

THE OLIGOCENE RODENT *ISCHYROMYS* AND
DISCUSSION OF THE FAMILY ISCHYROMYIDAE

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Ischyromys is one of the most common elements in Oligocene faunas of western North America. There are hundreds of jaws, partial and complete skulls, and much skeletal material of this genus in collections across the country. No attempt has been made in the present study to look at all this material. Rather, types of all described species have been examined and several large samples from localities of early and middle Oligocene age in Montana, South Dakota, and Nebraska have been treated statistically to determine variation and trends within the genus. There is some question as to whether *Ischyromys* ranges into the late Oligocene (Howe, 1966: 1209) and even if it does, there are no late Oligocene samples available that are adequate for statistical treatment.

Wood (1937), the last worker to review these rodents, recognized four species of *Ischyromys* and two of a second genus, *Titanotheriomys*. The present study demonstrates that only two of these species are valid, that both belong in the genus *Ischyromys*, and that *Titanotheriomys* is a synonym of Leidy's genus *Ischyromys*. In addition a third new species is here recognized, based upon material unavailable at the time of Wood's work. This material is from McCarty's Mountain, Montana, and represents what is probably the earliest known species of the genus. Morphologically it is the most primitive and appears to stand in an ancestral position to the later populations.

Wood (1937, 1955, 1959, 1962) has consistently separated the Ischyromyidae (*Ischyromys* and *Titanotheriomys* in his classification) from the Paramyidae. The family Ischyromyidae was erected by Alston (1876) for *Ischyromys*, and many later authors (for example, Matthew, 1910, Simpson, 1945, Wilson, 1949) referred *Paramys* and its relatives to this family. In his earlier work Wood included *Pareumys* in the Ischyromyidae, but Burke (1938) and Wilson (1940) have shown that

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this genus is a cylindrodontid, an assignment later followed by Wood (1955). Wood distinguishes the Ischyromyidae from the Paramyidae because the former have developed cheek-teeth with lophs or crests within which the primary cusps of earlier paramyids have been submerged, and because the ischyromids show some tendency towards a migration of the masseter off the ventral surface onto the anterior face of the zygoma. He states (1962: 247) "The limits of the Paramyidae have been set, in this paper, at the point where teeth, whose cusps are beginning to unite into crests, evolve into teeth whose crests are still clearly formed from cusps. As a result, the boundaries between the Paramyidae and the Sciuravidae or Pseudosciuridae are completely arbitrary." The Sciuravidae and Pseudosciuridae, as well as many other rodent families, were probably derived from paramyids, and at the time of origin of any one group, could not be separated from other contemporary paramyids. There are, however, many valid reasons for recognizing distinct families for these groups. Sciuravids had an extensive Eocene radiation and by the late early Eocene were quite distinct in dental and skull structure from paramyids. Pseudosciurids have a European history from the middle Eocene into the middle Oligocene, and as Lavocat (1951) has shown, were ancestral to the European Theridomyidae. Pseudosciurids were derived from paramyids but soon began to develop a fifth crest in the molars, and rapidly diverged from the typical paramyid condition. The ischyromyids (*sensu* Wood), however, never underwent a further radiation and in the short history of the genus *Ischyromys* there is no indication of appreciable departure from the typical late Eocene paramyid morphology. The four-crested condition of the molars was emphasized, but cusps are still prominent even in the latest population of the genus. Early Oligocene populations are only slightly advanced in this character over such late Eocene paramyids as *Rapamys* and *Mytonomys*, and are certainly no more advanced than the early Oligocene *Prosciurus*, which all workers consider a paramyid.

Although the actual ancestors of *Ischyromys* are not known, there has been general agreement that ischyromyids and paramyids, if not members of the same family, are certainly closely related. (For a comprehensive review of the history of ischyromyid and paramyid classification, see Wood, 1955, 1962.)

Evidence presented below shows that but a single genus with three species is contained within Wood's concept of the Ischyromyidae. In addition, the oldest species of the genus displays a number of features

that bridge the gap between the crested or lophate teeth of later *Ischyromys* and the cusperate teeth of other members of the family. The migration of the masseter onto the forward face of the zygoma is limited in all *Ischyromys* skulls examined and does not appear to be greatly different from the condition discussed by Wood (1962: 64-65, 82) for *Leptotomus*, particularly *Leptotomus grandis*. For this species Wood (1962: 82) states, "The infraorbital foramen is well forward, its median margin being appreciably in front of P³, and is markedly recessed. There is a broad slope of the maxillary between the foramen and the masseteric fossa on the zygoma. This suggests the possibility that this space between the foramen and the zygoma was in the process of expanding which could well have been a prerequisite for the "sciuromorph" type of zygomasseteric structure." This is exactly the condition seen in all *Ischyromys* skulls examined. In all other features of the skull and mandibles *Ischyromys* is similar to the genera included by Wood in the Paramyidae. I do not see any valid reasons for maintaining this genus in a distinct monotypic family removed from its close allies. It has been suggested (Burke, 1937; Wilson, 1949: 99) that the ancestors of *Ischyromys* are probably to be found within the family Sciuravidae (Sciuravinae of Wilson). Arguments are presented below against this view, however. The ancestry of this genus certainly is from one of the late Eocene paramyines, as suggested by Wood (1962: 243, fig. 90).

Ischyromys was undoubtedly derived from a paramyine, and is only separated from late Eocene paramyines such as *Leptotomus*, *Thisbemya*, and *Rapamys* by a few details of cheek-tooth morphology, none of which are any greater or of more fundamental importance than the differences seen between dentitions of the late Eocene genera themselves. I therefore consider *Ischyromys* and all the genera included by Wood (1962) in the Paramyidae to belong within a single family. This, by both priority and usage, is the family Ischyromyidae.

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Abbreviations used in the paper are: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; CM, Carnegie Museum; UM, University of Montana; YPM, Yale Peabody Museum; N, number; O.R., observed range; M, mean; s, standard deviation; V, coefficient of variation; B, estimate of the slope of Bartlett's "best fit" line; t, Student's t-statistic; P, tabulated probability from Student's t-distribution.

SYSTEMATIC REVIEW

Order Rodentia

Suborder Sciuromorpha

Family Ischyromyidae

Ischyromys Leidy, 1856

Ischyromys Leidy, 1856.

Colotaxis Cope, 1873a.

Gymnoptychus Cope, 1873b (in part).

Titanotheriomys Matthew, 1910.

TYPE: *Ischyromys typus* Leidy, 1856.

DIAGNOSIS: Upper and lower molars with four transverse crests; cusps most prominent in earliest species, becoming progressively more lophodont; infraorbital foramen vertically elongate oval, relatively large; masseter restricted to inferior border of zygoma and maxillary plate below infraorbital foramen; bulla co-ossified with skull; skeleton subfossorial.

RANGE: Early to late (?) Oligocene of western North America.

REFERRED SPECIES: *Ischyromys veterior* (Matthew) and *Ischyromys douglassi*, new species.

The skull, mandibles, dentition, and skeleton of *Ischyromys* have already been exhaustively described by Wood (1937) and the dentition more recently reviewed by Howe (1966). These descriptions will not be repeated here, although the skull of *I. douglassi* is compared in detail with that of *Paramys*. Wood demonstrated that the habitus was probably fossorial, somewhat similar to that of marmots and prairie dogs today, but *Ischyromys* was not as highly specialized for this niche as are *Marmota* and, particularly, *Cynomys*. The skeleton resembles most closely that of the Eocene *Paramys* and the modern *Aplodontia*. The skull resembles those of *Paramys* and *Leptotomus* in most details. The most notable exceptions are the co-ossified bulla of

Ischyromys (a character it shares with the other Oligocene ischyromyids, *Prosciurus* and *Cedromus*) and the much greater length of the pterygoid region in *Paramys*.

Since Wood's work of 1937 there has been no evaluation of the species within the genus *Ischyromys* and no attempt to establish species parameters or phylogenetic trends through the Oligocene. All species referred to *Ischyromys* are here considered and various changes through time within this conservative group are discussed.

Ischyromys typus

Ischyromys typus Leidy, 1856.

Ischyromys cristatus Cope, 1873a.

Gymnoptychus chrysodon Cope, 1873b.

Ischyromys chrysodon Cope, 1873c.

Ischyromys pliacus Troxell, 1922.

Ischyromys troxelli Wood, 1937.

TYPE: ANSP 11015, skull lacking anterior portion of rostrum, both zygomata, right P³-M¹, M³, and right bulla.

HORIZON AND LOCALITY: Type probably from middle Oligocene, White River Formation, South Dakota; *Colotaxis cristatus* from the Oligocene of Nebraska; *I. chrysodon* from the Oligocene of Colorado; type of *I. pliacus* from Cherry Creek, Wyoming; type of *I. troxelli* from the Middle Oreodon Beds, Sheep Mt., South Dakota.

DIAGNOSIS: Near size of *I. douglassi*, possibly slightly smaller; no conules present in lophs of upper molars; teeth four-crested; sagittal crest always present.

GEOLOGIC AND GEOGRAPHIC RANGE: Middle to possibly late Oligocene of the Great Plains.

DISCUSSION: *Ischyromys typus* is the common species of the Orellan and may extend into the Whitneyan (Howe, 1966: 1209). This species is larger than *I. veterior* but resembles it in most other respects.

Cope's two species were early realized to be synonymous with *I. typus*, but *I. pliacus* and *I. troxelli* have generally been considered to be distinct. Wood (1937: 191) states, "*I. troxelli* agrees closely with *I. typus* in size, differing, however, in a number of important characters from it. The interparietal is triangular, as in *I. pliacus*. The postorbital constriction is narrow as in that form, being only 8 mm. wide. The orbit, however, is long, being not only relatively, but absolutely, longer than in *I. pliacus*, and much longer than in *I. typus*."

On the basis of size and cheek-tooth pattern, the types of *I. troxelli* and *I. typus* are identical. The interparietal mentioned by Wood is

not preserved on the skull of *I. troxelli*; is unknown for *I. pliacus*, as the type of that species is a lower jaw; and is broadly triangular in *I. typus*. The postorbital constriction is 8 mm. in *I. troxelli* and 9 mm. in *I. typus*. In a series of *Ischyromys* skulls from McCarty's Mountain, Montana, the postorbital constriction varies from 8.0 mm. to 9.2 mm. within the population. The length of orbit, from the posterior opening of the infraorbital foramen to the sphenoidal fissure, is 21 mm. in the type skull of *I. typus* and 21.3 mm. in the type skull of *I. troxelli*. None of the features mentioned by Wood as distinctive for *I. troxelli* is significantly different from the conditions found in *I. typus*. *I. troxelli* is, therefore, a synonym of *I. typus*.

The type of *I. pliacus* is a lower jaw, YPM 12511, and hence cannot be compared directly to the type of *I. typus*. However, lower jaws are associated with the type of *I. troxelli* and these are indistinguishable from the *I. pliacus* jaw. Again on size and morphology there is no basis for recognizing two species. *I. pliacus* is a synonym of *I. typus*.

Ischyromys veterior Matthew

Figures 1-6, 13-15

Ischyromys veterior Matthew, 1903.

I. (Titanotheriomys) veterior Matthew, 1910.

Titanotheriomys veterior Wood, 1937.

Titanotheriomys wyomingensis Wood, 1937.

Ischyromys parvidens Miller and Gidley, 1920.

Ischyromys typus nanus Troxell, 1922.

TYPE: AMNH 9658, left mandible with P₄-M₃.

HORIZON AND LOCALITY: Early Oligocene, Pipestone Springs (including main locality and localities such as Fence Pocket and Little Pipestone), Jefferson Co., Montana. *Titanotheriomys wyomingensis* is from Beaver Divide Titanotherium Beds, also early Oligocene. *Ischyromys parvidens* is from the Oreodon Beds, Washington Co., South Dakota, probably early middle Oligocene. *I. typus nanus* is from the lower Oreodon Beds of the Warbonnet Ranch, 12 miles north of Harrison, Nebraska (Troxell, 1922: 124), middle Oligocene.

DIAGNOSIS: Smallest species of genus; molars four-crested, conules partially to completely submerged in lochs of upper molars; temporal crests not always fused into single sagittal crest.

GEOLOGIC AND GEOGRAPHIC RANGE: Early Oligocene of Montana to middle Oligocene of the Great Plains.

Discussion: Although this species was originally placed in the genus

Ischyromys, Matthew later (1910) erected a new subgenus, *Titanotheriomys*, for *I. veterior* and referred material from Beaver Divide to it. Wood (1937) elevated *Titanotheriomys* to full generic rank and separated the Montana and Wyoming populations as distinct species. Matthew (1910) stated that in *I. veterior* the preorbital portion of the skull was shorter than in typical *Ischyromys*, that there was no sagittal crest in *I. veterior*, and that the origin of the masseter was farther forward in this species than in *I. typus*. He based these conclusions primarily on skull material collected by Granger from Beaver Divide, Wyoming, in 1909, and not on material from Pipestone Springs, the locality from which *I. veterior* was described. Wood (1937) believed that these differences from other *Ischyromys* species warranted recognition of *Titanotheriomys* as a distinct genus of ischyromyid. Again his description of the skull of this genus was based on the Beaver Divide material, as no adequate skull material of *I. veterior* from Pipestone Springs was then available for study. Wood distinguished the Beaver Divide material as a new species, *I. wyomingensis*, and used this skull material to characterize the genus *Titanotheriomys*, although *I. veterior* was its type species.

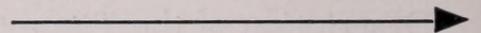
Wood (1937: 194) states that the skull of *I. veterior* is smaller than that of most species of *Ischyromys* but that it probably was near the size of *I. parvidens*, although no skulls were then known of that species. He goes on to discuss the much shorter muzzle, lack of sagittal crest, relatively larger braincase, and larger masseteric plate of *Titanotheriomys* in relation to *Ischyromys*. He places particular stress on the expansion of the maxillary which he states (1937: 195), "forms a considerable portion of the floor [of the orbit], as opposed to *Ischyromys*, where there is usually no such plate . . . In *Titanotheriomys*, however, the area of the origin of the masseter, below and behind the infraorbital foramen, continues the slope of the anterior face of the zygoma, instead of being horizontal, as in *Ischyromys* . . . In *Ischyromys*, the area of origin of the masseter is sharply limited to the ventral surface of the zygoma, posterior and below the infraorbital foramen. This area is not horizontal, but slopes upward at a lesser angle in *Titanotheriomys*."

Description of the *Titanotheriomys* skull was based upon one nearly complete skull (AMNH 14579) and the anterior portion, palate to incisors, of another (AMNH 14581) from Beaver Divide. Both skulls show considerable distortion, having been crushed dorso-ventrally after deposition, as well as some antero-posterior distortion along the

midline. This crushing has affected the depth of the rostrum, causing it to appear shallower than it must have been in life. Flattening has also caused expansion of the braincase laterally, causing it to appear wider and flatter than it must have been originally. The anterior end of the rostrum has been destroyed in both specimens, and the antero-posterior sliding of one half of the skull on the other has also caused some distortion in the muzzle. This does not appear to be too great, however. The anterior end of the zygoma has been little disturbed in AMNH 14579. It is unfortunate that neither Matthew nor Wood mentioned the condition of the material available in their discussions or illustrations of the skull structure in *Titanotheriomys*. As will be shown below, a great deal of the supposed difference between *Titanotheriomys* and *Ischyromys* is due to distortion in the Beaver Divide skull.

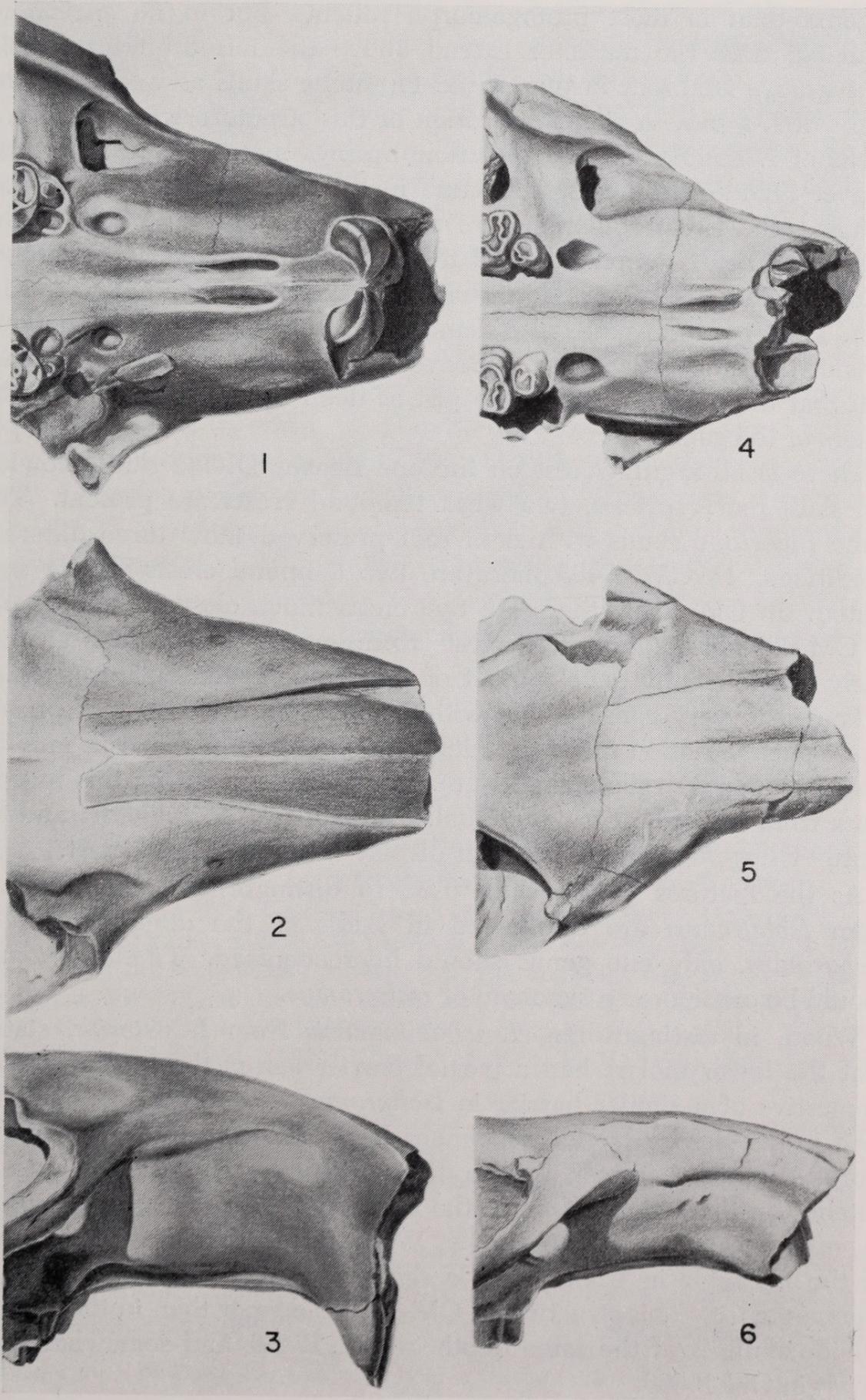
Several nearly complete skulls of *Ischyromys veterior* from Pipestone Springs are now available and allow for comparisons between *I. veterior*, *I. wyomingensis*, and other species of *Ischyromys*. One of the Pipestone skulls (CM 9058) is completely undistorted, although the right parietal, the basicranium, and the occiput are missing. A second skull (CM 17453), although badly broken, is not crushed, and shows the rostrum, anterior zygomatic root and plate, and the skull roof nearly intact. A third (CM 10660) is nearly complete but crushed in the manner described for the Beaver Divide skull.

The Pipestone Springs skulls demonstrate that the skull of *I. veterior* and that of *I. wyomingensis* are identical. The maxillary below the large oval infraorbital foramen slopes gently backward and does form part of the floor of the orbit as stated by Wood. However, this condition is also seen in the small portion of the masseteric plate preserved on the right side of the type skull of *I. typus*, is present on other skulls of *I. douglassi* from McCarty's Mountain, and indeed seems to be a general feature of all *Ischyromys* skulls examined. There is slight variation in the angle of the masseteric plate in various populations but nowhere have I seen it horizontal or even significantly different from the condition in *I. veterior*. In AMNH 14579 and CM 17453 there is a slight groove lateral to the infraorbital foramen indicating that part of the lateral masseter may have originated higher on the



Figs. 1-3. Ventral, dorsal, and lateral views of rostrum and anterior zygomatic root of the skull of *Ischyromys veterior*, CM 9058, approx. x 2.

Figs. 4-6. Same views of skull of *Ischyromys veterior*, AMNH 14579, type of "*Titanotheriomys wyomingensis*," approx. x 2.



zygoma than in most protogomorph rodents, but in no specimens available does the masseter extend above the infraorbital foramen. This groove is absent in two of the Pipestone skulls as well as in the skulls of *I. typus*. A slight indication of this structure is seen in some skulls of *I. douglassi*. The Pipestone Springs material and that from Beaver Divide are clearly the same in the structure of the zygoma.

Again the two populations are identical in shape and size of the rostrum. The diastemal length of P³-I in four Pipestone skulls averages 14.5 mm. In the somewhat distorted Beaver Divide skull, it is 13.8 mm. The Pipestone skulls also demonstrate that the apparent shallowness of the muzzle seen in the Beaver Divide specimens is an artifact and that the muzzle is relatively just as deep in this species as in the others of the genus.

There is no sagittal crest on the one Beaver Divide skull showing the skull roof. Instead, two weak temporal crests are present. The three Pipestone skulls with skull roof preserved show three different conditions. In CM 17453 there are two temporal crests widely separated. In CM 10660 there are two crests much closer together, and in CM 9058 a single sagittal crest is present. As these crests are entirely controlled by development of the temporal musculature, which is known to vary considerably within populations, it is not surprising to see such variation in this species. The variation in this case may be sexual or merely reflect slightly different development of this muscle mass from individual to individual. All skulls of *I. douglassi* and all those of *I. typus* that I have seen display a single sagittal crest.

As the features of the skull used to distinguish *Titanotheriomys* from *Ischyromys* are duplicated in skulls of the other species of *Ischyromys*, only one genus should be recognized. *Titanotheriomys* should be considered a synonym of *Ischyromys*.

Wood, in distinguishing *I. wyomingensis* from *I. veterior*, stated that the lower molars had a partial barrier across the median valley suggestive of a similar barrier in *Ischyromys*. This barrier cannot be seen in the Beaver Divide specimens because the teeth are too badly worn. Another character used to distinguish the two species, depth of notches on the external face of the paracones, also is lost in *I. wyomingensis* because of wear. Finally, Wood stated that the pit for part of the masseter in front of P³ is shallower in *I. veterior* than in *I. wyomingensis*. This structure in CM 9058 is deeper than in the Beaver Divide skull, is of the same depth in CM 17453, and somewhat shallower in CM 10660.

In view of the great similarity in all characters of the Beaver Divide and Pipestone specimens, only a single species should be recognized. The valid species is *Ischyromys veterior*.

Ischyromys parvidens (Miller and Gidley, 1920) is also here considered a synonym of *I. veterior*. In their original description Miller and Gidley distinguished this species from *I. veterior* on the basis of the shallower and more slender lower jaw of the latter. With the large sample of jaws now available, this distinction breaks down completely. On size of teeth and their morphology *I. parvidens* is certainly conspecific with *I. veterior*.

I. typus nanus (Troxell, 1922) which Wood refers to *I. parvidens* certainly represents *I. veterior*. Troxell's specimen comes from the Warbonnet Ranch north of Harrison, Nebraska. In the Carnegie Museum collections there are 17 jaws of *Ischyromys* that are probably from the same locality as Troxell's specimen. These were collected in 1901 by O. A. Peterson. As is shown below, a statistical study of this population, of the material from the Nebraska Orellan referred by Howe (1966) to *I. parvidens*, and of the *I. veterior* population from Pipestone Springs clearly demonstrates that all these samples represent but a single species.

*Ischyromys douglassi*¹ new species

Figures 7-12, 16-17, 19-20

TYPE: CM 1122, partial skull lacking parietals, left bulla, occiput, left P³ and M³.

HORIZON AND LOCALITY: Early Oligocene, McCarty's Mountain, Montana.

HYPODIGM: CM 1053, skull and jaws; 1120, parts of skeleton; 1122, skull; 1123, skull; 1125, right mandible; 1133, partial skull and RdP₄-M₂; 9254, left mandible; 9976, edentulous skull; 9986, LM₁-M₂; 9987, RP₄-M₃; 9995, RM₂-M₃; 10957, partial skull with RP³-M¹ and LP³-M³; 10963, RP₄-M₂; 10966, skull; 10967, skull and jaws; 10968, RM₂; 10969, RM₁-M₃; 16741, RP³-M¹ and LP₄-M₃; UM 0866, RP₄-M₃; 0932, RM₂-M₃; 1933, LP₄-M₁; 0936, LdP₄-M₃; 1801, LM₁-M₂; 1802, RP₄-M₃.

DIAGNOSIS: Near size of *Ischyromys typus*; metaconule distinct in upper molars, metaloph constricted at hypocone; lingual notch between protocone and hypocone shallow; hypolophid low, narrow, sometimes incomplete; small cusp on posterior slope of metalophid.

DESCRIPTION: The upper third premolar is large and rounded, presenting a single conical cusp with a small basin posterior to it. This basin is enclosed posteriorly by a thin ridge which merges into the

¹Named for Earl Douglass, who pioneered work on Tertiary mammals in Montana.

base of the single cusp both buccally and lingually. When completely unworn the tooth has a very shallow basin along the anterior face of the single cusp. This tooth is large in all *Ischyromys* and in many other ischyromyids, while in other sciuriform groups such as the Sciuridae, Aplodontidae, and Cylindrodontidae it has been reduced to a small, simple, peg-like structure, or lost entirely.

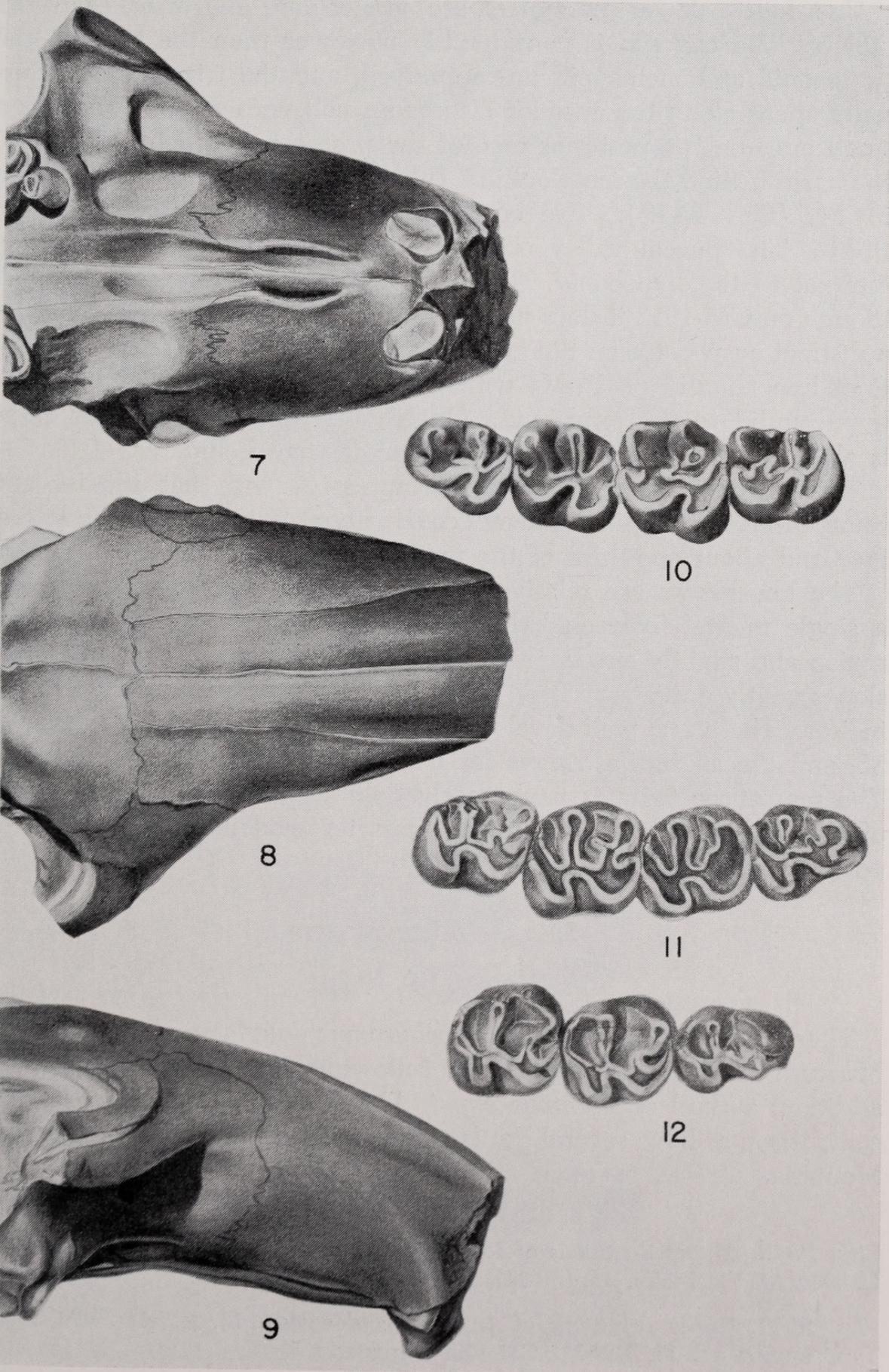
The fourth upper premolar (figs. 16-17) is basically similar in pattern to M^1 - M^2 except that the hypocone is not as fully developed, and the groove between the protocone and hypocone is not present. On M^1 and M^2 the protocone and hypocone are nearly of equal size, but the lingual groove between them is not as deep as that in *I. veterior* or *I. typus*. The protoloph is complete on P^4 - M^2 and there is no distinguishable protoconule. In contrast the metaloph on these teeth is either incomplete or only weakly joined to the hypocone, and the metaconule is always large and distinct. In one specimen, CM 10966, the metaloph sends a small, narrow spur into the slope of the protocone and is separated from the hypocone by a narrow notch. On P^4 there is a short spur directed anteriorly from the protoloph to the raised anterior cingulum ridge. This structure is not seen on M^1 - M^2 . The valley between the protoloph and anterior cingulum is closed on P^4 but open buccally on M^1 - M^2 . The posterior valley is closed on all teeth as the posterior cingulum fuses with the postero-internal slope of the metacone.

The third upper molar is quite variable both in size and morphology. In CM 10966 there is a small cusp, possibly a hypocone, behind the enlarged protocone, and there is also a distinct metacone, metaconule, and low metaloph. With the exception of the metaconule these structures are absent in all other *Ischyromys* examined, although complex M^3 posterior basins are common in Eocene ischyromyids such as *Thisbemys*, *Leptotomus*, *Paramys*, and *Rapamys*. In the other specimens of M^3 of *I. douglassi*, a large metaconule occurs, but there is no distinct hypocone, metacone, or metaloph.

The upper incisors are oval in cross section with slightly rounded anterior, lateral, and posterior faces. The medial margin is straight. Enamel is restricted to the anterior face, overlapping only slightly on the buccal margins of the teeth.

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Figs. 7-9. Ventral, dorsal, and lateral views of rostrum, and anterior zygomatic root of the skull of *Ischyromys douglassi*, CM 1122, approx. x 2.

Figs. 10-12. Lower dentitions of *Ischyromys douglassi*, 10. LP_4 - M_3 , CM 1053. 11. RP_4 - M_3 , CM 1125. 12. RP_4 - M_2 , CM 10963, all approximately x 3.5



The fourth lower premolars are longer and narrower than the molars. The trigonid is considerably narrower than the talonid, the protoconid and metaconid are appressed, and the trigonid basin usually opens along the anterior face as a small vertical slit. There is a small cusp on the posterior face of the protoconid which bulges into the basin behind the metalophid. This structure is quite prominent on M_1 - M_3 (figs. 10-12). The ectolophid is high and rather thick on P_4 - M_3 . The buccal valley on P_4 - M_3 is deep and curves posteriorly internal to the hypoconid. The hypolophid is usually complete, although on CM 1053 it does not reach the hypoconid but terminates in a distinct cusp between the entoconid and hypoconid. There is a distinct hypoconulid on P_4 - M_3 with little or no crest passing from the hypoconulid to the entoconid. On M_3 this posterior cingular ridge is elevated and passes into the base of the entoconid.

The lower incisors are quite compressed, with flat medial and rounded lateral margins. Enamel covers about two-thirds of the lateral face and about one-third of the medial face of the tooth.

The lower jaws are relatively heavy, although not deep. There is a single mental foramen below the dorsal surface of the diastemal region and slightly anterior to P_4 . The dorsal margin of the mandible slopes gently downward from P_4 and then rises in a smooth arc to the incisor. There is a well-developed pit between the alveolar border at M_3 and the ascending ramus for insertion of part of the temporalis. The masseteric fossa is very poorly delimited on the lateral margin of the ascending ramus, but the masseter evidently extended to a position below M_2 .

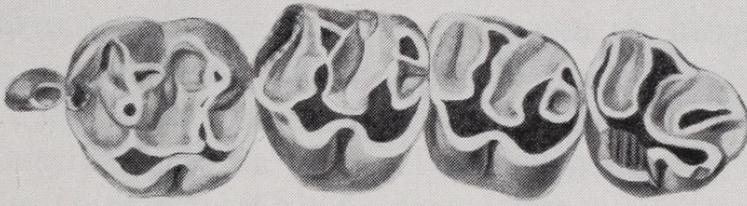
SKULL OF ISCHYROMYS

Figures 1-9, 18-20

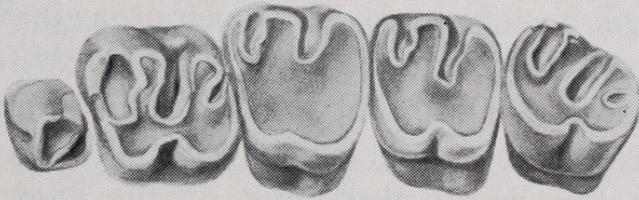
There are five partial skulls of *Ischyromys douglassi* in the Carnegie Museum collections on which the following description is based. In addition, a skull of *Paramys copei*, AMNH 4756, has been used for comparison as have several skulls of *I. veterior* from Pipestone Springs, Montana.

Fig. 13-15. Upper dentitions of *Ischyromys veterior*. 13. LP^3 - M^3 , CM 9058. 14. LP^3 - M^3 , AMNH 14579. 15. LP^3 - M^3 , CM 17453, all approx. x 6.

Fig. 16-17. Upper dentitions of *Ischyromys douglassi*. 16. LP^4 - M^2 , CM 1122, Type, approx. x 6. 17. LP^3 - M^3 , CM 10966, approx. x 5.



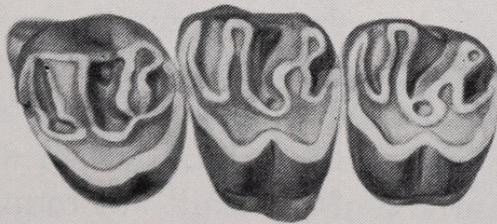
13



14



15



16



17

In over-all appearance the skull of *I. douglassi* is elongate, rather shallow through the cranium, and has an elongate, rather heavy, rostrum. In dorsal view the skull is narrow. The zygomatic arches are not preserved on any of the specimens of *I. douglassi*. The anterior root preserved on the type skull, however, suggests that the arches did not flare laterally to any great extent. In *I. veterior* the zygomatic arches are flattened laterally and pass directly posteriorly from the anterior zygomatic root. This is also the typical condition seen in *Paramys*, whereas in *Aplodontia* and *Cynomys* the arches flare out as they pass posteriorly. The dorsal surface of the skull is only slightly convex in lateral view from snout to occiput, as in *Paramys*. There is a slight bend in the basicranial axis in *I. douglassi*, comparable to that of *Aplodontia* and somewhat greater than that seen in *Paramys*. In general proportions the most striking difference between *Ischyromys* and *Paramys* is the great shortening of the pterygoid-alisphenoid region in *Ischyromys*. In *Paramys* the region between the posterior end of the tooth row and the foramen ovale is quite elongate, whereas in *Ischyromys* this region has been considerably shortened. In *Paramys* the alisphenoid canal is thus quite long and in *Ischyromys* is short. A condition similar to that in *Ischyromys* is seen in the skull of *Aplodontia*.

The occipital surface slopes very slightly to the rear from the dorsum of the skull to the condyles. This is also the condition in *Paramys* whereas in *Aplodontia* the occiput is vertical.

The nasals extend posteriorly to a line opposite the anterior zygomatic root. They are relatively narrow with the premaxillary extending considerably onto the skull roof. The frontal-premaxillary-nasal sutures form a rather straight line across the dorsal surface of the skull at the anterior end of the orbit. The maxillary does not quite reach to the dorsal surface of the skull but forms the sloping portion of the zygomatic root. The premaxillary-maxillary suture turns forward and then descends nearly vertically anterior to the root. The interorbital constriction is quite pronounced, with a slight protrusion anterior to the constriction, as seen in *Paramys* and *Sciuravus*. There is no postorbital process. The skull roof behind the orbits is either absent or badly damaged in all specimens of *I. douglassi*, but a low sagittal crest is present in CM 1123 quite similar to the crest seen in *Paramys copei*. The infraorbital foramen of *I. douglassi* is large and oval in shape. Under it is a rather broad plate of the maxillary for origin of part of the masseter. In *Paramys copei* there is only a small

rugose pit on the ventral border of the zygoma. The maxillary rises vertically above it to the inferior border of the infraorbital foramen. The *Ischyromys* condition is quite similar to that seen in *Leptotomus*, however, and no specimens show any indication that the masseter has spread off the ventral border of the zygoma. The posterior border of the anterior zygomatic root arises opposite P^4 and the infraorbital foramen opens well ahead of P^3 . In the maxillary just anterior to P^3 there is a well defined elongate depression showing the place of origin of part of the masseter.

The palate is of nearly uniform width and extends posteriorly to a line opposite the anterior end of M^3 . The maxillary-palatine suture lies on a line between P^4 and M^1 . The tooth rows converge only slightly posteriorly. In *Paramys* the palate extends opposite the posterior border of M^3 and the maxillary-palatine suture lies opposite the middle of M^1 .

The pterygoid region is quite short in *Ischyromys*—about half as long as it is in *Paramys*. This reduction is also seen in *Aplodontia* and in sciurids. The pterygoid plates are not well preserved in any specimens of *I. douglassi*. But it is obvious that both the entopterygoid and ectopterygoid plates were present and enclosed a narrow but rather deep trench for origin of the pterygoid musculature. The entopterygoid plate evidently did not reach the bulla, but the ectopterygoid plate did pass posteriorly to the foramen ovale.

Figures 18-20 show the interpretation here given to foramina in the alisphenoid and around the bulla in *Ischyromys*, with a reillustration of this area in the skull of *Paramys copei*, AMNH 4756. In *Ischyromys* the buccinator and masticatory foramina are separated by a thin bar of the alisphenoid as they pass laterally from the foramen ovale. In *Paramys* these foramina are farther forward, and the buccinator and masticatory nerves, as well as a branch of the internal maxillary artery, pass forward in the alisphenoid for a considerable distance anterior to the foramen ovale. The alisphenoid canal is also much longer in *Paramys* than in *Ischyromys*. The foramen ovale opens just anterior to the bulla in *Ischyromys*, as it does in *Paramys*. In *Ischyromys* there is a foramen at the anterior end of the pterygoid fossa which probably transmitted a vein connecting the internal maxillary veins. This canal and vein are present in sciurids and *Aplodontia* and probably, but not certainly, in *Paramys*.

Posteriorly between the bulla and the basioccipital, and overhung by the medial surface of the bulla, there are two foramina. The poster-

ior of these is here interpreted as the stapedia foramen, through which the stapedia artery passed. Just anterior to the stapedia foramen is another small foramen, believed to be the opening for the internal carotid artery, which then passed anteriorly between the bulla and basioccipital (but covered by the bulla) to enter the brain case at about the basioccipital-basisphenoid suture. In *Sciurus* only the stapedia artery is present (Guthrie, 1963), but in many other rodents both the stapedia and internal carotid are known. In *Paramys* a condition very similar to that suggested for *Ischyromys* seems to exist. Wood (1962: fig. 3C) has figured a foramen he calls the foramen lacerum posterius, at the postero-internal margin of the petrosal. He describes the foramen as having four distinct channels within it. The most anterior of these channels in my interpretation is probably a canal for the internal carotid artery, which passes medial to the promontorium through the petrosal and enters the brain case lateral to the foramen lacerum medium of Wood's figure. This course for the internal carotid corresponds almost exactly with that interpreted for *Ischyromys*. In *Ischyromys*, however, there is no evidence of a foramen lacerum medium. The bulla and petrosal are completely fused in *Ischyromys*, but in CM 1053 the thin bony spicules of the bulla were removed to show the bone flooring the brain case in this region. The course of the carotid can, I believe, be traced with some confidence. A single hypoglossal foramen is present just anterior to the condyle in *Ischyromys* and only one hypoglossal foramen is present in *Paramys copei*, AMNH 4756.

The basicranial region of *Ischyromys* is seen to be quite similar to that of *Paramys*. The major changes are a shortening of the pterygoid-alisphenoid area. As a result, the foramina in this area are much closer together in *Ischyromys*, and bulla and petrosal are completely fused in that genus. The number and relative positions of the openings for arteries, veins, and nerves have remained the same, however.

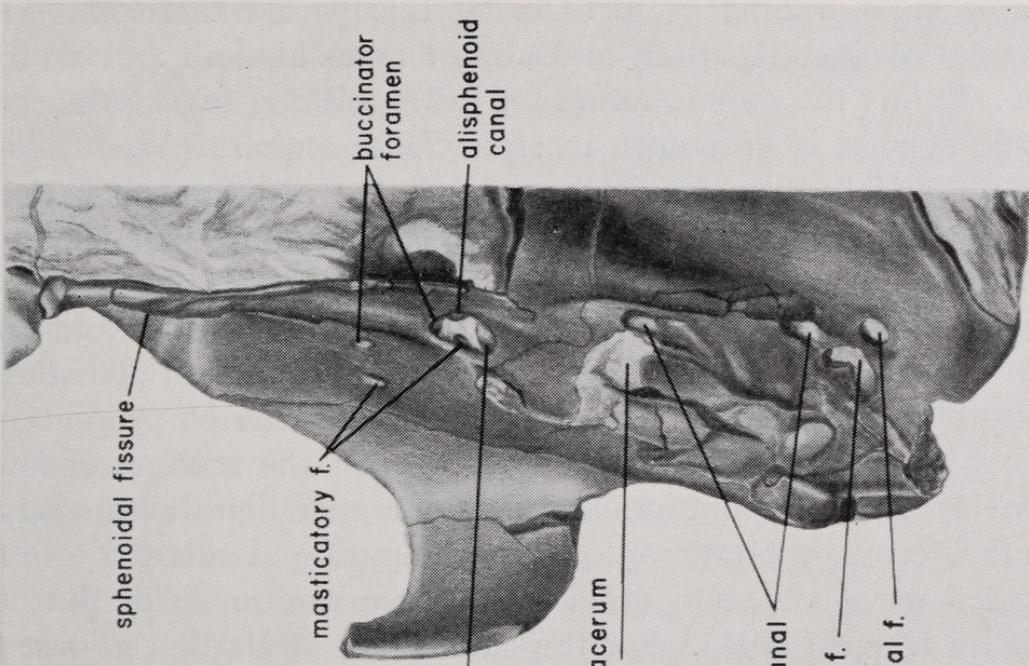
TRENDS WITHIN ISCHYROMYS

Ischyromys first appeared in the early Oligocene and probably persisted into the early late Oligocene. Thus its temporal range is no more

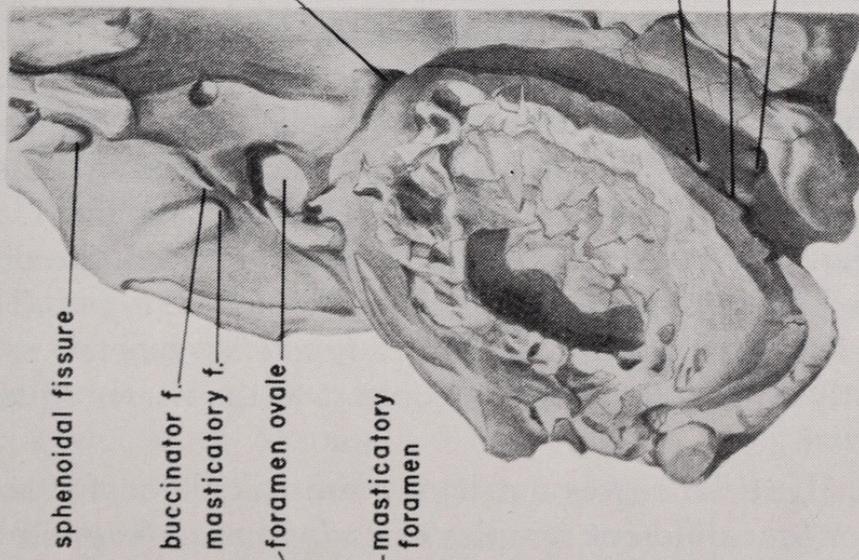
Fig. 18. Ventral view of basicranium of *Paramys copei*, AMNH 4756, x 3.

Fig. 19. Ventral view of basicranium of *Ischyromys douglassi*, CM 1122, Type, x 3.

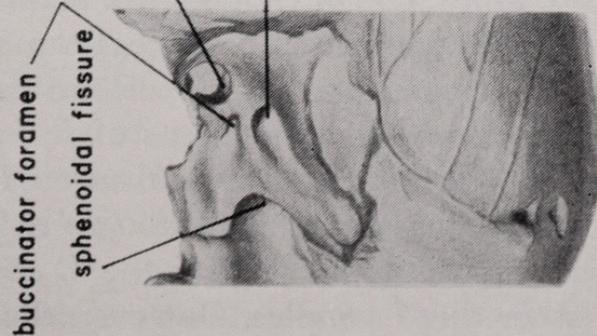
Fig. 20. Lateral view of orbit and anterior portion of ear region of *Ischyromys douglassi*, CM 1122, Type, x 2.5. This specimen was drawn with the dorsal surface of the skull at the bottom to allow for necessary lighting of this area.



18



19



20

than six to eight million years. During this period there was very little change in dental pattern and almost none in skull and skeletal structure. In fact the only criterion for distinguishing two of the three recognized species is difference in size. Some authors (Wood, 1937, Troxell, 1922, Galbreath, 1953) have suggested a difference in tooth proportions from species to species but this has never been demonstrated statistically.

Several large samples of *Ischyromys* from single localities and horizons were available for this study. They were evaluated statistically in an effort to demonstrate the presence or absence of proportional differences between species or through time. As the number of lower dentitions available far outnumbers that of upper dentitions, analysis only of the former was attempted. In computing standard deviation and coefficients of variation (tables 1-3), use was made of the data supplied by Howe (1966). For the calculation of Bartlett's "best fit" straight line in the regression graphs of figures 21-26, only data from specimens in the Carnegie Museum collections were used. Howe's raw data, which he kindly supplied, did not include paired measurements and hence could not be used in this type of problem.

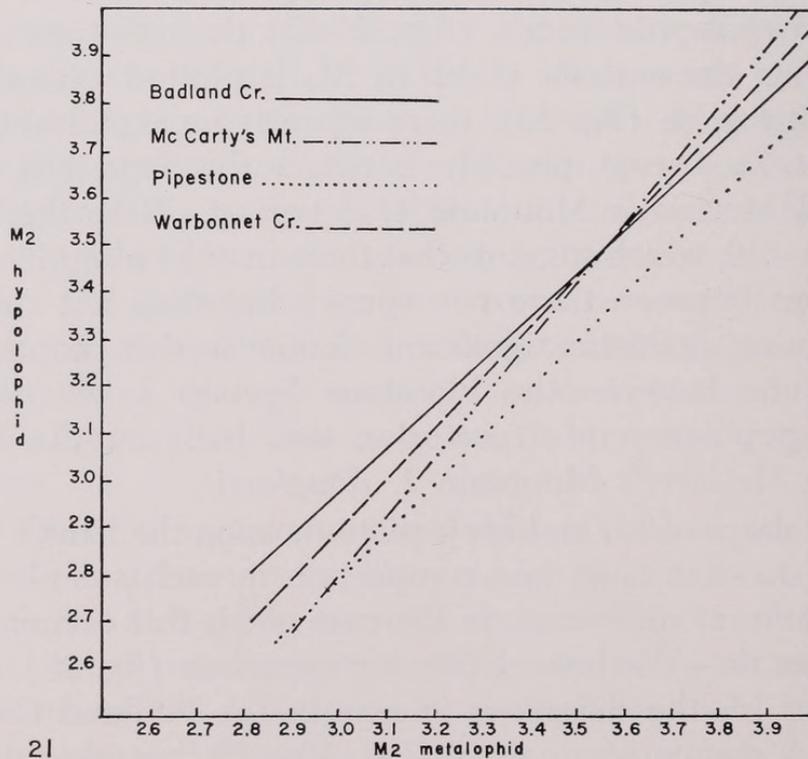
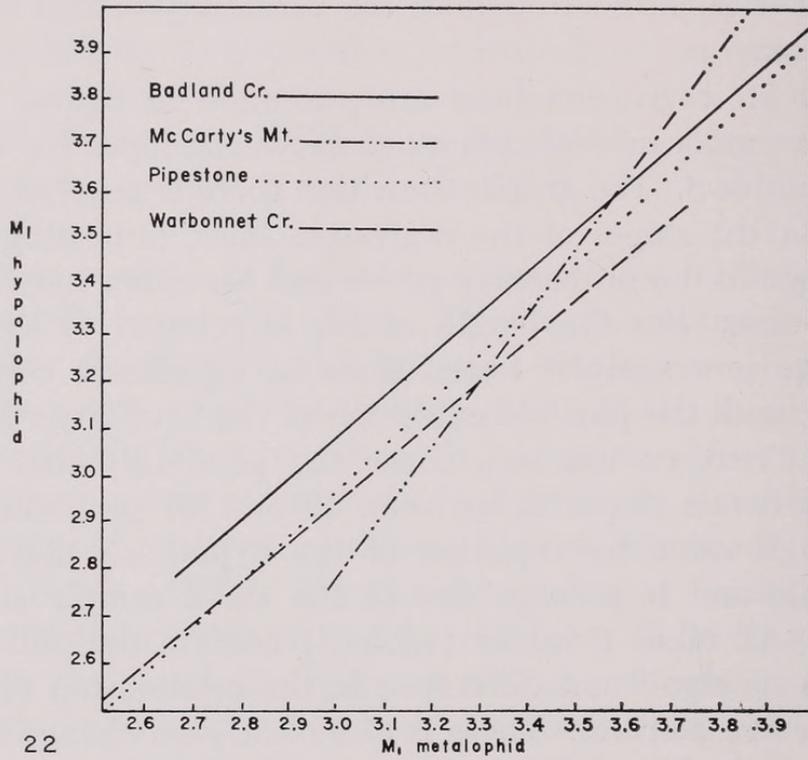
The standard meristic parameters for the species of *Ischyromys* are given for lower cheek teeth in table 2. *Ischyromys douglassi* and *Ischyromys typus* are quite close in size with *I. douglassi* having cheek teeth that are somewhat wider in relation to tooth length than those of *I. typus*. This is most notable in the transverse dimensions of M_1 and M_2 . In all other measurements, *I. douglassi* and *I. typus* are quite similar. All three samples of *I. veterior* average considerably smaller in all measurements than *I. douglassi* and *I. typus*. The molars of *I. veterior* agree with those of *I. typus* in general proportions, being slightly longer than wide in contrast to the nearly square molars of *I. douglassi*.

Bartlett's "best fit" regression lines were calculated for six pairs of variables for four different samples of *Ischyromys*. One sample represents a population of *I. typus*, one of *I. douglassi*, and two of *I. veterior*. There was a rather wide range in sample size, from 80 specimens for some measurements of *I. veterior* from Pipestone Springs, to a low of only 11 specimens for some measurements of *I. douglassi*. Sample sizes were adequate for all measurements taken on *I. veterior* and *I. typus* and were also probably sufficient for *I. douglassi*. The coefficient of variation was generally lower (table 2) for the *I. douglassi* measurements than for the other three samples. But even the lowest, $V=3.32$

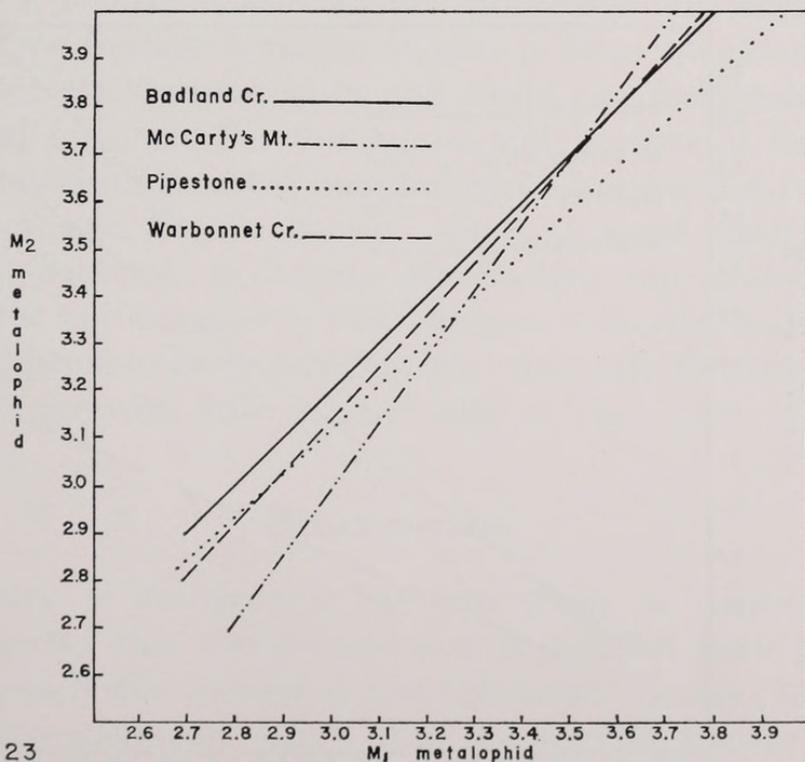
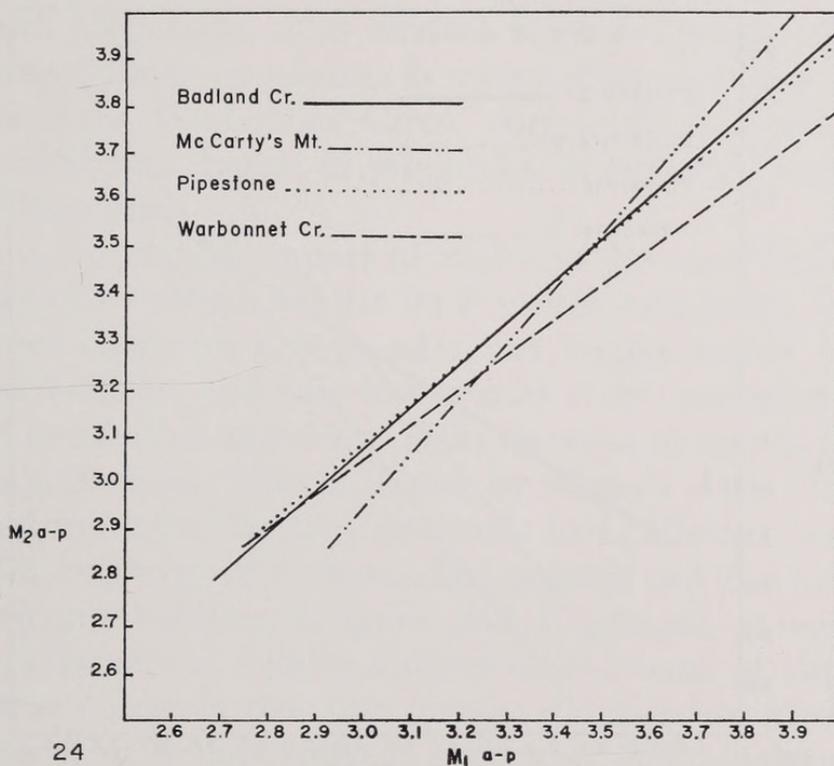
M₁ transverse metalophid, does not suggest that the sample is too small to provide a reasonable estimate of the variability of that character in the population.

The "best fit" regression lines are presented in figures 21-26, and the tests for significance of difference between slopes for each graph are given in table 3. The graphs show that there is generally very close agreement in the slopes of the regression lines, indicating that there is little change in the proportions of M₁ and M₂ either between species or through time. For the length of M₁ in relation to length of M₂ (fig. 24), the four samples tested show no significant difference between them, with the possible exception of the McCarty's Mountain—Warbonnet Creek comparison. Here the possibility that there is a difference between slopes is between 10 and 20 per cent. This is a relatively high value for rejection of the hypothesis that the slopes are the same, and is perhaps due to the small sample size for this comparison. All other P values (table 3) confirm the null hypothesis that there is no significant difference in the relationship of M₁ to M₂ for the other five pairings. There is also clearly no change in the relation of M₁ metalophid width to M₁ hypolophid width or of M₂ metalophid to M₂ hypolophid width, (figs. 21-22) through time or between species. When the anterior width of M₁ is plotted against the same measurement for M₂ (fig. 23), there again is no significant difference between species except possibly between the Pipestone Springs *I. veterior* and McCarty's Mountain *I. douglassi*. Here the P value is between .05—.10, which suggests that there may be a significant change in proportions between these two species but does not strongly confirm it. Arguing against a significant change in this proportion is the absence of one between the Pipestone Springs *I. veterior* and the Warbonnet population of *I. veterior*, and between the Warbonnet sample and McCarty's Mountain *I. douglassi*.

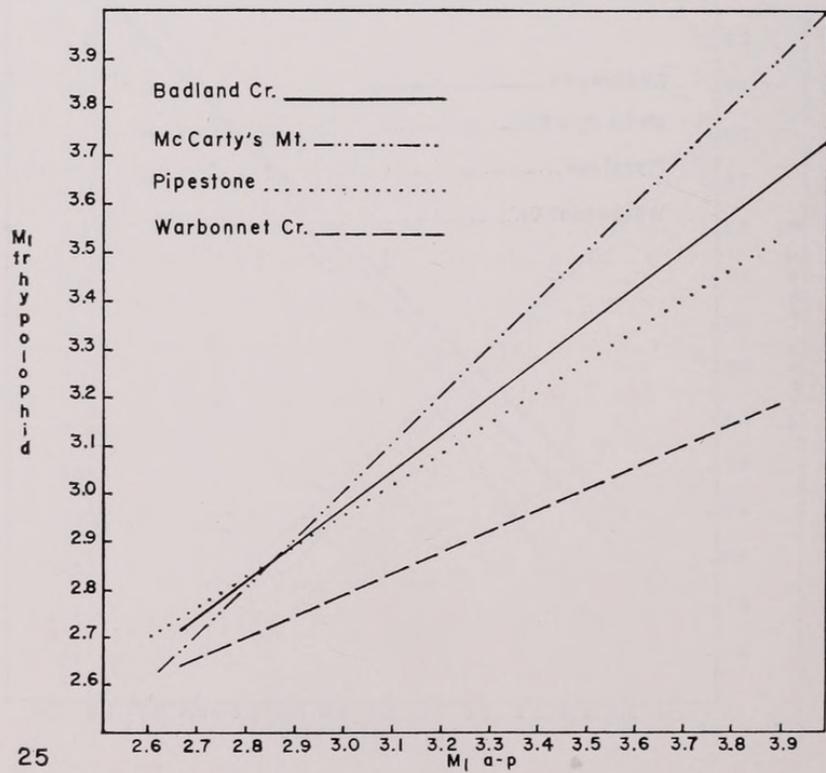
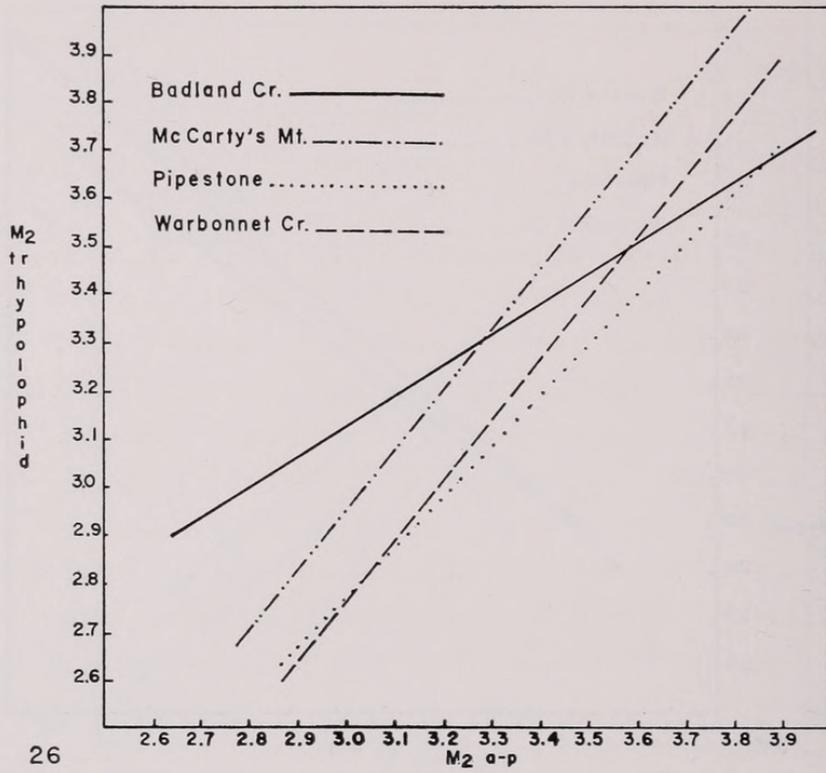
When the shape of M₁ and M₂ is plotted, using the length versus posterior width in each case, one comparison in each sample suggests a possibly significant difference. In the case of M₁ this occurs in the McCarty's Mountain—Warbonnet Creek comparison (fig. 25), where P is .05—.10. For M₂ the difference is seen in the Badland Creek—Warbonnet Creek comparison, where P is .10—.20, but close to .10. For M₂ (fig. 25) this may indicate a real divergence between *I. typus* and *I. veterior* by the middle Oligocene in the proportions of M₂, although a similar change is not found in M₁ where P is .50—.60 for these two species. The difference in M₁ shape between McCarty's Mountain



Figs. 21, 22. Bartlett's "best fit" regression lines for four populations of *Ischyromys*. Badland Creek=*I. typus*, McCarty's Mountain=*I. douglassi*, Pipestone Springs = *I. veterior*, Warbonnet Creek = *I. veterior*. **Fig. 21.** Variables M₂ hypolophid and M₂ metalophid. **Fig. 22.** Variables M₁ hypolophid and M₁ metalophid.



Figs. 23, 24. Bartlett's "best fit" regression lines for four populations of *Ischyromys*. Badland Creek = *I. typus*, McCarty's Mountain = *I. douglassi*, Pipestone Springs = *I. veterior*, Warbonnet Creek = *I. veterior*. **Fig. 23.** Variables M_2 metalophid and M_1 metalophid. **Fig. 24.** Variables M_2 a-p and M_1 a-p.



Figs. 25, 26. Bartlett's "best fit" regression lines for four populations of *Ischyromys*. Badland Creek = *I. typus*, McCarty's Mountain = *I. douglassi*, Pipestone Springs = *I. veterior*, Warbonnet Creek = *I. veterior*. **Fig. 25.** Variables M_1 tr hypolophid and M_1 a-p. **Fig. 26.** Variables M_2 tr hypolophid and M_2 a-p.

I. douglassi and the Warbonnet Creek *I. veterior* does show a real shift in tooth proportion. It is obvious from the graph (fig. 25) that the Pipestone Springs population is intermediate between *I. douglassi* and the younger Warbonnet Creek sample of *I. veterior*. In this lineage a significant change in proportion is indicated from the early to middle Oligocene.

In general, M_1 and M_2 appear to evolve in the same direction in the four populations studied. Of the 36 P values calculated, only four in four different character groups offer any suggestion of a difference between populations, and only in one case is this probably significant. One of the trends that is evident is an increase in size in the *I. typus* lineage through time. This is shown by Howe's data (1966: 1208). He assigned the later Orellan specimens to *I. pliacus*, which is here considered a synonym of *I. typus*, but pointed out the great overlap in measurements between *I. typus* and *I. pliacus*. Nevertheless, he believed *I. pliacus* was validly distinct on the basis of slightly larger size. There is no doubt that this lineage did increase in size through time. However, it is impossible to recognize individual specimens as belonging to *I. pliacus* unless they are quite large and *known to come from the upper Orellan horizons*. Given a large specimen of *Ischyromys* without stratigraphic data one could not distinguish between *I. pliacus* and *I. typus*. For this reason and because of the complete absence of any distinguishing morphological features I do not believe two species should be recognized. Given a good stratigraphic sequence of collections, a definite chronocline can undoubtedly be established for size increase in this lineage. A second lineage, that of *I. veterior*, appears to carry through from the early Oligocene into the middle Oligocene with little or no change in size.

RELATIONSHIPS

The ancestry of *Ischyromys* has long been in doubt. Matthew (1910) suggested that *Ischyromys* was descended from the Sciuravidae, particularly the Bridger genus *Sciuravus*. Burke (1937) reiterated this suggestion and stated that the middle Eocene *Sciuravus eucristadens* was reminiscent of the McCarty's Mountain *Ischyromys* material described here as *I. douglassi*. Wilson (1949) listed four factors suggestive of a sciuravid ancestry for *Ischyromys*, and three against such a relationship. Wood (1955) listed both paramyids and sciuravids as possible ancestors for *Ischyromys* but in 1962 he advo-

cated a paramyid ancestry alone, possibly from *Leptotomus* or a close relative.

In general the arguments for a sciuravid ancestry for *Ischyromys* have revolved around the lophate condition of the cheek teeth and the well developed hypocone of the upper molars. Both characters are clearer in the later forms than in the early Oligocene species. *I. douglassi* is the oldest known species of the genus and in this form the hypocone is not as completely separated from the protocone as it is in later forms. It is certainly less well developed than in various middle and late Eocene species of *Sciuravus* and is only slightly more distinct than in *Leptotomus* or *Rapamys*. In addition a metaconule is distinctly present in the metaloph of *I. douglassi*, whereas it is absent in *Sciuravus* but generally prominent in Eocene paramyines. Further, some specimens of *I. douglassi* show the metaloph passing into the protocone, reflecting the paramyine type of arrangement, not the sciuravid type in which the metaloph leads to the hypocone. The morphology of the upper dentition when closely examined shows many similarities to Eocene paramyines, but little or no resemblance to sciuravids.

Burke (1937: 7) emphasized the similarity of hypolophid development in *Sciuravus* and *Ischyromys* and the presence of a small cusp posterior to the metalophid on M_1 - M_3 in both genera. There are indeed certain superficial similarities in these structures in the two groups. However, these structures are also seen in some paramyines. While there is only the slightest hint of a crest from the entoconid towards the hypoconid or ectolophid in one species of *Leptotomus*, *L. bridgeri*, there is in *Rapamys* sp. B (Wood, 1962: fig. 52F & G) a well developed hypolophid. This structure has also developed in another ischyromyid group, the prosciurines. In addition, material of *Rapamys fricki*, in which the hypolophid has not reached the hypoconid, shows a small cusp on the posterior slope of the metalophid. This cusp is also present in some specimens of *Rapamys* sp. B from the late Eocene Badwater fauna. Further points against a sciuravid ancestry for *Ischyromys* are the absence of a mesoconid in *Ischyromys* (a point made by Wilson, 1949) and the high, well-developed ectolophid of *Ischyromys*, which is seen in *Rapamys* but not in *Sciuravus*.

In over-all skull structure *Ischyromys* appears closer to *Paramys* and *Leptotomus* than to *Sciuravus*, although they all share many features common to protrogomorphs in general. The rostrum of *Ischyromys* is relatively longer and deeper, and the infraorbital foramen is

larger than in *Sciuravus* (see Dawson, 1961). Also, the masseter has migrated more dorsally and anteriorly, somewhat compressing the infraorbital foramen in *Ischyromys*. This type of zygomasseteric-infraorbital foramen relationship is seen in *Leptotomus*, and is possibly suggested in the one maxillary fragment known for *Rapamys*. It is unknown in *Sciuravus*, however.

It seems quite clear that *Ischyromys* evolved from a late Eocene paramyine and has no special relationship to the Sciuravidae or *Sciuravus* other than that both are primitive protrogomorphous rodents. It is still impossible to be certain of the actual ancestor of *Ischyromys*. On dental evidence alone, however, the late Eocene *Rapamys* is quite close to what would be expected in an ancestral form. The lower cheek teeth of *Rapamys fricki* from the late Eocene of California and to an even greater extent those of an undescribed species of *Rapamys* from the late Eocene of Wyoming show the development of a hypolophid, an elevated ectolophid without mesoconid, and a small cusp or ridge from the posterior slope of the metalophid. The lower molars of *Rapamys* are more elongate than those of *I. douglassi*, being more nearly comparable to *I. veterior* in this regard.

The upper cheek teeth of *Rapamys fricki* are more complex than those of *Ischyromys*, having a number of small cusps in the position of the metacone. These were interpreted by Wilson (1940) as a divided metacone, and by Wood (1962) as a divided metaconule. In addition *Rapamys fricki* displays a number of crenulations in the enamel along the protoloph and metaloph. The upper teeth of *Rapamys* sp. B (Wood, 1962: fig. 52I) and undescribed specimens in the Carnegie Museum collections) are much simpler, however, showing a single metacone and metaconule. Some of these specimens have a complete protoloph, although the protoconule is distinct, while the metaloph is not joined to either the hypocone or protocone but terminates at the metaconule. In both species of *Rapamys* there is a separation of the protocone and hypocone with the molars taking on a rectangular occlusal outline.

In over-all aspect the teeth of *Rapamys* make the closest approach to those of *Ischyromys* and it is from within this genus that I believe the Oligocene *Ischyromys* evolved.

A suggested phylogenetic sequence is: (1) Evolution from the late Eocene *Rapamys* of a species of *Ischyromys* that maintained a rectangular occlusal outline of the lower molars while developing a complete hypolophid, complete metaloph with submergence of the metaconule

within it, and increase in the size and separation of the hypocone from the protocone. This lineage split sometime during the early Oligocene into two lines, one of large size, the *I. typus* sequence persisting into the early (?) late Oligocene, and the other, *I. veterior*, of smaller size, evidently dying out in the middle Oligocene. (2) Evolution from this first lineage of a species that evolved lower molars of more equal transverse and antero-posterior dimensions, the *I. douglassi* line, without the loss of a metaconule, only partially separated hypocone and protocone, and weaker metalophid. This species evidently became extinct in the early Oligocene.

There is no evidence that *Ischyromys* gave rise to any later group of rodents. The lineage survived through most of the Oligocene but died out before the close of the epoch. Throughout its history the zygomaseteric structure remained at the protrogomorph level and probably *Ischyromys* was unable to compete with one or another of several rodent groups. The latter, beginning in the late Eocene, were developing more sophisticated masticatory complexes. Although there is no direct evidence available, it is possible that *Ischyromys* was in competition with some of the early sciurids.

TABLE 1

MEASUREMENTS IN MILLIMETERS FOR *Ischyromys*

	N	O.R.	M	s	V
<i>I. veterior</i> Pipestone Springs					
P ⁴ a-p	18	3.2-3.7	3.47	.15	4.32
tr.	18	2.7-3.9	3.48	.31	8.91
M ¹ a-p	27	3.2-3.7	3.36	.12	3.57
tr.	27	3.1-4.0	3.47	.25	7.20
M ² a-p	23	3.1-3.5	3.30	.14	4.24
tr.	23	3.1-3.7	3.33	.20	6.01
M ³ a-p	12	2.9-3.3	3.11	.16	5.14
tr.	12	2.7-3.3	2.91	.18	6.19
<i>I. douglassi</i>					
P ⁴ a-p	5	3.0-3.7	3.42		
tr.	6	3.7-4.4	4.17		
M ¹ a-p	10	3.1-3.8	3.48		
tr.	10	3.6-4.5	4.13		
M ² a-p	8	2.6-3.8	3.35		
tr.	7	3.3-4.1	3.81		
M ³ a-p	7	2.9-3.9	3.46		
tr.	7	2.9-3.6	3.29		

(I. douglassi, cont'd.)

(Table 1, cont'd.)

Depth of mandible under M ₁	10.2 (5) ¹
Length of diastema, lower	10.0 (2)
Alveolar length P ₄ -M ₃	15.6 (6)
Length of skull	67.5 (1)
Length of palate	30.8 (2)
Length of diastema, upper	17.8 (2)
Width of rostrum at pmx-mx suture	16.7 (3)
Width of skull at postorbital constriction	8.5(4)

¹ Numbers in () represent number of specimens

TABLE 2

MEASUREMENTS IN MILLIMETERS, LOWER CHEEK TEETH, *Ischyromys*

	N	O.R.	M	s	V
P ₄ anteroposterior					
<i>I. veterior</i>					
Pipestone Springs	20	3.3-3.9	3.52	.17	4.83
Warbonnet Creek	14	2.9-3.4	3.19	.16	5.02
<i>I. parvidens</i> (Howe, 1966)	32	2.8-3.8	3.20	.24	7.50
<i>I. typus</i>					
Badland Creek	3	3.6-3.8	3.70		
<i>I. typus</i> (Howe, 1966)	58	2.7-4.2	3.60	.25	5.68
<i>I. pliacus</i> (Howe, 1966)	17	3.5-4.3	3.70	.21	5.68
<i>I. douglassi</i>	8	3.5-3.8	3.66	.10	2.73
M ₁ anteroposterior					
<i>I. veterior</i>					
Pipestone Springs	80	3.0-4.1	3.30	.17	5.15
Warbonnet Creek	20	2.9-3.5	3.18	.13	4.09
<i>I. parvidens</i>	53	2.9-3.6	3.20	.15	4.69
<i>I. typus</i>					
Badland Creek	37	3.1-4.0	3.53	.21	5.95
<i>I. typus</i> (Howe, 1966)	114	3.1-3.9	3.50	.17	4.86
<i>I. pliacus</i> (Howe, 1966)	32	3.3-4.1	3.70	.20	5.40
<i>I. douglassi</i>	12	3.4-3.8	3.65	.13	3.56
M ₂ anteroposterior					
<i>I. veterior</i>					
Pipestone Springs	80	3.0-4.1	3.32	.18	5.42
Warbonnet Creek	20	3.0-3.3	3.16	.09	2.85
<i>I. parvidens</i> (Howe, 1966)	52	2.8-3.4	3.10	.15	4.84
<i>I. typus</i>					
Badland Creek	37	3.1-4.0	3.54	.23	6.50
<i>I. typus</i> (Howe, 1966)	97	2.9-4.0	3.55	.18	5.07
<i>I. pliacus</i>	37	3.5-4.2	3.70	.15	4.05

(Table 2, cont'd.)

	N	O.R.	M	s	V
<i>I. douglassi</i>	12	3.5-3.9	3.71	.13	3.50
M ₃ anteroposterior					
<i>I. veterior</i>					
Pipestone Springs	50	2.9-3.9	3.26	.19	5.83
Warbonnet Creek	16	3.1-3.5	3.34	.12	3.60
<i>I. parvidens</i> (Howe, 1966)	29	3.0-3.8	3.30	.21	6.36
<i>I. typus</i>					
Badland Creek	10	3.8-4.0	3.86	.08	2.07
<i>I. typus</i> (Howe, 1966)	59	2.9-4.0	3.55	.15	4.23
<i>I. pliacus</i> (Howe, 1966)	25	3.5-4.0	3.75	.13	3.47
<i>I. douglassi</i>	11	3.5-4.2	3.84	.22	5.73
M ₁ transverse metalophid					
<i>I. veterior</i>					
Pipestone Springs	72	2.9-4.0	3.22	.23	7.14
Warbonnet Creek	17	2.7-3.0	2.89	.11	3.81
<i>I. parvidens</i> (Howe, 1966)	30	2.6-3.2	2.95	.15	5.08
<i>I. typus</i>					
Badland Creek	24	3.0-3.7	3.35	.19	5.67
<i>I. typus</i> (Howe, 1966)	97	2.8-4.0	3.40	.22	6.47
<i>I. pliacus</i> (Howe, 1966)	32	3.3-4.0	3.50	.16	4.57
<i>I. douglassi</i>	11	3.4-3.8	3.61	.12	3.32
M ₁ transverse hypolophid					
<i>I. veterior</i>					
Pipestone Springs	72	2.7-3.9	3.18	.24	7.55
Warbonnet Creek	17	2.6-3.1	2.85	.13	4.56
<i>I. parvidens</i> (Howe, 1966)	51	2.4-3.5	2.90	.23	7.93
<i>I. typus</i>					
Badland Creek	24	3.0-3.9	3.39	.20	5.90
<i>I. typus</i> (Howe, 1966)	101	2.9-4.0	3.55	.18	5.07
<i>I. pliacus</i> (Howe, 1966)	32	3.3-4.0	3.50	.17	4.86
<i>I. douglassi</i>	11	3.1-3.9	3.64	.21	5.77
M ₂ transverse metalophid					
<i>I. veterior</i>					
Pipestone Springs	72	3.0-4.1	3.32	.24	7.23
Warbonnet Creek	23	2.7-3.5	3.07	.15	4.89
<i>I. parvidens</i> (Howe, 1966)	34	2.8-3.5	3.10	.16	5.16
<i>I. typus</i>					
Badland Creek	25	3.2-4.0	3.55	.19	5.35
<i>I. typus</i> (Howe, 1966)	83	3.0-4.0	3.50	.20	5.71
<i>I. pliacus</i> (Howe, 1966)	35	3.4-4.0	3.65	.15	4.11

(Table 2, cont'd.)

	N	O.R.	M	s	V
<i>I. douglassi</i>	13	3.5-4.0	3.82	.15	3.93
M ₂ transverse hypolophid					
<i>I. veterior</i>					
Pipestone Springs	72	2.7-4.1	3.11	.37	11.90
Warbonnet Creek	23	2.6-3.5	2.97	.15	5.05
<i>I. parvidens</i> (Howe, 1966)	49	2.6-3.6	3.00	.21	7.00
<i>I. typus</i>					
Badland Creek	25	3.1-4.0	3.48	.19	5.46
<i>I. typus</i> (Howe, 1966)	83	2.9-3.9	3.45	.20	5.80
<i>I. pliacus</i> (Howe, 1966)	37	3.1-3.9	3.50	.18	5.14
<i>I. douglassi</i>	13	3.2-4.1	3.81	.26	6.83

TABLE 3

Student's t Test for Significance of Bartlett's "Best Fit"
Regression Lines¹ for Populations of *Ischyromys*

	B	degrees of freedom	t	P
M ₁ anteroposterior/M ₂ anteroposterior				
Pipestone Springs vs. Warbonnet Creek	.86 vs. 1.0	86	.117	>.9
Pipestone Springs vs. McCarty's Mt.	.86 vs. .61	94	.638	.5-.6
Pipestone Springs vs. Badland Creek	.86 vs. .89	111	.037	>.9
McCarty's Mt. vs. Warbonnet Creek	1.0 vs. .61	26	1.372	.1-.2
McCarty's Mt. vs. Badland Creek	1.0 vs. .89	43	.056	>.9
Warbonnet Creek vs. Badland Creek	.61 vs. .89	51	.961	.3-.4
M ₁ metalophid width/M ₂ metalophid width				
Pipestone Springs vs. McCarty's Mt.	.92 vs. 1.36	77	1.875	.05-.1
Pipestone Springs vs. Warbonnet Creek	.92 vs. 1.09	83	.634	.5-.6
Pipestone Springs vs. Badland Creek	.92 vs. 1.00	90	.092	>.9
McCarty's Mt. vs. Warbonnet Creek	1.36 vs. 1.09	22	.032	>.9
McCarty's Mt. vs. Badland Creek	1.36 vs. 1.00	29	.695	.8-.9
Warbonnet Creek vs. Badland Creek	1.09 vs. 1.00	36	.162	.8-.9
M ₁ metalophid width/M ₁ hypolophid width				
Pipestone Springs vs. McCarty's Mt.	.94 vs. 1.39	77	.243	.8-.9
Pipestone Springs vs. Warbonnet Creek	.94 vs. .87	83	.242	.8-.9
Pipestone Springs vs. Badland Creek	.94 vs. .82	90	.077	>.9
McCarty's Mt. vs. Warbonnet Creek	1.39 vs. .87	22	.010	>.9
McCarty's Mt. vs. Badland Creek	1.39 vs. .82	29	.235	.8-.9
Warbonnet Creek vs. Badland Creek	.89 vs. .82	35	.147	.8-.9
M ₂ metalophid width/M ₂ hypolophid width				
Pipestone Springs vs. McCarty's Mt.	1.02 vs. 1.23	78	.194	.8-.9
Pipestone Springs vs. Warbonnet Creek	1.02 vs. 1.06	88	.079	>.9

(Table 3, cont'd.)

	B	degrees of freedom	t	P
Pipestone Springs vs. Badland Creek	1.02 vs. .92	90	.123	>.9
McCarty's Mt. vs. Warbonnet Creek	1.23 vs. 1.06	30	.055	>.9
McCarty's Mt. vs. Badland Creek	1.23 vs. .92	32	.124	>.9
Badland Creek vs. Warbonnet Creek	.92 vs. 1.06	42	.062	>.9
M₁ a-p/M₁ hypolophid width				
Pipestone Springs vs. McCarty's Mt.	.64 vs. 1.00	76	.220	.8-.9
Pipestone Springs vs. Warbonnet Creek	.64 vs. .45	83	.326	.7-.8
Pipestone Springs vs. Badland Creek	.64 vs. .77	90	.043	>.9
McCarty's Mt. vs. Warbonnet Creek	1.00 vs. .45	23	1.784	.05-.1
McCarty's Mt. vs. Badland Creek	1.00 vs. .77	30	.176	.8-.9
Badland Creek vs. Warbonnet Creek	.77 vs. .45	37	.542	.5-.6
M₂ a-p/M₂ hypolophid width				
Pipestone Springs vs. McCarty's Mt.	1.06 vs. 1.27	77	.061	>.9
Pipestone Springs vs. Warbonnet Creek	1.06 vs. 1.26	88	.365	.7-.8
Pipestone Springs vs. Badland Creek	1.06 vs. .64	90	.266	.7-.8
McCarty's Mt. vs. Warbonnet Creek	1.27 vs. 1.26	30	.006	>.9
McCarty's Mt. vs. Badland Creek	1.27 vs. .64	32	.410	.6-.7
Badland Creek vs. Warbonnet Creek	.64 vs. 1.26	42	1.649	.1-.2

¹See figures 21-26 for plots of "best fit" regression lines.

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