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A GIANT RODENT FROM THE OLIGOCENE OF SOUTH DAKOTA

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The fossil rodent described in this paper is of remarkable interest on several counts. It is remarkably large, the largest rodent known from beds of comparable or greater age and scarcely equaled by any rodents except a few enormous forms in the South American Pliocene and North American Pleistocene. It is an unexpected survivor of a group, the Paramyinae, hitherto believed to have become extinct at about the close of the Eocene. It is a belated discovery, the more surprising in view of its large size, of a wholly new element in a fauna that is perhaps the most intensively collected and extensively studied of all fossil faunas.

The unique specimen was presented to the American Museum by Mr. Kenneth Briggs of Baker, Montana, who found it while cooperating with a Museum field party including Dr. Walter Granger, Mr.

Albert Thomson, and Mr. Junius Bird. It was found in Slim Buttes, Harding County, near the northwestern corner of South Dakota. These buttes, like others scattered in Harding County and adjacent Carter County, Montana, include outlying remnants of the White River Group, beginning some hundred miles north and slightly west of the more famous exposures in the Big Badlands. The Oligocene beds in the Slim Buttes are considerably folded and disturbed and the section is not clear, but assignment of the specimen to the Lower Brulé rests on the reliable authority of Mr. Thomson and on the nearby occurrence of more typical Lower Brulé fossils.

The specimen has been prepared by Mr. Thomson and all the illustrations in this paper were drawn by Mr. John C. Hermann.

TAXONOMY

ORDER RODENTIA VICQ D'AZYR, 1792

SUBORDER SCIUROMORPHA BRANDT, 1855

SUPERFAMILY APLODONTOIDEA MATTHEW, 1910 (HAPLODONTOIDEA GILL, 1872)

FAMILY ISCHYROMYIDAE ALSTON, 1876

Subfamily **Paramyinae** Matthew, 1921 (Paramyida Haeckel, 1895)

Tribe **Manitshini**, new

TYPE.—*Manitsha*, new genus.

KNOWN GENERA.—*Pseudotomus*, *Ischyrotomus*, *Manitsha*.

AUTHOR'S HYPODGM.—Type of *Pseudotomus hians*, several referred specimens of *Pseudotomus robustus*, especially Amer. Mus. No. 13091, type of *Ischyrotomus petersoni* and Amer. Mus. No. 2017, type of *Ischyrotomus eugenei* as described by Burke, and type of *Manitsha tanka*.

KNOWN DISTRIBUTION.—Middle and Upper Eocene and Middle Oligocene (Bridger to Lower Brulé formations, Bridgerian to Orellan ages) of western United States.

DEFINITION.—A lineage of large and robust paramyines. Incisors heavy, little compressed, without grooves, lower incisors becoming flattened on anterior faces. Cheek teeth broad, with simple, shallow, blunt patterns tending to develop transverse crests, upper cheek teeth approaching a pattern of four simple transverse crests united buccally and lingually. Skulls and jaws stoutly constructed throughout. Infra-orbital foramen small, low, not displaced by masseter. Anterior zygomatic root stout, nearly vertical, turning at an abrupt angle to the face. Ramus deep with projecting symphyseal flange.

Limbs and feet strong, developing elongate, moderately compressed claws.

MANITSHA SIMPSON, 1941

TYPE.—*Manitsha tanka*.

KNOWN SPECIES.—Type only.

AUTHOR'S HYPODIGM.—Type of *M. tanka* only.

KNOWN DISTRIBUTION.—Orellan of South Dakota.

DEFINITION.—A member of the Manitshini, as defined above, similar to *Ischyrotomus* and differing more than does that genus from other members of the tribe. Incisors relatively larger than in *Ischyrotomus* and less compressed transversely. Infraorbital foramen lower, relatively smaller. Anterior zygomatic root higher, its masseteric scar less horizontal. Rostrum and mandible deeper. Masseteric flange on mandible more, but symphyseal flange less, prominent. Digits of manus relatively stouter, unguals about

equally elongate and compressed, but notably deeper and more curved.

(Inadequate knowledge of *Ischyrotomus* leaves important generic comparisons incomplete, but the details listed suffice for establishment of the new genus.)

Manitsha tanka,¹ Simpson, 1941

Figures 1 to 4

TYPE.—Amer. Mus. No. 39081, most of skull and jaws with nearly complete dentition, most of right fore limb, and other fragments (listed below).

AUTHOR'S HYPODIGM.—Type only.

PROVENIENCE.—Near highway (as of 1940) on western side of Reva Pass, in northern part of Slim Buttes, Harding County, South Dakota. In "Oreodon Beds," Lower Brulé.

DEFINITION.—Sole known species of *Manitsha*, as defined above. Larger than any known relative.

DESCRIPTION

DENTITION.—The dental formula is $\frac{1.0.2.3}{1.0.1.3}$, as in all the Paramyinae. The teeth are all preserved except left P^3 and the incisor and M_3 in the right lower jaw.

The upper incisors are very robust, not much compressed transversely, all faces convex. The angle between anterior and medial faces is moderately sharp. The enamel extends little onto the lateral face. The anterior face is evenly convex, without groove. The compression index (100 times ratio of maximum anteroposterior diameter to width of enamel band) is 103 in the type, a low value for a paramyine.

As in most primitive rodents, the diastema is about equal in length to the cheek tooth series.

P^3 was present on both sides, although reduced to a vestige, but had dropped out after death. An isolated P^3 was found nearby in the matrix. It surely belongs to this individual and has been inserted in its probable position on the right side. It is one-rooted and the alveolus is about half way between tangents to the buccal and lingual faces of the other cheek teeth instead of being in contact with the lingual tangent as in most allied forms. The somewhat worn crown appears to have had only one rounded main cusp (the type of *Ischyro-*

tomus petersoni apparently had two), with two small flanking depressions.

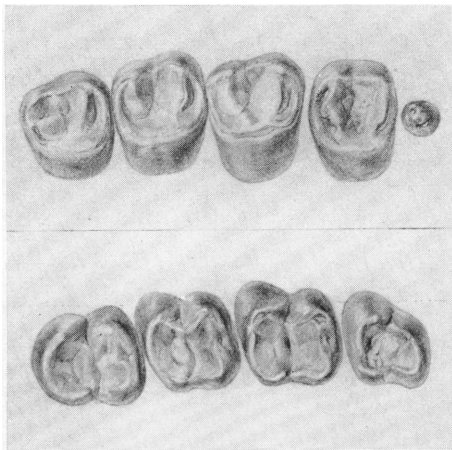


Fig. 1. *Manitsha tanka*, Simpson, 1941. Type, Amer. Mus. No. 39081. Right upper and left lower cheek teeth, crown views. $1\frac{1}{2}$ times natural size.

¹ *Manitsha*, "gopher (ground squirrel)," *tanka* "big," Dakota Indian (J. P. Williamson's Dakota Dictionary, American Tract Society). I am indebted to Mr. Thomson for suggesting the use of names from this dialect, recently spoken in the region where the fossil was found, and for lending me a dictionary of it. The name should be pronounced approximately *mahnéé-chah* (ch as in "church") *tahnk-kah* (not *tank-a*). *Tanka* is pronounced approximately like (and is in fact the same word as) the last two syllables of "Minnetonka."

The four upper grinding teeth are similar in general pattern although P^4 and M^3 are readily distinguished from the other two teeth in details. The pattern is simple and shallow, without deep folds or high cusps and crests. In the unique specimen the pattern is well shown, all the permanent teeth in place but only slightly worn, with dentine exposed only on the protocone of M^1 and nearly reached on M^2 . (Similarly on the lower teeth, dentine is well exposed on the buccal cusps of M_1 and just being reached on M_2 .) The tendency of the pat-

break into the adjacent buccal and lingual cusps. It is possible that a parastyle was present, as in most paramyines, when the tooth was unworn, but if so it was certainly less distinct than in *Paramys* itself, or even than in *Pseudotomus robustus* in which, nevertheless, its relative reduction is already suggested.

Paracone and metacone remain distinct cusps and are separated by a notch as seen in lateral profile, but there is a tendency to form a protoloph which is completed by small cuspsules between paracone and meta-

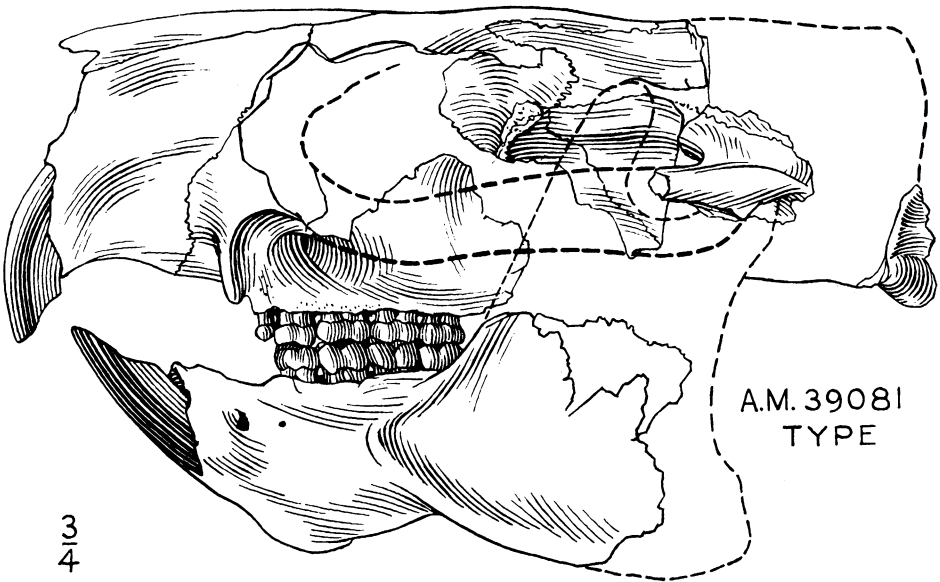


Fig. 2. *Manitsha tanka*, Simpson, 1941. Type, Amer. Mus. No. 39081. Skull and jaws, left lateral view. Parts in solid outline present in specimen, in part reversed from other side, with distortion corrected. Parts in broken outline restored by comparison with allied genera. $\frac{3}{4}$ natural size.

tern is to form an elevated rim on all sides of the tooth with two transverse crests dividing the shallow apical basin into three valleys. In comparison with allied forms, the striking character is an apparent tendency to form four transverse lophs (anteroloph, protoloph, metaloph, and posteroloph of Wood and Wilson, 1936, whose terminology I will use as far as applicable). Anteroloph and posteroloph are about equal to each other, lower than the other positive elements of the crown, and are simple, rounded crests. Both rise without

cone. These cuspsules are difficult to distinguish on teeth even slightly worn, especially on P^4 , but were surely present on M^{1-3} , at least. On M^{1-2} there was apparently only one such cuspsule and on M^3 there may have been one or two, the more posterior smaller. These cuspsules are unlike the mesostyle of *Paramys*, which is usually a single distinct cuspsule well external to paracone and metacone rather than one tending to unite these into an evenly curved ectoloph. Again an incipient stage of this manitshine development is

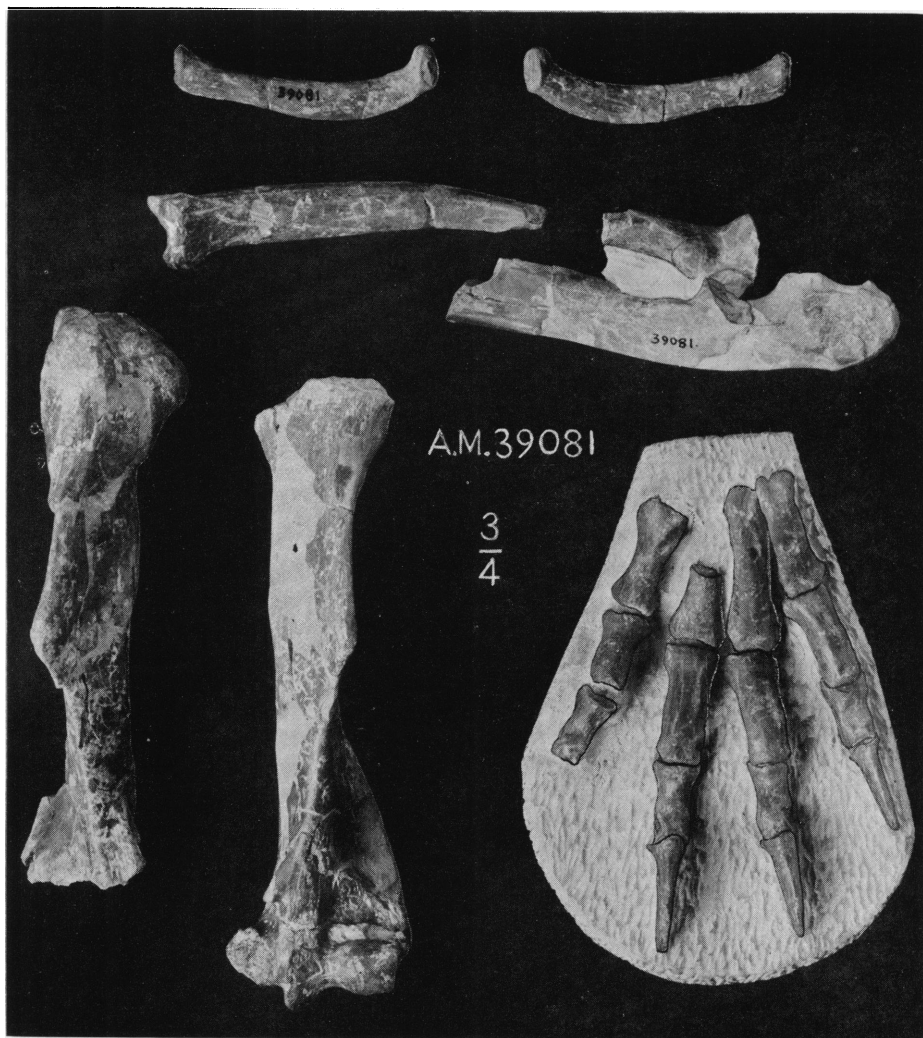


Fig. 3. *Manitsha tanka*, Simpson, 1941. Type, Amer. Mus. No. 39081. Skeletal remains associated with skull and jaws. Right and left clavicles, complete. Right radius, nearly complete (the two pieces do not make unequivocal contact but the missing part was probably not longer than a millimeter or two). Proximal end of right ulna. Right and left humeri, nearly complete. Most of right manus, mounted in a natural pose and not in a plane, so that the photograph is foreshortened. $\frac{3}{4}$ natural size.

visible in *Pseudotomus robustus*, in which there are one or two cuspsules more individualized than in *Manitsha* but in the same position. None of these cusp details can be made out on the upper teeth of any specimens of *Ischyrotomus* known to me.

The lingual side of the tooth is an elevated crescentic ridge rising to one main cusp, the protocone. No other can be

definitely distinguished on P^4 . On M^{1-2} the hypocone is faintly but surely distinguishable. It would merge completely with the protocone with very little more wear on these teeth. On M^3 it is still smaller and hardly distinguishable even with less wear. This poor differentiation of the hypocone is also foreshadowed in *Ps. robustus*.

The protoloph runs from the apex of the paracone to the buccal slope of the protocone, with which it fuses without running to the apex. This buccal end of the crest is very slightly and vaguely swollen, with no more definite suggestion of a protoconule. The metaloph is similar but it is more distinctly independent (less fused)

The lingual face is a long, smooth, oblique slope, while the buccal slope is much shorter and more vertical.

Aside from details already mentioned, P^4 is characterized by being more transverse than the other teeth and oval in contour. M^{1-2} are almost identical with each other in form and are subquadrate in outline.



Fig. 4. *Manitsha tanka*, Simpson, 1941. Life restoration, $\frac{1}{2}$ natural size. Lower right, sketch showing adjustment of main muscles, eye, ear, and skin outline to skull reconstruction, $\frac{1}{6}$ natural size.

at its buccal end and also more definitely (but still not sharply) swollen into a metaconule, which may have been double on P^4 when unworn. There is a distinction from the sharply distinct metaconule of *Paramys* (*sensu stricto*) and again *Ps. robustus* is intermediate in character.

There are no external or internal cingula.

M^3 is more nearly circular and shows the usual tendency toward rotation of the posterior elements and their reduction in height. The metaconule is more definite and not so loph-like.

One lower incisor had fallen out and was lost before burial. The other is preserved and shows the form well. The anterior

face is very flat and the angle with the medial face is sharp, that with the lateral face somewhat rounded. The compression index is 108, about equal to that of the upper incisor and also low for this group. In the type of *Ischyrotomus petersoni* the upper index is 131, lower 123. In that genus the form of the incisors is otherwise almost exactly as in *Manitsha*. In the type of *Pseudotomus hians* the upper index is about 116 (lower unknown) and in a specimen of *Ps. robustus* both upper and lower indices are 133. The widening and flattening of the anterior face is only incipient in *Ps. robustus* but is already definitely indicated in that early species.

The lower cheek teeth are basically paramyine but differ from *Paramys* and its closer allies in ways analogous to the differences in the upper teeth. The metaconid is the highest, sharpest, most distinctive cusp on all four teeth. The protoconid is much lower and is so small on P_4 that that tooth has a triangular outline, as in all paramyines but to as great a degree as in any. On P_4 the crest between these cusps appears to be single but on M_{1-3} it is formed by two elements of equal prominence, as is shown in this state of wear only by the presence of a small, dimple-like depression in the middle of this transverse elevation. Comparison with more primitive forms suggests that these elements be interpreted as anterolophid plus metalophid rather than as a double metalophid.

A short, low, vague, curved elevation joins the lingual bases of the protoconid and hypoconid, but this is so slight as hardly to deserve the name ectolophid and, at least in this stage of wear, does not appear to bear a distinct mesoconid. In any case this element is apparently less distinct than in the more typical paramyines. The apices of the hypoconid and entoconid are joined by a continuous single crest on the rim of the tooth, without any distinct development of cusps on it. This has more the structural relations of a posterolophid, with which hypolophulid II may have fused either phylogenetically or (improbably) by wear.

In the talonid basin on M_{1-3} there is a low, rounded, transverse crest between the anterobuccal base of the entoconid and a

point on the vestigial ectolophid near its junction with the hypoconid, not strongly united at either end. This is perhaps a vestigial hypolophulid I. On P_4 the basin shows traces of more complex and not definitely transverse wrinkling. Even allowing for wear, the enamel was evidently much less wrinkled and folded than in *Paramys*. There are no other distinguishable cusps or crests.

As in the upper teeth, most of the details of the lower cheek tooth pattern of *Manitsha* are foreshadowed in *Ps. robustus*, and *I. petersoni*, as far as known, is a suitable intermediate form. The pattern in *I. eugenei* is not adequately known and there is some suggestion that it is more aberrant.

The cheek teeth in all these species are decidedly brachyodont, but within this tribe they tend to have somewhat higher crowns than in the rest of the Paramyinae. There is, however, no definitely ascertainable difference in relative crown height between the Middle Eocene *Pseudotomus* and Middle Oligocene *Manitsha* and progressive hypsodonty is not present in this group. Some discrepancy in height between inner and outer sides, with the inner side higher on the upper teeth and the outer higher on the lower teeth, the so-called tendency toward unilateral hypsodonty, is characteristic of a great variety of mammals of many different orders and especially of primitive rodents. It occurs also in this group, but in *Ps. robustus* is not more pronounced than in *Paramys* or the Eocene Paramyinae in general. In *Manitsha* it is somewhat greater and there may have been some tendency in this direction. Comparison of *Manitsha* and *Pseudotomus* suggests that the net effect, in relation to the horizontal dimensions of the teeth, is more a relative lowering of the outer sides of the upper teeth and inner sides of the lower teeth than an elevation of the opposite sides, so that unilateral brachyodonty would be a more apt term in this case. Certainly the tendency is not strong enough to constitute a decisive resemblance to the cylindrodonts, in which true progressive unilateral hypsodonty is strongly present.

The upper teeth are insufficiently known

in the precursors of *Manitsha* and useful comparisons of size and proportions cannot be made. For the lower teeth, I have made comparisons based on Amer. Mus. No. 13091, referred to *Pseudotomus robustus*, Amer. Mus. No. 2017, referred to *Ischyrotomus petersoni*, the type of *Ischyrotomus eugenei* (data from Burke), and the type of *Manitsha tanka*. The following statements are true of these four specimens. The degree to which they are also true of the corresponding species cannot now be determined.

As a whole, the lower dentition of *I. petersoni* is slightly (not significantly) smaller than that of *Ps. robustus*. These two species were of approximately the same size. The lower dentition of *I. eugenei* is decidedly larger, about 134% of *Ps. robustus* for the cheek teeth,¹ while *M. tanka* is still larger, 144% of *Ps. robustus* (eleven cheek tooth dimensions) and 107% of *I. eugenei* (eight cheek tooth dimensions).

Ps. robustus, *I. petersoni*, and *I. eugenei* all have the lower incisor of about the same size relative to the cheek teeth but in *I. petersoni* it is slightly and in *I. eugenei* decidedly less compressed transversely than in *Ps. robustus*. In *M. tanka* the lower incisor is slightly larger, relative to the cheek teeth, than in any of the earlier species and is even less compressed than in *I. eugenei*.

P₄ has about the same relative size in all four forms, but in both *I. petersoni* and *I. eugenei* it is relatively slightly larger than in the other two species and it is broader than in *Ps. robustus* while in *M. tanka* it is of about the same relative size as in the latter form but narrower. The relative sizes of the molars are about the same in *Ps. robustus*, *I. petersoni*, and *M. tanka*, with M₁ perhaps a little enlarged in the latter, but in *I. eugenei* M₁ is relatively larger and M₃ is relatively smaller than in the other species, an effect opposite to the probable results of wear in this old specimen and so not attributable to that cause. In all three of the later forms, and in about

equal degree, M₁ and M₂ are slightly longer and narrower in proportions than are these teeth of *Ps. robustus*. In *M. tanka* M₃ is similarly elongated, but in *I. petersoni* this tooth has almost exactly the same proportions and form as in *Ps. robustus*. In *I. eugenei*, however, this tooth differs radically from any of its allies. Its width is about what would be expected in an animal of this size, but its length is relatively much less. In fact this M₃ is figured and measured by Burke as wider than long, which is not true of any other paramyine known to me, and these extraordinary proportions are accompanied by a flattening of the posterior face that is also unique. If this proves to be normal for the species, *I. eugenei* may be more aberrant in this tribe than appears at first sight, although there seems to be little doubt that it does belong here.

Some of the dental dimensions of *Manitsha tanka*, in millimeters, follow:

	Left	Right
Upper incisor: Maximum width on enamel face	..	9.7
Maximum (anteroposterior) diameter.....	..	10.0
P ³ : Maximum diameter of crown..	..	3.2
P ⁴ : Greatest anteroposterior length.....	7.5	7.3
Greatest transverse width...	10.1	10.1
M ¹ : Length.....	8.6	8.5
Width.....	10.7	10.7
M ² : Length.....	8.1	8.3
Width.....	10.6	10.2
M ³ : Length.....	7.8	7.9
Width.....	9.3	8.7
Lower incisor: Width of flattened anterior face.....	8.6	..
Greatest (anteroposterior) diameter.....	9.3	..
P ₄ : Length.....	7.6	7.3
Width, on talonid	7.5	7.5
M ₁ : Length.....	8.3	8.3
Trigonid width..	8.6	8.3
Talonid width...	9.0	9.0
M ₂ : Length.....	8.2	..
Trigonid width..	8.7	..
Talonid width...	8.9	..
M ₃ : Length.....	9.7	..
Trigonid width..	8.4	..
Talonid width...	7.6	..

¹ Geometric mean of eight cheek tooth ratios. Use of the geometric rather than arithmetic mean has no special advantage but is equally valid and happens to be easier in conjunction with graphic logarithmic methods that I use in order to facilitate comparisons of proportions.

SKULL.—The skull was broken both before burial and after exposure and is considerably crushed. Its preservation in general is poor, but many details are visible and the general structure can be reconstructed with reasonable security. The zygoma, proper, posterior part of the cranial roof, occiput, ear region, and most of the inferolateral cranial region are almost entirely missing, but the other parts of the skull are all at least partly preserved. The sutures are generally obscure and their description is tentative.

The palate is broad and nearly flat. The choanae extend to about the level of the anterior end of M^3 and the palatines appear to be unusually short, ending about opposite the posterior end of M^1 . The alveolar ridge (between P^3 and the incisor) is rounded and almost absent in the middle of the diastema. The anterior palatine foramina are relatively very small (probably a simple function of the large overall size of the skull) and are at a distance of about their own length from the incisors, which makes these unusually far in advance of the cheek teeth.

Even allowing for crushing, the rostrum was evidently unusually deep, perhaps as much as one and one-half times as deep as wide near the middle of the diastema, and similarly deep proportions seem to have characterized the whole skull in contrast with other ischyromyids. This tendency is barely indicated in the type of *Ischyrotomus petersoni* and is not visible in the only skull of *Pseudotomus* known to me (type of *Ps. hians*) which is, however, crushed dorso-ventrally. The rostrum is also short relative to the cranium. The premaxillo-maxillary suture runs almost vertically up the rostrum a short distance (about 5 mm.) anterior to the infraorbital foramen.

The infraorbital foramen is relatively very small, hardly larger than in many ischyromyids with skulls one-half to one-third as large as this. This relative size is doubtless in inverse proportion to gross skull dimensions in this group, in which the infraorbital foramen does not transmit and is not affected by the masseter. The rim of the foramen is only about 5 mm. anterior to a vertical plane at P^3 and only

about 11 mm. above the alveolar plane, an unusually low and posterior position, characteristic of paramyines but here exaggerated.

The anterior zygomatic root is aplodontoid and paramyine in basic pattern but in detail it is markedly unlike that of any other mammal known to me. It is very deep and its long axis is almost vertical, not inclined anterosuperiorly as in almost all allied rodents. This, too, seems to be a progressive specialization in this group. The inclination is still evident in *Pseudotomus hians*, almost absent in *Ischyrotomus petersoni*. The lower border of the free zygoma, where it departs from the root, is extraordinarily high, some 12 or 13 mm. above the alveolar plane and about on a level with the middle of the infraorbital foramen. In all other paramyine skulls known to me, even in the generally similar *Ischyrotomus*, it is very little above the alveolar level and definitely below the infraorbital foramen. As a result of this upward sweep of the root, the anterior end of the masseteric origin is inclined at more than 45° to the horizontal, while in allied forms it is almost horizontal.

The masseteric scar ends on the junction of the zygoma and its root and has none of the forward expansion seen in the Sciuroidea and incipient in a few ischyromyids (e.g., *Ischyromys troxelli*, *Titanotheriomys*). It is bounded above by a sharp crest which curves downward into an equally prominent but less sharp vertical ridge, anterior to which the zygomatic root has a flattened face almost at right angles to the rostrum. This ridge ends below in a small, well-defined knob anterior and slightly external to P^3 , from which it is separated by a rounded notch. The sharp turning in of the zygomatic root to the rostrum is present in less degree in *Ischyrotomus petersoni* and apparently foreshadowed in *Pseudotomus hians* in which, however, it would hardly be noteworthy were the later forms not compared. These early species do not show the ridge and knob developed in *Manitsha tanka* and in them the anterior face of the zygomatic root is about at the level of P^3 , while in the specimen here described it is well anterior to that tooth.

Although the process itself is not preserved, the remaining parts of the frontal suggest that there was a small true post-orbital process. Such a process, barely incipient but recognizable, occurs on the skulls of both *Ps. hians* and *I. petersoni* but is otherwise practically absent among ischyromyids.

The postorbital crests are not prominent and converge rapidly to the sagittal crest, which is sharp and single, as would be expected in so large a species.

The postorbital constriction is unusual if not unique, in being formed by a strongly defined, rounded groove, short anteroposteriorly and elongate in a nearly vertical direction, semicircular in horizontal section. It is bounded posteriorly by a strong, blunt prominence on the side of the braincase. A tendency to form a slight prominence here, usually barely distinguishable, is not uncommon among ischyromyids (e.g., *Titanotheriomys*) or even occasionally among more distantly related rodents, but this strong development and its structural details are very characteristic. Again *Pseudotomus hians* and *Ischyrotomus petersoni* are the most nearly similar of species in which this region is known. Both have a prominence differing only in detail from that of *Manitsha tanka*. Breakage in the two known skulls of those species (the types) shows that the prominence overlies the most anterolateral point of the cerebral hemisphere.

As nearly as I can make out the sutures, the frontal, parietal, squamosal, and alisphenoid all enter into at least the base of this prominence and all meet, or nearly meet, here. The parietal has a small, tab-like projection onto the upper surface of the prominence, which is unusual but not unique (cf. *Reithroparamys delicatissimus*).

A strongly prominent but not very sharp ridge runs posteriorly from the prominence just described. This ridge undoubtedly was continuous with the anterior edge of the posterior zygomatic root and glenoid fossa, although the connection is not demonstrated because the ridge is preserved only on the right side and this zygomatic root only on the left. This root and the glenoid fossa are simple and paramyine in

structure without being very distinctive. The fossa is broad and shallow, relatively short anteroposteriorly, and its posterior end evidently was open. The ear region is not preserved, but it is highly probable that the glenoid was entirely external to the ossified ear structures (as in other paramyines) instead of abutting against and being closed by an ossified meatus and the external part of the bulla (as it is in *Ischyromys troxelli*, for instance). In the absence of bone contacts, and of the mandibular condyle, the glenoid fossa cannot be exactly placed on the skull, but it was apparently somewhat high on the skull, far above the alveolar plane.

The occipital condyle seems to be more expanded dorsoventrally and anteroposteriorly and less transversely than in the smaller paramyines, a development probably shared in less degree by *Pseudotomus* and *Ischyrotomus*. The single condylar foramen and adjacent edge of the posterior lacerate foramen are placed about as in ischyromyids generally. The basioccipital-basisphenoid region is broad and rather flat.

No reliable standard measurements can be taken on the skull as preserved. The basal length, prosthion to condyles, must have been between 150 and 170 mm., probably about 160, as estimated from average ratios to skulls of *Ischyrotomus*, *Paramys*, and *Reithroparamys*. *Manitsha tanka* was thus larger than any living North American rodents.

MANDIBLE.—Both horizontal rami are preserved, without the coronoid, condylar, and angular processes. These can be most succinctly described as practically identical in structure with those of *Pseudotomus robustus* and *Ischyrotomus petersoni* except for being larger, deeper, and stronger. The symphyseal flange characteristic of these species is distinctly present but is relatively less prominent than in the available specimens of the earlier species. The anterior margin of the masseteric fossa is strongly marked, ending in a prominence at about the middle of the outer face of the horizontal ramus, beneath the posterior end of M_1 . In all three of the species in question the symphysis differs from that

of most allied forms by having a relatively small oval sutural area at the upper end only, below which the opposite rami are in contact only along a narrow, curving, flange-like rim without definite sutural union.

POSTCRANIAL SKELETON.—These elements were preserved: fragment of right scapula, complete left and right clavicles, most of the manubrium, right humerus except distal end, left humerus except proximal epiphysis, proximal half of right ulna, nearly complete right radius, right metacarpals II–V complete except proximal half of IV, phalanges of digits II–V complete except ungual of V.

The clavicle, not known in related species, is a stout, fully functional bone. The fore limb as a whole is almost identical in structure with that of *Pseudotomus robustus* except for its larger size and slight differences in proportion. The size relative to that of the head of the animal is almost the same. On the humerus the greater tuberosity is slightly stronger than in *Ps. robustus* and the deltoid crest, strong in both, projects relatively still farther in *M. tanka*. The width across the epicondyles is relatively slightly less in the latter, but the distal end is stout (anteroposteriorly), with the trochlear crests sharp and strong. The most noteworthy difference in the radius is that the capitular articulation in *M. tanka* has the least diameter shorter relative to the greatest diameter. As far as preserved, the ulna of *M. tanka* is almost exactly like that of *Ps. robustus* except for being slightly stouter, with strong crests and processes.

The metacarpals and phalanges also are very like those of *Ps. robustus*, but here the better preservation permits more adequate comparison of proportions. I have made an elaborate quantitative comparison of the proportions in one specimen each of *Pseudotomus robustus*, *Ischyrotomus petersoni*, and *Manitsha tanka*, which is not published in detail but which substantiates the following statements. Of course the statements are applicable to these individuals and their extension to the species as a

whole is dubious. In all three, the forefeet as a whole have about the same proportions to the jaws and dentitions.¹ The long dimensions of the preserved bones in *M. tanka* average (geometric mean) 138% those of *Ps. robustus* and the transverse dimensions 140%.

Except for the unguals (only one preserved) the digits of *I. petersoni* tend to be slightly stouter than in *Ps. robustus* but the difference is scarcely significant and on the whole these bones are almost alike in the two species. Aside from being much larger, these elements in *M. tanka* differ characteristically in proportions, all of them being notably stouter (or wider relative to the length) than in the earlier species. This difference is least in the first phalanges, which have nearly the proportions of *Ps. robustus*, and is strong in the metacarpals and second phalanges.

The unguals of *Manitsha tanka* are much longer than those of *Ps. robustus*, absolutely, relative to the size of the foot, and relative to their own widths. They are thus both more enlarged and relatively more compressed than in the Bridger form. Otherwise they are of the same general type in the two species, high and moderately curved. The one known ungual of *I. petersoni* (on digit IV) is also much more elongate than in *Ps. robustus* as Matthew pointed out (1910, p. 57), and length and width are relatively about the same as in *M. tanka*, both in proportion to each other and in proportion to the foot as a whole. The height, however, is relatively much less than in either of the two comparative species and this makes the curve of the upper surface less pronounced.

The unguals are thus the most characteristic feature of the manus in these three specimens: in *Pseudotomus robustus* short and deep, in *Ischyrotomus petersoni* long and shallow, in *Manitsha tanka* long and deep.

¹ Detailed measurements do not support Matthew's statement that the skeleton in *I. petersoni* is smaller in proportion to the skull than in *Ps. robustus*, nor is it true that the digits are relatively shorter in *I. petersoni*.

AFFINITIES

An opinion as to the affinities of this remarkable rodent is expressed by its taxonomic assignment on an earlier page and is in large part justified by the comparisons included in the description. That *Manitsha* is an ischyromyid, in the broad sense in which I define that family,¹ is so obvious as to require no special comment.

In the cheek-tooth pattern and a few other features, *Manitsha* has some striking likenesses to some of the cylindrodonts. There is considerable resemblance to primitive forms like *Mysons*, and perhaps still more to the Oligocene *Ardynomys*. Even before the discovery of *Manitsha*, this was noted by Burke (1936) as a resemblance between *Ardynomys* and *Ischyrotomus* (which is very like and approximately ancestral to *Manitsha*). Burke concluded that this is "nothing more than another interesting case of parallelism" and not an indication of close relationship, and I agree. *Ardynomys* and *Manitsha* may well have had a common ancestry in the Lower Eocene, but no closer relationship is likely. The parallelism was doubtless also aided by some community of habitus that would have been accompanied by some degree of convergence even without the basic structural similarity of their ancestry.

Manitsha is clearly more closely related to the Paramyinae than to any other ischyromyids. These forms, hitherto known from many western American deposits Tiffanian (Upper Paleocene, see Jepsen, 1937) to Duchesnean (latest or transitional Eocene) in age, include a number of different lineages (of what I would recognize as about tribal rank).

¹ The current great multiplication of taxonomic units is a practical necessity on the lower levels of taxonomy but is less necessary and is often inadvisable at higher levels. By the use of such neglected but valid and very useful ranks as tribes and subgenera, the number of steps in the hierarchy and the number of smaller units can be suitably increased for the purposes of specialized and refined studies without unnecessarily disturbing the larger units, such as families. The inclusive family names are more familiar to zoologists in general and are more useful and more comprehensible if kept in their older senses and broken up only if the assemblages are known to be definitely unnatural. The Ischyromyidae of older authors, approximately Ischyromyoidae of recent specialists, do still appear to be a natural group. Lesser categories amply suffice to indicate the variety and the probable interrelationships of the included forms.

The Bridgerian, Middle Eocene, paramyines have been longest known and most carefully reviewed, although even they are not yet satisfactorily classified. At least four, and probably more, groups now generally given generic rank are recognized. *Paramys*, type *P. delicatus*, is the type of the subfamily and was formerly made to include almost all the species of the subfamily. *Pseudotomus* was soon abandoned by its proposer, Cope, but was revived as a subgenus by Matthew (1910). The type is *Ps. hians*, known from a single specimen, a skull without teeth, but Matthew's paradigm was essentially specimens referred to "*Paramys*" *robustus*. Gidley (1919), however, suggested without discussion that *robustus* be placed in the otherwise Upper Eocene genus *Ischyrotomus*. As regards this point, the nature of the incomplete specimens concerned makes direct comparisons very limited, but it appears to me that *robustus* is probably no nearer to the type of *Ischyrotomus* than is *hians*, and quite possibly it is not as near. On the other hand there is no evidence that *robustus* and *hians* are generically or subgenerically distinct and there is some reason to believe that they are not. In the present state of knowledge, it is therefore more reasonable to keep *robustus* and *hians* together than to place one in *Ischyrotomus* and recognize the other as distinct under the name *Pseudotomus*. The genera are certainly closely related and might be placed together as subgenera under the names *Pseudotomus* (*Pseudotomus*) and *Pseudotomus* (*Ischyrotomus*), with *hians* and *robustus* placed in the former. I tentatively use both names in the generic form because I am not formally revising the whole group, and only use convenient designations of recognizable structural stages pending such revision.

Other Bridger groups, of less interest for the present study, are *Reithroparamys* Matthew, 1920, type "*Paramys*" *delicatus* and probably one or two others not yet named or clearly recognized (cf. "*Paramys*" *minutus* Wilson, 1937).

Among these forms, *Manitsha* is cer-

tainly closest to *Pseudotomus*. *Ps. robustus* could well be ancestral to *Manitsha* and various special points of comparison have been noted in the description on preceding pages. As far as known parts go, *Ps. hians* is no less close and although the molar structure cannot be compared, the skull structure characteristically foreshadows that of *Manitsha*. The skull structure is not known in *Ps. robustus*, but it is probable that it will prove to be very like that of *Ps. hians*.

Paramyines are also common in the Lower Eocene and hitherto have all been referred to *Paramys*, although it is doubtful whether any of them belong there in a strict sense. I do not recognize a definite precursor of *Pseudotomus* in these beds, but I have not attempted a careful review of the materials.

In the Upper Eocene Uintan and Uppermost Eocene (or according to some students Lowermost Oligocene) Duchesnean, paramyines also occur in great variety, but again their classification is highly confused. A number of little-known species are referred to *Paramys*, to which they may or may not belong. None seems to be particularly close to *Manitsha* so that they need not be reviewed here. More definitely distinguished Upper Eocene groups are *Ischyrotomus* and *Leptotomus*, both proposed as subgenera (Matthew, 1910) and later raised to generic rank (Burke, 1934), and *Rapamys* Wilson, 1940. Aside from being paramyine, the latter does not come into consideration as a close relative of *Manitsha*, from which it is sharply distinguished by the strong, circular metaconules, sharply crested ectolophids, and many other details. *Leptotomus* is less obviously distinct from *Manitsha*, but is probably no closer phyletically, as shown by the laterally compressed lower incisor, strong molar ectolophids, more complex and cuspidate talonid on M₃, more slender and elongate mandible, and other characters. *Leptotomus kayi* Burke, 1934, from the Duchesne River Formation has hitherto been the latest known paramyine, and hence closest to *Manitsha tanka* in age, but it is not the closest in relationship.

Ischyrotomus, on the other hand, is in

most respects very similar to *Manitsha*, as suggested by preceding comparisons, and seems surely to be the closest known ally of the new genus. Comparison has been primarily with the type, *I. petersoni*, from the Wagonhound Member of the Uinta Formation, and this statement of affinity rests on that basis. The several referred species add little on one side or the other. *I. eugenei* Burke, 1935, from the later Myton Member has been described on the basis of two rather poor specimens affording little opportunity for comparison but apparently consistent with this relationship. This has been the largest known paramyine, nearly but not quite as large as *Manitsha tanka*. The only slightly older *I. petersoni*, however, is no larger than the Middle Eocene *Ps. robustus*. On Gidley's authority, Peterson (1919) referred another Myton species, "*I.*" *gidleyi*, to this genus, but the reference is manifestly uncertain and, I think, probably wrong. The same uncertainty and probability of error applies to Gidley's reference of "*Paramys*" *compressidens*, also from the Myton, to *Ischyrotomus*. Very recently Wilson (1940) has described *I. californicus* from the Poway, of probable early Uintan age. Without questioning or substantiating the generic reference, I think that Wilson's descriptions and figures show a form somewhat less like *Manitsha* than is *I. petersoni* and casting no further light on the affinities of *Manitsha*. At the same time Wilson described *I. (?) tapensis*, from the Tapo Ranch Sespe, probably of later Uintan age, only doubtfully referred to *Ischyrotomus*. The characters separating this species from more typical *Ischyrotomus* also tend to separate it from *Manitsha* and it, too, fails to suggest any special affinity with the latter.

In their typical and best known species, at least, Middle Eocene *Pseudotomus* and Upper Eocene *Ischyrotomus* are surely related and apparently are successive stages of a distinctive (not necessarily single or direct) line of descent to which *Manitsha* could and probably does belong as a terminal member. In spite of the various marginal species of doubtful pertinence, this line is distinctive and readily definable. It seems convenient and justifiable to give

it a collective designation, which I have done by calling it a tribe, typified by *Manitsha* as the most specialized genus.

In view of the belated discovery of *Manitsha tanka*, it would be unwise to predict that no later form will be found, but at present this species is the last known survivor of the Paramyinae, so common in the Eocene. The missing Lower Oligocene (Chadronian) stage in this sequence will probably yet be found.

In each age in which they occur, the Manitshini include the largest known rodents (although, of course, they are united by structural features aside from size).

HABITAT, HABITS, AND RESTORATION

There is little objective evidence for a difference in facies of the Slim Buttes Lower Brulé from that of the Big Badlands. Dr. Granger and Mr. Thomson inform me that the beds physically resemble the typical *Oreodon* Beds except for being folded. The folding of these strata of course has no bearing on their deposition, but there was definite folding in this region also before this time, and these strata in addition to being folded themselves are angularly unconformable on the Cretaceous. It is thus possible, at least, that there were hills in the vicinity during the Middle Oligocene, in contrast with the main mass of White River sediments where the fauna seems to have been entirely derived from a plains environment. Except for *Manitsha*, the rather scanty known Slim Buttes fauna appears to be ecologically similar to that of the *Oreodon* Beds in the Big Badlands. The other rodents found were *Ischyromys* and *Eumys*, everywhere the common rodents of this fauna.

It has repeatedly been pointed out (by Matthew, Hatcher, Sinclair, McGrew, etc.) that the *Oreodon* Beds and their fauna represent a region predominantly of open plains. The contemporaneous channel deposits, *Metamynodon* Beds, represent a fluvial and gallery forest association. The fact that *Manitsha* had not previously been found and is still unknown from the Big Badlands, despite its large size and the

This gigantism may, on one hand, have assisted their survival beyond that of their smaller allies, and on the other hand it may have been involved in their ultimate extinction, since large size is a character the selective value of which is readily reversed by subtle environmental changes. Before the Miocene the only serious rodent rival of *Manitsha tanka* as to size, as far as I know, is *Tsaganomys altaicus*, from the Hsanda Gol of Mongolia. The skull of this species is almost as long as that of *Manitsha tanka* but much of this length was in the unusually elongated rostrum and the animal as a whole was apparently considerably smaller than *M. tanka*.

very intensive search of these exposures, proves either that it was extremely rare or that it did not form part of these faunules. In either case it seems probable that these deposits were not laid down in its favorite or normal habitat and that it was not camp-estral and, with less assurance, probably not fluvial. Strictly arboreal types are also rare in these deposits, although not unknown, and this might be the reason for the rarity of *Manitsha*, but it is more reasonable to believe that this was an upland animal, accidentally preserved here as a stray. The line of evidence is obviously and admittedly tenuous and the conclusion is more a reasonable guess than a serious deduction. A possible analogy is provided by *Marmota*, which is rare or absent in the treeless plains and open basins but is nevertheless abundant in adjacent uplands of the West. It is very unlikely to be preserved in recent plains sediments analogous to those of the Big Badlands, but might appear as a rarity in piedmont deposits or those of intermontane valleys and basins.

Manitsha was a strong gnawer, more so than recent sciurids, but nevertheless had brachyodont cheek teeth analogous with those of sciurids and not with such forms as the beavers in which the gnawing ability is more nearly similar. The cheek teeth are not equal to a bark diet, such as the incisors could well obtain. Perhaps the food included seeds, nuts, fruits, perhaps espe-

cially those with a heavy integument, as well as leaves, twigs, roots, and the like. *Manitsha* probably was not a leaping or a swift-running animal and may have relied more on ambling retreat to a place of vantage (burrow, rocks, trees, water?) than on flight. Its strong, short manus with great curved claws does not suggest a rapid runner but would be equally suitable for climbing or digging.

Aside from these inferences as to food and locomotion, the known parts of *Manitsha* and its allies give little good evidence as to habits or habitat.

Loomis (1903, p. 124) regarded *Paramys* as terrestrial: "As the limb bones are much heavier and the tuberosities well developed, and as the distal end of the humerus is expanded, it seems probable that these forms were terrestrial, not to say burrowing forms." It is not clear which of the several different adaptive types among the Paramyinae Loomis had in mind. His statement is inadequate as a generalization for the whole group (all of which he placed in *Paramys* as did most authors at that date). Speaking of *Paramys delicatus* (type of the genus), Matthew (1910, p. 52) disagreed: "The comparatively long neck and slender body, long tail, slender feet with sharp claws, all agree most nearly with arboreal animals, and, like the teeth, are most nearly comparable with the large tropical squirrels. Loomis regards *Paramys* as terrestrial, but it is in my opinion unmistakably adapted to an arboreal habitat." Matthew emphasized, however, that the Ischyromyidae (in about the same broad sense as that here adopted) included both arboreal and terrestrial forms, without specifying each in detail. He remarked of *Ischyrotomus petersoni* (1910, p. 57) that the unguals "are long, uncompressed, nearly round in cross section, little curved, and evidently specialized for fossorial habits."

Burke (1936, p. 147) quoted Matthew's conclusion as to *Ischyrotomus* with approval and pointed out many points of resemblance between that genus and *Ardynomys*, also believed to be terrestrial or fossorial. In both genera, as Burke notes, the skulls are robust, with angular muzzles, the lower

jaws are heavy, the symphysis has a flange, the lower incisors are flattened, molar bases broadened, hypoconid region large, and the tooth crowns are somewhat heightened unilaterally. Burke concludes that these characters "are to be found in various combinations in a number of terrestrial or fossorial rodents," and that they are adaptive parallelisms. He believes that *Ardynomys* was a sort of habitus vicar for *Ischyrotomus* and replaced the latter in the fauna after the extinction of the Paramyinae. This apparent functional similarity is not contradicted by the discovery that the Paramyinae did survive along with *Ardynomys*. The resemblances noted for *Ischyrotomus* exist equally in *Manitsha* and the habitus replacement by *Ardynomys* was at least incomplete in the Middle Oligocene. In spite of these resemblances there was certainly some habitus difference between *Ardynomys* and *Manitsha*, if only because the known species of the latter is about three times as large as *Ardynomys occidentalis*. It is interesting and perhaps significant that *Ardynomys*, like *Manitsha*, was rare and perhaps absent in the main, plains-deposited mass of White River sediments and is known (in America) only from a region that may have been hilly, or near wooded and hilly country, at the time (McCarty's Mountain, Montana).¹

The skeleton of *Pseudotomus robustus* is so similar to that of *Paramys delicatus* in all features likely to be of adaptive significance that no difference in habits is objectively apparent. I see no conclusive evidence for either arboreal or terrestrial habits in either genus, although inclined to agree with Matthew that the smaller Eocene paramyines were probably arboreal. In describing *Metacheiromys* (Bull.

¹ It is also interesting that another belated discovery of an unexpected survivor of an Eocene group, *Sinclairiella*, was probably an inhabitant of woods or forests (in this case because it was probably arboreal). The unique specimen, described by Jepsen, was found in the Big Badlands, but the animal is certainly very rare there, probably because of an environmental difference from the bulk of the fauna. It is likely that much of the contrast between our Eocene and Oligocene faunas is caused by differences in facies of the more abundantly fossiliferous deposits of the two epochs, those of the Eocene rich in upland and sylvan, those of the Oligocene in campestral, mammals.

Amer. Mus. Nat. Hist., LIX, 1931, pp. 315-319), I pointed out that the skeletal adaptations for semi-fossorial and for arboreal life may be so nearly identical as to be practically indistinguishable in fossils.

In the recent Sciuridae, terrestrial habits tend to be accompanied by shorter tails, although this is not invariable. Both *Pseudotomus robustus* and *Ischyrotomus petersoni* had unusually long and heavy tails, much as in *Paramys* in which this feature has been mentioned as evidence for arboreal habits. The tail is unknown in *Manitsha*. Tree squirrels tend to have short, fairly deep, well-curved unguals, more or less as in *Paramys* or *Pseudotomus*, while the larger, terrestrial to fossorial sciurids, e.g., *Cynomys* and *Marmota*, tend to have longer, straighter, and shallower unguals, more as in *Ischyrotomus petersoni*, justifying Matthew's inference that this suggests fossorial habits for that species. But the long, deep, curved unguals of *Manitsha* are not decisively of either type and would seem equally useful either for climbing or for digging. They evidently are not cursorial or strictly fossorial (as, for instance, in the geomyids).

The characters given by Burke as common to *Ischyrotomus* and various terrestrial or fossorial rodents do not appear to be directly related to terrestrial or fossorial activities but, in part at least, occur sporadically in rodents of relatively large size but of a wide variety of habits.

Perhaps the best evidence of terrestrial habitat for *Manitsha* and its allies is their large size. Among the most nearly comparable recent rodents, the Sciuridae, there is, indeed, no strong or exclusive correlation of size with habitat. In the North American fauna the ground squirrels have about the same size range as the tree squirrels or even average a little smaller. Our smallest sciurids, the chipmunks, are terrestrial, although less exclusively so than the other ground squirrels. Our largest squirrels, the fox squirrels, are truly arboreal, although somewhat more likely to be seen on the ground than some of the smaller tree squirrels. The largest of all squirrels, in the Oriental genus *Ratufa*, are arboreal. But even these giants are

smaller (except in tail length) than the largest living sciurids, the marmots, and the latter are strictly terrestrial. Moreover not even *Marmota* approaches the enormous size of *Manitsha*, in which the skull is about one and one-half times as long as in a large woodchuck. Without exception the few living rodents really comparable in size with this fossil are non-arboreal and either terrestrial or amphibious. There is a possibility that *Manitsha* was amphibious (some of the peculiarities signalized by Burke in *Ischyrotomus* are about as characteristic of amphibious as of terrestrial or fossorial rodents), but there is no good evidence that it was. If amphibious, it should perhaps have turned up before now in some of the closely searched channel sandstones of the Oligocene, which do contain animals of such associations, instead of being so rare a discovery and being found with purely terrestrial associations.

It is tempting to think of the more typical paramyines as a primitive arboreal stock analogous with the tree squirrels, of forms like *Ischyromys* as terrestrial rodents of the open plains, analogous with the prairie-dogs, and of the Manitshini as giant terrestrial forms analogous with the woodchucks. If, however, the present discussion serves no other purpose, it does show how speculative such a conclusion is.

In view of the striking character of *Manitsha* and of its popular as well as scientific interest, it seems worth while to present a restoration of the head (Fig. 4, drawn by John Hermann). The missing parts of the skull and jaws were reconstructed with reference to *Ischyrotomus* and the jaw musculature was sketched in with reference to *Aplodontia* and to the muscle areas as preserved. A generally sciuroid surface was then adapted to these underlying structures. In view of the rather stereotyped appearance of the head in the recent rodents of similar habitus (whether arboreal or terrestrial), this is likely to be about as true to life as such a restoration can be. The questionable points are, of course, possible color pattern, which is avoided by black-and-white drawing with no strong pattern, and the shape

and length of the ears, which are made small and rounded, more or less as in *Aplodontia* and all the medium-sized to large terrestrial sciurids.

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