Uintasoricinae, A New Subfamily of Early Tertiary Mammals (?Primates)

BY FREDERICK S. SZALAY

INTRODUCTION

The aims of the present study may be outlined as follows: (a) to gather all pertinent information on two closely related genera, *Niptomomys* and *Uintasorex*; (b) to establish family affinities for these genera; and (c) to examine briefly the ordinal affinities of microsyopids in the light of this allocation.

*Uintasorex* and *Niptomomys*, here placed in a subfamily of their own, are as reasonably referred to the Microsyopidae as can be determined from dental evidence alone. Because the ear region of *Microsyops* (including *Cynodontomys*) is decidedly more primitive than that of any known primate, unqueried allocation of the family to the Primates is not advisable.

The impetus to write the present paper was the discovery of a fragmentary, but important, specimen of *Uintasorex*. This discovery among the scraps in a museum drawer was made after an earlier study (Szalay, 1969) had already been completed. After studying a partial left dentary of *Uintasorex parvulus* (A.M.N.H. No. 55664), described by Simpson (in McGrew, 1959, p. 152) from Tabernacle Butte locality 5 of the University of Wyoming (upper Bridger beds), I re-examined the unidentified fragmentary specimens from the same locality, hoping to find

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additional material of insectivores or primates. One of these uncatalogued specimens proved to be the anterior part of the Uintasorex dentary A.M.N.H. No. 55664. The fragment has an intact anterior enlarged tooth in place and also shows the alveoli of the teeth posterior to it. The surprising find prompted a re-evaluation of Uintasorex and Niptomomys, the two genera I have long believed to be very closely related.

One of the conclusions presented in this paper, that Uintasorex and Niptomomys are microsyopids, was earlier suggested to me (personal communication in 1965) by Dr. Donald E. Russell of the Muséum National d'Histoire Naturelle, Paris. At that time, I was studying mixodectids, Paleocene and Eocene insectivores, primates, and microsyopids, but could not confirm or accept the astute suggestion. There was then no satisfactory evidence on which to base this conclusion with sufficient probability. Now, however, I believe that the evidence warrants the conclusions presented here.

Measurements were taken as I indicated on the figures of teeth of Microsyops (Szalay, 1969).

I thank Dr. Malcolm C. McKenna for his generous permission to study many specimens collected by him from the lower Wasatch beds of Colorado. These specimens were found after his work on the Four Mile fauna was published. His unselfish cooperation, in general, is deeply appreciated.

I am indebted to Dr. Bobb Schaeffer for the facilities to do research at the Department of Vertebrate Paleontology. I thank the following for permitting me to study specimens in their charge: Drs. Craig C. Black and Mary R. Dawson of the Carnegie Museum, Pittsburgh; Dr. Glenn L. Jepsen of Princeton University; Dr. Malcolm C. McKenna of the American Museum of Natural History; and Dr. Elwyn L. Simons of the Peabody Museum of Natural History, Yale University. I am indebted to Dr. Malcolm C. McKenna who critically read the manuscript and improved it by several suggestions.

Figures 6, 7, and 21 were skillfully prepared by Miss Biruta Akerbergs. All other illustrations were done by me.

ABBREVIATIONS

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
U.S.N.M., Division of Vertebrate Paleontology, United States National Museum, Smithsonian Institution
U.W., University of Wyoming
Y.P.M., Peabody Museum of Natural History, Yale University
AW, anterior width
SYSTEMATICS

ORDER ?PRIMATES

SUPERFAMILY MICROSYOPOIDEA (OSBORN AND WORTMAN, 1892),
NEW RANK

With a combination of a primitive eutherian ear region, the lack of
an ossified bulla, and with specializations in the teeth and cranium
that are clearly unique among early Tertiary mammals, the micro-
syopids cannot be allocated to any known superfamily of either the
Insectivora or the Primates. Because of their peculiar combination of
primitive and advanced morphology and their relative importance
in the Eocene faunas of North America the Microsyopidae warrant super-
family recognition of equal rank to the leptictoids, palaeoryctoids,
plesiadapoids, tupaiioids, lorisoids, tarsioids, or daubentonioids. The
groups cited diverge from their ancestry to approximately the same
degree that the microsyopids do from a primitive insectivoran or
primate ancestry.

FAMILY MICROSYOPIDAE OSBORN AND WORTMAN, 1892

UINTASORICINAE, NEW SUBFAMILY

INCLUDED GENERA: Uintasorex and Niptomomys.

DIAGNOSIS: Tiny microsyopids that differ from Microsyops (including
Cynodontomys) in their smaller size, in the construction of the trigonids,
in their relatively shorter lower molars, and in having more robust fourth
upper premolars and transversely narrower upper molars. The notch
between the entoconid and hypoconulid that characterizes all micro-
syopids is somewhat less distinct in the Uintasoricinae than in the
Microsyopinae.

1 Uintasorex has recently been reported (Black and Dawson, 1966) from the late
Eocene Tepee Trail Formation in Wyoming. Although I had no opportunity to examine
the specimen, illustrations of a single lower molar, at my disposal through the courtesy
of Dr. Peter Robinson, seem to confirm the identification.
Uintasoricines differ from anaptomorphs, omomyids, and adapids (including notharctines) in their talonid construction, in their peculiar mode of enlargement of the lower incisor, and in having two-rooted third upper premolars.

**HISTORY OF UINTASOREX AND NIPTOMOMYS**

1909: Matthew described the genotype of *Uintasorex* from the upper Bridger beds of Wyoming. He allocated *Uintasorex* to his newly established family Apatemyidae along with *Apatemys* and *Trogolemur*.

1910: Matthew, Gregory, and Mosenthal continued to associate *Uintasorex* with *Apatemys* and *Trogolemur*.

1916: Teilhard's (1916–1921) family Chiromyidae included *Uintasorex* in addition to various genera, such as *Plesiadapis*, *Phenacolemur*, *Mixodectes*, and *Trogolemur*. *Cynodontomys*, a microsyrpid, was also included in the heterogeneous family, but without any special mention of similarity other than the possession of an enlarged tooth, as in the listed genera.

1923: Schlosser's concept of Plesiadapidae included *Uintasorex*, *Trogolemur*, and *Apatemys*.

1934: Jepsen discontinued the previously standard practice of associating *Uintasorex* with apatemyids and plesiadapids. At that time the as yet poorly known *Uintasorex* could not be meaningfully allocated to any early Tertiary family, as Jepsen had conveyed.

1940: Simpson, in his series of studies on the earliest primates, placed *Uintasorex* in the Primates, *incertae sedis*, along with *Phenacolemur*, *Trogolemur*, and others.

1945: Simpson's mammal classification followed his 1940 stand on *Uintasorex*.

1958: Gazin compared *Uintasorex parvulus* to omomyids and anaptomorphs and noted that the genus was very *Omomys*-like in many features. He believed that *Uintasorex* was certainly a primate, but considered his allocation of it to the Anaptomorphidae tentative. The reduced number of teeth and the specialization of the front part of the dentition, however, prevented him from including *Uintasorex* in the Omomyidae. He astutely remarked that *Uintasorex* may prove to represent a distinct family.


1960: McKenna (1960) described a new species and a new genus, *Niptomomys dorenae*, from the lower Wasatch beds of northern Colorado. With a query, he allocated the genus to the Omomyinae of the family Anaptomorphidae. McKenna compared *Niptomomys*, known from both upper and lower teeth, with *Absarokius*, *Uintanius*, *Paronomys*, *Phenacolemur*, *Stockia*, *Omomys*, *Navajoicus*, and *Palaechiton*. He regarded *Niptomomys* as a primitive omomyine offshoot that had convergently developed paromomyine-like trigonids on M₂ and M₃.

1962: Gazin studied a specimen of *Uintasorex* cf. *U. parvulus*, and commented on its similarity to *Niptomomys*.

1963: Simons, in his review of Tertiary primates, apparently following Gazin and McKenna, classified *Uintasorex* as an anaptomorphid and *Niptomomys* as an omomyid.
1967: Simons considered *Niptomomys* (and also *Loveina* and *Teilhardina*) as the oldest representative of the Omomyidae.

**UINTASOREX MATTHEW, 1909**

*Uintasorex* Matthew, 1909, p. 545.

**Type:** *Uintasorex parvulus* Matthew, 1909.

**Included Species:** Type species and *Uintasorex* sp.

**Distribution:** Middle Eocene (Bridgerian) to late Eocene (Uintan) of North America.

**Diagnosis:** *Uintasorex* differs from *Niptomomys* in its smaller size, in the relatively greater width of the talonids compared with the trigonids, in the relative size of the paracone and metacone compared with absolute tooth size, and in the position of the conules on the upper molars. *Uintasorex* also appears to differ in having a small but distinct paraconid on P4.

**Dental Formula:** 1\(_1^?\)?, C\(_0^?\), P\(_{234}\), M\(_{123}\).

**Discussion:** Jepsen (1934, p. 304) suggested that the lower tooth formula of *Uintasorex* was more likely to be 1, 0, 3, 3, than 1, 1, 2, 3. Gazin (1958, p. 78), on the other hand, considered that the alveolus following the enlarged tooth housed a canine (because it is smaller than the one following it), “in order to be consistent,” probably meaning with his suggested dental formula of the Anaptomorphidae. Although Gazin may be correct, I believe that in general a canine alveolus is usually greater in diameter than the premolar following it, as is convincingly demonstrated in paromomyines, anaptomorphines, and omomyids. My interpretation of the dental formula is based on the belief, and therefore not on direct evidence, that *Uintasorex* is probably a microsyopid. In *Microsops* the upper canine is the smallest of the antemolar dentition, and one of the incisors is greatly enlarged. In known dentaries of *Microsops* that show the antemolar dentition, three antemolar teeth follow the noncaniniform enlarged tooth (presumably the incisor). Judged by the fact that the canine is the smallest tooth in the upper dentition, the lower antemolar teeth may represent the fourth, third, and second premolars. Based on this very tenuous comparison, I find Jepsen’s interpretation more likely than that of Gazin.

Well-defined interradicular crests are present on both the upper and lower molars of *Uintasorex parvulus*. The lower molars of *Niptomomys doreenae* also clearly show these crests. I had no isolated upper molars of the Wasatchian species for examination, but it is almost certain that the crests are also present on the upper molars of *Niptomomys*. 
Although direct evidence is entirely lacking, it seems to me that the upper and lower molars of Uintasorex are slightly more primitive than those of Niptomomys. A further discussion of this point must await the discovery of Paleocene microsyopines or uintasoricines.

There is as yet no way of deciding whether Niptomomys doreenae is ancestral to Uintasorex parvulus and U. sp., or not. The stratigraphic occurrence of the species would only suggest but not prove it. Judged by the teeth, N. doreenae was a very small mammal, but U. sp. was even smaller. If uintasoricines were microsyopids, their small size would contrast interestingly with that of the microsyopines, which steadily increase their absolute size from the earliest Wasatchian onward.

As microsyopines increased in size, the uintasoricines remained tiny or possibly became even smaller. By Bridgerian time Microsyops rivaled in size the largest species of adapids, such as the Bridger species of...
TABLE 1
NUMERICAL DATA (IN MILLIMETERS) OF Uintasorex parvulus FROM Upper Bridger Beds

<table>
<thead>
<tr>
<th></th>
<th>A.M.N.H. No. 12052</th>
<th>A.M.N.H. No. 55664</th>
<th>Y.P.M. No. 13519</th>
<th>OR</th>
</tr>
</thead>
<tbody>
<tr>
<td>P4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>1.05</td>
<td>—</td>
<td>1.00</td>
<td>1.00-1.05</td>
</tr>
<tr>
<td>PW</td>
<td>0.65</td>
<td>—</td>
<td>0.75</td>
<td>0.65-0.75</td>
</tr>
<tr>
<td>M1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>1.12</td>
<td>1.20</td>
<td>1.12</td>
<td>1.12-1.20</td>
</tr>
<tr>
<td>PW</td>
<td>0.90</td>
<td>1.03</td>
<td>1.00</td>
<td>0.90-1.03</td>
</tr>
<tr>
<td>AW</td>
<td>—</td>
<td>0.83</td>
<td>0.85</td>
<td>0.83-0.85</td>
</tr>
<tr>
<td>M2</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>—</td>
<td>1.20</td>
<td>1.09</td>
<td>1.09-1.20</td>
</tr>
<tr>
<td>PW</td>
<td>—</td>
<td>1.08</td>
<td>0.97</td>
<td>0.97-1.08</td>
</tr>
<tr>
<td>AW</td>
<td>—</td>
<td>0.90</td>
<td>0.85</td>
<td>0.85-0.90</td>
</tr>
<tr>
<td>M3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>—</td>
<td>1.22</td>
<td>1.25</td>
<td>1.22-1.25</td>
</tr>
<tr>
<td>PW</td>
<td>—</td>
<td>0.87</td>
<td>0.80</td>
<td>0.80-0.87</td>
</tr>
<tr>
<td>AW</td>
<td>—</td>
<td>0.85</td>
<td>0.75</td>
<td>0.75-0.85</td>
</tr>
<tr>
<td>From tip of symphysis to posterior border of M3</td>
<td>—</td>
<td>7.50</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Approximate length of symphysis</td>
<td>—</td>
<td>3.80</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Length of incisor crown</td>
<td>—</td>
<td>2.75</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Greatest depth of incisor crown</td>
<td>—</td>
<td>1.15</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

Notarchus, while at this time species of Uintasorex were among the smallest known in the North American Eocene mammal microfauna.

Uintasorex parvulus Matthew

Figures 1-7, 22-25

Uintasorex parvulus Matthew, 1909, p. 546.


Type: A.M.N.H. No. 12052, fragment of right dentary with P4-M1, collected at Henry’s Fork, Bridger D beds, Bridger Basin, Wyoming.

Hypodigm: The type; Y.P.M. No. 13519, from Twin Buttes, upper Bridger beds; and A.M.N.H. No. 55664, from University of Wyoming locality 5, upper Bridger beds, Tabernacle Butte area.

Specific Diagnosis: If Uintasorex parvulus should prove to be distinct from U. sp., then the genotype represents a species with larger average tooth size.
DESCRIPTION, INTERDEME AND INTRADEME VARIATION: The most complete specimen is A.M.N.H. No. 55664 from the upper Bridger beds at locality 5 (Hyopsodus Hill). The symphysis is long and unfused (figs. 3–5). The single mental foramen is invariably under P4 on the three known dentaries that show this part. The depth of the mandible on the known specimens is variable. It is relatively shallow on the type and on A.M.N.H. No. 55664. On Y.P.M. No. 13519 the dentary is con-
siderably deeper under $P_4$, $M_1$, and $M_2$ than at any other point of the specimen. In all probability, this difference is not a taxonomic one between Y.P.M. No. 13519 and A.M.N.H. No. 55664 from Hyopsodus Hill, although the specimens may have come from different demes of
the species. A.M.N.H. No. 55664 preserves the dental foramen, and a weak but distinct ridge for the insertion of the internal pterygoid.

Lower antemolar dentition: The enlarged incisor is very similar to that of Microsyops (including Cynodontomys), although that of Uintasorex...
is smaller and more slender. (For a description of Microsyops incisors, see Szalay, 1969.)

Anterior to P₄ and posterior to the enlarged incisor two teeth were present, presumably P₃ and P₂. The crowns of these two teeth are not
known. $P_3$ had closely compressed (anteroposteriorly) double roots, but $P_2$ (or possibly a canine) was a small, single-rooted tooth.

The wedge-shaped $P_4$ has an incipient talonid, a small metaconid, and a paraconid.

Lower molars: On the three lower molars the trigonids gradually become anteroposteriorly compressed from $M_1$ to $M_3$. On the first molar the trigonid is wide open linguually, with a relatively large lingual gap between the paraconid and metaconid. On $M_2$, and even to a greater degree on $M_3$, the paraconid and metaconid coalesce. The trigonid basin becomes completely surrounded by the paracristid (paralophid) and protocristid (protolophid). There is variation in the degree of constriction of the trigonids even among the small sample of *Uintasorex parvulus*.

The talonids are relatively much wider than the trigonids on all three molars. The characteristic proximity and sharp separation of the hypoconulid from the entoconid have been often noted.
Fig. 7. Above: Uintasorex sp., composite M1–3, C. M. Nos. 17277, 6465, and 13844, from the Green River Formation. Below: Uintasorex parvulus, Y.P.M. No. 13519, from the Bridger Formation.

DISCUSSION: Gazin (1962, p. 39) described a jaw fragment (U.W. No. 1646) from beds of Lost Cabin age, Red Desert region, Great Divide Basin. He allocated the M2–3 to Uintasorex cf. parvulus and published illustrations of the specimen (Gazin, 1962, pl. 5, fig. 4). Gazin correctly noted that the specimen, although much smaller, is clearly related to Niptomomys doreenae.

The discussion under Uintasorex sp., below, pertains also to U. parvulus.

Uintasorex sp.

Figures 7–10, 22–25

A fine collection of tiny Uintasorex teeth was made by the Carnegie Museum personnel from the middle Eocene Green River Formation, Powder Wash, Utah (T. 7 S., R. 25 E., Uintah County). Gazin (1958) discovered this sample in the Carnegie Museum collection and noted
TABLE 2
STATISTICAL DATA OF Uintasorex sp. FROM Powder Wash, Green River Formation, Utah

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>OR</th>
<th>M</th>
<th>S</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>9</td>
<td>1.00-1.20</td>
<td>1.09±0.02</td>
<td>0.06</td>
<td>5.98</td>
</tr>
<tr>
<td>PW</td>
<td>9</td>
<td>0.75-0.95</td>
<td>0.85±0.02</td>
<td>0.06</td>
<td>6.96</td>
</tr>
<tr>
<td>AW</td>
<td>9</td>
<td>0.65-0.85</td>
<td>0.74±0.02</td>
<td>0.07</td>
<td>9.08</td>
</tr>
<tr>
<td>M2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>11</td>
<td>0.90-1.10</td>
<td>1.01±0.02</td>
<td>0.06</td>
<td>5.70</td>
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<tr>
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<td>11</td>
<td>0.75-0.95</td>
<td>0.86±0.02</td>
<td>0.05</td>
<td>6.26</td>
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<tr>
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<td>11</td>
<td>0.70-0.85</td>
<td>0.78±0.02</td>
<td>0.05</td>
<td>6.98</td>
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<tr>
<td>M3</td>
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<td></td>
</tr>
<tr>
<td>L</td>
<td>5</td>
<td>1.10-1.15</td>
<td>1.08±0.03</td>
<td>0.07</td>
<td>7.02</td>
</tr>
<tr>
<td>PW</td>
<td>5</td>
<td>0.68-0.90</td>
<td>0.75±0.04</td>
<td>0.09</td>
<td>12.07</td>
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<tr>
<td>AW</td>
<td>5</td>
<td>0.60-0.80</td>
<td>0.68±0.04</td>
<td>0.08</td>
<td>12.30</td>
</tr>
<tr>
<td>M1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>14</td>
<td>0.90-1.15</td>
<td>1.01±0.02</td>
<td>0.06</td>
<td>6.13</td>
</tr>
<tr>
<td>AW</td>
<td>14</td>
<td>1.08-1.25</td>
<td>1.17±0.01</td>
<td>0.05</td>
<td>4.03</td>
</tr>
<tr>
<td>M2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>10</td>
<td>0.87-1.05</td>
<td>0.96±0.09</td>
<td>0.06</td>
<td>6.17</td>
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<tr>
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<td>10</td>
<td>1.00-1.25</td>
<td>1.17±0.03</td>
<td>0.09</td>
<td>7.99</td>
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<tr>
<td>M3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L</td>
<td>5</td>
<td>0.75-0.90</td>
<td>0.80±0.03</td>
<td>0.06</td>
<td>7.65</td>
</tr>
<tr>
<td>AW</td>
<td>5</td>
<td>0.82-0.90</td>
<td>0.87±0.02</td>
<td>0.04</td>
<td>4.25</td>
</tr>
</tbody>
</table>

(p. 79). I believe correctly, that it may represent a distinct species. At that time he preferred to treat the sample with Uintasorex parvulus.

The following Carnegie Museum specimens, each representing one or several isolated molars, make up the catalogued sample: C.M. Nos. 6414, 6415, 6450, 6457, 6465, 6474, 13844, 13846, 13849, 13850, 17272-17290.

Although statistical data for Uintasorex sp. and numerical data for Uintasorex parvulus are given in tables 1 and 2, comparison of the two samples is at present biologically meaningless. Whereas the upper and lower teeth of the Green River sample are relatively well represented, the Bridger genotype is known from only three specimens.

One of the reasons for not referring the Powder Wash sample of Uintasorex to U. parvulus is the possibility that the upper molars of U. parvulus, once they become known, may prove to be qualitatively different from those of U. sp. As far as the morphology of the lower teeth is concerned, no consistent differences can be ascertained between the poor sample of U. parvulus and the fair sample of U. sp.
As the graphs of figures 22–25 suggest, there appears to be a real size difference between the two samples of Uintasorex, in spite of the scarcity of the Bridger specimens.

The qualitative differences between the upper molars of Uintasorex
FIG. 9. *Uintasorex* sp., left upper molars from the Green River Formation. *Left row, from top down*: C.M. No. 6474, M3; C.M. No. 17277, M1; C.M. No. 6474, M1. *Right row, from top down*: C.M. No. 13844, M3; C.M. No. 17279, M1; C.M. No. 6465, M1.

*sp.* and those of *Niptomomys doreenae*, although quite real, require careful study of the specimens (see the stereophotographs) to be discerned. In general, the upper molar teeth of *Niptomomys* are more massive and

FIG. 10. *Uintasorex* sp., right upper molars from the Green River Formation. *Left row and upper two of right row*: C.M. No. 6465. *Lowest in right row*: C.M. No. 13846. Top and bottom teeth on left are M1's; the remaining ones are M2's.
denser in appearance than those of Uintasorex sp., which may or may not be a factor of the larger size of Niptomomys doreenae. Absolute size may, however, influence this feature. Under the discussion of differences between Niptomomys and Uintasorex, the more specific differences of the upper teeth are treated in detail.

Niptomomys McKenna, 1960


**Type:** *Niptomomys doreenae* McKenna, 1960.

**Included Species:** Type species only.

**Distribution:** Early Eocene (Wasatchian) of North America.

**Diagnosis:** Because *Niptomomys* and *Uintasorex* are the only known genera of the subfamily Uintasoricinae, the diagnostic differences between the two taxa are given under the generic diagnosis of *Uintasorex*.

**Dental Formula:** The known dental formula of *Niptomomys* is the same as that of *Uintasorex*.

**Discussion:** McKenna (1960) noted that the *P*⁴ and *M*¹ of *Niptomomys* strongly resemble those of *Omomys*. He added that the undeveloped hypocone on the molars and the lack of parastyle and metacone on *P*⁴, the omomyine and tarsiid resemblances of the genus, are confined to *Tarsius, Omomys*, the “... Teilhardina-Loveina-Wasatchian ‘Omomys’ complex,” and, less closely, to *Navajovius*. In conclusion, on the upper dentition, he considered the upper cheek teeth to be a minute version of those of the Bridgerian *Omomys*. McKenna stated that the upper molars of *Palaechthon* could have been structural ancestors of those of *Niptomomys*. Although McKenna failed to compare *N. doreenae* with its closest relative, *Uintasorex parvulus*, he realized that *Niptomomys* did not fit well into either the Paromomyinae or the Omomyinae. His 1960 views on the affinities of *Niptomomys* are summarized under the historical resume of *Uintasorex* and *Niptomomys*.

The homologies of the lower antemolar dentition discussed under *Uintasorex* apply equally to *Niptomomys*.

It must be stressed again that the similarity between *Uintasorex* and *Niptomomys* is very great. The differences, on the other hand, are consistent and easily recognizable, and are of such qualitative nature that generic separation is warranted. If a perfect intermediate were to be found, both in morphology and temporal distribution, then a convincing case might be made for uniting the species in one genus. Were the fossil record to improve and gradually suggest that *N. doreenae* and *U. parvulus* diverged from a common ancestry, then, I believe, an even more secure generic distinction could be maintained.
The following differences exist between *Niptomomys doreenae* on the one hand and *Uintasorex parvulus* and *U.* sp. on the other. Both the lower and upper molars of *Niptomomys*, in addition to their larger absolute size, are more square than those of *Uintasorex*. The talonid of lower molars of *Uintasorex* is considerably wider transversely, relative to the trigonid, than that of *Niptomomys*. *Niptomomys* lower molars, consistently from many different localities, support the reality of this difference. The upper molars of *Niptomomys* can be compared only with those of *Uintasorex* sp. from Powder Wash, because upper teeth from Bridger beds are not known to me. *Niptomomys* upper molars have slightly smaller paracones and metacones in relation to the lingual half of the tooth. Either because of the reduced relative size of the paracone and metacone, or because of the enlargement of the lingual half of *Niptomomys*.

Fig. 11. *Niptomomys doreenae*, A.M.N.H. No. 80955, edentulous left dentary fragment from East Alheit Quarry.
upper molars (the latter is more likely), the conules are closely crowded to the buccal cusps. Both the paraconule and the metaconule are clearly on the buccal half of the upper molar. In *Uintasorex* sp., however, the paracone and the metacone are relatively larger and the conules are approximately halfway between the imagined buccal and lingual halves of an upper molar. The $M^1$ of *Uintasorex* sp. appears to
Fig. 13. *Niptomomys doreenae*, from Hackberry Hollow, Gray Bull beds, P.U. No. 17833, left P₄-M₃.

be more constricted anteroposteriorly on its lingual half in comparison with the buccal half than that of the few known *Niptomomys* M₁'s.

Although the sample of fourth lower premolars of *Uintasorex* is small, the paraconid on P₄ is consistently more distinct than that of *Niptomomys*.

*Niptomomys doreenae* McKenna

Figures 11-25

*Niptomomys doreenae* McKenna, 1960, p. 63.

Cf. *Niptomomys* sp.: McKenna, 1960, p. 65.

Type: U.C.M.P. No. 44081, right dentary with M₂-₃, collected from Kent Quarry, lower Wasatch beds, Colorado (see McKenna, 1960).

Fig. 14. *Niptomomys doreenae*, from Despair Quarry, A.M.N.H. No. 80055, left $P_4$-$M_3$.

Nos. 59692, 59694, 80055. From Timberlake Quarry: U.C.M.P. No. 46987, A.M.N.H. No. 80958. From East Alheit Quarry: A.M.N.H. No. 59655, 80079, 80080, 80955, 80957, 80959-80963. From Gray Bull beds, various localities given in parentheses: P.U. Nos. 17412, 17833, 17885 (Hackberry Hollow, sect. 28, T. 55 N., R. 101 W., Park County, Wyoming), 17880 (Twisty Turn Hollow, same section, township, and range), 17897 (Bone Hill, SE. $\frac{1}{4}$ of sect. 16 to NW. $\frac{1}{4}$ of sect. 21, T. 54 N., R. 97 W., Big Horn County, Wyoming), A.M.N.H. Nos. 16829 (upper Gray Bull beds), 16828 (lower Gray Bull beds), Y.P.M. No. 23600 (Yale University locality 97b). From Lysite beds: Y.P.M. No. 18711 (Yale University locality 31).

**Specific Diagnosis:** Only known species of the genus.

**Description, Interdeime and Intra deime Variation:** Mandible: The most complete dentary is A.M.N.H. No. 80955 (fig. 11), an edentulous horizontal ramus from East Alheit Quarry. From the shape of the
dentary, the position of the dental foramen, and the relative size of similar small mammals in the Four Mile fauna, the specimen probably represents *Niptomomys doreenae*. The large mental foramen was under the anterior root of P₄. There were four antemolar teeth in the dentary: a double-rooted P₄ and P₃, a single-rooted tooth, probably P₂, and the enlarged anterior tooth.

Lower antemolar dentition: Of the antemolar teeth other than the enlarged incisor, the crown is known only in P₄. The most pronounced manifestation of the paraconid is on P.U. No. 17833 (fig. 13) where it is incipient. It is usually absent as from the East Alheit Quarry
TABLE 3

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*Quarry samples from East Alheit, Sand Kent, Despair, and Timberlake quarries of the lower Wasatch beds (Four Mile fauna of McKenna, 1960) and scattered collections from Gray Bull beds at various localities are treated together. No meaningful statistics can be computed for any of the isolated samples because of scarcity of specimens. Figures 22-25 should be consulted for the distribution of the parameters of teeth from various localities.

sample (fig. 12). The small metaconid and the incipient talonid are consistently present on P4.

Lower molars: The lower molars have been satisfactorily described by McKenna (1960, p. 64). Probably the most remarkable variation concerns the degree of closure of the trigonid on M1. The trigonid is relatively wide open in A.M.H.N. Nos. 80961, 80962, and 80963 from East Alheit Quarry (fig. 12). The relation of the paracristid to the
Fig. 16. Above: *Niptomomys doreenae*, from Hackberry Hollow, Gray Bull beds, P.U. No. 17833, left dentary, fragment with P₄-M₃. Below: *Uintasorex parvulus*, from Bridger beds, Y.P.M. No. 13519, right dentary fragment with P₄-M₃. Both are medial views.
Fig. 17. Above: Niptomomys doreenae, from Hackberry Hollow, Gray Bull beds, P.U. No. 17833, left dentary fragment with P₄–M₃. Below: Uintasorex parvulus, from Bridger beds, Y.P.M. No. 13519, right dentary fragment with P₄–M₃. Both are lateral views.
protocristid is roughly the same in A.M.N.H. No. 80055 from Despair Quarry and in P.U. No. 17833 from the lower Willwood beds at Hackberry Hollow. Whereas on A.M.N.H. No. 16829 from the upper Gray Bull beds the M₁ trigonid is like the trigonids listed above, that of A.M.N.H. No. 16828 from the lower Gray Bull beds is distinctly
more constricted anteroposteriorly. The paracristid is about as close to the protocristid as it is usually on $M_2$ of *N. doreenae*.

The greatest size discrepancy within this species is between A.M.N.H. No. 16828 from lower Gray Bull beds and A.M.N.H. No. 16829 from upper Gray Bull beds (fig. 15).

Upper antemolar dentition: $P^3$ was double-rooted, lacking a lingual root. The crown of this tooth is not known. Two specimens show the relative size and position of this tooth: A.M.N.H. No. 80958 from Timberlake Quarry and Y.P.M. No. 18711 from Yale University Lysite locality 31. The roots of the small $P^3$ in A.M.N.H. No. 80958 are at the level where the $P^4$ is constricted between the buccal and lingual halves. Judged by the position of the broken roots at the base of the crown, the crown of $P^3$ leaned in a posteroventral direction. In Y.P.M. No. 18711 also, only the roots are preserved, but the posterior root is in a more lingual position and relatively larger than that of A.M.N.H. No. 80958. Because the buccal border of $P^3$ was more medial than that of $P^4$, the large buccal root appears to be a third, lingual root.

$P^4$ is a large tooth with a robust paracone, small protocone, small parastyle, small metastyle, a trace of the precingulum, and a strong postcingulum. On the unworn $P^4$ in Y.P.M. No. 18711 there is an incipient metacone.
Upper molars: The most characteristic feature of the molars is the conspicuous proximity of the conules to the buccal cusps and the slightly smaller size of the metacone compared with the paracone. The latter trait is merely primitive. The metacrista is too short to support a metastyle. As a rule, M\textsuperscript{1} is the widest transversely and M\textsuperscript{3} is the narrowest transversely of the upper molars. The slight, incipient meso-style displayed by the M\textsuperscript{1} of P.U. No. 17412 from Hackberry Hollow is not shared by any of the few known specimens of upper teeth.

**DISCUSSION:** The first specimens of this species were collected 47 years prior to McKenna's (1960) naming and description of the taxon. There is no doubt that A.M.N.H. Nos. 16828 and 16829, both collected in 1913, and all subsequently found specimens from Gray Bull beds belong to *Niptomomys*.

Prolonged study of the hypodigm resulted in a firm conviction that these specimens could not be allocated to more than one species. Admittedly, upper molars and the antemolar dentition are poorly represented, and large samples of these elements may result in the naming of new species in the future. Were some qualitative or very slight size differences demonstrated within large samples, sexual dimorphism would have to be accounted for before taxonomic separation could be justified.

McKenna (1960, p. 65) noted that two specimens, one from Kent Quarry (U.C.M.P. No. 44082) and another from Timberlake Quarry (U.C.M.P. No. 46978), seemed to differ sufficiently from his concept of *N. doreenae* to make their reference to the latter questionable. He treated these specimens under "cf. *Niptomomys* sp." McKenna's remark that "the species represented is the smallest known primate. . . ." indicates clearly that he considered these specimens to represent a species distinct from *N. doreenae*. I have no reasonable doubt, however, that these two specimens are merely individuals at the small end of the size spectrum of *N. doreenae*.

**SYSTEMATIC POSITION OF THE UINTASORICINAE**

Views of previous students on *Uintasorex* and *Niptomomys* are briefly surveyed under the historical résumé, and some other pertinent aspects are given under the generic and specific discussions. The arguments presented here in favor of microsyopid ties of the new subfamily are based on dental evidence alone and must be viewed with caution.

The proportions of the upper molars and the construction of the trigonid on the lower molars of early Wasatchian *Microsyops* are distinctly more primitive than those of the Uintasoricinae.
One of the most diagnostic features shared by uintasoricines and microsyopines is the characteristic notch between the closely twinned hypoconulid and entoconid. In comparison with most Paleocene and Eocene primates and with most primitive Paleocene and Eocene Eutheria this feature is specialized and hence is highly useful as evidence bearing on affinity. This proximity of the hypoconulid to the entoconid sets Uintasorex and Niptomomys apart from the anaptomorphids and omomyids, primate families to which past authorities have relegated these genera. Were it not for this feature, the morphology of the lower
molars, particularly the trigonid construction, would be easily assessed as reflecting affinities to *Phenacolemur* or *Stockia*. McKenna (1960, p. 64–65) has stated that this feature of *Niptomomys* is probably convergent and shared because of special affinity (presumably meaning that they were all primates) between these forms.

With a knowledge of the almost-complete dental morphology in mind, there is little doubt that the *Phenacolemur*-like trigonid of *Uintasorex* and *Niptomomys* is convergent with that of *Phenacolemur*. *Necrolemur* cf. *zitteli* (Hürzeler, 1948, fig. 35) shows a convergently similar sequence from *M*₁–*M*₃.

Gazin (1958, p. 77) noted great similarities between the upper molars of *Uintasorex* and those of *Omomys*. McKenna (1960, pp. 63–64) also remarked on the similarities between the upper molars of *Niptomomys* and those of *Omomys*. One cannot but agree, in general, with Gazin’s and McKenna’s observations. As Gazin stated, the precingula and postcingula of the upper molars of *Uintasorex* from the Green River beds are not continuous as are those of *Omomys*.

Although uintasoricine upper molars are indeed very *Omomys*-like, it is equally important to point out that the taxa have very generalized

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**Fig. 21. Niptomomys doreenae.** Above: A.M.N.H. No. 80958, right P₄–M₃, Timberlake Quarry. Below: A.M.N.H. No. 80055, left P₄–M₃, Despair Quarry.
tritubercular (not tribosphenic) upper molars. The only notable specialization, the continuous precingulum and postcingulum in *Omomys*, is not shared with the older *Niptomomys* or with the roughly contemporaneous *Uintasorex*. Sharing these generalized tritubercular features and not sharing specialized characters cannot be a basis for advocacy of special affinity. *Omomys* and uintasoricines do not share advanced characters that would make the discussion of their ties very meaningful.

If *Uintasorex* shares a two-rooted P۳ with *Niptomomys* (a very probable assumption considering the similarity of the two genera) then the Uintasoricinae are set apart from anaptomorphids, omomyids, and necrolemurids in lacking a lingual root for the third upper premolar. Judged from the leptictid and palaeoryctid condition, a three-rooted P۳ is very likely primitive for most eutherians. Also, there is no evidence to contradict the assumption that the most primitive condylarths and most Paleocene and Eocene primates had three-rooted P۳'s. The condi-

![Figure 22. Scatter diagram of length/width (posterior width for the lower teeth) of the cheek teeth of *Niptomomys dorenae* (Gray Bull, Four Mile, and Lysite localities), *Uintasorex parvulus* (Bridger localities), and *Uintasorex* sp. (Powder Wash).](image-url)
tion of the P3 in Microsyops (including Cynodontomys) from the early Wasatchian Gray Bull and lower Wasatch beds is not known. It is known, however, that a very pronounced trend to molarize P4, and also slightly P3, was already under way among microsyopines during early Wasatchian. Judged from the lower teeth, it is quite possible that P3 in the early Wasatchian species was only two-rooted. P3 is two-rooted in the Tiffanian Navajovius kohlhaasae and in a new species of Navajovius? (Szalay, 1969) from the Wasatchian San José Formation of the San Juan Basin.

If the Uintasoricinae (and the Microsyopinae) are primates or derived from leptictids, the two-rooted P3 is very likely a specialized character, as is also probably that of Navajovius and the hypothetical rodent ancestor of Wood (1962).1

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1 Future discoveries may provide evidence for a common origin of rodents and microsyopids, or for rodent origins from uintasoricine microsyopids. I believe that the rela-
Although Uintasorex, Niptomomys, and Microsyops share the presence of interradicular crests, these structures also occur in anaptomorphids, omomyids, Erinaceoids, mixodectids, several specimens of leptics, and picrodontids. Interradicular crests undoubtedly evolved independently several times.

The newly discovered enlarged tooth of Uintasorex bears no resemblance to the known enlarged incisors of anaptomorphids and omomyids, but incisor construction is poorly known in the two latter families. In omomyids only the incisors of the Uintan Ourayia uintensis are known adequately (P.U. No. 16431). No adequate anaptomorphine incisors have
tively primitive paramyid ear region, with an ecotympanic auditory bulla (for the evidence, see Wood, 1962), supplies additional arguments against derivation of rodents from plesiadapids which possess a petrosal-ecotympanic auditory bulla. Although further discussion of this subject would be premature, McKenna (personal communication) and I are in agreement that these alternatives are more probable than McKenna's (1961) and Wood's (1962) suggestion for a plesiadapid origin of rodents.
Fig. 25. Scatter diagram of length/width (posterior width for the lower teeth) of the cheek teeth of *Niptomomys doreenae* (Gray Bull, Four Mile, and Lysite localities), *Uintasorex parvulus* (Bridger localities), and *Uintasorex* sp. (Powder Wash). See figure 22.

been described or illustrated. I can, however, allocate isolated incisors from the large samples of the Four Mile fauna collected by McKenna to *Tetonius homunculus*. These enlarged incisors of the anaptomorphine *Tetonius* are very similar in construction to those of *Paromomys*, *Palaechthon*, and *Palenochtha*. Isolated incisors of the three latter genera are known from the Torrejonian Swain Quarry. In *Tetonius*, *Paromomys*, *Palenochtha*, and *Palaechthon*, as well as in the advanced omomyid *Ourayia*, the incisors display a rather strong quasibilateral symmetry. Known incisors of both *Uintasorex* and *Microsyops* show very pronounced asymmetry between the buccal and lingual sides. Incisors of *Microsyops* have been described and illustrated in detail in Szalay (1969), and the incisor of *Uintasorex* is clearly shown in figures 3 to 6. No other early Tertiary group of mammals known to me, with possible relevance to the uintasoricines or to microsyopines, has incisors similar to those of *Uintasorex* and *Microsyops*. I interpret the sharing of this specialized tooth as a highly probable indication of close relationships. The identical lower tooth formula of
the three genera (*Uintasorex*, *Niptomomys*, and *Microsyops*) gives additional support for their close mutual ties.

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