Paleo Bios

A NEW SPECIES OF *GREGORYMYS* (RODENTIA, GEOMYIDAE)

FROM THE MIOCENE OF COLORADO

by

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ABSTRACT

Gregorymys larsoni n. sp. is a very late survivor of the *Gregorymys* lineage. It is known only from the Derby Peak fauna of late Barstovian or early Clarendonian age. Radiometric dates obtained from volcanic rocks above and below the sediments from which the Derby Peak fauna was collected range from approximately 13 to 10 million years before present. *G. larsoni* is temporally disjunct from all previously described species of the genus and may represent a population surviving only within a persistent refugium.

INTRODUCTION

A small collection of mammals was obtained from Derby Peak in Garfield County, Colorado by a University of Colorado party in 1967. The geology of the area was studied in subsequent years and radiometric ages were determined for rocks above and below the fossiliferous sediments. Because the stage of evolution of one of the rodent taxa represented in the collection appears anomalous with respect to the remainder of the fauna and the radiometric dates, this rodent was studied in detail to determine its affinities. It is described here as a new species and the geologic and faunal evidence bearing on the age of the deposit is discussed.

Measurements of the holotype were made with an EPOl Measuring Microscope and are shown in Table 1. Acronyms used are AMNH (= American Museum of Natural History), CM (= Carnegie Museum), FMNH (= Field Museum of Natural History), UCM (= University of Colorado Museum), and UCMP (= University of California Museum of Paleontology).

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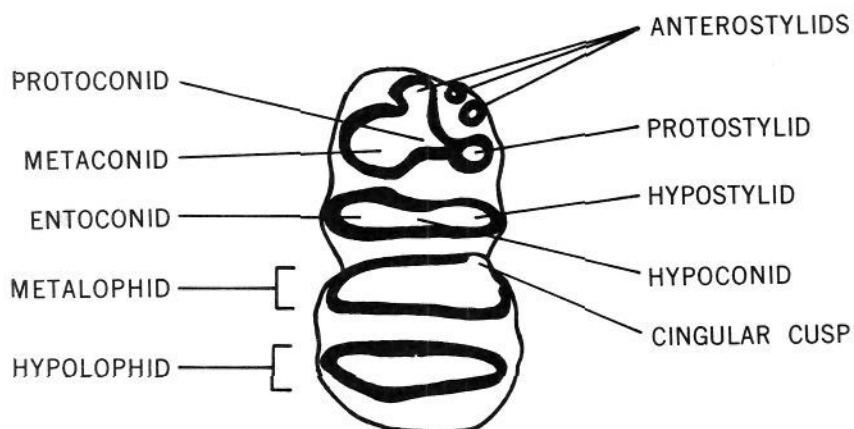
Figure 1. Cheek tooth cusp terminology for *Gregorymys larsoni*.
The major metalophid and hypolophid cusps occupy the same relative
positions on the molars as on P$_4$.

The cheek tooth cusp terminology employed here (Fig. 1) is that of
Rensberger (1971:110). The terminology for P$_4$, however, is used
only in a topographic sense. Cusp homologies are not implied. If
Gregorymys is ultimately descended from *Heliscomys*, which had only
three cusps on P$_4$, then one of *Gregorymys*' principal cusps is a
neomorph not homologous with the four principal cusps of general-
ized rodent teeth. Several attempts have been made to homologize
geomyoid P$_4$ cusps assuming that *Heliscomys* had lost one principal
cusp (*e. g.*, Shotwell, 1967; Lindsay, 1972), but none of these is
entirely satisfactory. I have therefore used names topographically
for simplicity and clarity.

SYSTEMATICS

Superfamily Geomyoidea Weber, 1904

Family Geomyidae Gill, 1872

Subfamily Entoptychinae Miller and Gidley, 1918

Gregorymys Wood, 1936

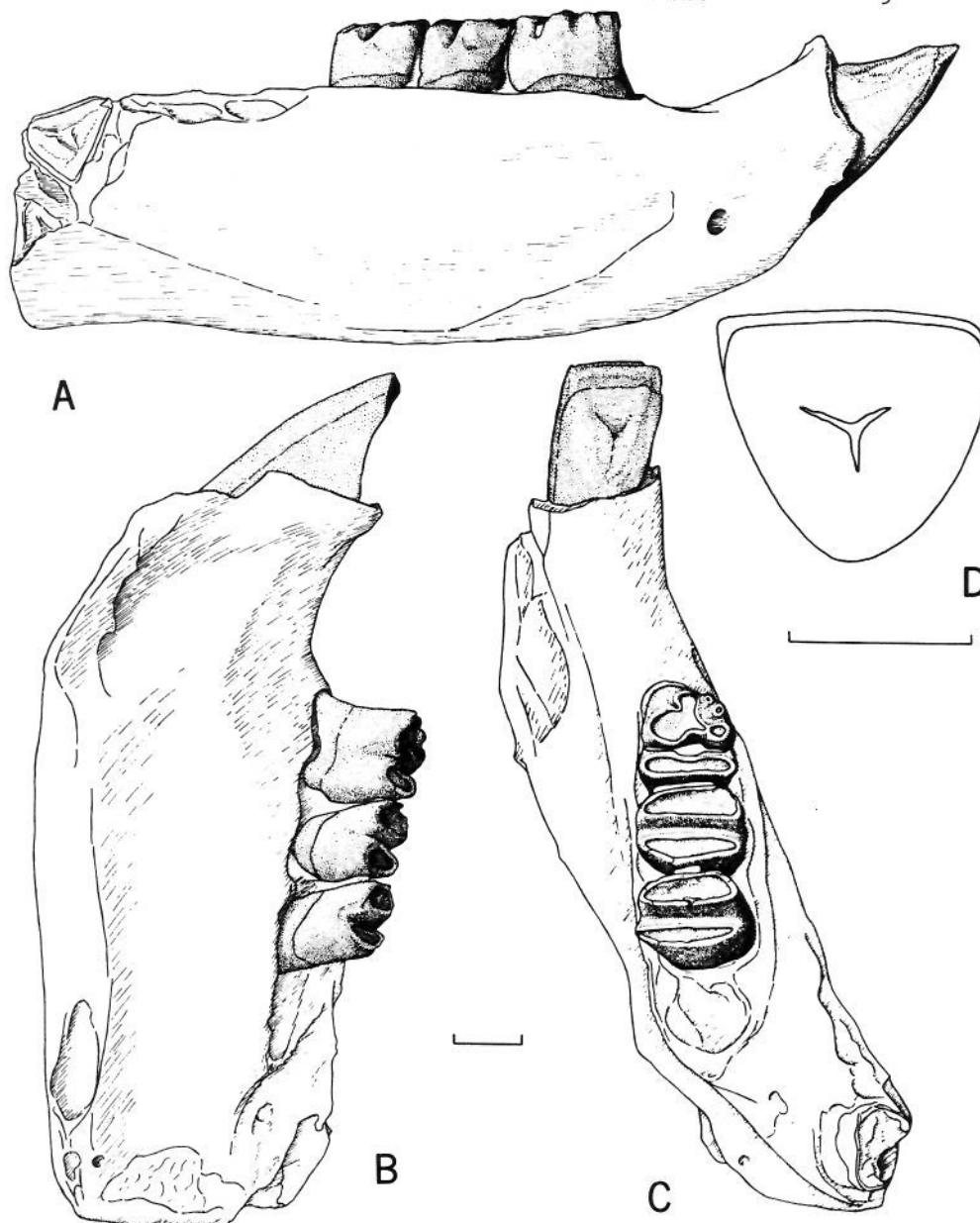*Gregorymys larsoni* new species

(Figure 2)

Figure 2. *Gregorymys larsoni* n. sp., UCM 29745. A. Lateral view. B. Lingual view. C. Occlusal view. D. Cross-section of incisor. Scale bars equal 1 mm.

Holotype: UCM 29745, right mandibular ramus with I-M_2.

Hypodigm: Type only.

Etymology: Patronym for Dr. Edwin E. Larson, who discovered the type locality and has been instrumental in deciphering the Cenozoic history of the area.

Locality: UCMP locality V76III, Derby Peak, Garfield County, Colorado. Detailed locality information may be obtained from the Museum of Paleontology, University of California, or the University of Colorado Museum.

Age: Late Barstovian or early Clarendonian.

Diagnosis: Very small species of *Gregorymys* (Table 1); mandible shallow (Table 1); diastema short (Table 1); protoconids and hypoconids weakly developed.

Description: The mandible is shallow for the genus. Its depth is 70% of P_4-M_3 length as opposed to 83% in AMNH 12895, referred by Wood (1936) to *G. curtus*, and 107% in CM 8999, the type specimen of *G. kayi* (Wood, 1950). The diastema is shallow and much shorter than in any previously described specimen of *Gregorymys*. Its length is less than half the P_4-M_3 length, whereas the diastema is approximately two-thirds as long as the cheek tooth row in FMNH 12221, the type specimen of *G. riggsi* (Wood, 1936) and CM 8999. The masseteric crest is low but sharply defined. It extends in a smooth arc from below the posterior portion of the diastema, immediately posterior to the small mental foramen, to a point below the hypolophid of M_2. A weak, rounded crest begins at the posterior end of the masseteric crest and follows the ventral margin of the incisor alveolus into the ascending ramus. This is distinctly different from the condition In AMNH 12895, where the masseteric crest is sharply angled and there is no crest posterior to it along the incisor alveolus. The angle is missing, but it extended anteriorly as far as M_3. The symphysis is rugose. A shallow genioglossal fossa lies immediately posterior to its dorsoventral midpoint. A narrow ventrolingual crest, presumably the area of insertion of M. digastricus, extends from the symphysis to a small ventral process below P_4. A rugose swelling near the ventral margin of the mandible below the hypolophid of P_4 may have been the area of origin of M. transversus mandibulae. A similar swelling occurs in some specimens of *G. curtus*. The prominent chin process seen in some specimens of *G. curtus* is lacking.

P_4 has three anterostylids, of which the most lingual is the largest, arranged in an arc anterolinguad of the metalophid. The lingual anterostylid differs from that in other described specimens of *Gregorymys* in its greater size and more labial position. In this respect it most closely approaches the type specimen of *G. riggsi*. The metalophid has only a very weak protoconid that has not yet united with the protostylid. The hypolophid has equally

developed entoconid and hypostylid but a weak hypoconid. The pos-
terior margin of the hypolophid is straight, in contrast to the
more arcuate hypolophids of other specimens, particularly AMNH
12909, referred to *G. formosus* by Wood (1936) and to *G. curtus* by
Macdonald (1970). With increased wear a small enamel lake would
develop between the anterostylids and the metalophid as in AMNH
12909. At a still later wear stage, a lake would form between the
metalophid and hypolophid as they would unite first labially and
then lingually. This is a result of the weak development of the
central cusp in each of these lophids.

M_1 and M_2 also show weak development of the protoconid and hy-
poconid in contrast to other species of the genus. The cingular
cusp of the metalophid is slightly lingual to the protostylid,
causing the labial margin of the metalophid to lie oblique to the
anteroposterior axis of the tooth row on both M_1 and M_2. This is
typical of M_2 in other species of *Gregorymys*, but in most previ-
ously described specimens the anterolabial cusp and protostylid
are equally labial on M_1. With increased wear the metalophids and
hypolophids would unite medially and labially at almost exactly
the same time. A very short-lived enamel lake would thus be form-
ed on the labial half of the tooth. The lophids would then unite
progressively more lingually. The lophid unions in FMNH 12221
(*G. riggsi*) would be similar, although in that specimen the first
connection is definitely at the labial margin and the medial con-
nection is slightly linguad of that in *G. larsoni*. In all other
species, the valley between the lophids is very deep in the center
of the tooth so that a persistent central enamel lake is formed.

Cement is present around the roots and slightly above on P_4 and
it extends well up on the crowns of M_{1-2}, particularly labially.
This development of cement exceeds that seen in specimens of *G.
curtus*, is very similar to *G. riggsi*, and is less than in *G. doug-
lassi* (Wood, 1936) and *G. kayi* (Wood, 1950).

The lower incisor is broad, flat anteriorly, and triangular
in cross-section. The enamel is thin and is almost entirely con-
fined to the anterior surface. The triradiate pulp cavity is i-
dentical to that in AMNH 12895 (*G. curtus*). The root is not pre-
served, but the incisor extended posterodorsally at least above
the occlusal surfaces of the cheek teeth. The incisor is larger
relative to the cheek teeth than in any other species of *Gregory-
mys* (Table 1).

Discussion: Certain aspects of geomyoid superspecific taxonomy
are fundamental to an understanding of *G. larsoni's* relationships
to other members of this superfamily. Shotwell (1967:10) included
the subfamilies traditionally grouped as Geomyidae within Hetero-
myidae. Rensberger (1971:151) advanced additional reasons for
this arrangement and acknowledged the probable artificiality of
the geomyid-heteromyid dichotomy, but retained the dichotomy in
order to emphasize "the fossorial attributes of the Entoptychinae
and Geomyinae" (1971:66). However, a recent study of the skeleton

Table 1. Measurements (in millimeters) of *Gregorymys larsoni* and selected comparative measurements of other species.

Measurement	UCM 29745 G. larsoni	AMNH 12895 G. curtus	FMNH 12221 G. riggsi	CM 8999 G. kayi
P_4-M_3 alveolar distance	6.60	8.10	7.45	7.80
P_4 anteroposterior (occlusal)	1.52	----	----	----
transverse metalophid	1.47	----	----	----
transverse hypolophid	1.60	----	----	----
M_1 anteroposterior (occlusal)	1.33	----	----	----
transverse metalophid	1.64	----	----	----
transverse hypolophid	1.62	2.31	2.39	2.30
M_2 anteroposterior (occlusal)	1.41	----	----	----
transverse metalophid	1.60	----	----	----
transverse hypolophid	1.66	----	----	----
M_3 anteroposterior (alveolus)	1.24	----	----	----
transverse (alveolus)	1.29	----	----	----
I anteroposterior	1.42	----	----	----
transverse	1.53	1.75	1.96	1.99
anteroposterior/ transverse	0.928	----	----	----
enamel thickness	0.03	----	----	----
Length of diastema	3.17	7.30	5.05	5.10
Depth of mandible below P_4	4.62	6.70	6.50	8.00

of *Schizodontomys* (Munthe, 1975), an entoptychine *sensu* Wood (1936), indicates that this animal was not fossorial, but semi-saltatorial.

Gregorymys is a pivotal genus with regard to familial taxonomy of these rodents. Galbreath (1967:278-280) has summarized many of the similarities of *Gregorymys* to geomyines on one hand and heteromyines on the other. He concluded that placing *Gregorymys* in either Geomyidae or Heteromyidae might obscure its true relationships. This seems certainly to be the case even with the limited suite of morphologic characters available for comparison in this study. While its overall size, length of diastema, and size and shape of incisor argue for *G. larsoni* being a geomyid, its P_4 morphology, depth of mandible, and certain characters of the molars appear to place it in the Heteromyidae.

Despite the fact that all the above arguments support the inclusion of heteromyids and geomyids within a single family, such

an arrangement is never likely to win general acceptance. Both
family names are very solidly entrenched in the scientific liter-
ature. The most compelling argument against fusing the two fami-
lies is the ease with which their modern representatives may be
morphologically differentiated, although, as noted by Wood (1937),
this morphologic disparity is largely a reflection of different
habits. Neozoologists would be understandably skeptical of plac-
ing *Thomomys* and *Dipodomys* in the same family based solely on evi-
dence provided by extinct taxa whose exact relationships to modern
subfamilies are uncertain. With some misgivings, I have attempted
to place *G. larsoni* within the traditional geomyoid taxonomic
framework.

The subfamily assignment of *Gregorymys* to the Entoptychinae is
based on its close similarity to *Entoptychus*. However, the very
prominent anterior cingulum on *Gregorymys'* P_4 clearly separates it
from *Entoptychus* and has led some authors (Wood, 1936:4; Shotwell,
1967:48-49) to place it closer to the heteromyines than the ento-
ptychines in dental anatomy. Reeder (1956:411) considered *Gregory-
mys* to be a heteromyid and closely related to *Heteromys* on the ba-
sis of similarities in their DP_4s. The same evidence, however, was
used by Hibbard (1954:357) to suggest that *Gregorymys* might be an-
cestral to the geomyines. Rensberger (1971), who considered more
morphologic characters than any previous worker, retained *Gregory-
mys* within the Entoptychinae and that conclusion is followed here.

No genus other than *Gregorymys* is closely comparable to the
Derby Peak specimen. The distinctive cusp arrangement of P_4, the
relative sizes of the cheek teeth, the development of cement on
the cheek teeth, and the broad, triangular incisor are found in
combination only in *Gregorymys*. Certain heteromyines, notably
some specimens of *Peridiomys* and *Diprionomys*, approach *G. larsoni's*
peculiar method of uniting the lophids of P_4 more closely than pre-
viously described species of *Gregorymys*, but characters of their
mandibles and especially their incisors clearly set them apart
from *G. larsoni*. Similarly, the molar lophid connections of some
heteromyines and some geomyines proceed as in *G. larsoni*, but char-
acters either of the mandible and incisor or of P_4 exclude these
taxa from close relationship.

In most respects, *G. larsoni* is more similar to the type of *G.
riggsi* than to the other previously described specimens of the
genus. None of these specimens approach *G. larsoni* in overall size,
length of diastema, or depth of mandible, but *G. riggsi* is similar
in P_4 morphology, sequence of lophid unification in M_{1-2}, height of
crown, and development of cement.

I consider all *G. larsoni's* diagnostic characters to be derived
(autapomorphies). This certainly seems to be true with respect to
commonality of characters, since all other described specimens of
Gregorymys are alike in being much larger than *G. larsoni* and hav-
ing deeper mandibles, longer diastemas, and more prominent proto-
conids and hypoconids. *G. larsoni's* small dimensions would appear

to place it in a primitive (plesiomorphic) position with respect
to the other species of the genus when size trends in other groups
of mammals are considered. The trend toward larger size through
phylogeny is observed frequently enough to be considered an evolu-
tionary "law", and *G. larsoni* appears to violate this law. How-
ever, some geomyoid rodents are notoriously variable in size.
This is true of modern gophers and the sample of *Gregorymys for-
mosus* studied by Macdonald (1970) is adequate to establish that it
is also true of *Gregorymys*. The lengths of four P_4s from the same
locality are recorded by Macdonald (1970:37) as 1.14, 1.52, 1.95,
and 2.46 mm. Given this magnitude of potential variability and
the unusual biogeographic circumstances under which *G. larsoni*
may have evolved, its size seems less of an evolutionary anomaly,
although it is presently impossible to determine whether the Derby
Peak specimen is a small individual or a typical member of a dwarf
taxon. It should be noted that the three dimensional diagnostic
characters are probably at least partially correlated and are pos-
sibly united in a single size-dependent functional-morphologic
complex. They may therefore be considered aspects of a single
feature, but each nevertheless serves to distinguish *G. larsoni*.

I do not propose to construct a formal phylogeny of *Gregorymys*
or attempt to place *G. larsoni* within such a phylogeny at this
time. The lack of detailed population studies, the poor strati-
graphic control for many of the published specimens, and the abun-
dance of unpublished material prevent an understanding of the in-
terspecific relationships within the genus. In fact, the genus
needs a revision. It has not been extensively studied since it
was described in 1936 and several species evidently referable to
the genus remain to be described (*e. g.*, Robinson, 1968:195). The
only population of *Gregorymys* which has ever been studied consists
of 15 specimens assigned to *G. formosus* by Macdonald (1970). This
sample shows very great dimensional variation in tooth measurements
and no statistical treatment was attempted, presumably because the
sample was so small and variable, so that it does not provide an
understanding of potential ranges in size or morphologic charac-
ters within *Gregorymys'* populations. Large samples of *Gregorymys*
are evidently available for study (*e. g.*, Macdonald, 1972:30), but
such studies have not been undertaken.

Storer (1975:105) suggests that *Gregorymys* may be ancestral to
Lignimus, a dominantly Clarendonian genus. Transitional forms
which might support this relationship have not been reported, but
it is at least clear that *G. larsoni* has nothing to do with a
Gregorymys-Lignimus morphocline. *G. larsoni* may be characterized
as a persistent survivor of the Arikareean *Gregorymys* morphotype.

AGE AND CORRELATION

The Derby Peak fauna containing *Gregorymys larsoni* has not been
studied in detail. It consists of Equidae, Rhinocerotidae, Cameli-
dae, Antilocapridae, and *Mylagaulus laevis* (Larson, 1968; P. Robin-
son, personal communication). These taxa are not particularly

useful for correlation purposes, but the presence of antilocaprids and *Mylagaulus* precludes an age earlier than Hemingfordian. Morris Skinner of the American Museum of Natural History has examined a horse mandible from Derby Peak (UCM 29747) and considers it most similar to specimens from the Lower Snake Creek fauna of Nebraska. Based upon the stage of evolution of this horse, he believes the Derby Peak fauna to be approximately 13.5 m.y. old (personal communication).

K-Ar ages have been determined for many of the volcanic rocks interbedded with vertebrate-bearing sediments in the area surrounding Derby Peak (Larson, 1968; Larson *et al.*, 1975). An age of 10.3 ± .5 m.y. was obtained from the flow immediately above the unit containing the Derby Peak fauna. No rocks below the vertebrate locality on Derby Peak itself have been dated, but flows immediately underlying and interbedded with similar sediments containing poorly preserved vertebrate remains on "W" Mountain and Trapper's Peak nearby have produced dates. Their ages range from 12.4 ± .5 m.y. to 13.4 ± .5 m.y. These ages indicate that the Derby Peak fauna lived between 13 and 10 million years ago.

This faunal and radiometric age evidence strongly suggests that the Derby Peak fauna is equivalent to late Barstovian or early Clarendonian faunas in age (Evernden *et al.*, 1964; Lindsay, 1972). *Gregorymys* has previously been reported only from late Arikareean and early Hemingfordian deposits. A single "entoptychine" tooth has been reported from sediments as young as Clarendonian or Hemphillian in Wyoming (Love, 1961:35), but the data are insufficient to evaluate this occurrence. The species with the closest apparent relationship to *G. larsoni*, *G. riggsi*, is known only from "Arikaree Beds" of Wyoming. Therefore, *G. larsoni* is anomalous in stage of evolution and the possibility that the specimen was redeposited from older sediments must be considered. There are older fossiliferous sediments in the area of Derby Peak. These are the Group 1 rocks of Larson *et al.* (1975), which range in age from 24 to 20 m.y. This age would be consistent with the stage of evolution of *G. larsoni* and a number of unstudied specimens of *Gregorymys* have been collected from deposits of this age east of Derby Peak (Robinson, 1968). However, there is no evidence that the specimen of *G. larsoni* was redeposited. It shows the same type of preservation and does not seem to be more abraded than the other specimens from Derby Peak, which all were apparently transported prior to deposition.

BIOGEOGRAPHY

The *Gregorymys* lineage, based upon its previously recorded occurrences, appeared to have become extinct by middle Hemingfordian time, approximately 18 million years ago. Its presence in the Derby Peak fauna is unexpected. Persistence of a primitive morphological type such as *G. larsoni* could occur through isolating mechanisms which protect it from competition. Topographic isolation in a high-altitude mountain basin may be suggested as such a mechanism

in this case, but the geologic evidence for isolation of this kind
is not strong. The existence of isolated early Miocene deposition-
al basins in northwestern Colorado is well documented, but the per-
iod of volcanism during which the Derby Peak sediments were deposi-
ted seems to have been characterized by widespread steppes which
connected previously isolated basins and were inhabited by a uni-
form biota (Izett, 1975; Larson *et al.*, 1975; earlier work cited
therein). The widespread tectonism which resulted in the present
intermontane basins of northwestern Colorado did not begin until
nine or ten million years ago. However, the White River Plateau,
of which Derby Peak is presently an outlier, has been a positive
structural and topographic feature since its origin in the late
Cretaceous. Kucera's (1968) studies show that it was shedding sed-
iments into the basins to the north during deposition of the Derby
Peak sediments. Furthermore, his observations on the depositional
characteristics of the basalt flows in the Derby Peak area indicate
that many of the flows are very localized. It is therefore possi-
ble that *Gregorymys larsoni* could have inhabited one or several
very small intermontane basins where it was effectively isolated
from competitors.

It is interesting to note that Robinson (1968) has observed spe-
ciation of early Miocene entoptychines in the area east of Derby
Peak which was apparently at least partially controlled by the same
isolated intermontane basin type of topography suggested above. If
a population of the type mentioned by Robinson became isolated in a
high valley on the slopes of the White River Plateau, and if that
valley provided a refugium while the lower basins to the east grad-
ually fused, bringing their previously isolated entoptychines and
other later-evolved rodents into competition with one another, the
population remaining in the high valley might well develop into the
sort of taxonomic compromise represented by *G. larsoni*.

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