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A Note on *Toxotherium* (Mammalia, Rhinocerotoidea) from Natrona County, Wyoming

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In 1961 H. E. Wood, 2nd, erected the genus and species *Toxotherium hunteri* on the basis of a ramal fragment from the Cypress Hills in Saskatchewan, Canada. The type of *T. hunteri* is from the Cypress Hills Formation, which Wood considered early Oligocene. During the summer of 1958 a ramal fragment of a *Toxotherium*-like animal was found in the earliest Oligocene or latest Eocene deposits of the Bates Hole region of Natrona County, Wyoming, by Morris F. Skinner and Ted Galusha of the Frick Laboratory, the American Museum of Natural History. Certain characters separate the Bates Hole specimen, specifically at least, from *T. hunteri,* but until more evidence is available we are assigning it to Wood's genus. It is coincidental that the Bates Hole specimen is fragmented in nearly the same way as the one from Cypress Hills. However, the basal part of a tusklike tooth is present and reveals the remarkable character which Wood (1961) noted in the "curious bulbous alveolus" of his specimen.

We are indebted to Dr. Malcolm C. McKenna for help and guidance. We wish particularly to thank Mr. Morris F. Skinner for valuable assistance in identifications and for preparing and sectioning specimens for this study. Mr. Skinner also furnished the stratigraphic notes, section,

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and photograph of the type locality. Thanks are given to Dr. Leonard B. Radinsky who constructively read the manuscript and gave helpful advice, and to Dr. Dale Russell of the National Museum of Canada in Ottawa for the cast of the type of *Toxotherium hunteri.*

The following abbreviations are used:

F.A.M., Frick American mammals, the American Museum of Natural History
N.M.C., National Museum of Canada, Ottawa
U.S.N.M., United States National Museum of the Smithsonian Institution, Washington, D. C.

ORDER PERISSODACTYLA

SUBORDER CERATOMORPHA

SUPERFAMILY RHINOCEROTOIDEA

FAMILY *INCERTAE SEDIS*

TOXOTHERIUM WOOD, 1961

TYPE: *Toxotherium hunteri* Wood (1961).

Toxotherium woodi,[1] new species

TYPE: F:A.M. No. 42901 (fig. 4); a partial left ramus with broken root of a tusklike tooth, dP_2 (broken)–dP_4, M_1, M_2 (alveolus broken), and right detached M_1. The ramus is missing posterior to M_1, but enough remains to show an abrupt rise of the lingual side of the ramus immediately behind M_1 and the enlarged alveolus for M_2 germ which is not present. The relative diameter and length of the massive tusklike tooth suggest that it is permanent. Other interpretations can be given to the tooth series, but the one here designated seems the most appropriate.

LOCALITY: Ledge Creek No. 2, NE. ¼, sect. 22, T. 29 N., R. 82 W., 7 to 8 miles southeast of Alcova, Natrona County, Wyoming (figs. 1, 2).

ZONE: From a set of deposits of Duchesnean or Chadronian age, containing what is referred to here as the "Red Fauna" in reference to the red clay from which the fauna was taken. Various manuscript names have been proposed for these beds, but it is not known whether formal lithic names have been applied. The specimen was found at an elevation of 6365 feet on the talus, between 100 and 105 feet above the base of the section at this place, and about 10 feet above the main "Red Fauna" but definitely below the major part of what appears to be the Chadronian deposits of the Bates Hole area (see fig. 3). A recent study by Evernden,

[1] The specific name is for Dr. Horace E. Wood, 2nd.

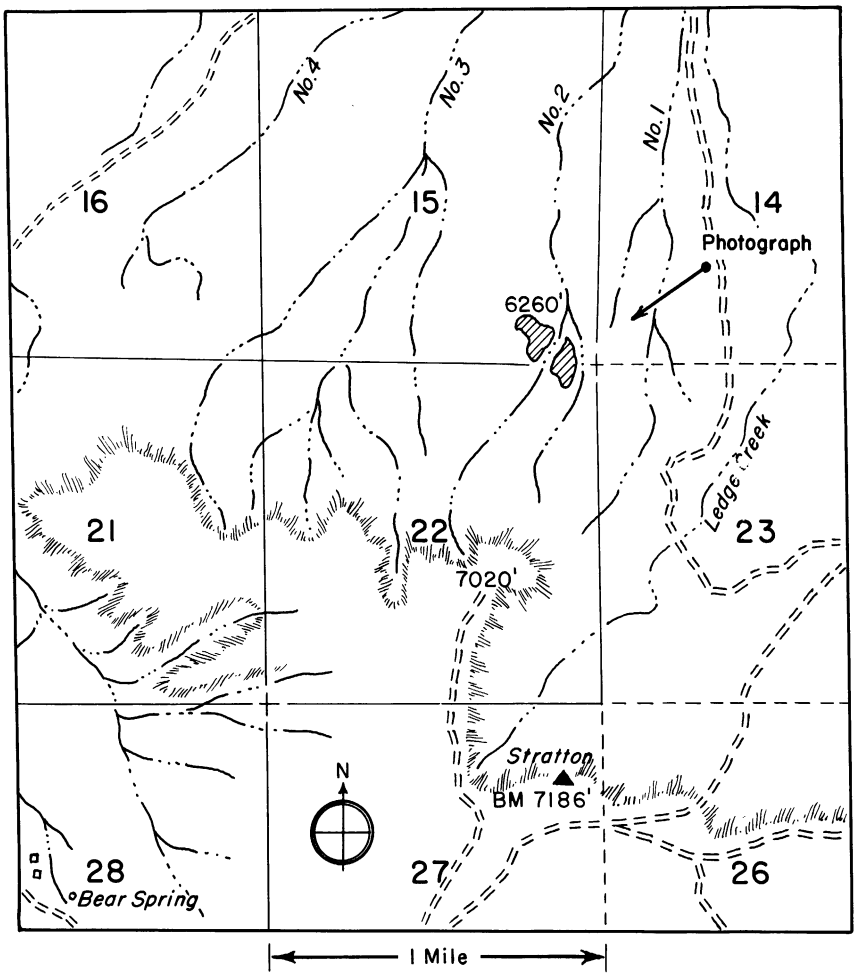

FIG. 1. Portion of United States Geological Survey Bear Springs Quadrangle, 1951 edition, showing "Red Fauna" area (shaded) of Ledge Creek No. 2, Natrona County, Wyoming. The site of figure 2 is indicated by an arrow. The Stratton bench mark and the top and bottom of the section are indicated in feet.

Savage, Curtis, and James (1964) indicates that these beds are about 35 million years old (p. 185, KA 895, Lone Tree Gulch, Ash B). No matrix samples for potassium-argon dating were collected from the Ledge Creek deposits, but the deposits correlate readily with those of Flagstaff Rim where a suite of potassium-argon samples was collected and tested

FIG. 2. Site of "Red Fauna" at center of photograph. Arrow indicates collecting locality for type of *Toxotherium woodi,* new species, F:A.M. No. 42901, NE. 1/4, sect. 22, T. 29 N., R. 82 W., Natrona County, Wyoming. View to southwest from east side of Ledge Creek No. 1 shows exposures on Ledge Creek No. 2 where section (fig. 3) was made.

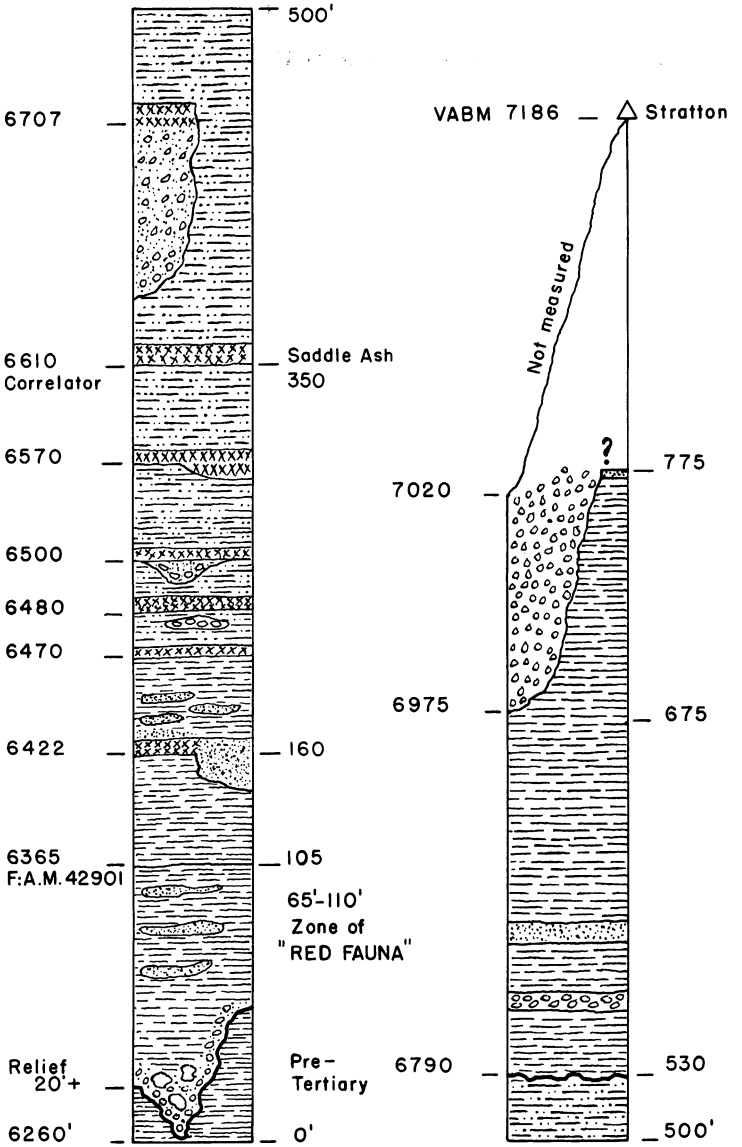

FIG. 3. Ledge Creek No. 2 section. Base of section started at junction of east and west draws of Ledge Creek No. 2. Section measured across dip and corrected as much as possible; diagrammatic only to demonstrate the occurrence of F:A.M. No. 42901, the type of *Toxotherium woodi*, new species. Main part of section in NE. 1/4, sect. 22, T. 29 N., R. 82 W., Natrona County, Wyoming. For reference point on elevation, see United States Geological Survey Bear Springs Quadrangle, 1951 edition. Elevation of main ash zones indicated. Lithic description of siltstones and channel omitted.

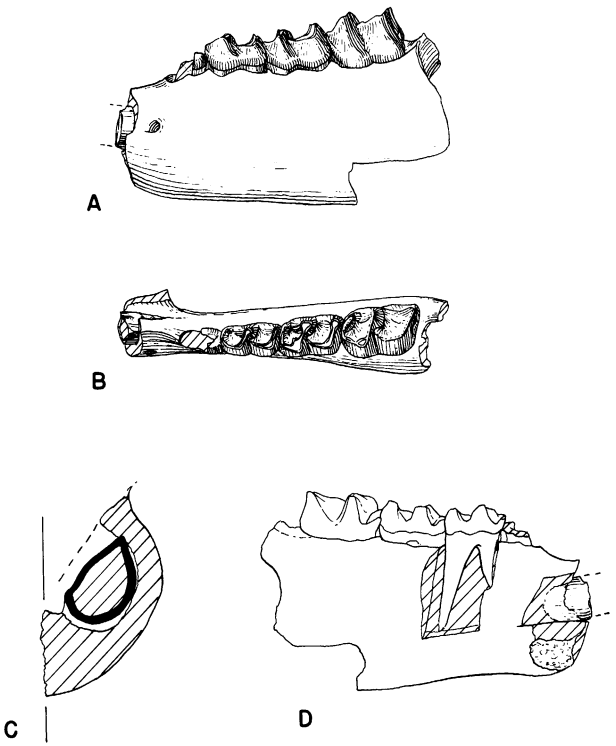

FIG. 4. A. Lateral, buccal view of the type of *Toxotherium woodi*, new species, F:A.M. No. 42901, a partial left ramus with broken tusk, dP_2 (broken)–dP_4, M_1, M_2 (alveolus broken). Note abrupt rise of ramus behind M_1 and the enlarged alveolus for the germ of M_2 which is not present. ×1. B. Occlusal view of the type of *Toxotherium woodi*, new species, F:A.M. No. 42901, showing the difference in size and wear of M_1 in relation to dP_{2-4}. ×1. C. Cross section of tusk and symphysis of type of *Toxotherium woodi*, new species, F:A.M. No. 42901. ×2. D. Lingual view of type of *Toxotherium woodi*, new species, F:A.M. No. 42901, showing excavated and exposed roots of dP_3 and tusk. ×1.

by Evernden and his co-authors. The Ledge Creek deposits are about 16 airline miles southeast of Flagstaff Rim.

ASSOCIATED FAUNA: In addition to the ramal fragment of *Toxotherium woodi*, new species, the "Red Fauna" consisted of the following forms, identification of which was not carried beyond the genus except for *Hyracodon: Hyracodon petersoni, Leptomeryx, Pseudocynodictis, Agriochoerus, Ictops,* titanothere, turtle, and unidentified jaws and limb fragments of artiodactyls.

DESCRIPTION: A section taken from the lingual side of the ramus of

T. woodi (fig. 4D) shows that the alveolus of the "tusk"[1] extends almost to the posterior border of the symphysis. The enamel of the tusk is thick and extends well back but not to the extreme base of the root, which is open, a condition usually reflecting prolonged growth. The semi-ovoid shape of the tusk in cross section and its proportionately large size (about 41% of the ramal depth) are outstanding (see fig. 4C, and measurements on p. 11). The tusk in cross section has a prominent dorsal ridge and a less prominent ventrolingual ridge. The procumbent position and shape of the rounded buccal side and the flattened lingual side between the ridges compare favorably with many rhinocerotoid tusks, if size is not considered. The measurements in millimeters of the tusk of the type of *T. woodi* (F:A.M. No. 42901) are as follows: depth of tusk at break, 5.8; thickness of enamel band of tusk, 0.8; depth of ramus below tusk, 5.4; depth of ramus at break, 13.6; width of pulp cavity of tusk, 4.1; depth of ramus above tusk, 2.4.

It is apparent that *Toxotherium* had a short symphysis. In *T. woodi* the posterior end of the symphysis is almost even with the anterior border of the dental series, and the portion of the diastema remaining indicates that it, too, was comparatively short. When the specimen is viewed from above, the angle formed between the median suture of the symphysis and the midline of the horizontal ramus is close to 20 degrees, indicating a wedge-shaped mandible. The remaining part of the horizontal ramus behind M_1 rises abruptly, which indicates a high-rising coronoid, as would be expected in a juvenile specimen. The deep, convergent rami, plus the short symphysis, suggest that *T. woodi* was brachycephalic. A single mental foramen is 1.2 mm. anterior to the alveolus of dP_2 and 3.7 mm. below the diastema (fig. 4A).[2]

The dental formula of *Toxotherium* as displayed by the two specimens standing for the types of *T. hunteri* and *T. woodi* has been the source of much speculation. X-rays of the type of *T. woodi* and a section removed from the lingual side below dP_3 (fig. 4D) show that no germs were present or developing. Whereas the dentition of *T. hunteri* seems almost certainly

[1] For the sake of brevity and clarity, we use Matthew's (1931) term "tusk" for the first tooth anterior to the main dental series. Wood (1961) referred to it as a bulbous-rooted front tooth (incisor or canine). Lydekker (1880, p. 140) expressed doubt over the terminology of this part and apparently anticipated the various terms of Leidy, Cope, Lucas, Osborn, Wood, and others. The nomenclature of these tusklike teeth has not been stabilized, so far as we know.

[2] Dr. Dale Russell (personal communication) stated that the type of *T. hunteri* has a small foramen about the diameter of the shaft of a pin below the anterior part of P_3 alveolus. We have added the foramen to Wood's figure (fig. 5A of the present paper).

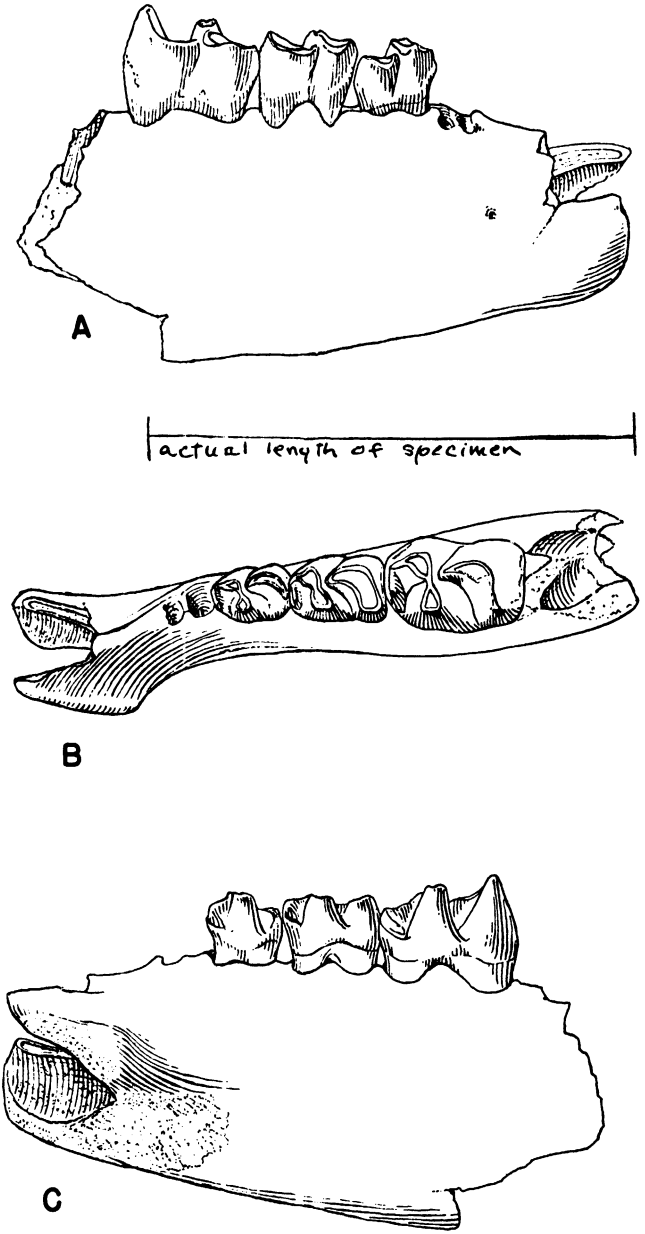

FIG. 5. *Toxotherium hunteri*, holotype, N.M.C. No. 8918, right mandibular ramus, with P_3 (alveolus), P_4–M_2. After Wood (1961). A. Buccal view. Mental foramen not shown on Wood's figure is included here. B. Crown view. C. Lingual view. All approximately ×1.3.

to be mature, that of *T. woodi* is immature in nearly all aspects except for the relative depth of the horizontal ramus and the tusk, which appears to be permanent. In *T. woodi* the M_1 is identifiable by an abrupt increase in size and less wear on the crown in relation to the preceeding teeth. The sharp rise of the ramus and the enlarged alveolus posterior to M_1 are significant signs of immaturity.

Ten *Hyracodon* jaws from early immaturity to early maturity were sectioned to enable us to observe tooth replacement, root resorption, and the formation of dental sacs for permanent premolars. Although differences in tooth replacement between *Hyracodon* and *Toxotherium* specimens would be expected, the roots of the deciduous premolars of *Hyracodon* are long as in *T. woodi,* and there is no indication of resorption until the M_2 germ is formed.

One specimen (cf. *Hyracodon,* F:A.M. No. 42904) duplicates in nearly every detail the stage of wear and development of *T. woodi;* the deciduous premolars are worn, the M_1 is fully erupted but unworn, and the ramus posterior to M_1 rises abruptly. No permanent premolar germs have formed, and the roots of the deciduous premolars are long and show no resorption.

Wood's interpretation of *T. hunteri* is P_1 (alveolus)–P_4. We interpret the dentition of *T. hunteri* as P_3 (alveolus)–M_2 and the enlarged area posterior to M_2 as an indication of an alveolus for M_3. In *T. hunteri* M_1 is more worn than M_2, and both are large and molariform; P_4 is relatively small and much less molariform than M_{1-2}. If the teeth of *T. woodi* are dP_{2-4}, M_1, as here considered, the premolar series was shortened by the loss of P_1 only, not by both P_1 and P_2 as in *T. hunteri.* In some of the rhinoceroses, tapirs, and horses, the first premolar erupts with the milk teeth, is not replaced, and in some of these groups never develops. *Toxotherium* may exemplify a modification of the dental formula involving reduction of the premolar series with extreme enlargement of the tusk.

Because of the fragmented evidence and age difference, dental comparisons between *T. woodi* and *T. hunteri* are confined to the first molar. The M_1 of *T. woodi* is less worn than that of *T. hunteri,* but the cusp patterns are basically rhinocerotoid, and the anteroposterior and transverse dimensions are nearly equal. The M_1 metaconid and entoconid are sharper, the valley between them is deeper, and the ramus is about 20 per cent smaller in *T. woodi* than in *T. hunteri,* all differences that might be expected to indicate the immaturity of *T. woodi.*

Comparisons were made with *Lophialetes* and *Schlosseria* of the Irdin Manha of Mongolia, since Wood remarked on a conceivable subfamily relationship to the Lophialetinae. Radinsky (1965), in his study of tapirs from late Eocene faunal zones of Asia, proposed a new family, the

Lophialetidae, which included *Lophialetes, Schlosseria,* and a diminutive form, *Breviodon.* Radinsky questioned but included two more pygmy genera in his new family, *Rhodopagus* and *Pataecops.*[1] The size (diminutive) and the rhinocerotoid cheek-tooth pattern of *Toxotherium* suggest a possible relationship to the Asian lophialetids. However, the lophialetids have no heavy tusk, which is in direct contrast to the greatly enlarged one in the wedge-shaped jaw of *Toxotherium.* A figure of the type ramus of *Schlosseria magister* (A.M.N.H. No.20241; Matthew and Granger, 1926, figs. 1 and 2) illustrates a ramus with a long, slender symphysis and pronounced buccal cingula on the lower cheek teeth.

Comparisons were made between *Toxotherium* and *Schizotheroides,* an enigmatic genus of perissodactyls so far known only from an upper dentition. Hough (1955, p. 34), on the basis of two upper teeth (M^{2-3}, U.S.N.M. No. 20205), described *Schizotheroides parvus*[2] from upper Eocene deposits at Sage Creek, Montana, and questionably referred it to the chalicotheres. Radinsky (1964, pp. 23–24) believed that the absence of a distinct protoconule was a strong argument for removing *Schizotheroides* from the Chalicotherioidea and that Hough's genus more nearly resembled the Tapiroidea in cusp pattern. However, because of limited evidence, Radinsky left *Schizotheroides* in the Perissodactyla, *incertae sedis.* If the upper dentition of *Toxotherium* is ever found in association with the lower, it is doubtful that it will be referable to *Schizotheroides.* The cusp pattern of *Schizotheroides* is not rhinocerotoid, and, thus far, we have never noted an instance in which upper dentition with heavy cingula, as in *Schizotheroides,* was combined with lower dentition with no cingula, as in *Toxotherium.*

Superficially *T. woodi* resembles *Hyracodon* in the wedge shape of the jaw and the shortness of the symphysis. In detail, *Toxotherium* is quite different. The lingual-buccal cingula of *Hyracodon* dentition are lacking in *Toxotherium,* and *Hyracodon* lacks the extremely heavy tusk of *Toxotherium.* Although relatively heavier and larger, the tusk of *Toxotherium* may be said to resemble others of the rhinocerotoids, for example, *Metamynodon.*

In the course of comparing *T. hunteri* and *T. woodi* with members of the Perissodactyla, we made some extremely close matches in dental pattern. If it were not for the fortuitously preserved area around the tusk of

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[1] Radinsky (1966, p. 222) stated: "*Pataecus* Radinsky, 1965 (p. 212) a late Eocene tapiroid, is a junior homonym of *Pataecus* Richardson, 1844, a perciform fish. I therefore propose the generic name *Pataecops* to replace *Pataecus* Radinsky, 1965."

[2] Hough (1955, p. 34) spelled the new genus *"Schizotheriodes."* She also misspelled the superfamily name Chalicotherioidea and another genus, *Chasmotheroides,* transposing the "o" and the "i" in each case. According to the International Code, 1961, Article 32 (a) (ii) and Article 33 (a) (i), we are correcting the spelling of this genus to read *Schizotheroides.*

Toxotherium, T. woodi might be referred to *Caenolophus progressus* Matthew and Granger (1925), a small late Eocene rhinoceros from the Shara Murun Formation of Inner Mongolia. The molar cusps of *Toxotherium* are also similar to those of *Triplopus cubitalis,* but the cusp pattern is basic to all rhinocerotoids.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) OF LOWER JAWS AND TEETH OF *Toxotherium*

	T. woodi F:A.M. No. 42901	*T. hunteri*[a] N.M.C. No. 8918
Diastema, dP_2 to break	5.2[b]	—
Diastema, P_3 to break	—	8.7[b]
Depth below dP_3	17.2	—
Depth below P_4	—	24.6
Length, dP_3–M_1	26.6	—
Length, P_4–M_2	—	32.6
Length, dP_2 (broken)–M_1	32.1	—
Length, P_3 (alveolus)–M_2	—	37.5
Length, dP_2 (broken)	6.0	—
Width, dP_2 (broken)	3.4	—
Length, dP_3	7.8	—
Width, dP_3	4.6	—
Length, P_3 (roots)	—	4.9
Length, P_4	—	8.3
Width, P_4	—	5.6
dP_3, enamel height, tip of entoconid to base of enamel	5.0	—
Length, posterior root, base of enamel to end of root	12.9	—
Length, dP_4	8.8	—
Width, dP_4	5.1	—
Length, M_1	10.0	10.3
Width, M_1	6.3	6.1
Length, M_2	—	14.1
Width, M_2	—	8.0

[a] Measurements from Wood (1961), but dentition as herein interpreted.

[b] Owing to break on specimens, accurate measurements cannot be given.

All comparisons between *Toxotherium* and other forms of rhinoceroses (or tapirs with rhinocerotoid-like molar patterns) fail when the massive tusk of *Toxotherium* is considered. A family relationship to the Amynodontidae is not suggested here, but there is a similarity in the size of the tusk in relation to the abbreviated dental series. But again the *Toxotherium*

tusk is relatively heavier and more pronounced than that of any observed amynodont.

When and if other specimens are found, or as yet unrecognized specimens in other collections are recorded, *Toxotherium* may well be assigned a place in a new family or subfamily of the Rhinocerotoidea. The present study is too inconclusive to do more than show the differences between *T. hunteri* and *T. woodi* and record a southern extension of the range of the genus from Saskatchewan to Wyoming. The place of *Toxotherium* in the North American late Eocene or early Oligocene mammalian fauna is nearly as enigmatic as Wood found it.

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