

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 ^e	79 ^e	—
A.M.N.H. No. 26666	"Irdin Manha" beds, 7 miles W. of Camp Margetts	—	—	83	65 ^e
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 ^e	—
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 ^g	—	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 P²-M¹, and 26672, M¹⁻³, P₂-M₃. 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 P₃-M₃ (described by Wood, 1963), and A.M.N.H. No. 26643, an incomplete skull with very damaged teeth. The M³ 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 DP₃₋₄, M₁₋₂, from 7 miles southwest of Camp Margetts, matches in size comparable teeth in a jaw with P₁-M₃ (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

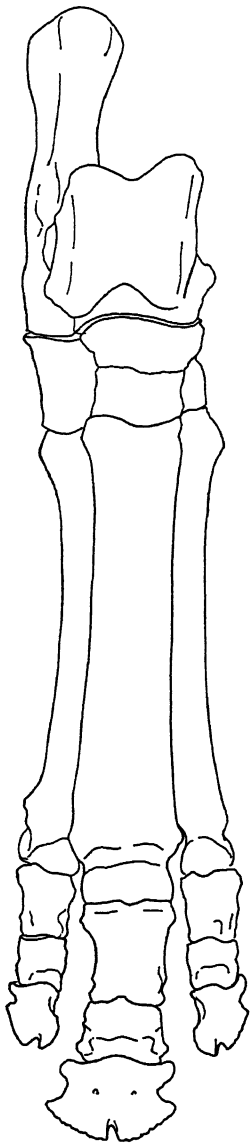


FIG. 10. Hind foot of *Forstercooperia sharamurenense*, new combination, A.M.N.H. No. 20288. $\times 1/2$.

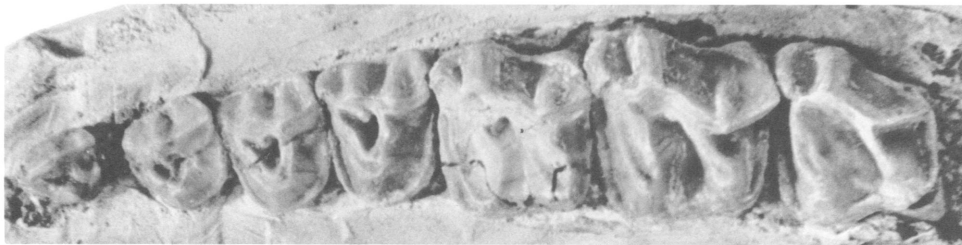
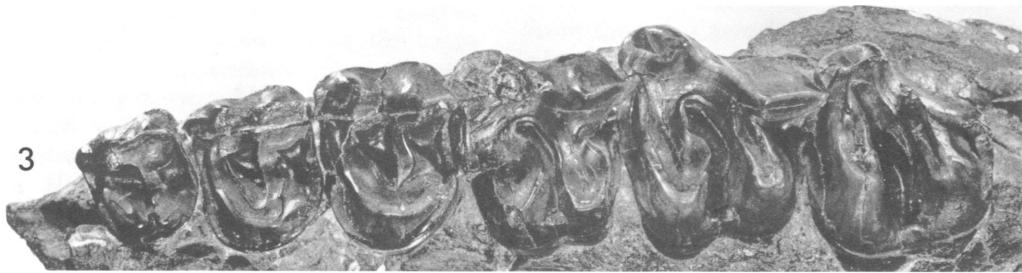
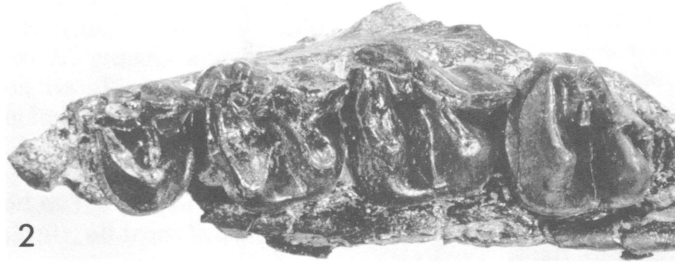
specimens are larger representatives. In this case the other Camp Margetts specimens would represent a new species, characterized by its small size and, possibly, by less reduced M^3 metacones. Stratigraphic correlations between the "Irdin Manha" beds of the Camp Margetts area at various localities and 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 sharamurenense* 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 M^3 , 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 M^3 of *F. sharamurenense*. It is 25 per cent smaller than M^3 of *F. sharamurenense* 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 M^3 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. sharamurenense* in Shara Murun beds is illustrated in text figure 10.



1. *Triplopus implicatus*, new combination, A.M.N.H. No. 2341. $\times 1.5$
2. *Triplopus obliquidens*, A.M.N.H. No. 1972. $\times 1.5$
3. *Triplopus rhinocerinus*, new combination, type, Y.P.M. No. 13331. $\times 1.5$
4. *Triplopus? proficiens*, new combination, from the Ulan Shireh beds, A.M.N.H. No. 21552. $\times 1.5$
5. *Epitriplopus uintensis*, type, C.M. No. 3007a, P²-M³. $\times 1.5$

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.

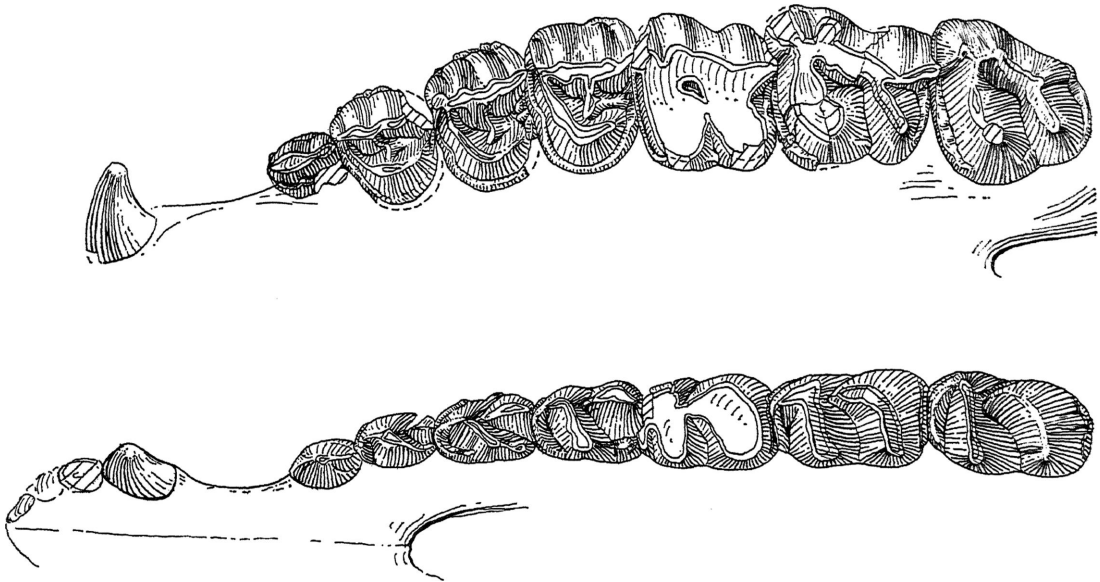


FIG. 11. Upper and lower dentition of *Forstercooperia? grandis*, new combination, U.C.M.P. No. 69722. $\times 2/3$.

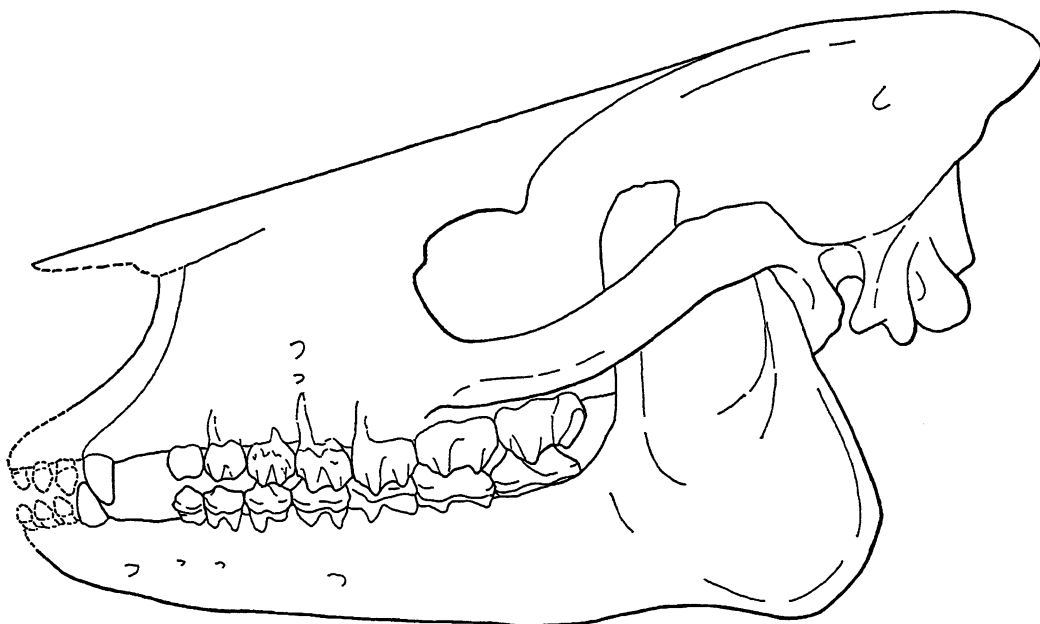


FIG. 12. *Forstercooperia? grandis*, skull and mandible, drawn from U.C.M.P. No. 69722. $\times 1/3$.

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 *Hyracondon*, 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 M^3 's of *Epitriplopus* and *Ardymia*, 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 I^1/I_2 and loss of the others), and this character should be considered diagnostic of the family (see p. 5). The loss of the M^3 metacone, on the other hand, is of no adaptive significance (for mastication) once the M_3 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 M^2 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 DP^1-M^1 , 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

Prohyracodon: 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 M^{1-3} , 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. M^{1-2} relatively longer and narrower than in *Prohyracodon*, and with a pronounced antecrochet. M^3 with no trace of a metacone.

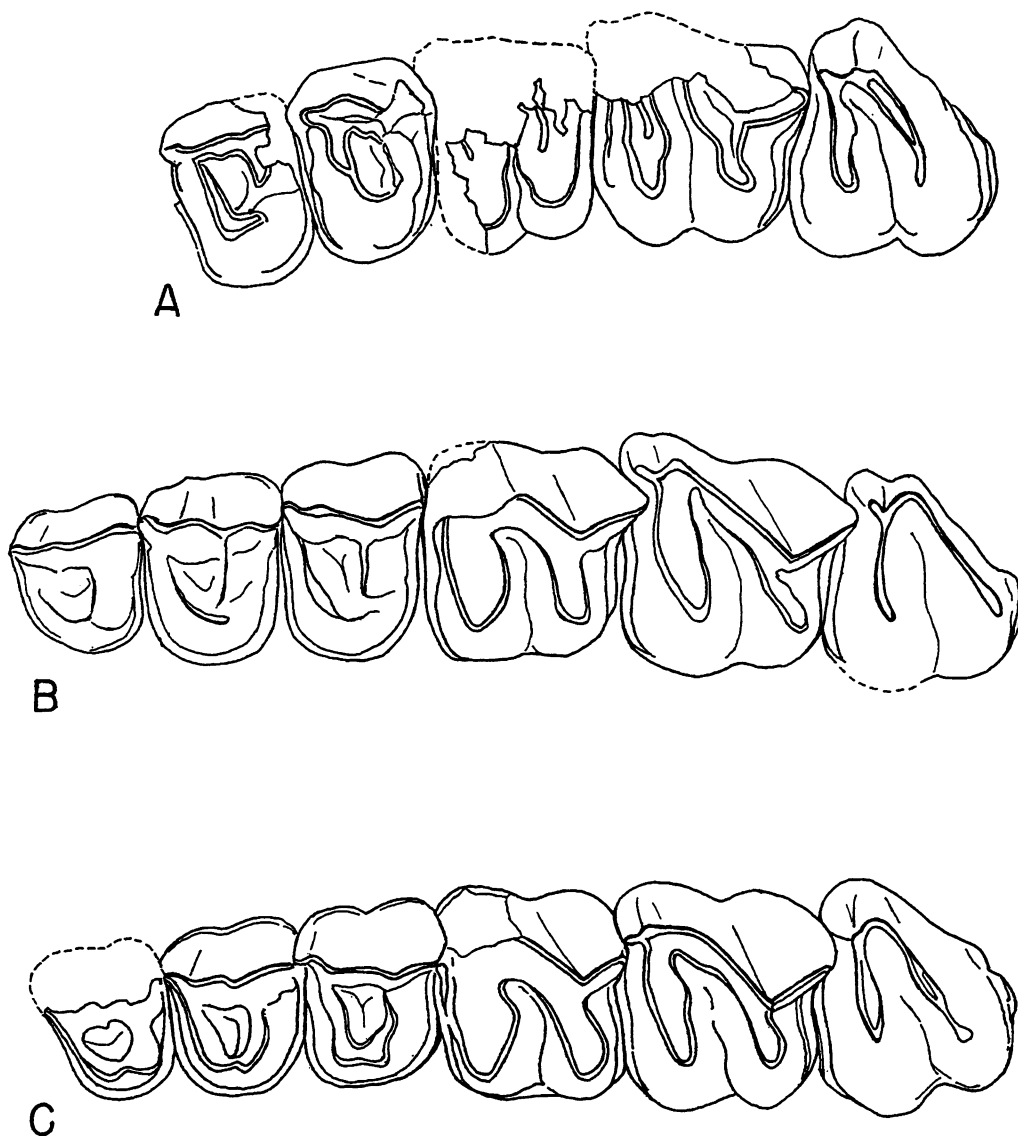


FIG. 13. Upper dentitions of *Prothyracodon*, taken from Chow and Xu (1961, fig. 2). A. *P. orientale*. B. *P. meridionale*, type. C. *P. progresssa*, type (= *P. meridionale*). All $\times 1.5$.

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 M^3 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 *Prothyracodon orientale* in lacking the M^3

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 M^2 , loss of the M^3 metacone, a peculiar cusp pattern on P^2 , and a tridactyl manus. The first two characters are valid (see revised diagnosis above). However, what Wood interpreted as incompletely calcified crowns of P^2-3

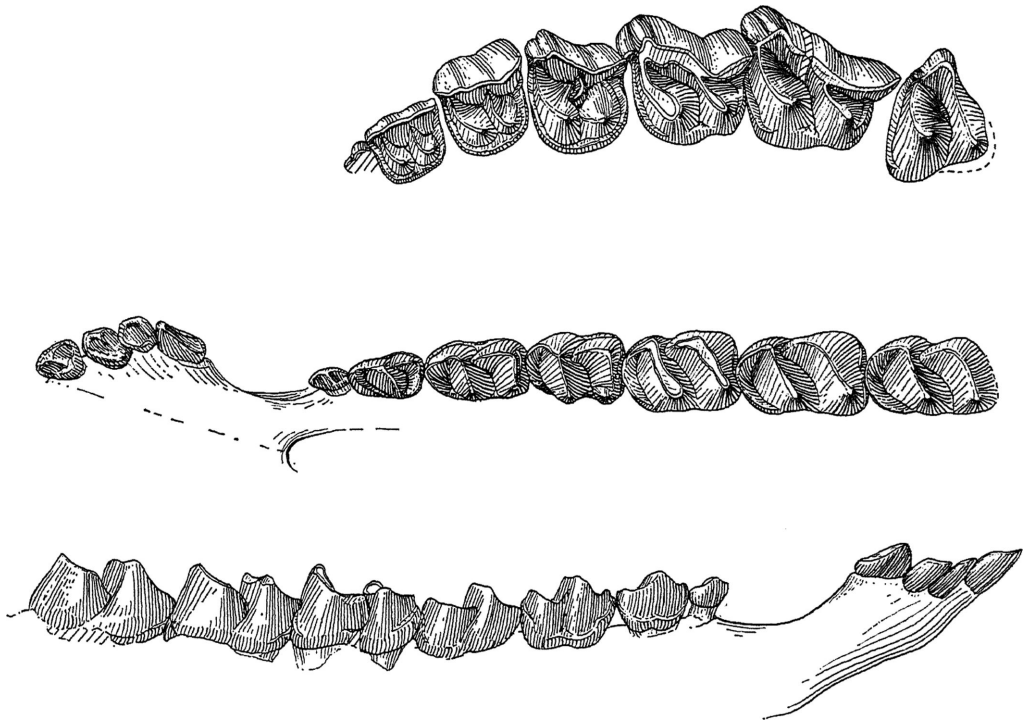


FIG. 14. *Epitriplopus uintensis*, type, C.M. No. 3007a. Top: P²-M³. Middle and bottom: Lower dentition in occlusal and labial views, respectively. The premolars were unerupted but in this figure are restored in adult position. All $\times 1$.

were actually lumps of matrix covering those teeth. Further preparation has revealed preciously 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. uiniensis*.

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

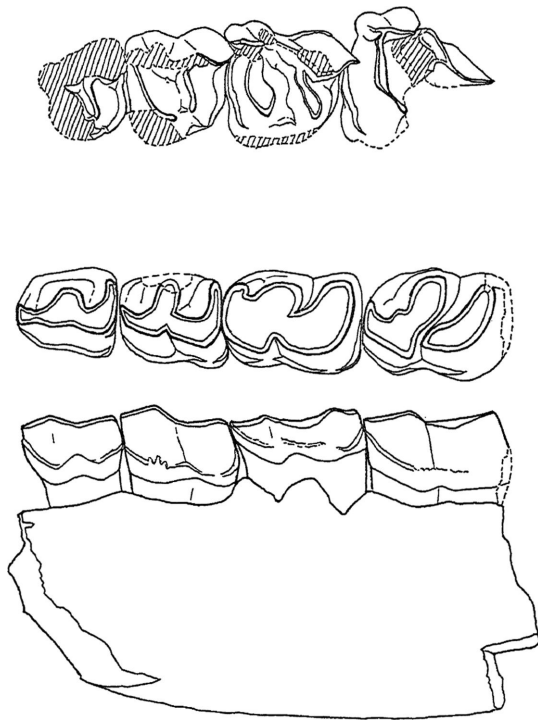


FIG. 15. Duchesnean *Epitriplopus*. Top: *E. medius*, type, C.M. No. 11915, P_3^2 - M^2 . Middle and bottom: "*Mesamynodon medius*," type, C.M. No. 11762, P_3 - M_2 in occlusal and labial views, respectively. All $\times 1$.

Epitriplopus medius, but may belong to the same species. The P_{3-4} of C.M. No. 11762 have prominent labial cingula, as do those teeth in *E. wintensis*.

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 M^{1-2} (the posterior half of these teeth is particularly narrow), less labially situated molar parastyles, and higher-crowned teeth. The long, narrow M^{1-2} of *Epitriplopus* resemble those teeth in the Asiatic Oligocene genus *Ardynia*, from which *Epitriplopus* differs in having more molariform P^{2-4} , a less reduced premolar series (P^1 is lost and P_2 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 M^{1-3} averaging 60 mm. Crown height index, 0.88. Incisors approximately equal-sized, small and slender, grading from spatulate at I_1^1 to pointed in I_3^3 . Canines approximately the same size and shape as I_3^3 . Premolars submolariform; P_1 lost. Premolar and molar paracones not delimited posteriorly from the ectolophs. M^{1-2} with large antecrochet and protocone set off by vertical grooves; these features less pronounced in M^3 . M^3 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 M^{1-3} , about 65 mm. Incisors slender and spatulate, increasing slightly in size anteriorly. Canines small and slender. P_1^1 lost; premolars submolariform. M^3 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.

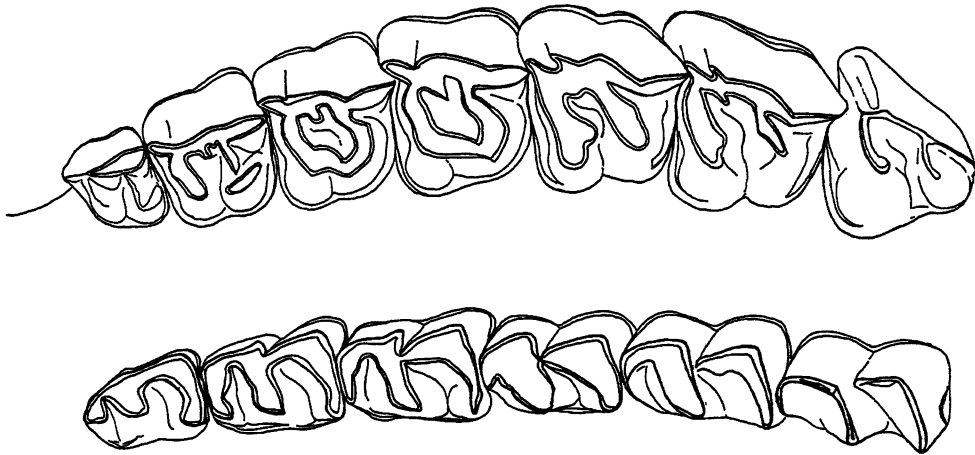


FIG. 16. Upper and lower dentition of *Hyracodon nebraskensis*, A.M.N.H. No. 11296. $\times 1$.

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^2 - 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 pres-

ence of canines and three pairs of lower incisors. A short postcanine diastema is followed by P^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 mid-length; 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

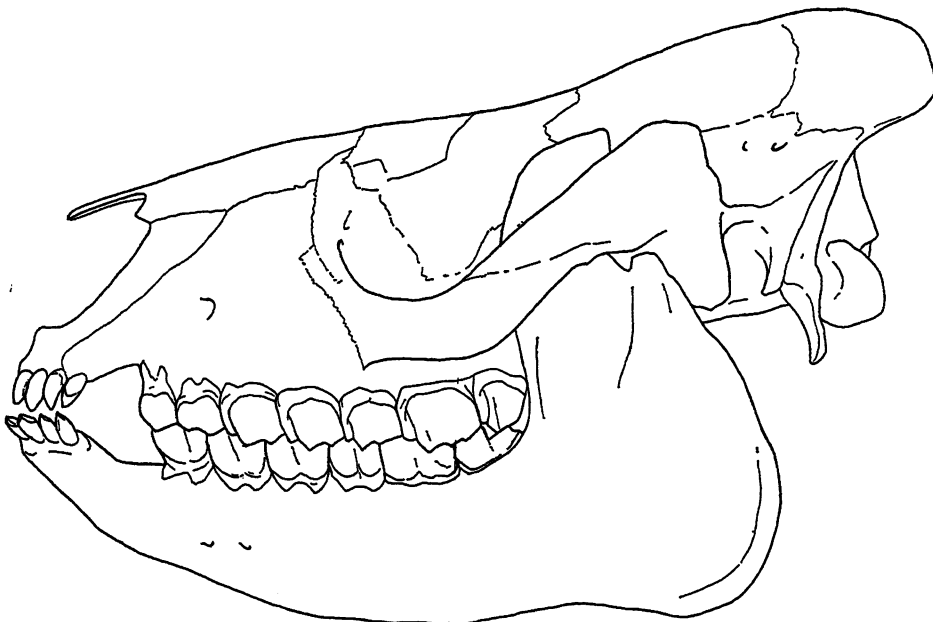


FIG. 17. Skull and mandible of *Hyracodon nebraskensis*, reversed from Scott (1941, pl. 89). $\times 1/2$.

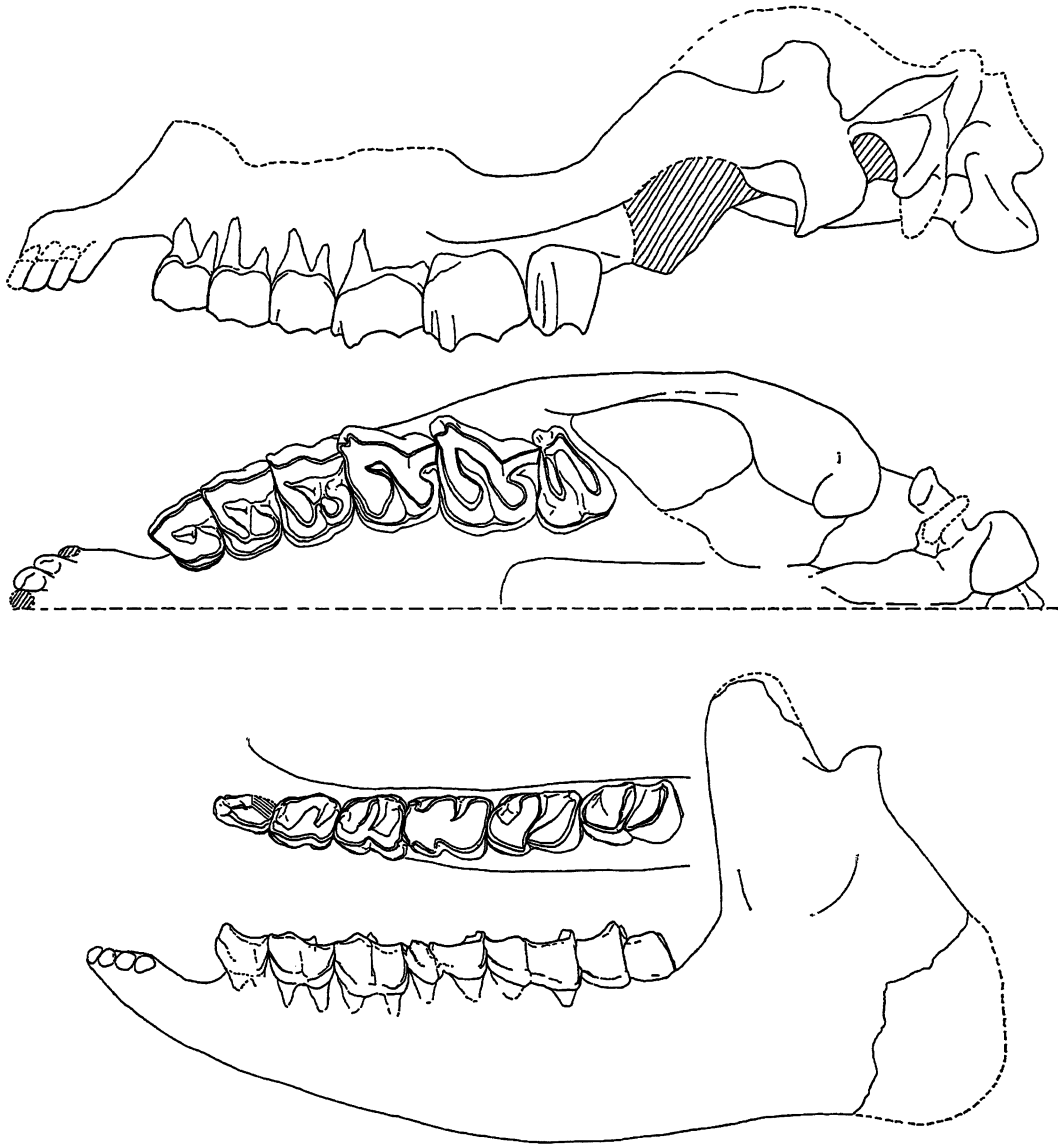


FIG. 18. *Triplopides rieli*, new genus and species, type, C.M. No. 9370. *Top and middle*: Incomplete skull and upper dentition in lateral and ventral views, respectively. *Bottom*: Mandible with lower dentition in occlusal and labial views. All $\times 1/2$.

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 P¹. 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. kazakhstanensis* (Beliajeva, 1952), new combination.

RANGE: Early to Late Oligocene of Asia.

REVISED DIAGNOSIS: Medium-sized hyracodontids; length of M¹⁻³, approximately 60 mm. Teeth relatively high crowned: crown height index higher than 1.10. Incisors spatulate, increasing in size anteriorly; canines slightly smaller than I³. Relatively long post-canine diastema. Premolar series shortened: P¹ lost, P² reduced in size. P₃₋₄ molariform; P³⁻⁴ non-molariform, with protoloph-meta-loph loop. M¹⁻² relatively long and narrow, with oblique cross crests; M³ 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. kazakhstanica*, 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. kazakhstanensis*, 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 *Ardynia 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 P₂ 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 kazakhstanensis differs from *Ardynia praecox* in having relatively larger P₃₋₄ (the length of P₃₋₄ divided by the length of M₁₋₃ is 0.53 in *P. kazakhstanensis* and averages 0.43 in *A. praecox*). However, the P₂ of *P. kazakhstanensis* is reduced almost as much as that of *A. praecox*, and the difference in size of P₃₋₄ is not enough, in my opinion, to warrant separation on a generic level. Therefore I assign *P. kazakhstanensis* to *Ardynia*. *Ergilia kazakhstanica* Gromova, 1960, probably represents the feet of *A. kazakhstanensis* (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 kazakhstanensis* (Beliajeva, 1952) new combination (including *Ergilia kazakhstanica* Gromova).

Gabunia (1964, p. 74) proposed the species *Ardynia plicidentata* for a DP³ or DP⁴ and an M¹ or M² from the Late Oligocene Benara

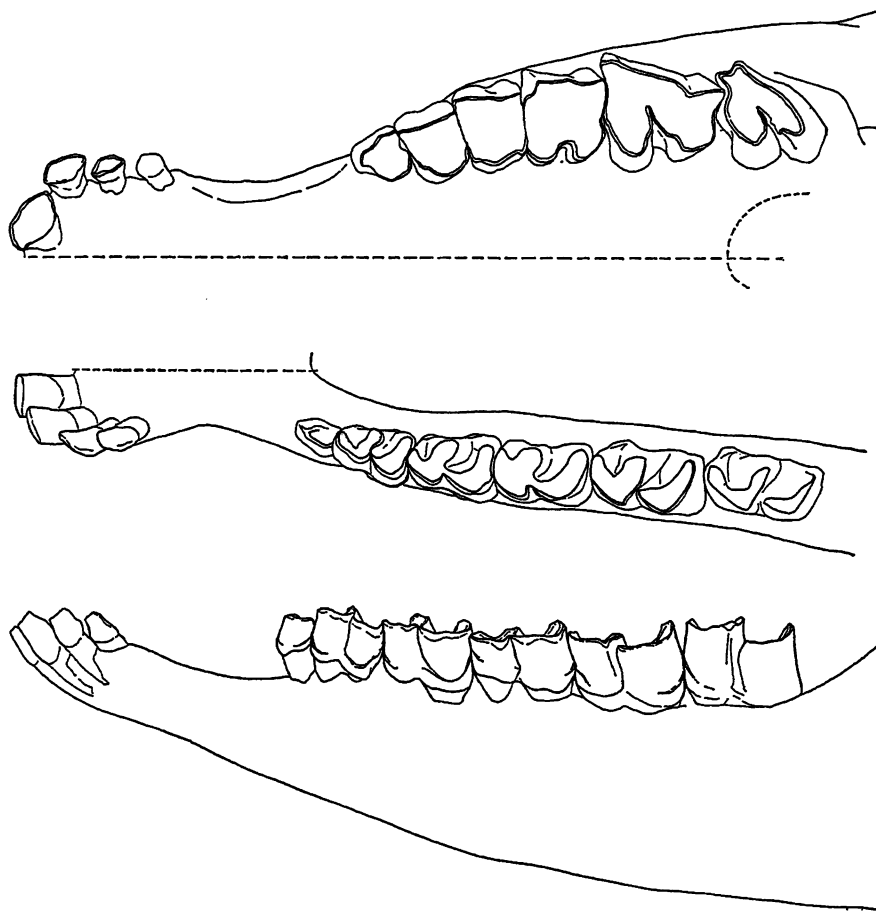


FIG. 19. *Ardynia*. Top: Upper dentition of *A. praecox*, A.M.N.H. No. 26039. Middle and bottom: Lower dentition of *A. kazachstanensis*, new combination, A.M.N.H. No. 26183, in occlusal and labial views, respectively. All $\times 2/3$.

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, *Ronzootherium 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

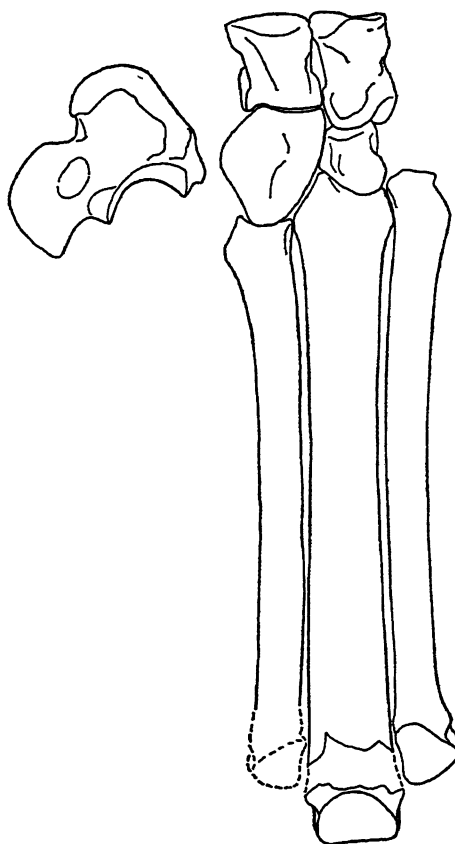


FIG. 20. Carpal bones of *Ardynia praecox*, A.M.N.H. No. 26039. The magnum is shown in lateral view also. $\times 3/4$.

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 *Ronzootherium? 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 *Epiacetherium* a maxillary from the Middle Oligocene of Kazakhstan, with a large C^1 alveolus

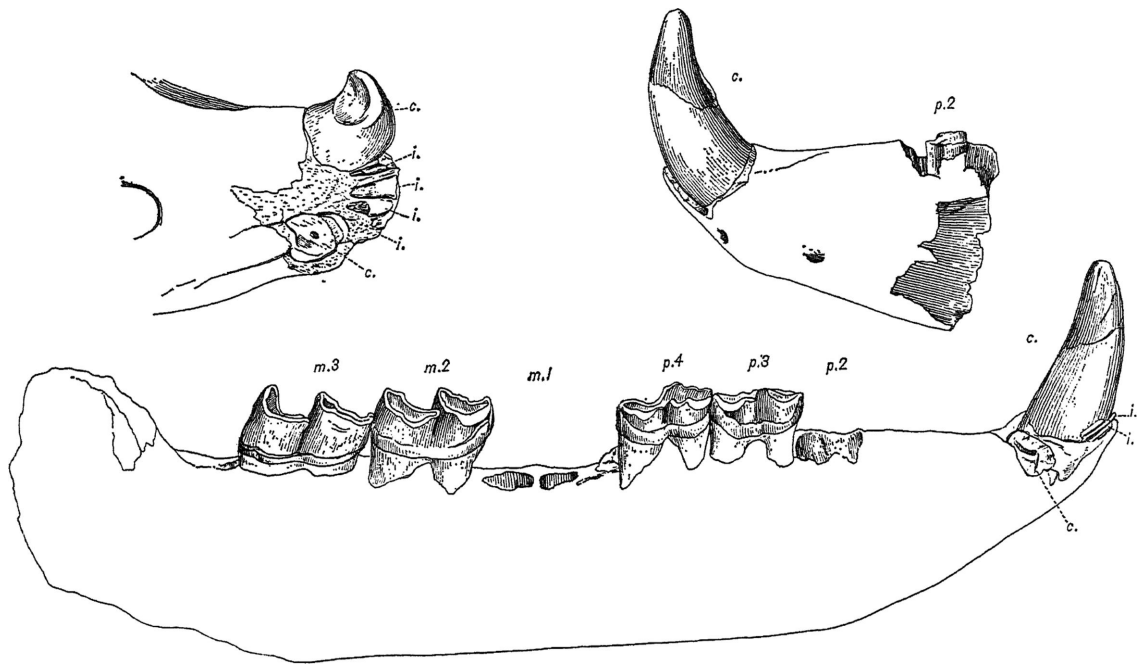


FIG. 21. Mandible of *Allacerops*. From Osborn (1900, fig. 2). $\times 1/2$.

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-

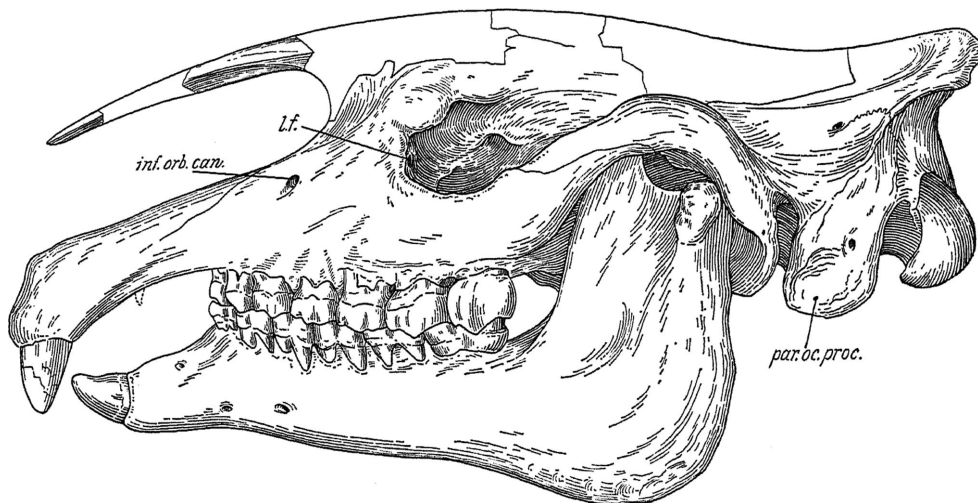


FIG. 22. Skull and mandible of *Indricotherium transouralicum*, from Granger and Gregory (1926, fig. 1). The skull, A.M.N.H. No. 18650, is the type of "*Baluchitherium grangeri*." $\times 1/10$.

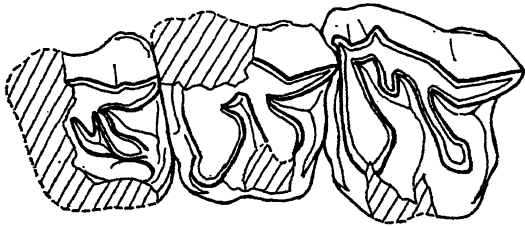


FIG. 23. "*Hyracodon primus*," type, C.M. No. 11914, P⁴-M². ×1.5.

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, unguigrade 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 *Epi-triplopus 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 *Teihardia 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 *Teihardia 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 EVOLUTION

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

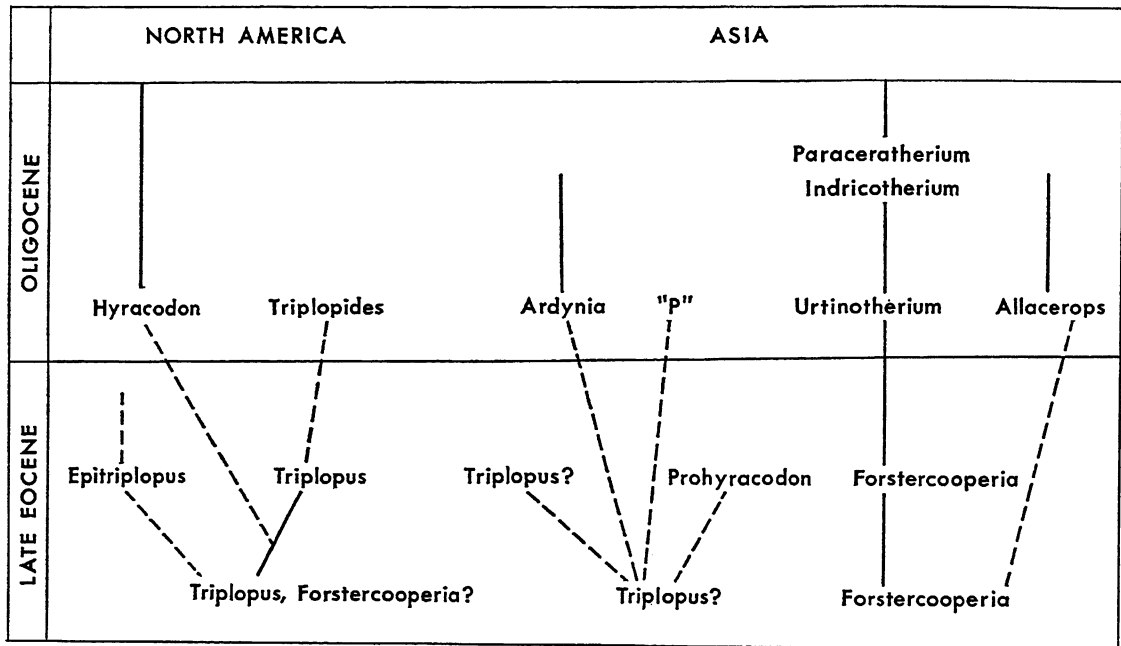


FIG. 24. Suggested phylogeny of the Hyracodontidae. "P" represents "*Prohyracodon turgaiensis*". *Allacerops* occurs also in Europe.

M¹⁻² ectolophs and concomitant increase in height of lower molar paralophids and meta-
lophids, suggesting increased emphasis on vertical shear along those labial ridges, reduction in size of parastyles, reduction in size and lingual deflection of the M³ 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 Rhinoceroidea.

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 M^3 metacone (compare *Triplopus implicatus* and *T. rhinoceros*). 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 M^3 metacone. A contemporary of *Hyracodon* in the Early Oligocene of North America is the genus *Triplopides*, which is unusual in that it has lost P^1 . The incisors of *Triplopides* appear to have been relatively slender and spatulate, with a slight size decrease posteriorly. The M^3 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 M^3 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 "*Prohyracodon*" *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 M^3 metacone, and, in at least one line, enlargement of the nasal incision (compare *F. confluens* with *F. sharamuraenense*). 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 M^3 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.

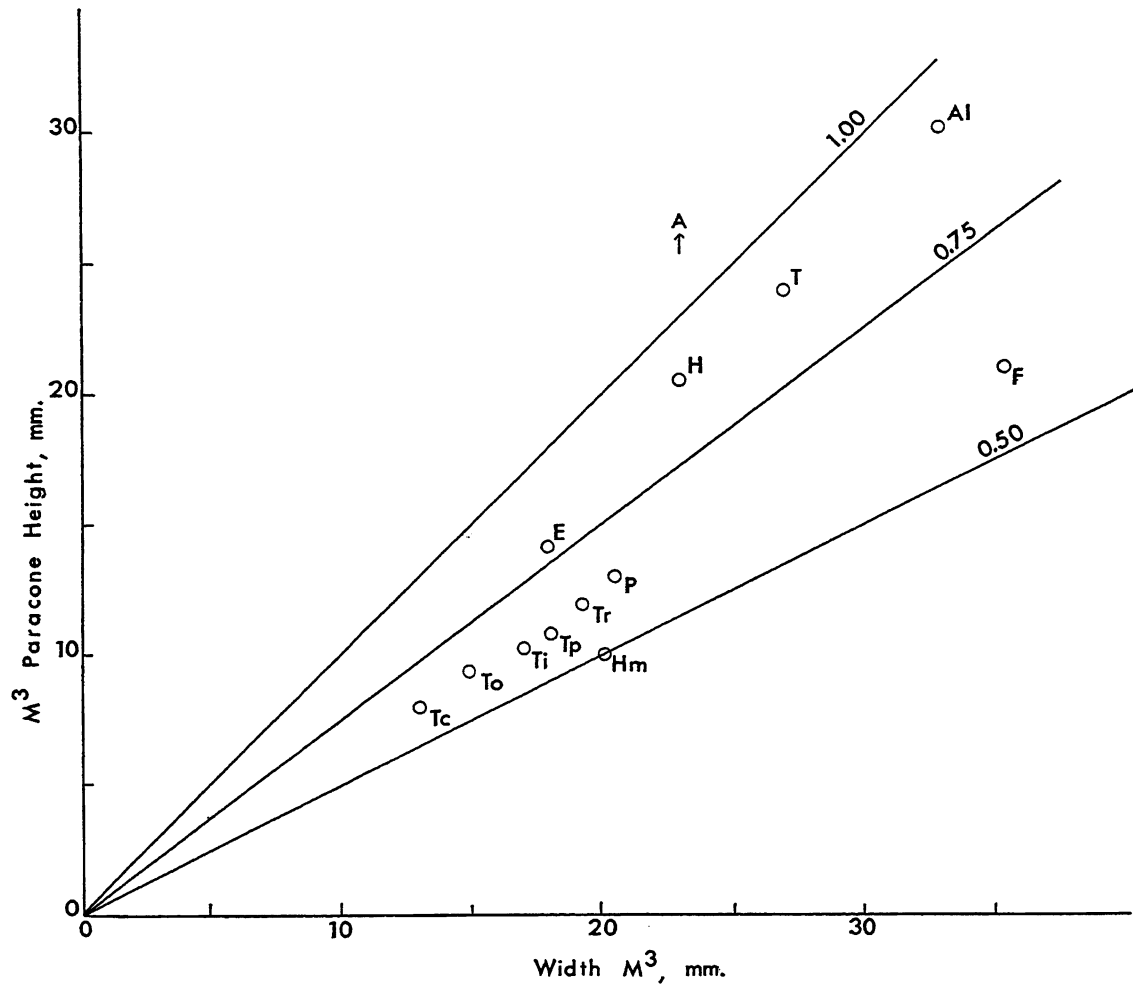


FIG. 25. Scatter diagram, showing relationship of M^3 paracone height to M^3 width in the Hyracodontidae. *Indricotherium*, which falls off the scale used here, has M^3 's averaging 70 mm. in height and 100 mm. in width.

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 M^3 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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