ON THE GENUS *DIKKOMYS* (GEOMYOIDEA, MAMMALIA)

by

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SUMMARY

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ABSTRACT

The geomyoid genus *Dikkomys* is well represented in a sample from the Black Bear Quarry II local fauna of Early Hemingfordian age in Bennett County, South Dakota. Isolated unworn P/4's of *Dikkomys matthewi* WOOD have a prominent median cristid (sagicristid) with a connection to the metaconid and the hypolophid. With wear, P/4 does not become as molariform as P/4 because of this cristid.

A large sample of the Whitneyan heteromyid *Proheteromys nebraskensis* WOOD contains variants of the P/4 with on incipient sagicristid in approximately 18 percent of the population. The upper dentition and lower molars of *Proheteromys nebraskensis* are sufficiently generalized to indicate probable ancestry to *Dikkomys*.

INTRODUCTION

This paper is part of a larger study of Black Bear Quarry II (Hemingfordian) geomyoids still in progress. Some conclusions we are making are based on our knowledge of *Proheteromys* from Black Bear Quarry II and from the Brule and Sharps Formations of South Dakota.

Black Bear Quarry II is an early Miocene locality and has yielded an excellent fauna of microvertebrates (Green 1972, 1977, Green and Martin 1976, Martin and Green 1979, Holman 1976). This material was recovered by acetic acid treatment of the matrix in the field (Green 1970). Details concerning the quarry may be found in Green (1972).

Among the teeth of geomyoids are a series of isolated lower and upper teeth and several mandibular fragments with partial dentitions of *Dikkomys*. These form the largest number of teeth from a single locality and add to our knowledge of the relationship of the genus to other geomyoids. *Dikkomys* is the earliest known geomyine. *D. matthewi* was first described by A.E. Wood (1936). The type consists of an isolated P/4 with isolated M/1, M/2, and M1/ as paratypes. These teeth from the Harrison Formation of Nebraska were found in ant hills. Galbreath referred a mandible from the Wounded Knee Rosebud fauna (see Macdonald, J. R. 1970, p. 41) to the species. Macdonald, J. R. (1970) lists one other specimen from the Rosebud Formation. Russell (1968) in a reclassification of the Geomyinae established the Tribe Dikkomyini for the genera *Dikkomys* and *Pliosaccomys*. This has not been generally followed by later workers. Black (1961) described *D. woodi* from the Deep River Formation (Miocene, Upper Hemingfordian). Munthe (1971) made some preliminary conclusions regarding the temporal range of the genus based on specimens referred to *D. woodi*. Further study of additional material by Munthe (personal communication, March, 1979) indicates that *D. woodi* does not belong in *Dikkomys* but is referable to the Florentyaminae. Martin (1976) referred isolated teeth from the Batesland Formation (Hemingfordian) to *D. matthewi* stating that they were identical with teeth from BBQ II. The Batesland Formation lies just above the Rosebud Formation. *Dikkomys* is a monotypic genus.

Acronyms used are : AMNH, American Museum of Natural History ; F:AM, Frick Collection American Museum of Natural History ; FMNH, Field Museum of Natural

History ; SDSM, Museum of Geology, South Dakota School of Mines and Technology ; YPM, Yale Peabody Museum. Abbreviations used are : AP, anteroposterior diameter ; Tr, transverse diameter ; BBQ II, Black Bear Quarry II. Measurements are in millimeters.

In addition to the BBQ II material of *Dikkomys*, the following specimens (or casts) have been examined. AMNH 22720 (holotype, right P/4) ; AMNH 22721 (left M/1, left M/2, right M1/) ; FMNH P26284 (right mandible with P/4-M/3) ; F:AM 97826 (maxillary fragment with P4/-M2/) ; YPM 14038 (holotype of *D. woodi*, left mandible with P/4-M/1).

The anatomical terminology for the teeth that is used in this paper differs from that of Rensberger (1971, 1973) who does not recognize separate protoconid and metastylid cusps in P/4 and that of Lindsay (1972) who does not recognize the entoconid in P/4.

All previously described specimens of *Dikkomys* are well worn. It is this wear that gives *Dikkomys* a typical geomyid appearance. However, in the BBQ II collection of teeth there are a number of unworn specimens. These teeth demonstrate a complicated pattern quite unlike the simple figure eight pattern usually seen in geomyids. It necessitates the introduction of two new terms, the *sagicristid* and the *cristid mesiobliqua*. The sagicristid is defined as follows : In P/4 of Geomyoidea, a ridge or crest usually in the midline (fig. 1). It may extend from the anterior end of the tooth to the posterior. It may be entire or partial. It may be low on the valley floor of the tooth of rise as a crest to crown level. Storer (1975) called the sagicristid a longitudinal ridge and Black (1963) called it a median crest. The cristid mesiobliqua is found in the lower molars of Geomyoidea. It is a crest extending diagonally from the inner border of the protoconid to the inner border of the entoconid connecting the labial and lingual moieties of the tooth.

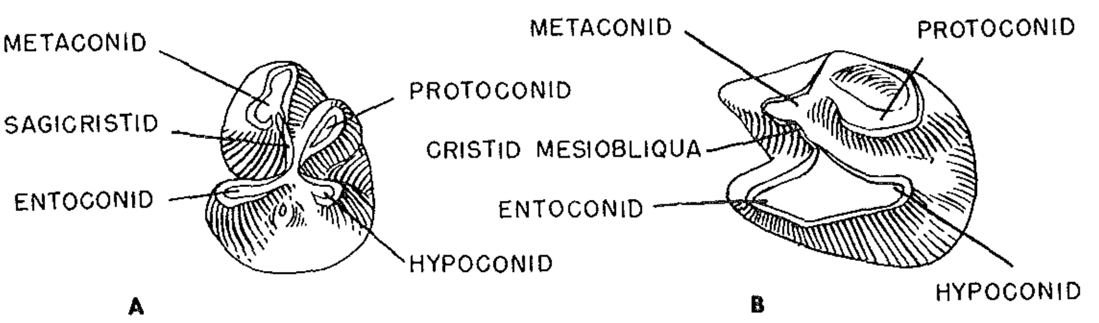

Figure 1. — Dental terminology used in this paper ; right P/4 and M/1.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA BOWDICH, 1821

Family GEOMYIDAE GILL, 1872

Subfamily GEOMYINAE BAIRD, 1857

DIKKOMYS WOOD, 1936

Dikkomys matthewi WOOD

Holotype : AMNH 22720

Referred specimens : SDSM 8289 A through SDSM 8289 P, 16 isolated P/4 ; SDSM 8325, right mandibular fragment with P/4-M/1 ; SDSM 8340, left mandibular fragment with P/4-M/1 ; SDSM 8412, right mandibular fragment with broken P/4, M/1-M/2 complete, root of M/3 ; SDSM 8752, 18 isolated M/1 ; SDSM 8753, 29 isolated M/2 ; SDSM 8754, 11 isolated M/3 ; SDSM 8755, 8 isolated P4/, and one broken P4/ ; SDSM 8756, 8 isolated M1/ ; SDSM 8757, 13 isolated M2/ ; SDSM 8758, 6 isolated M3/.

LOWER DENTITION

Three stages of wear groups have been arbitrarily established. These are : young adult, mature adult, and old adult. P/4 ; SDSM 8289 A - SDSM 8289 E represent wear phases in young adults, SDSM 8289 F - SDSM 8289 L phases of mature adult, and SD SM 8325, 8340, and 8412 are in a late mature stage of wear.

— SDSM 8289 A. This is the least worn tooth and does not seem to have had any wear at all. The anteroconid is centrally located below the top of the crown. It is connected to a posterobuccally directed anterior cingulum. Their is a slight discontinuity between the anterior cingulum and metaconid. The metaconid is somewhat triangular in shape with the apex pointing buccally. The sagicristid is well developed, separated from the anteroconid, and is not so high as the metaconid or protoconid. A small anterolabial crest connects the sagicristid to the metaconid. Another small crest (? anterior cingulum) joins the sagicristid to the protoconid. The hypoconid and entoconid are connected in the center with a junction to the sagicristid. The posterior cingulum exists as two tubercles.

— SDSM 8289 B. The tooth is also unworn. It differs in some respects from 8289 A. The sagicristid lacks the small anterobuccal crest to the protoconid. In this tooth, the entoconid has a small spur directed anteriorly toward the posteriorly directed arm of the metaconid. The posterior end of the sagicristid branches and is firmly joined to the entoconid and hypoconid respectively. The two cuspulids of the posterior cingulum are joined together and a projection from the central one connects it to the sagicristid.

— SDSM 8289 C is broken at the anterior end and is slightly less worn than SDSM 8289 D. In this tooth (D) the anterior cingulum is nearly connected to the protoconid. The valley between the metaconid and sagicristid is isolated as a fossetid. A crest from

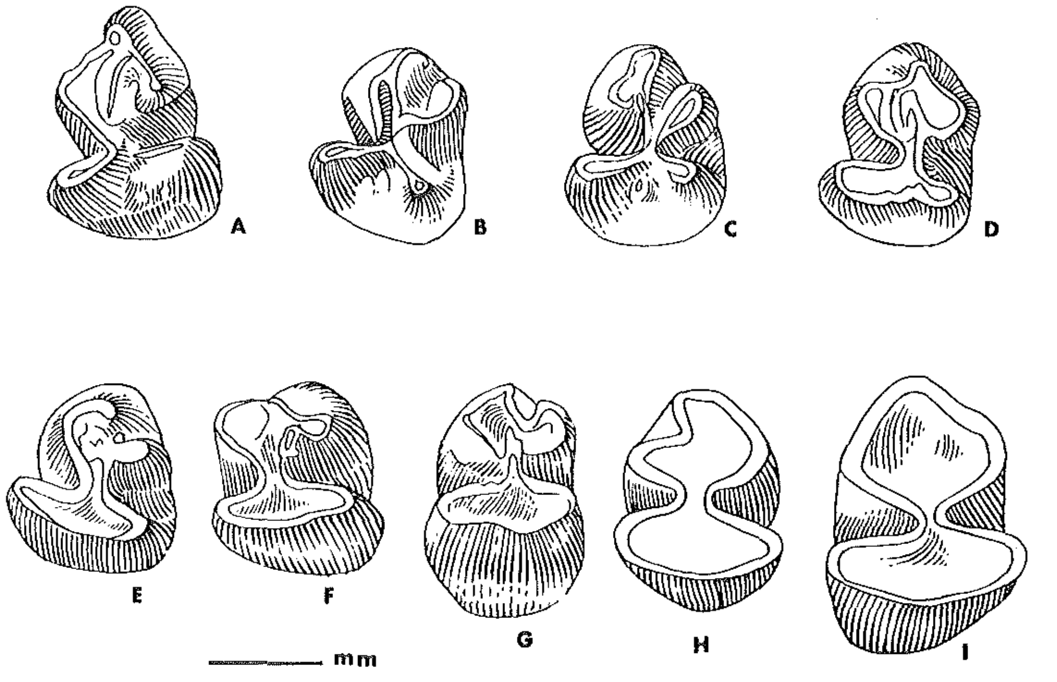

Figure 2. — *Dikkomys matthewi* P/4 arranged in order of wear.
A. SDSM 8289 A, left ; B. SDSM 8289 B, right ; C. SDSM 8289 E, right ; D. SDSM 8289 D, right ; E. SDSM 8289 G, right ; F. SDSM 8289I, left ; G. SDSM 8289 J, right ; H. SDSM 8289 L, left ; I. SDSM 8289 N, right.

the entoconid is connected to the metaconid. The valley between the entoconid and posterior cingulum is reduced to a plain with a slight enamel gap at the posterior end. SDSM 8289 E is as in 8289 D. SDSM 8289 F - SDSM 8289 H essentially have the same wear. The valley between the anteroconid and protoconid is still well developed. The entoconid, hypolophid, and posterior cingulum are united as a well developed hypolophid. The bridge of the sagicristid between the metaconid and protoconid gradually broadens. SDSM 8289 I - SDSM 8289 L show that continued wear reduces the anterobuccal groove to a small notch. The metalophid is well developed. SDSM 8289 M and O. The anterobuccal notch is gone. The tooth now has a typical geomyid eight shape. SDSM 8289 P. The lateral grooves are almost gone. A remnant of the anterobuccal notch is still present.

Similar stages of wear are given for M/1. SDSM 8752 A - SDSM 8752 E represent young adult phases, SDSM 8752 F - SDSM 8752 H mature adult, and SDSM 8752 F - SDSM 8752 H mature adult. In young adults, there is no anteroconid on M/1. The protoconid is higher than the metaconid and they are separate. The protoconid and metaconid are higher than the hypoconid and entoconid. The anterior cingulum and meta-

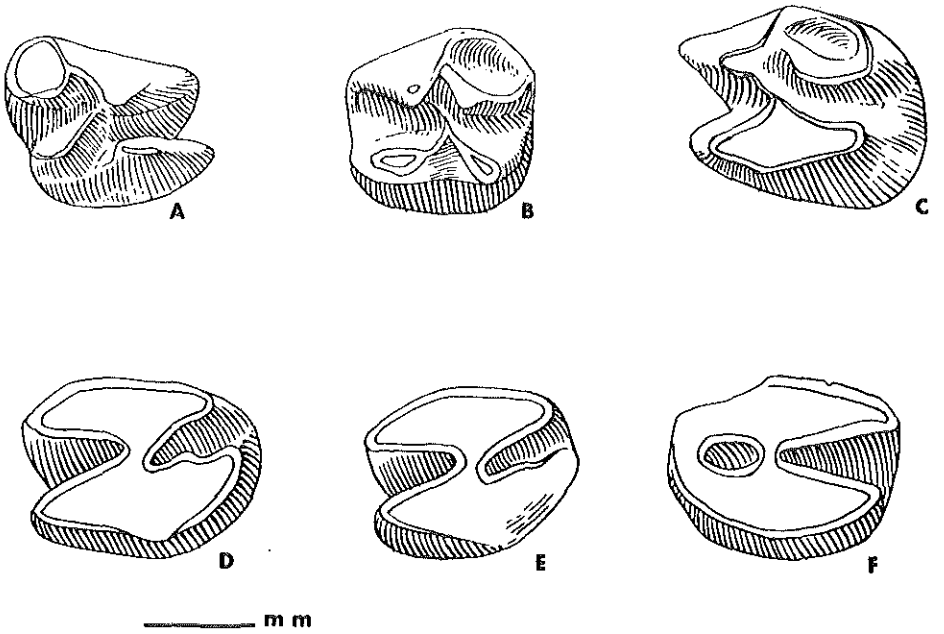

Figure 3. — *Dikkomys matthewi* M/1 arranged in order of wear.
A. SDSM 8752 A, left ; B. SDSM 8752 C, right ; C. SDSM 8752 D, right ; D. SDSM 8752 F, left ; E. SDSM 8752 F, left ; F. SDSM 8752 J, left.

conid surround an anterolingual fossettid. The hypoconid is higher than the entoconid. The cristid mesiobliqua begins at the center of the protoconid and is posterolingually directed to the entoconid. The posterior cingulum is slightly tuberculated. An entostylid is present or absent. A complete posterior cingulum is sometimes present. In some young adult teeth, a short lived fossettid develops between the protoconid and metaconid. This occurs when a crest develops from the metaconid and reaches the cristid mesiobliqua. When this happens, wear soon removes it. When the posterior cingulum is present it joins the entoconid and hypoconid to form a small fossettid which is soon gone with wear. In mature adults, the anterolingual fossettid is obliterated. The protoconid and metaconid are fused into a metalophid. The hypoconid and entoconid are fused into a hypolophid. The metalophid and hypolophid are centrally connected by an anteroposteriorly directed short cristid mesiobliqua. There is beginning of the closure of the lingual valley. In old adults, the lingual valley is closed, forming a lingual fossettid. The buccal valley never closes and is open to the base of the tooth. Although there are no M/1 in the collection showing such a condition, if a tooth were to be worn enough, the lingual fossettid would disappear with enough wear.

M/2 is slightly smaller than M/1 with the same wear pattern. M/3 is smaller than M/2, but is otherwise the same.

UPPER DENTITION

Unlike the lower teeth where the molars differ in structure from the premolar, the upper premolars and molars have the same structure and pattern. The changes in wear given below are for P4/-M3/. Three groups have been arbitrarily set up : young adult, mature adult, and old adult. As we have no associated upper and lower teeth we have no way of associating these age groups with those of the lower teeth, except by inference.

The youngest tooth, an M1/, still retains its cuspate condition. In the protoloph there are two small anterostyles about half way up from the crown. Not all teeth have anterostyles. The paracone and protocone are distinct as in the protostyle. In the metaloph, the metacone and hypocone are distinct. A small valley separates the hypocone from a large entostyle. The entostyle is connected to the protocone by a short crest. In the unworn tooth, the top of the crest is below the surface of the crown. Until some wear takes place, the buccal and lingual valleys are continuous. A posterior cingulum is present in the unworn M1/. With wear, it is quickly incorporated into the posterior border of the tooth.

The next stage of wear is seen in a P4/. This tooth has no anterostyles. The protostyle is unworn and still isolated. The protocone and paracone are united by an enamel band. The metacone and hypocone are united. The entostyle is still distinct but is joined to the hypocone by a short enamel strip and likewise to the protocone.

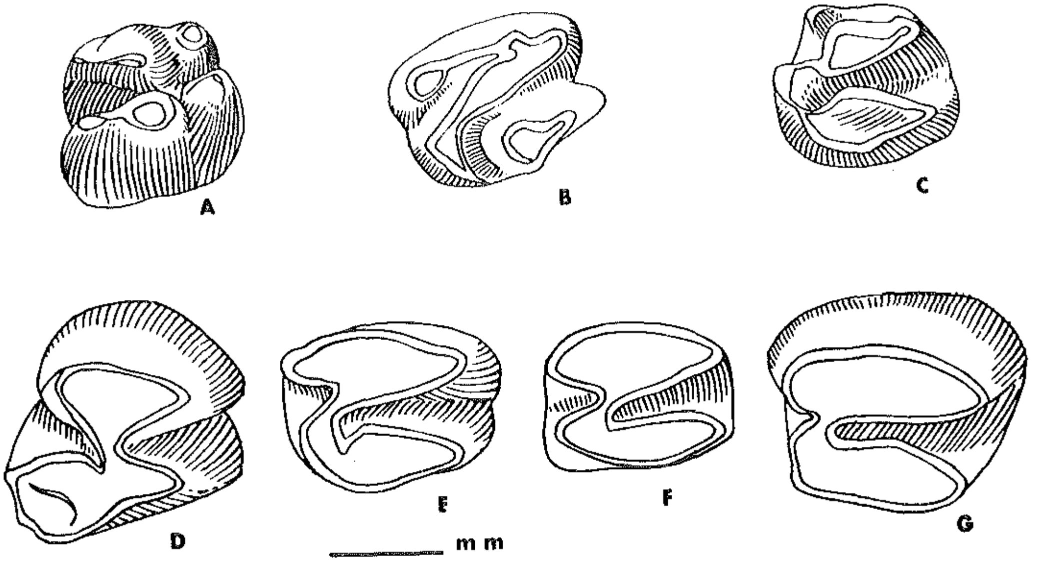

Figure 4. — *Dikkomys matthewi* upper teeth arranged in order of wear.
A. SDSM 8757 A, right M2/ ; B. SDSM 8757 B, left M2/ ; C. SDSM 8755 A, left P4/ ; D. SDSM 8756 A, left M1/ ; E. SDSM 8756 C, left M1/ ; F. SDSM 8757 E, left M2/ ; G. SDSM 8756 F, left M1/.

In the next stage, the protostyle is incorporated into the protoloph and is no longer distinct. The hypocone, at first separated from the metacone as an enamel ring soon loses its distinctness and becomes one with the metacone. The same is true of the entostyle. When this stage is reached, the young adult phase is over. The mature adult with a protoloph and metaloph still retains the lingual valley. Old age is reached when the lingual valley is gone and the two lophs are united lingually. At this stage, the tooth is U shaped with the open end facing buccally.

COMMENT

The Arikareean was an important time in the history of the geomyoids for several lineages of descent became established. Various authors have recognized heteromyine, perognathine, florentiamyine, pleurolicine, and entoptychine lines at this time. In addition, the geomyine line surely was present because of the level of development seen in *Dikkomys*, the earliest recognized geomyine which appears in the Hemingfordian. Derivation of these diverse lines has been the object of much interest especially since Wood's (1935) review of the Heteromyidae. Recent studies by Rensberger (1971, 1973 A, 1973 B) have provided valuable insights into the study of these groups. Independently, we have been collecting materials related to this problem. Green has assembled the sample of *Dikkomys* just described and Bjork a large sample of heteromyids from the Whitneyan of South Dakota. Informal discussions between the two authors leads to the conclusion that the Whitneyan sample is important because of the variations present, especially in the P/4.

The Whitneyan sample consists of over 250 upper and lower jaws with two or more teeth from a stratigraphically restricted zone in the upper Brule Formation in the Badlands National Park. This sample is very interesting because the morphology of the sample includes variants that include the species of *Proheteromys* recognized by J. R. Macdonald (1963, 1970) from the overlying Sharps Formation. This presents a problem which cannot be resolved with confidence because the species recognized by Macdonald may be valid within the Sharps Formation but sample sizes for each of these species are very small. Until the Sharps material is representative, we place the Whitneyan sample in *Proheteromys nebraskensis* WOOD 1937.

Although the specimens are low crowned especially when compared with *Dikkomys*, similarities with early geomyoids are apparent. Perhaps the most surprising feature in the *Proheteromys* sample is the presence of an incipient sagicristid. In approximately 18 % of 56 specimens of *Proheteromys nebraskensis* P/4's a median structure is present between the protoconid and metaconid.

The remaining dental features seen in *Proheteromys nebraskensis* are quite generalized for a heteromyid. This is in marked contrast to the specialized nature of *Heliscomys*, *i.e.* dominantly a tri-cusped P4/, all cheek teeth are cuspidate rather than lophate and a tubercle for the attachment of the M. masseter superficialis. Rensberger (1973) has remarked that this may be due to the small size of *Heliscomys* and a preference for insects in the diet. We regard *Heliscomys* as a small heteromyid of the Oligocene and unrelated to the post-Whitneyan diversification of geomyids.

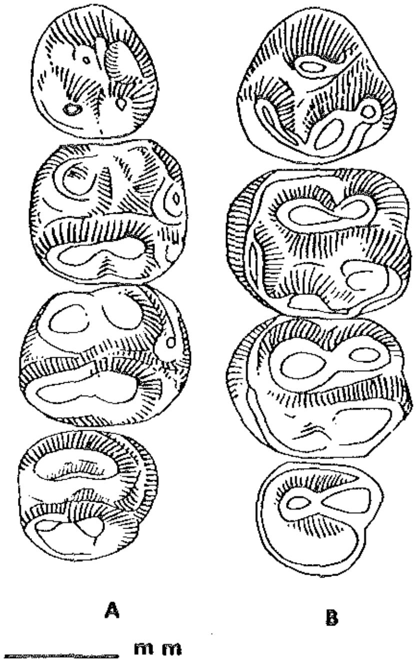

Figure 5. — *Proheteromys nebraskensis* ;
A. SDSM 10,000, right P/4-M/3 ;
B. SDSM 10,001, left P4/-M3/.

Modification of the upper molars of *Proheteromys nebraskensis* to the *Dikkomys* pattern required heightened crown and establishment of a lingual connection of the protoloph and metaloph. Such a connection requires separation of the cingular cusps in M1/ but not necessarily in M2/. This is consistent with the character of the cingular cusps of M1/ and M2/ in *Proheteromys nebraskensis*. The pit for the attachment of the tendon of *M. masseter superficialis* is typical of geomyoids and not tubercular as in *Heliscomys.*

CONCLUSION

The sagicristid first appears as a variation in *Proheteromys* during the Whitneyan and becomes a permanent structure in *Dikkomys*. It is our opinion that this provides very strong evidence that *Proheteromys* is ancestral to *Dikkomys* and as a stem genus unites the heteromyids and geomyids into a cohesive group. The variations seen in P/4 from BBQ II specimens are present in the South Dakota Whitneyan specimens in our collection. *Proheteromys* with its myriad of variants makes an excellent ancestor for other Arikareean geomyoids as well.

In unworn teeth of *Dikkomys* the ancestral condition of *Proheteromys* is rapidly eroded by wear as the more advanced condition comes into view. The more advanced pattern is added at the base of the tooth. Chaline (1974) has demonstrated the same situation in the *Mimomys-Arvicola* line, referring to the phenomenon as palingenesis. He also believes that palingenesis is a partner of hypsodonty. This seems to be the case in the *Proheteromys-Dikkomys* line.

R. J. Russell (1968) postulated the mode of wear in the dentition of *Dikkomys*. His starting point was a specimen of *D. matthewi* WOOD (incorrectly called *D. woodi*), FMNH N° P 26284 and from this specimen he inferred an earlier stage of wear. This postulate is incorrect in that we now know that P/4 possesses a well developed sagicristid in its earliest stage and that in the lower molars the lophids are connected by the cristid mesiobliqua.

	APa	APp	AP	Tra	Trp
A	1.10	0.55	1.70	1.10	1.50
B	0.70	0.55	1.60	1.00	1.40
C	0.80	0.40	1.40	0.90	1.35
D	0.90	0.45	1.45	1.10	1.30
E	0.85	0.50	1.65	1.05	1.35
F	1.00	0.75	1.90	1.30	1.65
G	0.90	0.45	1.45	0.90	1.50
H	0.85	0.50	1.50	1.05	1.20
I	0.70	0.40	1.50	1.20	1.50
J	0.80	0.60	1.60	1.10	1.45
K	0.90	0.50	1.55	1.05	1.45
L	1.00	0.75	1.85	1.30	1.60
M	1.15	0.65	1.90	1.20	1.60
N	1.15	0.80	2.00	1.55	1.80
O	1.00	0.70	1.80	1.20	1.45
P	–	–	1.50	1.10	1.45
8325	0.95	0.65	1.60	1.25	1.50
8340	1.10	0.65	1.75	1.25	1.55

Measurements - *D. matthewi*, SDSM 8289 (A-O) P/4 in mm.

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