A REVIEW OF THE RHINOCEROTOID FAMILY HYRACODONTIDAE (PERISSODACTYLA)

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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

TAXONOMY

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_{3-1}^{3-1}, C_{1-0}^{1-0}, P_{4-3}^{4-3}, M_{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.*

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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 P^2, the greater progressiveness of P^4, the greater reduction of the posterior buttress of M^3" (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 M^1 but appears to be absent from M^2 and M^3. The presence or absence of an M^1 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 M^3. The degree to which the M^3 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.

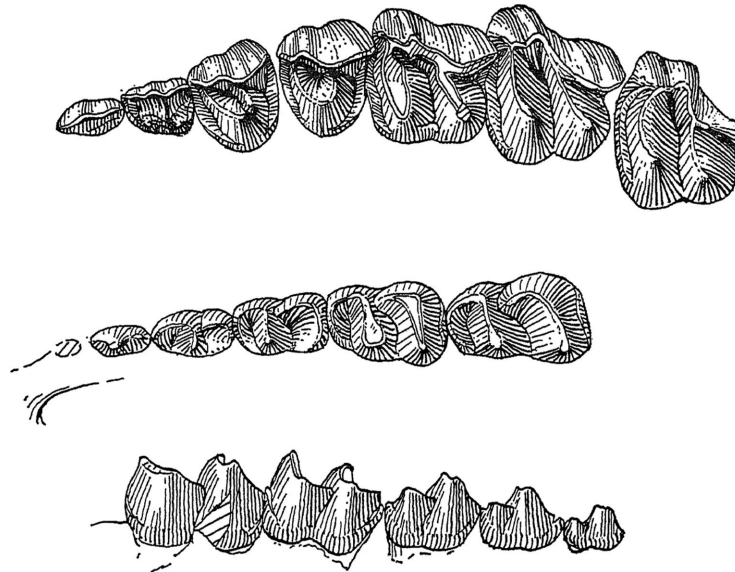*Triplopus cubitalis* is distinguished from

FIG. 1. *Triplopus cubitalis*, type, A.M.N.H. No. 5095. *Top:* P¹–M³, M²⁻³ reversed from opposite side. *Middle and bottom:* P₂–M₂ 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

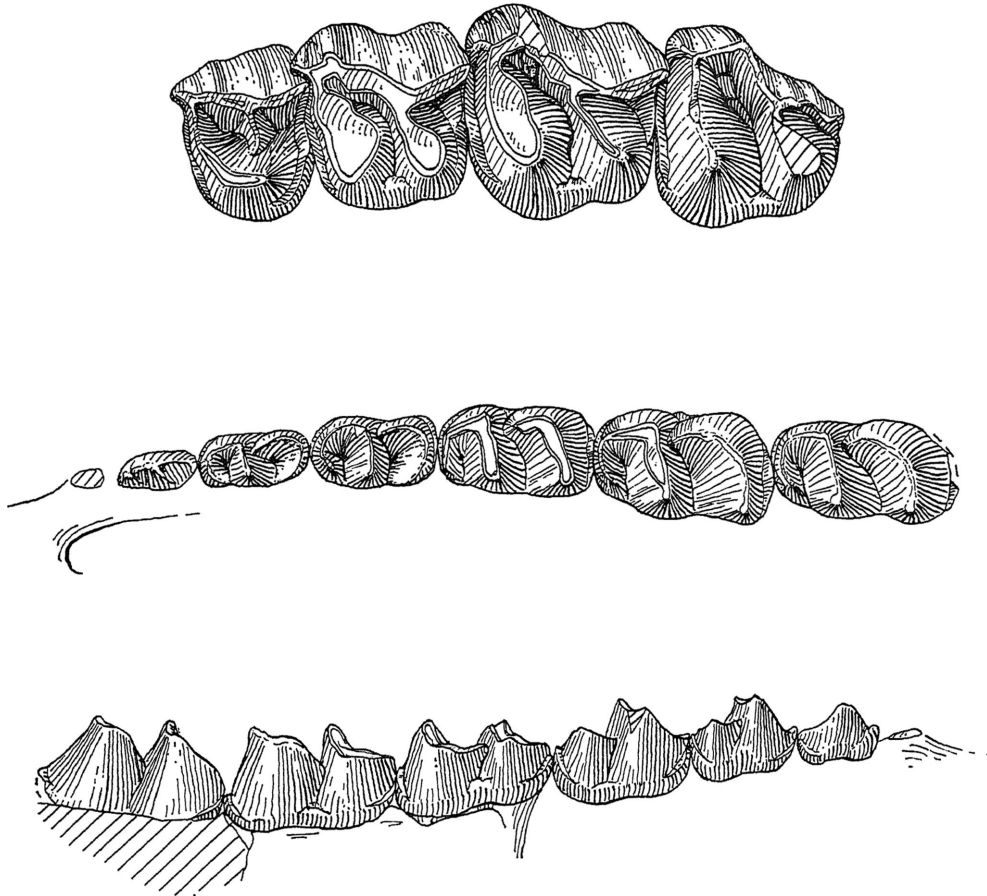|	N	O.R.	M
P_1			
L	2	4.8–5.3	5.05
W	2	2.5–2.8	2.65
P_2			
L	2	6.9–6.9	6.9
W	2	3.2–3.6	3.4
P_3			
L	1	—	8.0
W	1	—	4.5
P_4			
L	3	8.3–9.0	8.73
W	3	5.8–6.3	6.10
M_1			
L	5	9.8–11.5	10.60
W	5	6.5– 8.7	7.54
M_2			
L	3	11.9–12.0	11.93
W	3	7.8– 9.0	8.37
M_3			
L	3	12.8–14.1	13.63
W	3	8.0– 8.7	8.40
L M_{1-3}	3	34–37	35.33

FIG. 2. *Triplopus implicatus*, new combination. *Top:* A.M.N.H. No. 2341, P⁴-M³. *Middle and bottom:* A.M.N.H. No. 2342, P₂-M₃, 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 P³.

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 P² (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 M³ 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 M³ metacone is small and lingually deflected, as in younger and more advanced *Triplopus* specimens. M¹⁻² 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 M^3 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 M^3 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
P^1	—	—	—
P^2			
L	1	—	8.1
W	1	—	9.0
P^3			
L	2	9.3– 9.6	9.45
W	2	12.0–12.5	12.25
P^4			
L	3	10.0–11.7	10.97
W	3	14.0–17.2	15.53
M^1			
L	4	13.1–14.8	13.95
W	4	15.9–17.5	16.70
M^2			
L	3	15.5–16.9	16.13
W	3	17.2–18.7	17.87
M^3			
L	5	14.8–17.2	15.76
W	5	16.2–19.3	17.48
L $M^{1–3}$	3	44–49	46.33
P_1	—	—	—
P_2			
L	2	8.0–9.1	8.55
W	2	4.8–5.5	5.15
P_3			
L	3	9.8–11.2	10.37
W	3	6.4– 6.8	6.63
P_4			
L	6	10.3–12.8	11.70
W	6	7.4– 9.2	8.38
M_1			
L	7	12.7–14.0	13.56
W	7	8.4–10.0	9.21
M_2			
L	6	14.6–16.5	15.58
W	6	9.6–11.0	10.13
M_3			
L	3	16.5–18.0	17.20
W	3	10.3–11.5	10.80
L $M_{1–3}$	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 P^4 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-
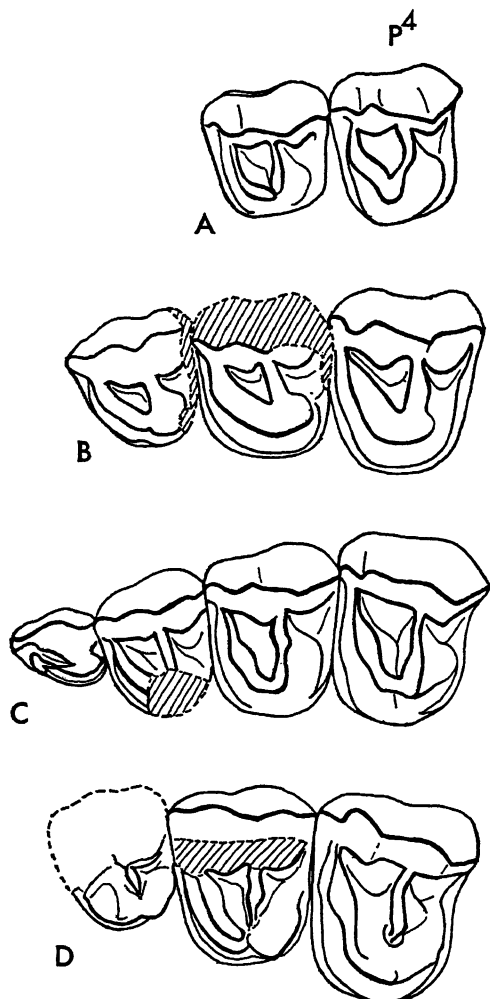
P⁴

FIG 3. Upper premolars of *Triplopus obliquidens*, 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 M³ 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 M³ 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 M³ 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.
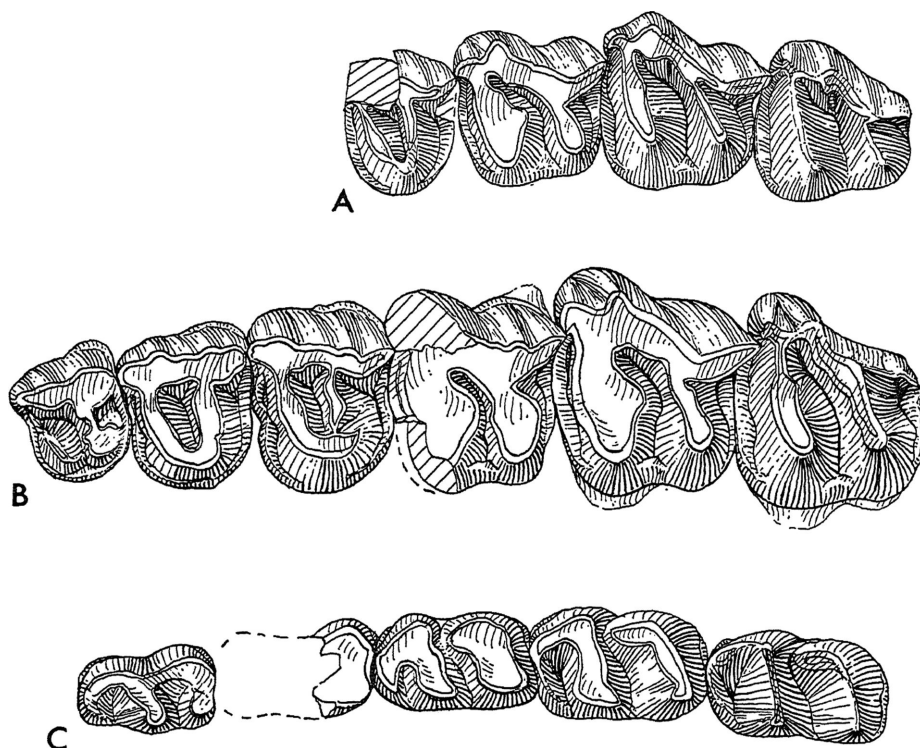
The skull of *Triplopus*, as interpreted from a

FIG. 4. *Triplopus* from the Uinta Basin. A. *T. obliquidens*, A.M.N.H. No. 1972, P⁴–M³. B, C. *T. rhinocerinus*, new combination, type, Y.P.M. No. 13331, P²–M³ and P₃–M₃. In C, P₃ 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 M³ (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-
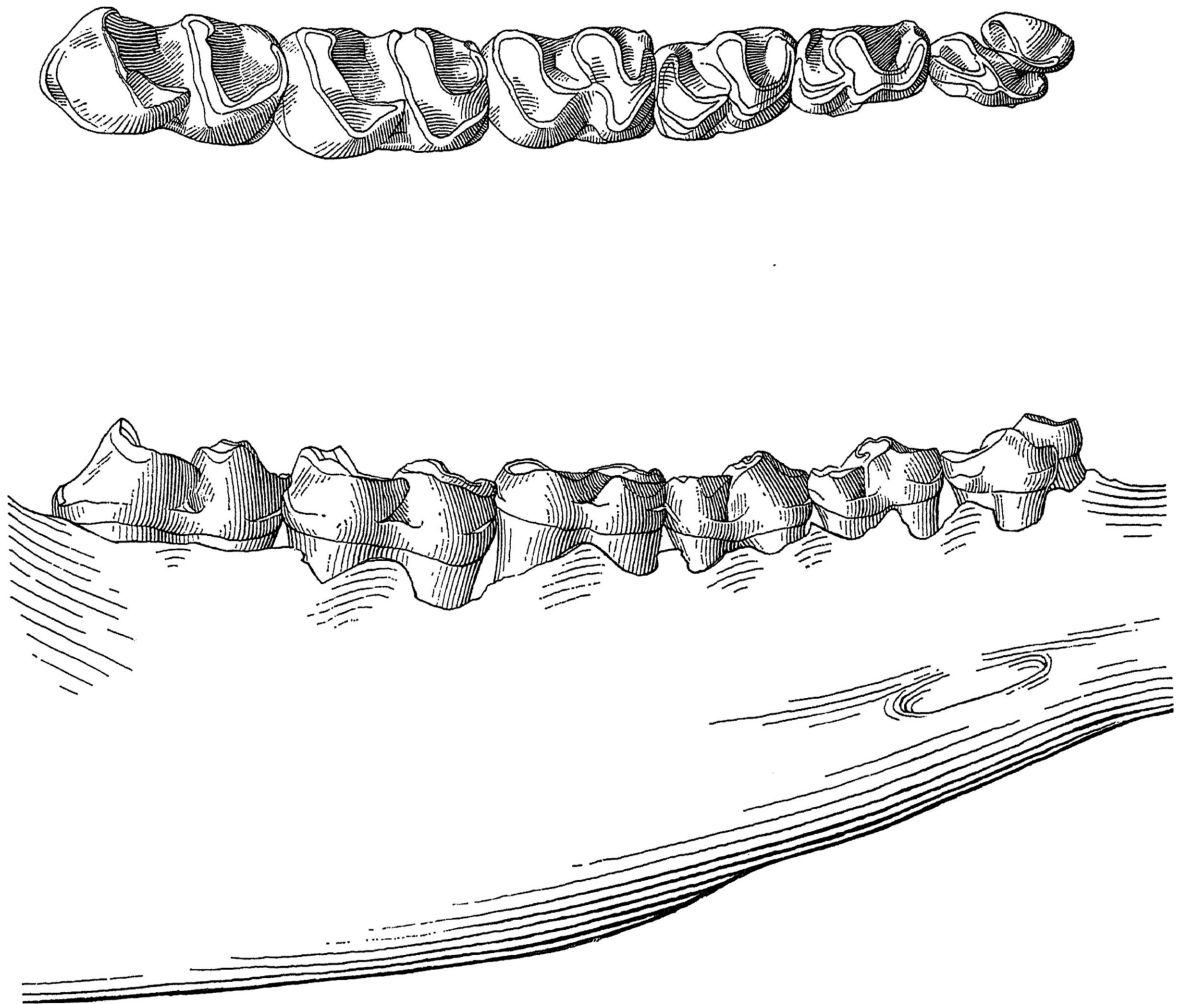
FIG. 5. *Triplopus? proficiens*, new combination, type, A.M.N.H. No. 20141, P_1–M_3. From Matthew and Granger (1925c, fig. 9). ×1.5.

larged I_2 is not congeneric with *T.? proficiens*; it may belong to the tapiroid *Teleolophus medius*.) The upper premolars have a pro-toloph-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 tapi-roid-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
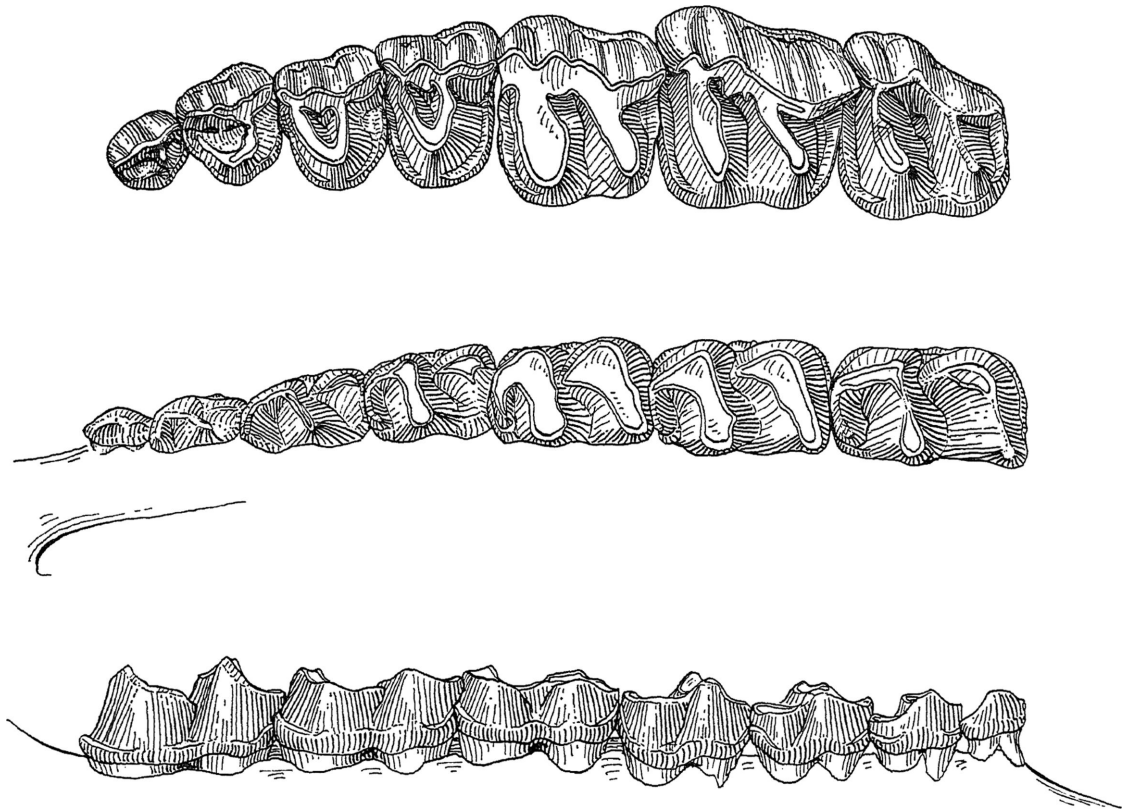
FIG. 6. *Triplopus? proficiens*, new combination, from the Ulan Shireh beds. *Top:* A.M.N.H. No. 21552, P¹–M³. *Middle and bottom:* A.M.N.H. No. 26124, P₁–M₃, in occlusal and labial views, respectively. All ×1.5.

Manha *Triplopus? proficiens*, and have the same pointed posterior border on M₃. A.M.N.H. No. 26673, a maxilla with extremely worn P¹–M² 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 (M₂₋₃), and 81872 (M³), represent a small hyracodontid, *Triplopus? progressus* (Matthew and Granger, 1925), new combination. In A.M.N.H. No. 20298, the length of M¹⁻³ is 35 mm.; the other two specimens represent somewhat smaller individuals. *Triplopus? progressus* is more advanced than *T.? proficiens* in the reduction of M³ 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 M¹⁻³ 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.

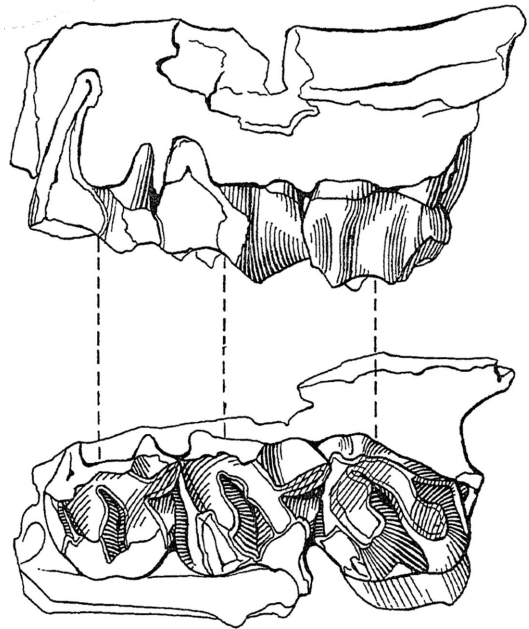Twenty-four years after describing *Forstercooperia*, Wood (1963) erected a second

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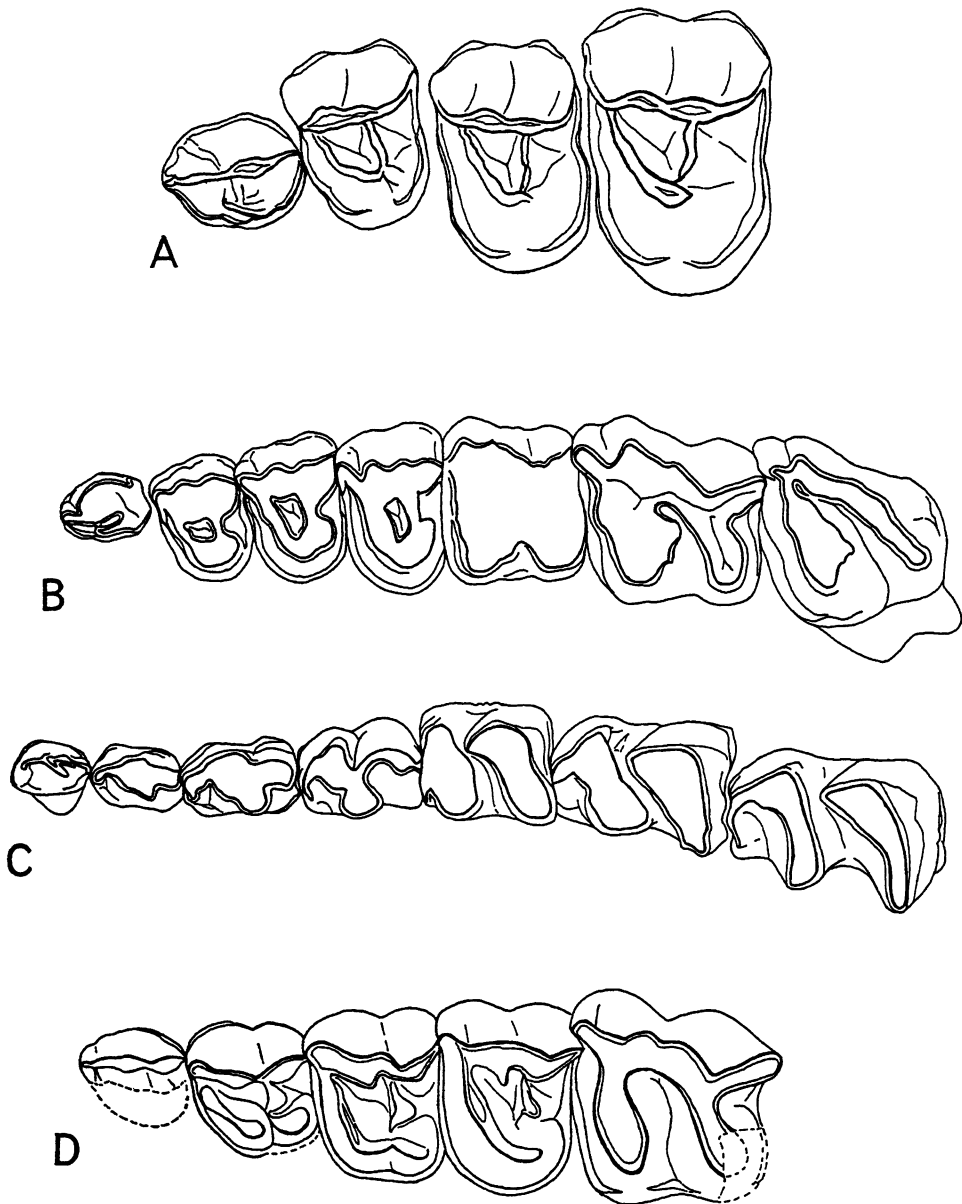
FIG. 8. Teeth of *Forstercooperia*. A. *F. totadentata*, type, A.M.N.H. No. 20116, P^{1-4}, from Wood (1938, fig. 5). B, C. *F. confluens*, new combination, type, A.M.N.H. No. 26660, $P^1_{\bar{1}}$–$M^3_{\bar{3}}$, reversed from Wood (1963, fig. 2). D. *F. sharamurenense*, new combination. P^1–M^1,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

Triplopus (e.g., *T. rhinocerinus*) in being tri-
angular, with only a low swelling on the poste-
rior face of the confluent metaloph and ecto-
loph representing the metacone. The remain-
ing molars are typically rhinocerotoid and pre-
sent 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. tota-
denta* occurs (see Radinsky, 1964, for a dis-
cussion of Late Eocene stratigraphy in Inner
Mongolia).

The third-named genus of large, Late Eo-
cene, 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 di-
mensions than *Forstercooperia totadentata*, and
is known from a few skulls, mandibles, and
postcranial elements from the late Late Eo-
cene 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 (I¹ 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 en-
larged 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 P³ (see text fig. 9), and slightly more
molariform, although still submolariform, pre-
molars. The metacone swelling in the one M³
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
M³ 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 differ-
ences in dentition I consider indicative of
specific-level differentiation only, but the
difference in nasal incision retraction may be
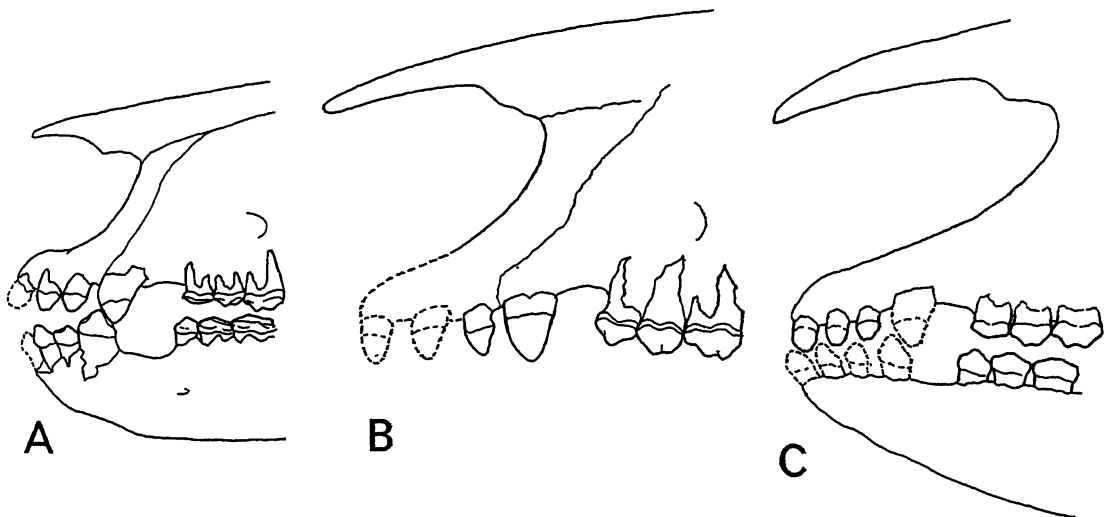more significant. However, since nothing is

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 M^1 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 M^{1-3} estimated from premolar-molar indices in the other species at about 140 mm.) and *F. confluens* (M^{1-3}, 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* (M^{1-3}, 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 C^1 and P^2–M^3, 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 P^1–M^3; A.M.N.H. No. 22101, an incomplete mandible with P_3–M_3, and A.M.N.H. No. 22102, P_4–M_3. 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"