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Erwin Hinckley Barbour

Thompson M. Stout

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DIPLOLOPHUS

BY ERWIN HINCKLEY BARBOUR AND THOMPSON M. STOUT

THE rich and varied nature of the mammalian faunas of the White River Oligocene has been recognized for many years, but the exact geologic succession is only now becoming known. In these faunal assemblages the rodents and lagomorphs appear to have been important elements, perhaps numerically as abundant in the Oligocene as are these same groups at present.

One of the results of the extensive field work of the last few years (particularly from 1931 to 1938) by University of Nebraska State Museum field parties has been a very large stratigraphic collection of Oligocene mammal remains. In this collection Oligocene rodents and lagomorphs are now represented by several thousand specimens, a stratigraphic study of which is in progress. It is the purpose of this paper to report upon recently discovered material of one of the least known of the Oligocene rodents, *Diplolophus,* and to record definitely its stratigraphic occurrence in the area explored.

The genus *Diplolophus* is at present known from only the one species, *D. insolens,* established by Dr. E. L. Troxell (1923, p. 157-8, figs. 1-2)[1] upon a specimen found by Professor O. C. Marsh in 1870. The species *Diplolophus parvus* established at the same time by Dr. Troxell (1923, p. 158-9, figs. 3-5) is now considered to be a species of *Proheteromys* (Wood 1935A, p. 170-2).

The writers wish to express thanks to Doctors Malcolm R. Thorpe and G. Edward Lewis of the Yale Peabody Museum and to Doctors C. Lewis Gazin and C. W. Gilmore of the United States National Museum for

[1] See Bibliography, page 36.

kind permission to examine types. Dr. H. E. Anthony has allowed comparison study with modern murid material in the American Museum of Natural History. Mr. Childs Frick, Dr. Walter Granger, and Mr. C. Bertrand Schultz have given much-appreciated assistance. Mr. J. J. Burke and Dr. A. E. Wood have given helpful suggestions. The figures have been drawn to scale by the junior author, with all specimens shown as left-hand for convenience in comparison.

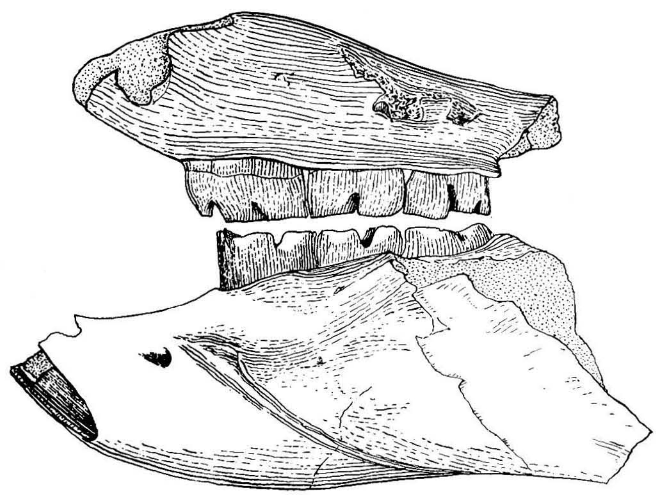

Fig. 13.—Side view of left ramus and maxillary of probably the same individual of *Diplolophus insolens* Troxell, referred. N. S. M. 9-5-7-36 S. P. ×5.

DESCRIPTION OF MATERIAL

RODENTIA, Incertae Sedis

Diplolophus insolens Troxell 1923

Diplolophus insolens Troxell, 1923.
Gidleumys adspectans Wood, 1936.

Holotype.—Yale Peabody Museum, Cat. No. 10368, right ramus with M_1–M_3. (Original field number 118), (Fig. 14*H*).

Type Locality.—Collected by Professor O. C. Marsh, on Cherry creek, August 22, 1870, according to the label with the type. This specimen appears to have been collected by Professor Marsh on the very same day as the holotype of *Ischyromys pliacus* Troxell (1922, p. 124), Yale Peabody Museum No. 12511, according to an identical label with the latter. Location of Cherry creek, is given, however, in the case of *Diplolophus insolens,* by Dr. E. L. Troxell as "near Scottsbluff, Nebraska" (Troxell 1923, p. 157), while for *Ischyromys pliacus* this location is stated by Dr. Troxell (1922, p. 124) as "Cherry creek, Colorado." Evidence that the Colorado location is possibly correct occurs in a letter written by Professor Marsh on August 12, 1870, to Professor J. D. Dana, telling of the work in northeastern Colorado. This letter was later published (see Amer. Jour. Sci., 1870, (2), L, p. 292; ibid., 1871, (3), I, p. 142-3). The possible association of the holotype of *Diplolophus insolens* with the holotype of

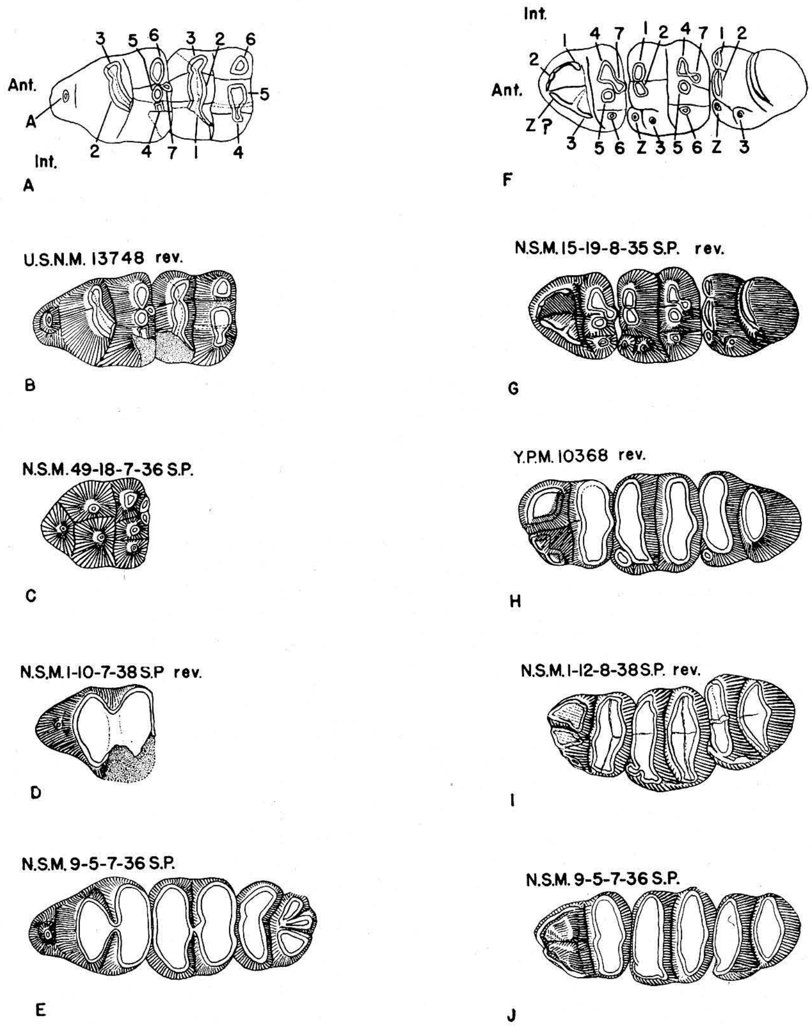

Fig. 14.—Dentitions of *Diplolophus insolens* Troxell, referred. *A*, Diagram of little-worn left upper molars, M^1–M^2, to show nomenclature of cusps referred to in text. *B*, Little-worn right upper molars, M^1–M^2, reversed to appear left; U. S. N. M. 13748 (Holotype, *Gidleumys adspectans*). *C*, Little-worn left upper molar, M^1; N. S. M. 49-18-7-36 S. P. *D*, Well-worn right upper molar, M^1, reversed (Anterocone very small), N. S.M. 1-10-7-38 S. P. *E*, Well-worn left upper molars, M^1–M^3; N. S. M. 9-5-7-36 S. P. (see also *J*). *F*, Diagram of little-worn left lower molars, M_1–M_3, to show nomenclature of cusps referred to in text. *G*, Little-worn right lower molars, M_1–M_5, reversed; N. S. M. 15-19-8-35 S. P. *H*, Moderately worn right lower molars, M_1–M_3, reversed; Y. P. M. 10368 (Holotype, *Diplolophus insolens*). *I*, Moderately worn right lower molars, M_1–M_3, reversed; N. S. M. 1-12-8-38 S. P. *J*, Well-worn left lower molars, M_1–M_3; N. S. M. 9-5-7-36 S. P. (see also *E*). $\times 5$.

Ischyromys pliacus may be of some importance, because the recent collections of the University of Nebraska State Museum disclose that these two species are both probably good index fossils for the uppermost faunal level of the middle Oligocene in northwestern Nebraska. Neither of these species has thus far been identified in the collections from stratigraphic levels lower in the Brule formation, although one large specimen of *Ischyromys* is known from the collection in the middle portion of the Chadron formation.

Referred Specimens.—University of Nebraska State Museum specimens: From Sioux county collecting locality 14, northwest of Crawford, Nebraska: No. 15-19-8-35 S.P., a right ramus with M_1–M_3; No. 49-18-7-36 S.P., an isolated left M^1; and No. 1-10-7-38 S.P., a right maxillary fragment with M^1 (Figs. 14*C*, *D*, G).

From Sioux county collecting locality 17, near top of badlands escarpment to the east of Toadstool park, northwest of Crawford, Nebraska: No. 9-5-7-36 S.P., a left maxillary with M^1–M^3, and left and right rami of mandible with both M_1–M_3 found closely associated and almost certainly belonging to the same individual (Figs. 13; 14*E*, *J*).

From Sioux county collecting locality 6, north of Harrison, Nebraska: No. 1-12-8-38 S.P., a right ramus with M_1–M_3, collected *in situ* (Fig. 14*I*).

All of the referred specimens mentioned above are from University of Nebraska State Museum collecting localities northwest of Crawford and north of Harrison, in Sioux county, Nebraska. Exact section locations for these localities are preserved in the records of the University of Nebraska State Museum. All of these specimens are from almost exactly the same geologic level, the uppermost faunal level of the Orella member ("*Oreodon* zone") of the Brule formation in this area, at a level (C^3) 60 to 65 feet above the base of field division C of this member or 10 to 25 feet below the top of division C, and 140 to 160 feet above the base of the Orella member. For a preliminary statement regarding a suggested lithologic subdivision of the Brule formation into Orella member ("*Oreodon* zone") and Whitney member ("*Leptauchenia* zone") in northwestern Nebraska, see Schultz & Stout (1938).

Also referred to *Diplolophus insolens* on the basis of the other referred specimens is United States National Museum No. 13748, a right maxillary with M^1–M^2 (not left P^4–M^1) from the Oligocene of South Dakota, other data lacking. This specimen is the holotype of *Gidleumys adspectans* Wood (1936, p. 3-4, fig. 2; 1937, p. 217-18, fig. 39), here considered to represent the little-worn partial upper dentition of *Diplolophus insolens* (Fig. 14*B*).

Generic and Specific Characters.—Dentition: cheek teeth 3/3. Size slightly larger than contemporary *Eumys*, M^1–M^3 length measuring about 8 mm., and M_1–M_3 length about 6.8 to 7.8 mm. Molars brachydont-hypsodont, becoming more massive and rounded with age, and characterized by prominent transverse ridges separated by deep transverse valleys (bilophodont condition). Molars further characterized by one unique and very prominent accessory cusp, Z (Fig. 14*F*), situated antero-externally on the second and third lower molars, and by the isolated anterior basal cusp A on the first upper molar (Fig. 14*A*). The number of roots on the cheek teeth are not certainly known without excavation except that the anterior root of M^1 is single and situated over the anterior cusp, and the posterior root of M_3 is also single and of the width of the tooth. The lower incisor is triangular in cross-section.

STAGE OF LITTLE WEAR ON LOWER MOLARS.—(Fig. 14*F*). Anterior lophid (metalophid) of M_1 of two parts and divided by a shallow longitudinal valley, with the triturating surface basin shaped, reducing upon wear to three more or less distinct cusps. The posterior lophid (hypolophid) of M_1 in early stages of wear is composed of three primary cusps, 4, 5, and 6, with an accessory cusp, 7, situated postero-external to cusp 4.

The anterior lophid (metalophid) of M_2 is composed of three main cusps, 1, 2, and 3, with the unique antero-external accessory cusp Z, mentioned above. The posterior lophid (hypolophid) of M_2 is like the hypolophid of M_1, described above.

Table 1.—Comparative Measurements of Diplolophus. ¶

LOWER DENTITION	Y.P.M. 10368 Right	N.S.M. 9-5-7-36 S.P. Left	Right	N.S.M. 1-12-8-38 S.P. Right	N.S.M. 15-19-8-35 S.P. Right
Cr. M_1–M_3, maximum	7.75 A	7.2	7.2	6.8	7.25
Alv. M_1–M_3, internal	7.9 A	7.2	7.25	6.8	7.4
Cr. M_1–M_2, maximum *	4.8	4.7	4.6	4.3	4.45
Cr. M_2–M_3, maximum †	5.2	4.6	4.6	4.6 A	4.8
Cr. M_2–M_3, triturating	4.35	4.25	4.2	3.9 A	3.8
Cr. M_1, anterop. maximum ‡	2.5	2.5	2.5	2.3	2.3
Cr. M_1, tr. ant. maximum	2.25	2.1	2.1	2.05	2.1
Cr. M_1, tr. post. maximum	2.45	2.35	2.3	2.35	2.3
Cr. M_2, anterop. triturat.	2.25	2.2	2.1	1.95	2.0
Cr. M_2, tr. ant. maximum	2.75	2.6	2.6	2.65	2.6
Cr. M_2, tr. post. maximum	2.65	2.55	2.5	2.65	2.5
Cr. M_3, anterop. maximum §	3.2	2.5	2.6	2.6	2.5
Cr. M_3, anterop. triturat.	1.95	2.1	2.05	1.9	1.6
Cr. M_3, tr. ant. maximum	2.6	2.4	2.45	2.5	2.4
Cr. M_3, tr. post. maximum	2.0	2.0	2.0	2.15	2.05
Depth ramus below M_1	5.0	5.45	5.5	5.2	

UPPER DENTITION	U.S.N.M. 13748 Right	N.S.M. 9-5-7-36 S.P. Left	N.S.M. 49-18-7-36 S.P. Left	N.S.M. 1-10-7-38 S.P. Right
Cr. M^1–M^3, maximum		7.9		
Alv. M^1–M^3		8.2		
Cr. M^1–M^2, maximum *	5.6	5.8		
Cr. M^1–M^2, ext. base crown	5.35	5.5		
Cr. M^2–M^3, maximum †		4.4		
Cr. M^1, anterop. maximum ‡	3.5	3.6	3.1	3.0
Cr. M^1, anterop. ext. base	3.05	3.2	3.0	3.0
Cr. M^1, anterop, triturat.	3.05	3.1	2.6	2.8
Cr. M^1, tr. at anterocone	1.5	1.5	1.5	1.4
Cr. M^1, tr. ant. maximum	2.45	2.4	2.35	2.3 A
Cr. M^1, tr. post. maximum	2.65	2.75	2.5	2.5 A
Cr. M^2, anterop. triturat.	2.15	2.25		
Cr. M^2, tr. ant. maximum	2.6–	2.8		
Cr. M^2, tr. post. maximum	2.55	2.65		
Cr. M^3, anterop. maximum §		2.2		
Cr. M^3, anterop. triturat.		2.15		
Cr. M^3, tr. ant. maximum		2.45		
Cr. M^3 tr. post. maximum		2.05		

¶ Measurements to .05 mm. approximate. Abbreviations: A—approximate; tr—transverse; ant—anterior; post—posterior; anterop—anteroposterior; ext—external; triturat—triturating. Abbreviations of institutions: Y.P.M.—Yale Peabody Museum; U.S.N.M.—United States National Museum; N.S.M.—University of Nebraska State Museum.

* Measured from most anterior point on crown of $M^1/_1$ to posterior edge of the triturating surface of $M^2/_2$.

† Measured from anterior edge of triturating surface of $M^2/_2$ to posterior base of the crown of $M^3/_3$.

‡ Measured from most anterior point on crown of $M^1/_1$ to posterior edge of the triturating surface.

§ Measured from anterior edge of triturating surface of $M^3/_3$ to posterior base of the crown.

The anterior lophid (metalophid) of M_3 is similar to the metalophid of M_2. The posterior lophid (hypolophid) of M_3 appears to consist of a single ridge or crest, and even when little worn no accessory posterior cusps can be made out.

STAGE OF LITTLE WEAR ON UPPER MOLARS.—(Fig. 14*A*). M^1 with a distinctive isolated anterior basal cusp, A, situated lower than the remainder of the tooth, becoming minute with extreme wear. The anterior loph (protoloph) of M^1 consists of only the two cusps 2 and 3, of which cusp 2 is the larger and situated internal to cusp 3. The posterior loph (metaloph) of M^1 consists of three cusps, 4, 5, and 6, with small accessory cusps, 7a and 7b, situated posterior to and between cusps 5 and 6.

The anterior loph (protoloph) of M^2 is composed of the three cusps, 1, 2, and 3, and the posterior loph (metaloph) consists of the three cusps 4, 5 and 6. Due to imperfect preservation of the only little-worn M^2 available (U.S.N.M. 13748), the presence or absence of accessory cusps on the posterior loph of the little-worn M^2 cannot be determined.

M^3 is known only in the well-worn stage, with the anterior loph (protoloph) a single ridge, but with the posterior loph (metaloph) composed of three cusps. Of these posterior cusps, the median cusp is situated posterior to and between the other two (Fig. 14*E*).

STAGES OF ADVANCED WEAR.—(Figs. 14*D*, *E*, *H*, *I*, *J*). With advanced wear the pattern of the molar teeth appears to have been reduced to a simple set of flattened ridges. The antero-external cusp Z on M_2 and M_3 becomes progressively incorporated into the ridge, but it is still faintly distinguishable in even advanced stages of wear (Figs. 14*I*, *J*). The anterior half of M_1 retains the basin-shaped triturating surface even with advanced wear, but the prominence and appearance of the anterior cusps appear to be quite variable, depending upon age and preservation of the specimen. The usually prominent and distinctive anterior basal cusp, A, of M^1 (Figs. 14*A*, *B*, *C*, *E*) becomes minute and is scarcely distinguishable with extreme wear (Fig. 14*D*), although it is still large on N.S.M. 9-5-7-36 S.P. (Figs. 13, 14*E*).

Discussion. THE PROBLEM OF CUSP TERMINOLOGY.—The nomenclature to be applied to the cheek teeth of *Diplolophus* is difficult to determine.

One possible interpretation, however, is the application of the heteromyid cusp terminology of Wood & Wilson (1936, p. 388-91, figs. 1b, 2b) in the sense of geographic location of cusps (not cusp homology) as follows:

Upper Molars: A—anterocone; 1—protostyle; 2—protocone; 3—paracone; 4—entostyle; 5—hypocone; 6—metacone; 7a and 7b—cusps of uncertain correlation. (Fig. 14*A*).

Lower Molars: 1—metaconid; 2—protoconid; 3—protostylid?; 4—entoconid; 5—hypoconid; 6—hypostylid; 7—cusp of uncertain correlation; Z—antero-external accessory cusp occupying a position similar (but anterior) to that of the protostylid in the heteromyids according to the Wood-Wilson terminology. (Fig. 14*F*).

There are several other possible interpretations as to the geographic nomenclature of these cusps, but the arrangement and placement of the various cusps in *Diplolophus* (Figs. 14*A*, *F*) suggests that cusp addition in this genus has been on the protomere (inner side of maxillary cheek teeth and outer side of mandibular cheek teeth, as defined by Miller & Gidley 1918, p. 434, footnote 2). Against this interpretation and the nomenclature suggested above is the relatively large size of cusp 3 on the lower second and third molars, which may indicate that cusp addition might have been instead along the midline of the last lower molars. In such a case cusp 3 would probably be termed the protoconid and cusp 2 perhaps the metaconulid, with cusp 6 the hypoconid and cusp 5 perhaps the entoconulid. A correspondingly different interpretation as to the names to be applied to the inner and middle cusps of the upper cheek teeth would then also be necessary. However, because cusp Z is evidently accessory on the lower second and third molars, and because cusp 1 is absent (not developed) on the first upper molar, the heteromyid cusp nomenclature applied as here in the geographic sense is probably to be preferred.

Summary.—The family relationships and affinities of *Diplolophus* have been in doubt since this form was first made known and must still remain so, despite the discovery of the new material here described. Only the characters of the skull may be expected to settle definitely the systematic position of this interesting genus. Comparisons with the little known John Day Miocene rodent, *Palustrimus lewisi* Wood (1935B, p. 370-1, figs. 2-3), are not attempted at this time since the holotype of this species has not been examined by the writers.

In a recent fundamental work on the Oligocene rodents, Dr. A. E. Wood has pointed out the similarity in tooth pattern between *Diplolophus* and geomyoid rodents (Wood 1937, p. 258), remarking, however, the presence of only three teeth in *Diplolophus* in contrast to the four teeth of geomyoids. This difference in dental formula, together with differences in apparently fundamental details of tooth pattern, seems to the present writers to be of considerable importance. In this connection it may be remarked that the rodent described as *Gidleumys adspectans* as an undoubted Oligocene geomyoid (Wood 1936, p. 3-4; 1937, p. 217-18) now appears to be conspecific with *Diplolophus insolens* and thus probably had three teeth instead of four teeth in each jaw.

The limiting possibilities as to the relationships of *Diplolophus* have been well summarized by Wood (1937, p. 259) as follows:

> It is therefore at present impossible to determine the relationships of this form. It may be a pathologic individual of one of several unknown or poorly known phyla of geomyoids. It may represent a new family of geomyoids which early lost the third molar and subsequently paralleled the other families as they have paralleled each other. Or it may represent an entirely distinct stock, belonging to the "Myomorph" group, which, after losing the premolar, developed dental similarities to the Geomyoidea. As suggested by Dr. G. E. Lewis [Wood 1935B, p. 371, footnote], there are certain interesting similarities to the Muridae in the pattern of *Diplolophus*, which may or may not be of significance.

To this statement of possible affinities very little can at present be added, except to note that the holotype of *Diplolophus insolens* is almost certainly not pathologic since other specimens are now known with the same dental formula. Further discussion of family relationships must await the discovery of skull material of this unique Oligocene rodent.

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