (compare *Triplopus implicatus* and *T. rhinocerinus*). A contemporary of *Triplopus* in the Late Uintan fauna, and presumably derived from an early species of *Triplopus*, the North American genus *Epitriplopus*, is characterized by precociously molariform premolars and precociously high-crowned teeth (see text fig. 25). A second lineage for which *Triplopus* is a suitable ancestor is that of the well-known North American Oligocene genus *Hyracodon*, characterized by slender, approximately equal-sized, spatulate to pointed incisors and canines, and the retention of the M³ metacone. A contemporary of *Hyracodon* in the Early Oligocene of North America is the genus *Triplopides*, which is unusual in that it has lost P¹. The incisors of *Triplopides* appear to have been relatively slender and spatulate, with a slight size decrease posteriorly. The M³ metacone is lost in *Triplopides*.

A descendant of *Triplopus* in the Late Eocene of Asia is the poorly known genus *Prohyracodon*, which is advanced over *Triplopus* only in having lost all vestiges of the M³ metacone. *Prohyracodon* ranged as far west as eastern Europe. In the Oligocene of Asia the genus *Ardynia* represents yet another group of hyracodontids which was probably derived from *Triplopus*. *Ardynia* is characterized by relatively high-crowned teeth (more so than those of any other hyracodontid), relatively large spatulate incisors, a long postcanine diastema, and a shortened premolar series. These features suggest that *Ardynia* was more of a grazer and fed on harsher vegetation than did the other hyracodontids. Finally, the species *"Prothyracodon" turgaiensis* indicates the presence in Oligocene faunas in Asia of a hyracodontid with unspecialized anterior dentition.

All the hyracodontids mentioned so far were small to barely medium-sized animals, and in those genera in which the feet are known, *Triplopus*, *Hyracodon*, and *Ardynia*, the manus is tridactyl and relatively long and slender, indicating specialization for running. Presumably the same specialization was present in *Epitriplopus*, *Triplopides*, and *Prohyracodon*.

The remaining genera of hyracodontids are medium-sized to gigantic animals. The most primitive species of *Forstercooperia*, the North American *F.? grandis*, differs from contemporaneous primitive species of *Triplopus* only in its (considerably) larger size. However, the other species of *Forstercooperia*, all Asiatic, show a divergent specialization in their stubby canines and pointed, rather than spatulate, incisors. Evolutionary trends within *Forstercooperia* include premolar molarization, reduction and loss of the M³ metacone, and, in at least one line, enlargement of the nasal incision (compare *F. confluens* with *F. sharamurenense*). Some species of *Forstercooperia* probably gave rise to the Oligocene *Paraceratherium-Indricotherium* group, which is characterized by gigantic size and a peculiar incisor specialization—the first pair of incisors are enlarged, stubby, and conical, with the lower one procumbent, and the posterior incisors and canines are lost. The Early Oligocene genus *Urtinotherium*, known only from a mandible, provides an intermediate form between *Forstercooperia* and *Paraceratherium*.

The last lineage of hyracodontids is represented in Oligocene faunas in Europe and Asia by the genus *Allacerops*, which is characterized, among hyracodontids, mainly by its lack of specialization. The cheek teeth display the degree of premolar molarization, hypsodonty, and loss of M³ metacone seen in most Oligocene hyracodontids. The canine is primitively large, possibly slightly hypertrophied. The lower incisor alveoli indicate that only two pairs of incisors were present. If *Allacerops* was derived from *Forstercooperia*, it must have split off early in the history of *Forstercooperia*, before the anterior dental specializations appeared in that genus.

Various subfamily groupings have been proposed for the Hyracodontidae, but in view of our present ignorance of phylogenetic relationships between genera (only the *Forstercooperia-Urtinotherium-Paraceratherium* sequence seems reasonably well established), I believe it best for the present to omit formal suprageneric categories in the Hyracodontidae.

A visual summary of crown height indices is presented in text figure 25. All Late Eocene forms, with the exception of *Epitriplopus*, have about the same crown height index, and the points fall on an approximately straight line on an arithmetic scale, indicating the apparent absence of an allometric growth factor in crown height within the size range represented.
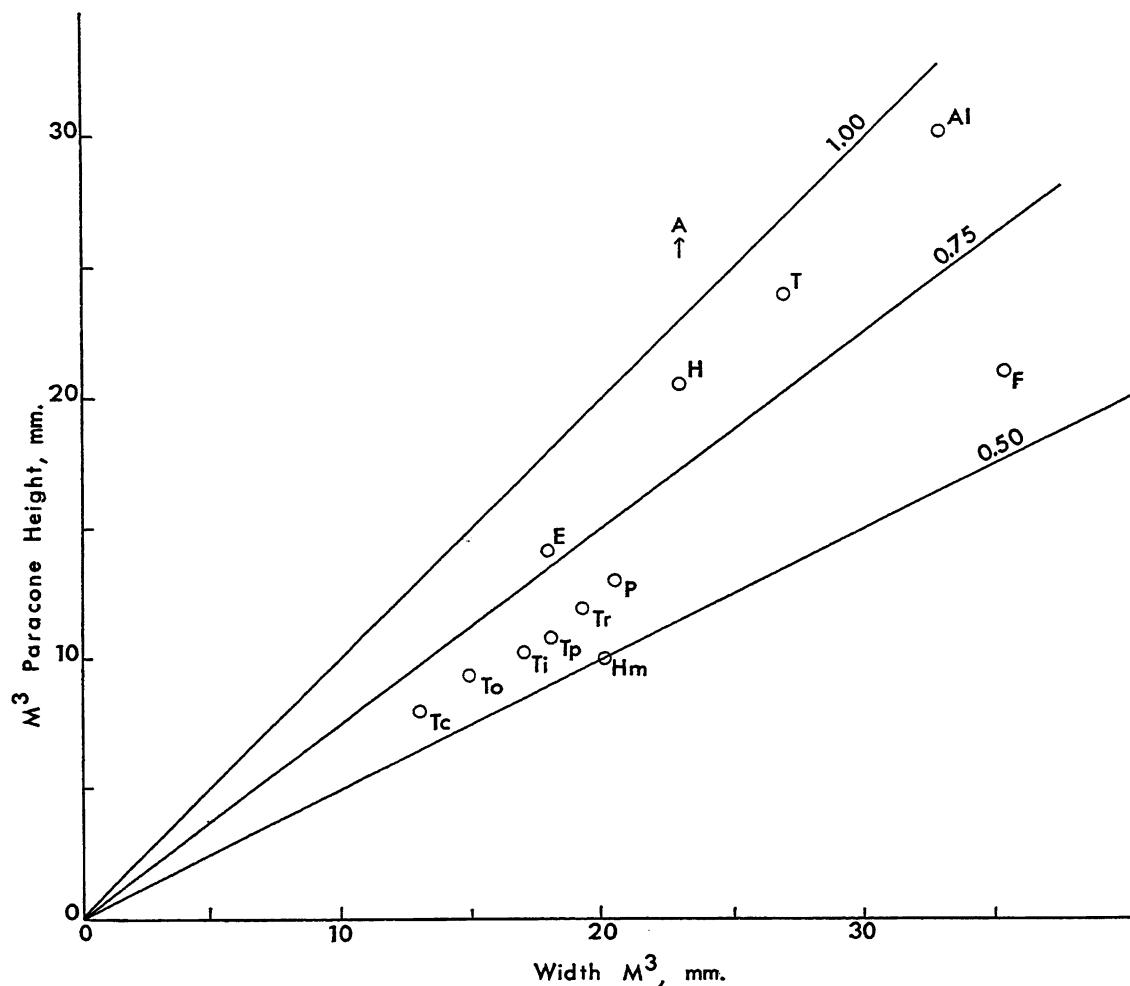
Fig. 25. Scatter diagram, showing relationship of M³ paracone height to M³ width in the Hyracodont-idae. *Indricotherium*, which falls off the scale used here, has M³'s averaging 70 mm. in height and 100 mm. in width.

Abbreviations: A, *Ardynia* (height, more than 25 mm.); Al, *Allacerops;* E, *Epitriplopus;* F, average of *Forstercooperia* species; H, *Hyracodon;* Hm, Bridger B *Hyrachyus modestus* (included to show the ancestral condition); P, *Prohyracodon;* T, *Triplopides;* Tc, *Triplopus cubitalis;* Ti, *Triplopus implicatus;* To, *Triplopus obliquidens;* Tp, *Triplopus? proficiens* from the Ulan Shireh beds; Tr, *Triplopus rhinocerinus*.

Three of the Oligocene genera, *Hyracodon,* *Triplopides,* and *Allacerops,* have about the same crown height index, again with the apparent absence of an allometric growth factor. *Ardynia* has unusually hypsodont teeth. In *Indricotherium,* which falls off the scale used here (the width of M³ averages 100 mm.), the

index is low, averaging 0.70. This low index suggests for the *Forstercooperia-Urtinotherium-Paraceratherium-Indricotherium* line either a negative allometric factor in tooth height or the lack of the evolutionary trend toward hypsodonty seen in the other hyracodontid lineages.

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