56.9,32P(1181):14.71.

Article VI.— ON THE OSTEOLOGY AND RELATIONSHIPS OF *PARAMYS*, AND THE AFFINITIES OF THE ISCHYROMYIDÆ.

By W. D. Matthew.

The Ischyromyidæ are a family of primitive Rodents characteristic of the American Eocene, with a few survivors in the Lower and Middle Oligocene of this country. They are the oldest known fossil rodents, appearing first in the Lower Eocene (Wasatch) and are practically the only known group until the end of the Eocene. They are thus of especial interest in tracing the history and evolution of the Rodentia and the relationship of the various modern families.

The best known genera are *Ischyromys* Leidy, of the Lower and Middle Oligocene (White River group), and *Paramys* Leidy, of the Lower, Middle, and Upper Eocene (Wasatch, Wind River, Bridger, Washakie and Uinta formations). Imperfect skulls and some parts of the skeleton of these two genera have been described and figured by Cope (1885) and their relationships considered by subsequent students of the Rodentia. The remaining genera have been known only from jaws, and mostly from very incomplete descriptions, so that almost nothing is known of their affinities.

The present contribution is based chiefly upon a series of fine skeletons and skulls of Rodentia from the Bridger formation (Middle Eocene) obtained by the American Museum Expeditions of 1903–6. This material gives us for the first time a fairly complete knowledge of the osteology of the oldest known fossil rodents. It furnishes very important evidence in regard to the evolution of the Simplicidentate Rodents, and the relationships of the several modern groups.

The modern rodents have been thoroughly studied and extensively monographed by various writers, but comparatively little attention has been paid by these writers to their geological history. This is not surprising in view of our very imperfect knowledge of the extinct forms. Fossil rodents are very numerous and varied, but not in proportion to their modern abundance, and on account of their small size the great majority are very imperfectly known, principally from jaws or teeth. They first appear in North America in the Lower Eocene (Wasatch), in Europe in the Middle or Upper Eocene (Egerkingen), in South America in the Pyrotherium beds (Upper Eocene or Oligocene), in Africa in the Fayûm deposits (Upper Eocene or Oligocene). In other parts of the world nothing is known of their first

appearance, as early Tertiary deposits are unknown, or fossil mammals have not been found in them.

The ordinal characters of the Rodentia are well marked at their first appearance, and they do not appear to be directly derivable from any known Basal Eocene or Cretaceous mammals. The later Tertiary rodents are for the most part nearly related to living genera, and are referred to modern families. The North American Eocene rodents and a part of the Oligocene genera are referred to the extinct family Ischyromyidæ. The genera of the European Eocene and Oligocene have been in part referred to the extinct families Theridomyidæ and Pseudosciuridæ. There are also several aberrant specialized groups of later Tertiary rodents which are placed in extinct families.

Family ISCHYROMYIDÆ *Alston*, 1876.

Alston included in this family *Ischyromys* Leidy, 1856, and perhaps *Pseudotomus* Cope, 1872, with the following definition: "Dentition as in Sciuridæ. Skull resembling Castoridæ, but with the infra-orbital opening large, a sagittal crest, no postorbital processes, palate broad, basioccipital keeled." *Plesiarctomys*, *Paramys* and *Sciuravus* he referred to the Sciuridæ. Cope in 1884 defined the family as follows:

"Dentition as in Sciuridæ; infraorbital foramen large, superior; pterygoid fossa large, with well developed exterior as well as interior walls; a sagittal crest." The description of the infraorbital foramen as "large" is somewhat misleading; it is not larger than in *Aplodontia*, and is not large as in Hystricomorphs, nor superior in position as in the Myomorphs. The sagittal crest is not present on *Sciuravus*. The keeled basioccipital is present only in *Ischyromys*.

On our present knowledge the family may be defined as follows:

Infraorbital foramen small or of moderate size, round, postero-inferior in position, situate close to the antero-inferior margin of the orbit, and facing forward and downward, so that it was probably not traversed by any portion of the masseter. Origin of masseter wholly limited to the zygomatic arch, not extended forward on the side of the muzzle in advance of the orbits.

Dentition $\frac{1.0.2.3}{1.0.1.3}$; teeth brachyodont, sciurid in pattern or with imperfect transverse crests. Palate broad and grinding surfaces approximately horizontal.

Tympanic bulla incompletely ossified and loosely attached in earlier genera (complete in *Ischyromys*).

Zygomatic arch moderately deep, jugal extending upward in front of orbit to meet the lachrymal. Premaxillæ broad posteriorly, almost exclud-

ing frontals from contact with maxillæ. Nasals long, and broad posteriorly; facial extension of lachrymals not large. No postorbital processes on frontals; post-tympanic plate of squamosal broad; mastoid exposure small.

Neck moderately long, tail very long and strong; limbs and feet of moderate length, arboreal to terrestrial in adaptation; manus tetradactyl with vestigial pollex; pes pentadactyl, lateral digits well developed; scaphoid, lunar and centrale separate.

Paramys *Leidy*, 1871.

Paramys LEIDY, 1871, Proc. Acad. Sci. Phila., Vol. XXII, p. 231 (published Nov. 28, 1871); Ext. Vert. West. Terrs., p. 109, pl. vi.

Pseudotomus COPE, 1872, Pal. Bull. No. 2, issued, Aug. 3, 1872; Proc. Am. Phil. Soc., Vol. XII, p. 467.

Plesiarctomys COPE, 1877, Ext. Vert. New Mex., p. 170; 1885, Tert. Vert., p. 175.

?*Plesiarctomys* BRAVARD, 1848–52, in Gervais, Zool. et Pal. Franc., pt. ii, expl. pl. xlvi.

Nomenclature. This genus was founded upon three species from the Bridger formation, *P. delicatus, delicatior* and *delicatissimus* Leidy, known

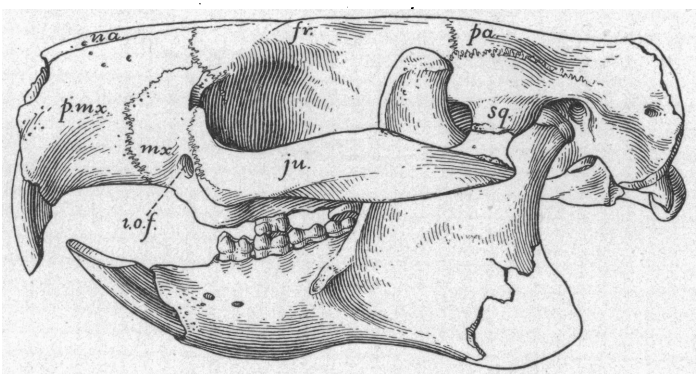

Fig. 1. *Paramys delicatus*, skull and lower jaw, natural size, No. 12506. Lower Bridger, Wyoming.

only from parts of lower jaws. *Pseudotomus*, type *P. hians* Cope, was based upon a skull from the same formation, lacking the cheek teeth and otherwise defective, but with complete incisors. Both genera were subsequently synonymized by Cope with *Plesiarctomys* Bravard, type *P. gervaisi* Brav., based upon an incomplete lower jaw from the Upper Eocene of France. This identification has been generally accepted, but in recent years several

authors [1] have revived Leidy's genus, although without giving any reasons for separating it from *Plesiarctomys*.[2]

It is entirely probable, in my opinion, that *Plesiarctomys* and *Paramys* are identical or closely allied genera, although there are some marked differences between the teeth of the typical species. In *Plesiarctomys gervaisi*, according to Gervais's figure, p_4 is short and small, more reduced than in *Arctomys*, and the molars increase regularly in width and length from p_4 to m_3. In *Paramys delicatus*, p_4 is a much larger tooth, longer than m_{1-2}, and as wide as m_1; its two anterior cusps are more separated and of larger size. Other species of *Paramys*, however, especially *P. robustus* and *P.* (*Ischyrotomus*) *petersoni*, approach very closely to the type of *Plesiarctomys* in dentition. Unfortunately Gervais does not figure the outside of the jaw, so that

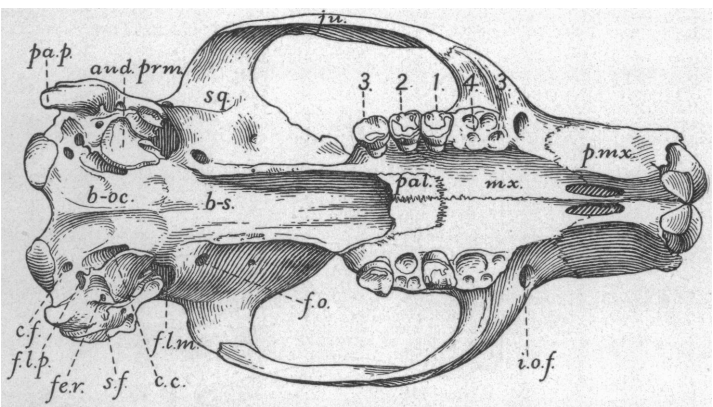

Fig. 2. *Paramys delicatus*, under view of skull, natural size, No. 12506. *Aud. prm.*, auditory prominence of petrosal; *b.-oc.*, basioccipital; *b.-s.*, basisphenoid; *c.c.*, carotid canal; *c.f.*, condylar foramen; *fe.r.*, fenestra rotunda; *f.l.m.*, foramen lacerum medium; *f.l.p.*, foramen lacerum posterius; *f.o.*, foramen ovale; *i.o.f.*, infraorbital foramen; *ju.*, jugal; *mx.*, maxilla, *pal.*, palatine; *pmx*, premaxillary; *pa.p.*, paroccipital process; *s.f.*, stylomastoid foramen; *sq.*, squamosal.

we do not know whether the French genus resembled *Paramys* or *Sciurus* in the more important diagnostic characters which would determine its family relations. I have failed to find any figures or descriptions of European specimens which would throw any additional light on this point; pending a reëxamination of the type in the British Museum, I regard the identity of the two genera as *sub judice*, and retain Leidy's name provisionally for the American forms.

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[1] Zittel, 1893; Osborn, 1895; Matthew, 1899; Hay, 1902; Loomis, 1907.

[2] Except Osborn, 1895, the single hint of distinction there given being inapplicable to the type species of the two genera.

Generic Characters. Dentition $\frac{1.0.2.3}{1.0.1.3}$. Teeth sciurid in pattern but anterior ledge of upper molars rudimentary, entoconid a distinct cusp instead of a marginal ledge, paraconid and metaconid less widely separated than in modern Sciuridæ. Cusps low, more or less marginal, little or not at all crested; upper molars tritubercular, hypocone absent or small; lower molars with broad shallow basin heels. Incisors broad or of moderate width, with convex anterior face (except subgen. *Ischyrotomus*, infra).

Skull proportioned as in *Arctomys*, but with shorter muzzle and longer basicranial region. Preorbital region as in *Aplodontia*, the infraorbital foramen of moderate size, facing partly downward, situate just in advance of p_3 and mainly below the level of the orbit. Origin of masseter wholly behind infraorbital foramen, as in *Aplodontia*, not extended forward above

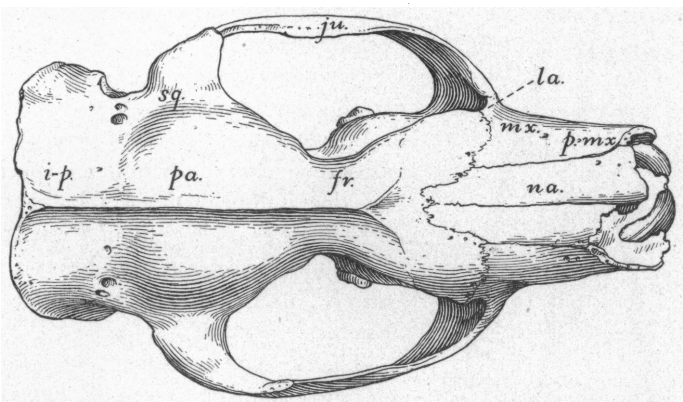


Fig. 3. *Paramys delicatus*, top view of skull No. 12506.

it as in Sciuromorpha generally, nor beneath the major portion of it, as in Myomorpha, nor through it as in Hystricomorpha (and to a varying extent in Myomorpha), but wholly confined to the zygomatic arch, and not reaching the skull in front of the arch. Postorbital constriction narrow, no postorbital processes. Premaxillæ very wide posteriorly (*cf. Aplodontia*) almost excluding contact between maxillæ and frontals. Facial expansion of lachrymal limited, as in *Arctomys*. Sagittal crest low, but extending forward in advance of postorbital constriction. Parietals long, reaching forward nearly to postorbital constriction. Post-tympanic process of squamosal broad, completely overlapping mastoid region, save for a small lateral exposure between paroccipital and post-tympanic processes. Paroccipital process short, projecting backward rather than downward. Bulla absent in all our specimens, probably incomplete and loosely attached (as in *Sciuravus*).

The alisphenoid canal and the larger tunnel internal to it are much as in *Arctomys*, and the transverse canal perforating the basisphenoid is apparently present but not large. There is a considerable vacuity between petrosal and alisphenoid, suggestive of the Hystricomorph condition, but it may have been wholly covered in by the bulla.

In the lower jaw, the anterior border of the masseteric fossa is much further back than in Sciuridæ, mental foramen beneath p_4, diastema decidedly shorter than in any Sciurids, symphysis mandibuli extended backward along lower border of jaw to a point beneath m_1, the border being more or less angulate at this point. Coronoid process much longer and broader than in Sciuridæ (*cf. Aplodontia*); the angle (see Fig. 7) is a vertical plate, not inflected along its inferior border as it is to a varying extent among Rodentia generally (except Duplicidentata). The relation of the angle to the incisive alveolus is more like that of Sciuromorpha and Myomorpha than Hystricomorpha, but varies somewhat in the different species. In none does it show the marked lateral position of the angle characteristic of Hystricognathi, and in most species it may be said to arise entirely from the inferior border of the alveolus.

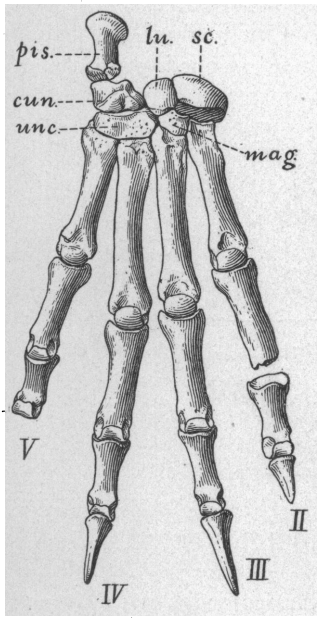


Fig. 4. *Paramys robustus*, fore foot, natural size, No. 13091.

The skeleton is proportioned much as in the larger squirrels, relatively larger than in *Arctomys*, especially in the hind limbs. The vertebræ are longer, especially in the cervical and lumbar regions, the lumbar spines much higher. The tail is very long and stout, much exceeding the presacral series in length, and the caudal vertebræ, beyond the first five or six, are much elongate. The limbs and feet are comparatively slender. The humerus has an entepicondylar foramen and no epitrochlear perforation. Its tuberosities are of the usual rodent type, the deltoid crest is strong and ends abruptly about the middle of the shaft. The head of the radius is round-oval. The ulnar shaft is broad and flat. The manus has four functional digits and a rudimentary pollex. Scaphoid, lunar and centrale are separate, and a radial sesamoid (pre-pollex) is present. The phalanges are long, the unguals[1]

[1] Excepting in the subgenus *Ischyrotomus* (infra).

sharp, high, compressed, not fissured at the tips, the penultimate phalanges somewhat asymmetric. The femur has a moderate third trochanter, set two fifths down on the shaft. The patellar trochlea is rather broad and shallow, patella flat and small, fabellæ well developed. Tibia and fibula separate, the latter comparatively well developed, its shaft equalling the metapodial shafts in size. Astragalus much like that of *Arctomys*, except for the less vertical depth of the head. The pes has five well developed digits, the first considerably shorter than the others. The phalanges are slender the penultimate series somewhat asymmetric, the unguals sharp and compressed, like those of the manus. Presence of a pre-hallux is not demonstrated.

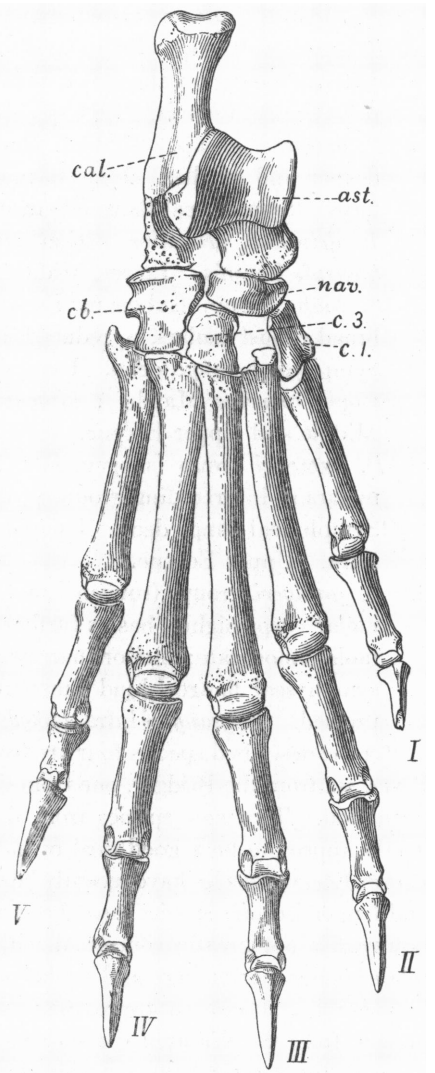


Fig. 5. *Paramys robustus*, hind foot, natural size, No. 13091.

Species of Paramys. Sixteen species of this genus have been described from the Wasatch, Wind River, Bridger, Washakie and Uinta formations. With two exceptions they are based upon parts of jaws or teeth. *P. sciuroides* Scott and *P. copei* Loomis are founded upon skull and jaws with parts of the skeleton. The genus embraces a wide range in size, and in the proportions and construction of the teeth, far wider than any modern Sciurid genus. It is a commendable custom, however, to draw generic lines much wider among extinct than among living species, on account of our imperfect knowledge of the fossil forms. I continue therefore to refer these species to *Paramys*, distinguishing the most aberrant ones as subgenera.

The species may be grouped as follows:

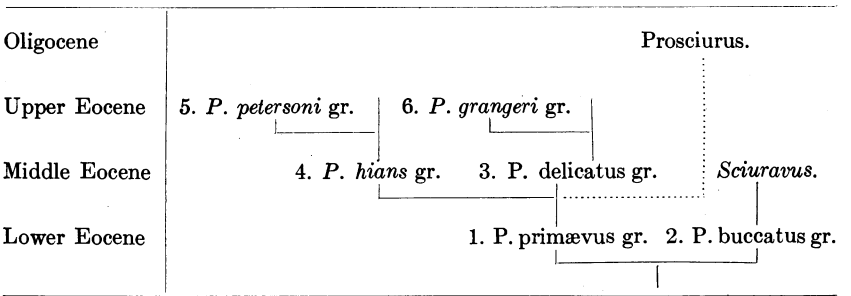
1. *P. buccatus* group. Very small, molars approaching *Sciuravus* in structure, sub-quadrate with well developed cusps, basins reduced. *P. buccatus* Cope, *atwateri* Loomis. Lower Eocene.
2. *P. primævus* group. Small species with low marginal cusps and broad shallow basins on the lower molars. *P. primævus, excavatus, quadratus, major* Loomis. Lower Eocene.
3. *P. delicatus* group. Medium sized species with cusps larger, basins deeper and smaller. Incisors moderately wide, with convex anterior faces. Symphyseal flange slight or none. Unguals high, compressed. *P. delicatus, delicatior, delicatissimus*, Leidy, *sciuroides* Scott, *copei, bicuspis* Loomis. Lower, Middle and Upper Eocene.
4. *P. hians* group. (subgenus *Pseudotomus* Cope). Large species with broad robust molars, p_4 reduced, incisors very wide, convex anteriorly. Symphyseal flange deep. Unguals as in preceding group. *P. hians* Cope, *robustus* Marsh, ? *uintensis* Osborn, ? *superbus* O. S. & S. Middle and Upper Eocene.
5. *P. petersoni* group (subgen. nov. **Ischyrotomus**). Large species with molars as in preceding group, p_4 reduced, incisors wide, flat anteriorly. Symphyseal flange deep. Unguals long, not compressed. *P. petersoni* infra. Upper Eocene.
6. *P. grangeri* group (subgen. nov. **Leptotomus**). Large species with molar cusps higher, basins further reduced, p_4 not reduced, breadth of molars moderate; incisors narrower, compressed, convex anteriorly; no symphyseal flange; hind limbs relatively large; unguals high, compressed. *P. grangeri* infra, *leptodus* Cope. Upper Eocene.

Of the described species four are from the Wasatch, three from the Wind River, six from the Bridger, one from the Washakie and two from the Uinta formation. Two new species from the Uinta are here described. There would appear to be a good deal of individual variation in the teeth. The Lower Eocene species have recently been revised by Dr. Loomis; the Middle and Upper Eocene species have been reviewed for the present study, which however is not greatly concerned with species distinctions except as they relate to the morphology and evolution of the group. The species exhibit in general a successive approximation towards the sciurid pattern in the molars, from the Wasatch species with broad flat crowns and low marginal cusps, to those of the Uinta with higher cusps, reduced basins, and a tendency to cross-cresting. They vary widely in size, the largest equalling the Canada porcupine, the smallest not exceeding the red squirrel. The Wasatch species are all comparatively small. The teeth are readily interpreted as of the tritubercular pattern, with large heels on the lower molars. I find myself

quite unable to agree with Dr. Loomis (1907, p. 126, fig. 1) in his interpretation of the lower molars; the cusp which he calls paraconid is in my opinion the metaconid, and his metaconid the entoconid.

The relations of the several groups I take to be approximately as follows:

Phylogenetic Relations of the Species of Paramys.



Wasatch Species.

P. buccatus Cope, 1874. P_4–m_3 = 11 mm. (calculated from the upper molars of the type). Loomis refers this species to *Sciuravus*, but Cope's description and figures appear to me to agree much better with *Paramys*.

P. atwateri Loomis, 1907. P_4–m_3 = 12.5 mm. Like the preceding species this has some resemblance to *Sciuravus*. It is possibly a larger variety of *P. buccatus*.

P. primævus Loomis, 1907. P_4–m_3 = 15 mm. This appears to be the common form of the Wasatch. Cusps low and marginal, basins broad and shallow. Individual variation wide, especially in size.

P. quadratus Loomis, 1907. P_4–m_3 = 18 mm. Distinguished by larger size, and broader more robust teeth.

Wind River Species.

P. copei Loomis, 1907. P_4–m_3 = 13.5 mm. The type of this species is the skull, jaws and part of skeleton described and figured by Cope in 'Tertiary Vertebrata' under the name of *Plesiarctomys delicatissimus*. Dr. Loomis distinguishes it from Leidy's species by the double anterior cusp of p_4, lower cusps and broader basins on the molars.

P. bicuspis Loomis, 1907. P_4–m_3 = 13.5 mm. Distinguished from *P. copei* by the twinning of the mesostyle.

P. major Loomis, 1907. P_4–m_3 = 16.5 mm. Distinguished from the

two preceding species by larger size, from *P. delicatior* by slenderer proportions, broader basins, and smaller cusps to the molars.

P. excavatus Loomis, 1907. P_4–m_3 = 12 mm. A small species with broad basins and small marginal cusps, and wide incisors. Although typically from the Wind River, it is very like the smaller specimens of *Paramys* from the Wasatch.

Bridger Species.

P. delicatus Leidy, 1871. P_4–m_3 = 19 mm. This is the type of the genus, and is represented by abundant material in our collections. I refer to it several skeletons more or less complete, the best being No. 12506, skull, lower jaw, all the vertebræ except two dorsals and a few distal caudals, one fore limb and both hind limbs; No. 13090, skull with most of fore and hind limbs, various vertebræ, etc.; No. 11593, skull, parts of lower jaw, limb bones, etc.; and some twenty upper and lower jaws, parts of skulls and other fragmentary material. All of these are from the lower or middle beds, the highest level being the top of Horizon C. The specimens from the middle beds (Horizon C), show a slight reduction of p_4 in comparison with those of Horizon B, and the cusps are a little more robust, the central basin reduced.

The more important characters are stated under the generic description. The specific characters are as follows:

Skull about as large as in *Arctomys monax*, body more elongate, especially in cervical and lumbar regions, tail nearly four times as long. Fore limbs about a tenth longer, hind limbs about a third longer than in *A. monax*. Femur and tibia of equal length. The entire length of the animal was about a meter, of which more than half was tail. The proportions run much as in the larger squirrels, but the skull is much more like that of a woodchuck. 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.

Principal measurements (see also table of comparative measurements):

Length of skull	89.
7 cervical vertebræ	60.
12 dorsal " , est'd (10 preserved measure 113 mm.)	137.
7 lumbar "	133.
3 sacral "	42.
?29 caudal " , est'd (24 preserved in series, 473 mm.)	540.
Total length of skeleton including tail, est'd	1001.
Fore limb. Length (phalanges estimated)	215.
Hind limb, length	296.
Hind foot, length	104.

P. delicatior Leidy, 1871. P_4–m_3 = 15.3 mm. This is the most abundant species of the Bridger, about three fourths of our specimens being referable to it. All are upper and lower jaws, except for certain unprepared skeletons provisionally placed here. It is closely allied to *P. delicatus* and

Fig. 6. *Paramys delicatus*, restoration of skeleton, one-fourth natural size. Shaded portions from No. 12506, outlined portions from other specimens of *Paramys*, dotted outlines adapted from the modern squirrel. Drawn by Erwin Christman.

separable in the dentition only by smaller size and somewhat more slender proportions. The infraorbital foramen of the skull is distinctly smaller in proportion.

P. delicatissimus Leidy, 1871. P_4–m_3 = 12.6. This small species is rather scarce and not well represented in our collections. The jaw is more slender, the diastema less deeply notched, the incisor relatively more compressed.

P. robustus Marsh, 1872.[1] P_4–m_3 = 22.5. The type of this species is stated to consist of two lower molar teeth, m_{2-3}. Other fragmentary specimens are referred by Marsh to the species, including a lower incisor. Three specimens in our collection agree with Marsh's type, so far as the published

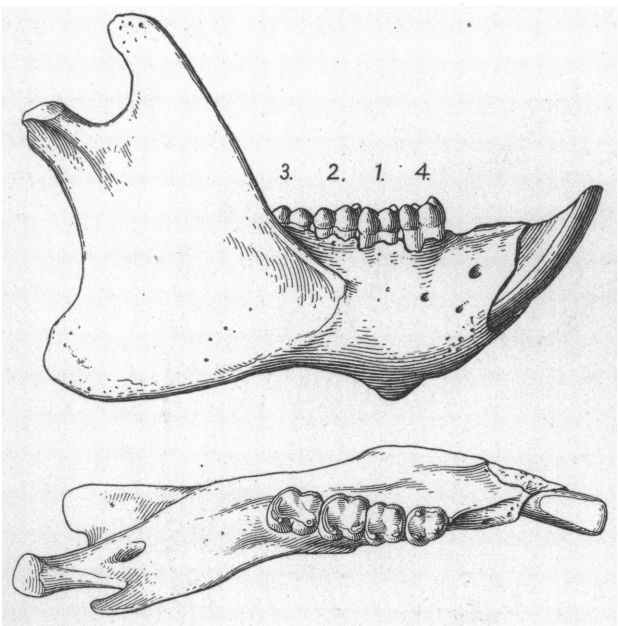


Fig. 7. *Paramys robustus*, lower jaw, natural size, external and superior views. No. 13091. Lower Bridger, Wyoming.

description and measurements permit comparison. Of these, two are lower jaws, the third, no. 13091, is a skeleton, incomplete, but finely preserved. This specimen (Figs. 4, 5 and 7) includes three upper teeth, a complete lower jaw, scapula, pelvis, and both fore and hind limbs practically complete, many of the presacral and caudal vertebræ, and numerous fragmentary ribs, etc.

The species is very clearly distinct from *P. delicatus*. The teeth are larger, much broader, p_4 proportionately shorter and smaller, the jaw much

[1] Amer. Jour. Sci., Vol. iv, p. 218 (separata issued August 17).

deeper with the symphysis extended backward and downward in a prominent flange on the inferior margin beneath m_1. The antero-inferior border of the masseteric fossa is much more prominent, and shows a suggestive approach toward the hystricomorph construction of the angle. The angle lies wholly in a vertical plane, lacking the inflection of the inferior border characteristic of most modern rodents. The coronoid process is large, high and broad.

The skeleton indicates an animal nearly as large as the American beaver, but of different proportions, much like the larger squirrels, and agreeing closely with *P. delicatus* except for the more elongate lower limbs and feet. The more important skeleton characters have been noted in the generic

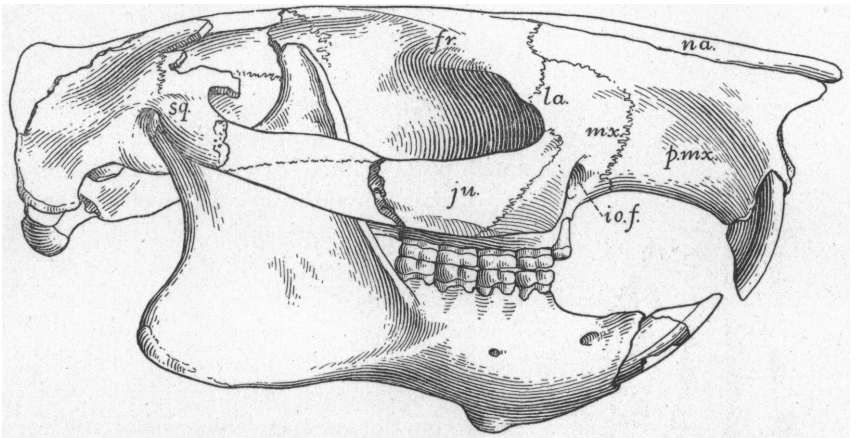


Fig. 8. *Paramys (Ischyrotomus) petersoni*, skull and lower jaws, No. 2018, type specimen, natural size. Telmatotherium beds of Uinta Basin, Utah.

description. The total length of this species must have been about four feet, half of this being tail.

P. hians (Cope, 1872). Type, a skull, No. 5025, Am. Mus. Cope Coll., considerably crushed and lacking the cheek teeth, top of braincase and zygomata. It is distinguishable from *P. robustus* by the much broader incisors, no other comparisons being practicable. No referred specimens in our collections. *Paramys superbus* O. S. and S., 1877, known only from a part of a lower incisor, may be identical with *P. hians*.

This species is the type of *Pseudotomus*, which may prove to be a valid genus, or at least generically distinct from *Paramys* if not from *Plesiarctomys*; but until better direct evidence appears, it may be regarded as a subgenus. *P. robustus* is much better known, but appears to be an annectant form with *Paramys* s. s., although nearer to *P. hians*.

Washakie Species.

P. leptodus Cope, 1872. P_4–m_3 = 21 mm. This species, type No. 5026, a lower jaw from the Upper Washakie, is considerably larger than *P. delicatus*, but with a slender narrow incisor. The molar cusps are more prominent, the basins of the teeth more reduced. The heel of m_3 is not so broad and quadrate as in the Bridger species, and the entoconid is placed further forward. *P. grangeri* (infra) is a closely related species of somewhat larger size.

P. cf. delicatus Leidy. A specimen from the Lower Washakie, No. 13215, parts of jaws and fragments of skeleton, agrees quite nearly with this Bridger species.

Uinta Species.

P. sciuroides (Scott, 1887). P_4–m_3 = 12 mm. This is one of the smallest species of the genus. The type is a well preserved skull and jaws with parts of the skeleton in the Princeton Museum. Professor Scott has pointed out certain approximations in the dentition to *Sciurus* as compared with the older forms.

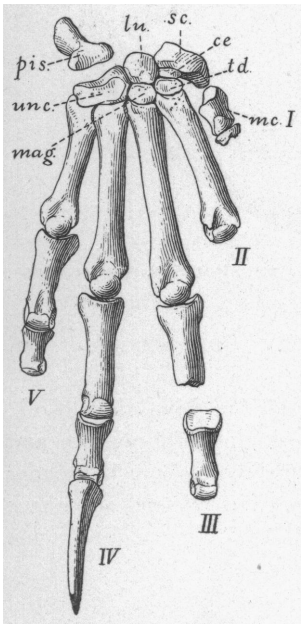


Fig. 9. *Paramys* (*Ischyrotomus petersoni*, fore foot, natural size, type specimen.

P. uintensis Osborn, 1895. A much larger species, comparable in size and characters with *P. robustus*, but no satisfactory comparison of the two can be made on account of the fragmentary nature of the types. The type of *P. uintensis*, Am. Mus. No. 1901, consists of m^{1-2}, m_2 and an incomplete lower incisor. No referred material.

P. **petersoni** sp. nov. P_4–m_3 = 23 mm. Type, No. 2018, Am. Mus., a skull, jaws and partial skeleton found by O. A. Peterson in the Telmatotherium level in 1895. It is a little larger than *P. hians* of the Bridger, and may be distinguished by the much longer skull, narrower incisors, longer diastemata, etc. It is the largest species of the genus. Teeth broad and robust as in *P. hians* and *robustus*, muzzle peculiarly angular. Anterior face of lower incisors flat, as in Castoridæ, Geomyidæ, etc., a marked distinction from any other species of this genus.

The greater part of the skeleton is preserved in the type, but has not yet been prepared. The proportions of the fore and hind limbs are much as in *P. delicatus* and *robustus*, but the entire skeleton is smaller in proportion to the size of the skull. The manus shows four functional digits, a short, stout pollex and a radial sesamoid (pre-pollex). The unguals are of very different type from those in *P. delicatus, robustus* or *grangeri*; they are long, uncompressed, nearly round in cross section, little curved, and evidently specialized for fossorial habits. Scaphoid, lunar and centrale separate, digits somewhat shortened from the proportions of the other species.

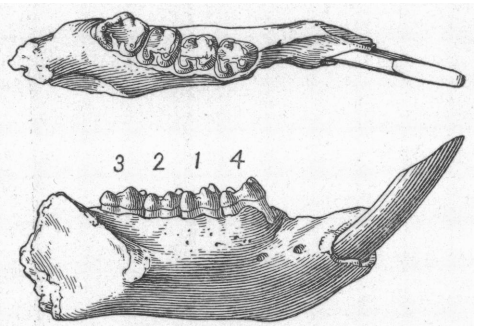


Fig. 10. *Paramys* (*Leptotomus*) *grangeri*, lower jaw, superior and external views, natural size. Type specimen, No. 2016, Uinta beds, Utah.

P. **grangeri** sp. nov. P_4–m_3 = 23 mm. Type, Am. Mus. No. 2016, a lower jaw with fragmentary skeleton, from the top of the Telmatherium Beds, found by Walter Granger in 1895. This species is closely related to *P. leptodus* of the Washakie, but larger and more robust. The incisor is narrow, slender, longer and more procumbent than in the *P. delicatus* group, and much more compressed. Diastema longer, molars less basined, the enamel not rugose. Entoconid of m_3 more anterior, hypoconid more postero-median in position, connecting crests between protoconid and hypoconid generally more prominent. P^4 more trigonal in outline, metaconule more prominent than metacone.

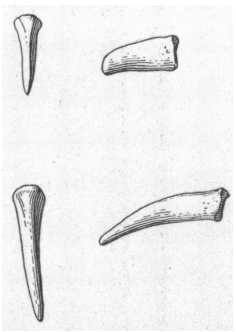


Fig. 11. Claw phalanges of fore foot in *P. grangeri* (upper) and *P. petersoni* (lower), natural size, dorsal and lateral views.

P_4–m_3 one tenth longer than in *P. leptodus*, the molars one fourth to one sixth wider.

A second specimen found by Mr. Granger in 1906 in the Upper Washakie, is referable to this species. It consists of lower jaw, p^4 and fragments of skeleton.

The limb bones in *P. grangeri* are more robust than in *P. delicatus*, and the proportionate size of the hind limb is considerably greater. The scaphoid and lunar of the left side in the type specimen are united, those of the right side separate; this probably indicates a tendency to fusion of the two bones. The centrale

Comparative Measurements.

	P. primævus.	P. quadratus.	P. atwateri.	P. buccatus.	P. bicuspis.	P. copei.	P. major.	P. excavatus.	P. delicatus.	P. delicatior.	P. delicatissimus.	P. robustus.	P. hians.	P. leptodus.	P. sciuroides.	P. uintensis.	P. petersoni.	P. grangeri.
Skull, total length						75.			90.				95+		61.		109	
" width across arches									51.				72				54	
Skull, width muzzle									22.						25		23	
" " occiput									35.5								42	
" height "									23.								24	
" length of diastema						17.			20.								21	
Skull, length m^3 to for. ov.									19.									
Skull, length for. ov. to condyles									25.									
Skull, width postorb. constriction						10.			11.						10		16	
Skull, width palate betw. molars									13.									
Lower jaw, total length						40.			67.			75.			28		77	
Lower jaw, height, angle to coronoid						31.			40.			50.5					45	
Lower jaw, depth beneath m_2						10.			12.6	10.6	8.5	18.					17	13.
Lower jaw, length diastema						6.			6.8		6.3	9.8					11.5	13.
Dentition, p^3–m^3						14.5			19.5						13	(21.8)		
" p_4–m_3	15.	18.	12.5	11.	14.	13.5	16.5	12.	19	15.3	12.6	(12.5)		21.	12		23	23
Upper incisor, transverse									5			5.1	7			4.	6.	
Upper incisor, antero-post.									5.8			7.1	8.5			4.2	7.	
Lower incisor, transverse									3.2	3.2	2.5	4.8		2.4	2.		4.8	2.9
Lower incisor, antero-post.									4.8	4.2	3.8	6.7		3.8	3.		6.	4.1
Fore-limb, humerus, length						60			72			81			43.		76.	53.
Fore-limb, radius. length									55			66						
Fore-limb, manus, length																		(65)
Hind limb, femur, length									97			115						(121)
Hind limb, tibia, length									95			124			36			
Hind limb, pes, length									104			137						
Vertebræ, seven cervicals									60									
Vertebræ, nineteen dorsolumbars									(270)									
Vertebræ, sacrum									42									
" twenty-nine caudals									(540)									

remains separate, as usually among rodentia. The fore-foot is somewhat more elongate than in *P. delicatus*, the ungual phalanges are of similar type but less compressed. The hind limb is one third larger throughout than in *P. delicatus*, and of more robust proportions.

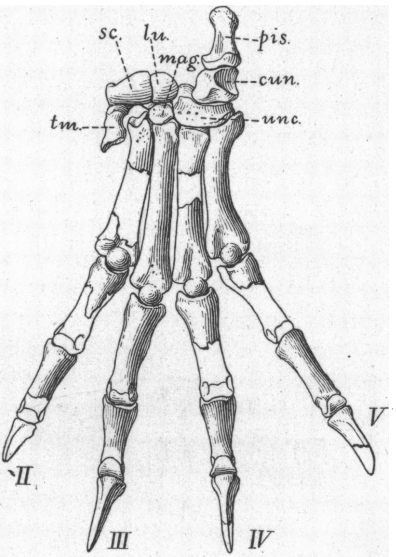


Fig. 12. *Paramys* (*Leptotomus*) *grangeri*, fore foot, natural size. No. 2016, Type.

Sciuravus *Marsh*, 1871.

Sciuravus MARSH, 1871, Amer. Jour. Sci., Vol. II, p. 122. Separata issued July 1871.

Plesiarctomys (in part) COPE, 1884. Not of Bravard.

Paramys (in part) ZITTEL, 1893; MATTHEW, 1899; HAY, 1902. Not of Leidy.

Sciuravus LOOMIS 1907, MATTHEW 1909.

This was the first genus of rodents described from the American Eocene, but on account of the brief and inadequate description has been mostly confounded with the better known *Paramys*, which, however, it antedates by about five months. Loomis in 1907 showed that the genera were distinct.

Sciuravus is nearly related to *Paramys*, but includes smaller species with quadritubercular upper molars. The dental formula, $\frac{1.0.2.3}{1.0.1.3}$, is the same as in *Paramys* and the general proportions of the teeth much the same as in the small species of that genus. The protocone and hypocone of the upper molars are distinct, well separated, sub-equal. In the lower molars the entoconid is placed further forward, and a strong ridge from the hypoconid runs inward behind it along the posterior margin of the tooth. This ridge may be compared in position with the hypoconulid, but is doubtfully homologous with the hypoconulid of other orders, and is well marked on all the molars. The molar cusps are more distinct than in *Paramys*, the basining of the crown less apparent. The pattern is a marked approach toward those of *Ischyromys* and *Gymnoptychus* (= *Adjidaumo*).

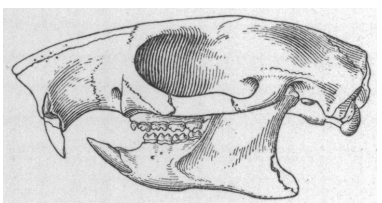


Fig. 13. *Sciuravus nitidus*, skull and lower jaw, side view, natural size, No. 12551. Lower Bridger, Wyoming.

The skull is very like that of *Paramys* except for a longer muzzle, more slender proportions, and absence of sagittal crest. In size and general proportions it compares with the rat (*Mus decumanus*). The tympanic bulla is incompletely ossified and loosely attached to the skull; it has no tubular meatus, the ossification comprising little besides the tympanic ring. What is known of the skeleton agrees with *Paramys* except for the lesser width of the distal end of the humerus. The carpals and the number of digits are unknown.

No satisfactory revision of the species can be undertaken without a restudy of the types of this and allied genera which at present I know only from Marsh's descriptions. Our material, provisionally referred to the genus

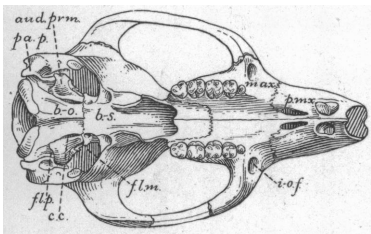


Fig. 14.

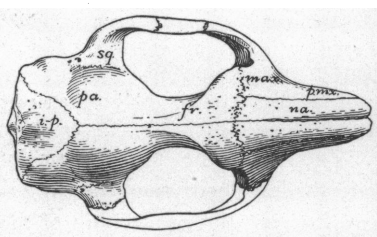


Fig. 15.

Fig., 14. *Sciuravus nitidus*, under view of skull, natural size, No. 12551. *Aud. prm.*, auditory prominence; *pa.p.*, paroccipital process; *f.b.-o.*, basioccipital; *b.-s.*, basisphenoid; *c.c.*, carotid canal; *f.l.m.*, foramen lacerum medium; *f.l.p.*, foramen lacerum posterius; *i.o.f.*, infra-orbital foramen.

Fig. 15. *Sciuravus nitidus*, top view of skull, natural size, No. 12551.

and identified through the courtesy of Dr. Loomis, consists of two nearly complete and several incomplete skulls, with fragmentary skeletons associated, and numerous upper and lower jaws.

Mysops *Leidy*, 1873.

A smaller animal than *Sciuravus*, with narrower teeth, upper molars less quadrate, the inner cusps less distinctly separate, the centre of the crown more basined. Lower molars narrower, the anterior pair of cusps higher and more crested, the entoconid more central in position. Construction of antorbital region as in *Sciuravus* and *Paramys*.

The genera *Tillomys*, *Taxymys* and *Colonomys* Marsh are known only from fragments of jaws or separate teeth, and Marsh's brief descriptions do not satisfactorily separate them from *Sciuravus*. The smaller referred species of *Tillomys* is perhaps identical with *Mysops*.

Ischyromys *Leidy*, 1856.

The structure of the skull in this genus has been described and figured by Leidy and Cope. It has the same primitive construction of the antorbital region as in *Paramys*, *Sciuravus* and *Mysops*, save that the infraorbital foramen is somewhat larger, and its anterior opening faces somewhat more downward. This direction appears to preclude its transmitting any portion of the median masseter, nor is there any evidence of the attachment of the muscle to the surface of the bone in front of or above the foramen. The characters of the antorbital region are throughout closely comparable with *Aplodontia*. The tympanic bullae are large, completely ossified, and always attached to the skull, unlike the Eocene genera. The attachment of the masseter on the lower jaw is limited anteriorly as in *Paramys*, the anterior

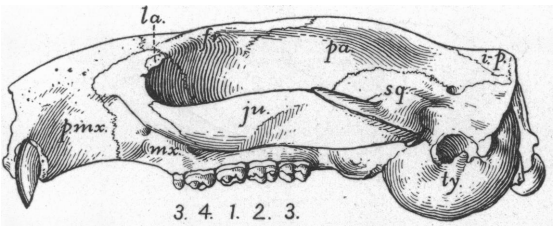


Fig. 16. *Ischyromys typus*, skull, natural size, Oreodon beds, S. Dakota. No. 694.

border of the masseteric fossa extending forward only to a point beneath m_2. The mental foramen is further forward than in *Paramys*, not so far as in *Arctomys*.

The skeleton of this genus is almost completely determinable from specimens in our collections, but in their present state of preparation the characters can be only partially stated. The cervicals are much shorter than in *Paramys*, not as short as in *Arctomys*. The tail was long and heavy. The humerus has an entepicondylar foramen and a prominent deltoid crest produced into a distinct process. The breadth of the ulnar shaft is intermediate between *Paramys* and *Arctomys*. The third trochanter of the femur has the same position as in *Paramys*; in Sciuridæ it is higher up on the shaft.

The dentition is a direct derivative of that of *Sciuravus* by partial conversion of its cusps into transverse crests.

SPECIES OF *Ischyromys.*

A. *Ischyromys* s.s. Incisors of moderate width, muzzle heavy and deep, skull with low sagittal crest, arches moderately deep, no masseter attachment on side of muzzle.

1. *I. typus* Leidy, 1856. Oreodon Beds, South Dakota and elsewhere. Length of skull, incisors to condyles, 63 mm. Teeth wider transversely with lower crowns and heavier enamel.

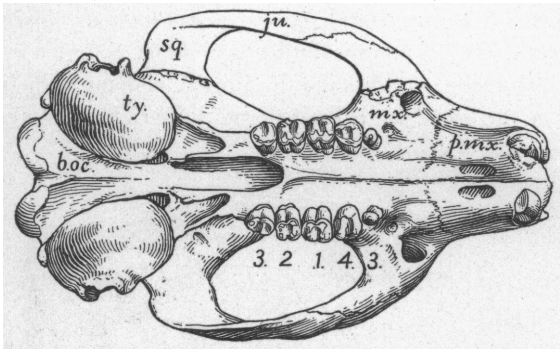


Fig. 17. *Ischyromys typus*, under view of skull, natural size. No. 694, Oreodon Beds, S. Dakota.

2. *I. cristatus* (Cope, 1872). Syn., *Gymnoptychus chrysodon* Cope, 1872. Oreodon Beds, N.-E. Colorado. Teeth narrower transversely

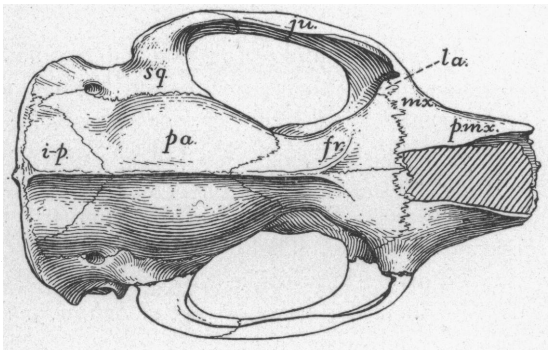


Fig. 18. *Ischyromys typus*, top view of skull. No. 694.

than in *I. typus*, with higher crowns and thinner enamel; skull and teeth usually smaller and sagittal crest sometimes incomplete anteriorly.

B. **Titanotheriomys,** new subgenus. Incisors narrow, muzzle small, no sagittal crest but an indistinct lyrate area; zygomata slender, superior border of origin of masseter extended forward on muzzle in an indistinct ridge.

3. *I.* (*T.*) *veterior* Matthew, 1903. Length of skull, incisors to condyles, 54 mm. Cheek-teeth much as in *I. cristatus* but heel of m_3 narrow with incomplete crest.

The skull proportions of this last species, as determined from a fragmentary skull from the type locality (Pipestone Springs, Montana) and a skull and skeleton (No. 14579) from the Titanotherium beds of Wyoming, differ so widely from the typical *Ischyromys* that I am obliged to place it in a separate subgenus. It belongs to a distinctly older horizon than *I. typus* or *cristatus* and is in some respects more primitive, but in the antorbital construction shows a definite advance towards the Sciurid type.

Prosciurus *Matthew,* 1903.

In the description of *Sciurus* (*Prosciurus*) *vetustus* from the Lower Oligocene, I stated that these earlier Oligocene squirrels were probably generically distinct from any modern sciurids, although the distinctions then observed did not warrant separating them as more than a subgenus. Review of the White River material, somewhat augmented since that date, shows additional characters which certainly warrant raising *Prosciurus* to the rank of a distinct genus, and apparently it should be included in the Ischyromyidæ rather than the true Sciuridæ. The anterior margin of the masseteric fossa is under m_2 as in *Paramys, Ischyromys,* etc., instead of under p_4 or m_1 as in Sciuridæ. This appears in the types of *S. relictus* and *wortmani* Cope and in two undescribed jaws from the White River. The relations of the infraorbital foramen in the type of *S. vetustus* were apparently as in the Ischyromyidæ and certainly not as in the Sciuridæ. From these indications I judge that these species retained the primitive construction of the antorbital region. *Sciurus ballovianus* Cope, from the John Day, appears, on the other hand, to have assumed, at least in part, the true Sciurid conditions in this region, so far as may be judged from the imperfectly preserved skull. I leave it therefore in the modern genus, and transfer the other three species under *Prosciurus,* to the Ischyromyidæ. The Miocene squirrels, known only from a few jaws, appear to be true Sciurids, as are *S. chalaniati* and *feignouxi* of the Upper Oligocene of Europe.

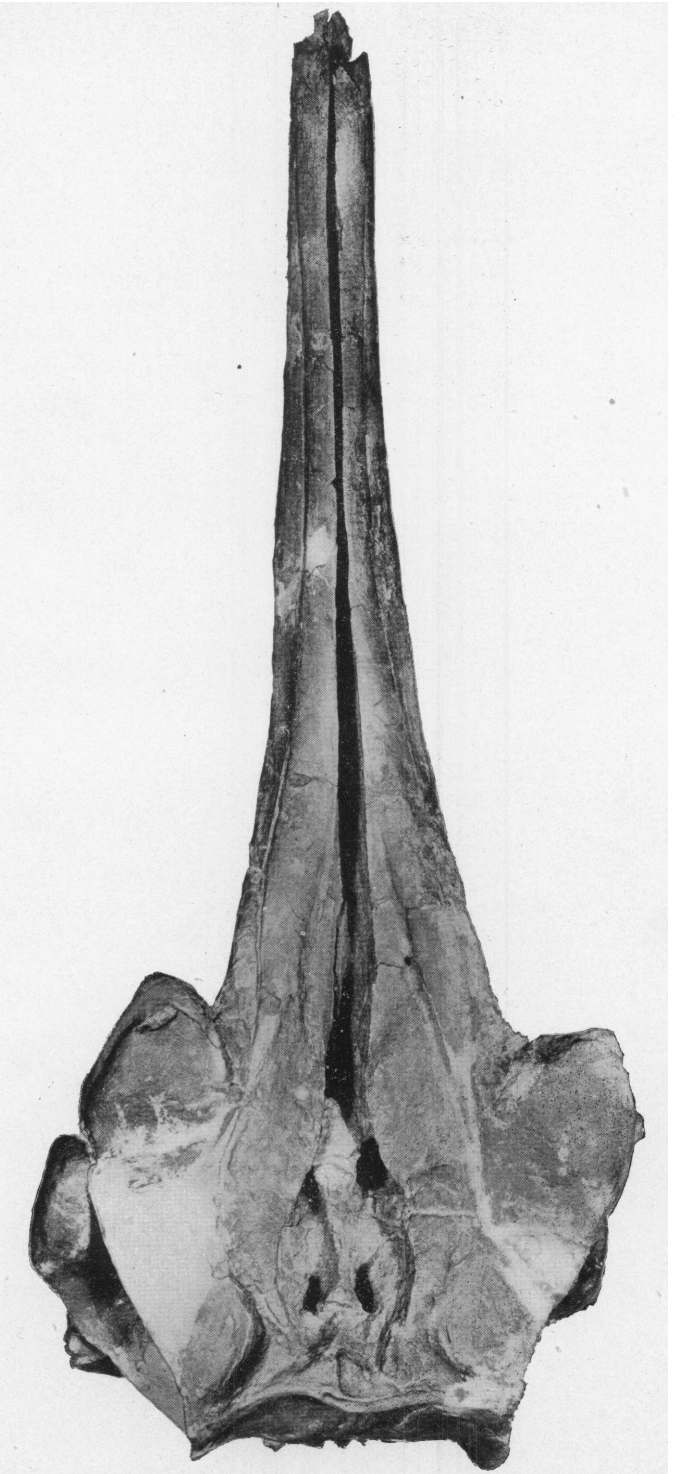
Cylindrodon *Douglass*, 1901.

This genus appears also to exhibit the primitive construction of the antorbital region, so far as can be judged from the upper jaw figured by me in 1903, and should apparently be separated from the Castoridæ on this ground, while from the Ischyromyidæ it is distinguished by the dental formula. The fundamental pattern of the molars is apparently much as in *Steneofiber*, but it is also quite near to certain of the Theridomyidæ, with which it agrees better in what little is known of the antorbital region, except that the antorbital foramen is small, while in the European family it is said to be large. There is no tendency towards the Hystricomorph construction of the angle such as is observable in several of the Theridomyid genera. None of the Ischyromyidæ come near *Cylindrodon* in tooth-pattern. It may best be referred provisionally to the Ischyromyidæ.

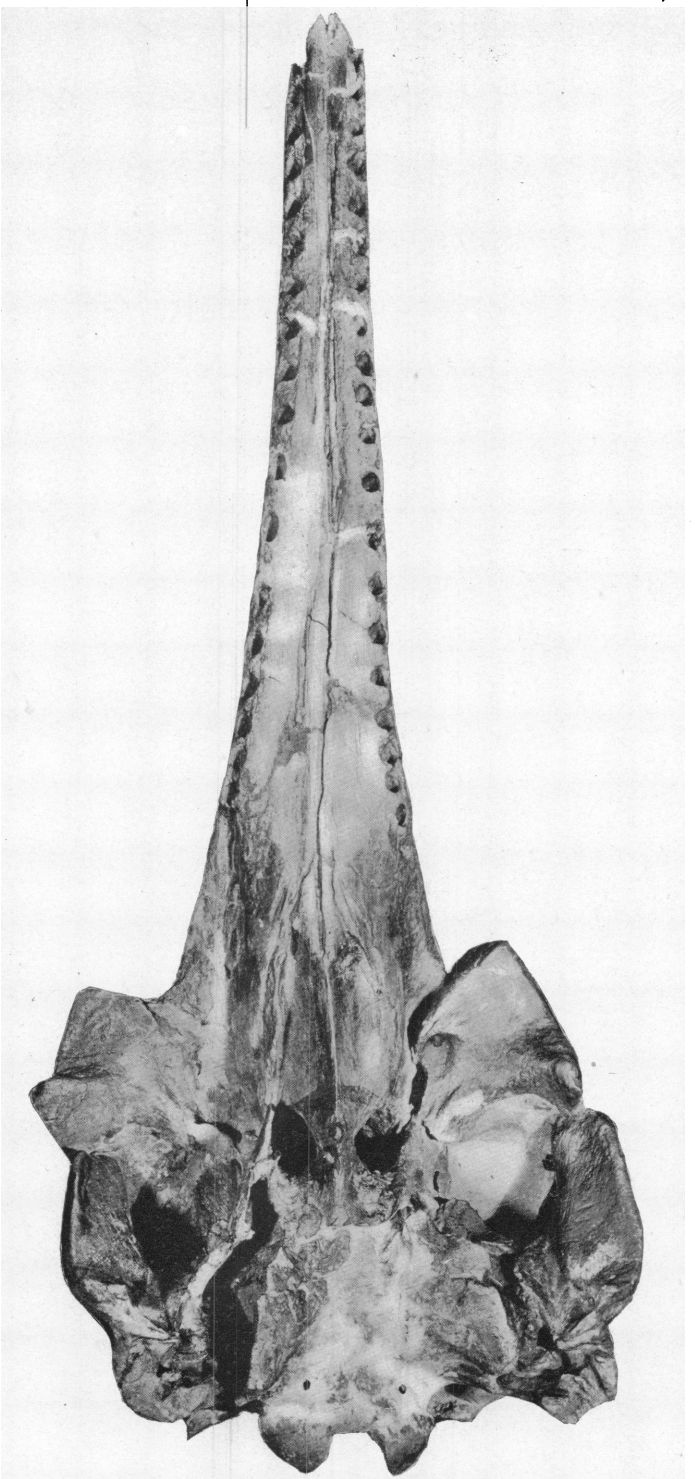
Affinities of the Ischyromyidæ.

From their geological position we should expect this family to be more or less directly ancestral to the later groups of rodents and to represent the common stock from which they have differentiated. This appears to be substantially the case, so far as the Simplicidentata are concerned. They give little or no hint as to the ancestry of the Lagomorpha, which are not included in the following discussion.

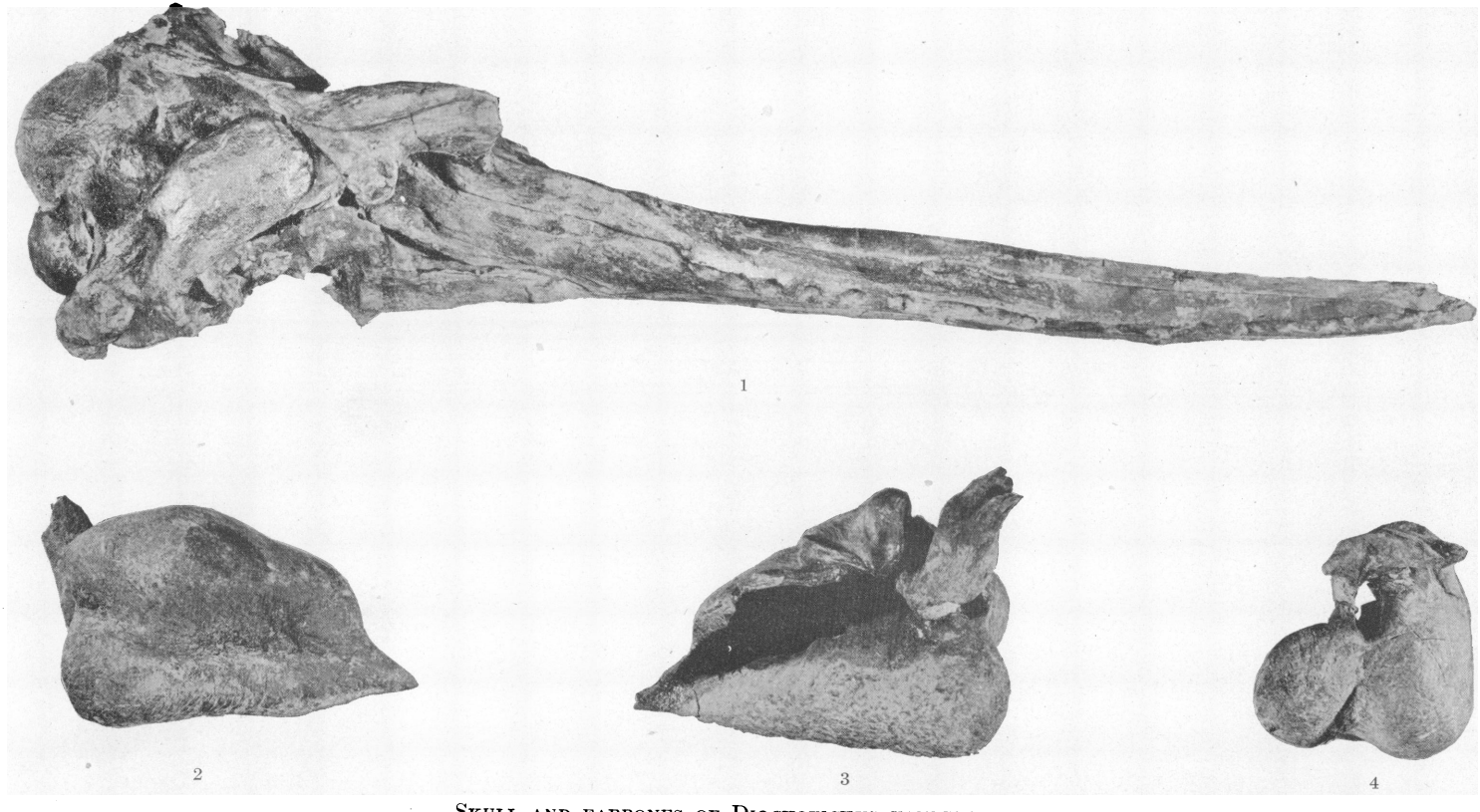
The structure of the antorbital region in the Ischyromyidæ must be regarded as the primitive construction among the rodentia generally. It agrees most nearly with the construction in other orders of mammalia, especially the more primitive mammals. In nearly all modern rodents the masseter is extended forward so as to gain a strong attachment on the side of the muzzle in advance of the orbit, thus giving it increased leverage on the incisors. In the Sciuromorpha (except *Aplodontia*), the *external* portion of the masseter is extended forward *above* the infraorbital foramen, which is small, and opens considerably in front of the zygoma and low down on the muzzle. In the Hystricomorpha the *inner* portion of the masseter is extended forward *through* the infraorbital foramen, which is much enlarged and faces more upward. In the Myomorpha the *external* part of the masseter is extended forward on a plate projecting from the root of the zygoma and *overlapping* the infraorbital foramen, partially dividing it into two unequal parts, of which the small lower division transmits the nerve, while a part of the *inner* portion of the masseter is extended forward through the large upper division of the foramen to gain an attachment on the side of the skull.



SKULL OF DIOCHOTICHUS VANBENEDENI.



Skull of Diochotichus vanbenedeni.



SKULL AND EARBONES OF DIOCHOTICHUS VANBENEDENI.

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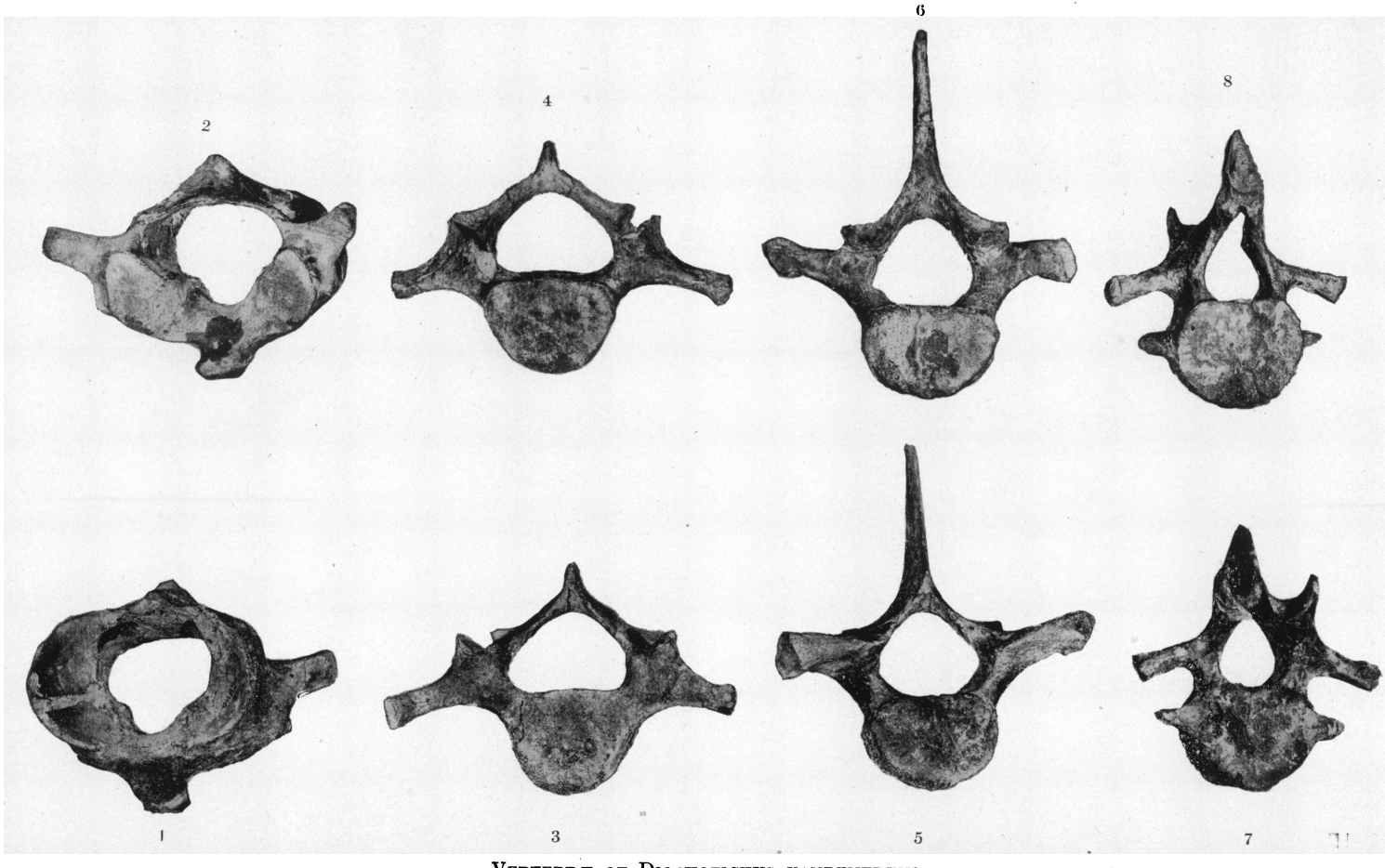
SKULL AND RIBS OF DIOCHOTICHUS VANBENEDENI.



Vertebræ of Diochotichus vanbenedeni.

This forward extension of the masseter is carried furthest in the most progressive members of the three principal groups of Simplicidentate rodents. The primitive condition is universal in the Eocene, common in the Oligocene, rare in the Miocene, and among modern rodents is preserved only in a few aberrant and exceptional types, most perfectly in *Aplodontia.*

In the lower jaw the Ischyromyidæ are likewise unmistakably primitive. They retain the vertical uninflected angle characteristic of most placental mammals, but rare among rodents. In nearly all modern rodents the angle is inflected or twisted by the hypertrophy of certain parts associated with the specialization of the masseter. In most of the Hystricomorpha, and in the Bathyergidæ, the antero-inferior border of the masseteric fossa is raised into a prominent ridge projecting outward, so that the angle appears to originate anteriorly from the external side of the incisive alveolus. In the Sciuromorphs and Myomorphs this does not occur, but the postero-inferior border of the masseteric fossa, as also in some Hystricomorphs, is extended and inflected, while the posterior point of the angle is more or less everted. The primitive condition is most nearly retained in this respect among the Muridæ — *Aplodontia* is highly specialized — the Sciuridæ less so. The masseteric fossa is also considerably extended anteriorly in most modern rodents, and the coronoid process reduced (except in *Aplodontia*).

The imperfectly ossified bulla, short backwardly directed paroccipital process, posterior extension of the nasals and premaxillaries, narrow post-orbital constriction, etc., are all primitive Eutherian cranial characters, common to nearly all Eocene mammals, generally or always lost in modern rodents, as they are to a varying extent in other orders.

The dentition of the Ischyromyidæ is that of the Sciuridæ and Aplodontiidæ, the most primitive of modern rodents in this respect. The skeleton agrees in proportions and construction with the arboreal squirrels, but retains one primitive character lost in all modern rodents except *Bathyergus,* the separate lunar and scaphoid of the carpus. The feet are very sciuroid, and while they are the most generalized rodent feet, they show the distinctive characters of the order already firmly fixed, in the peculiar reduction of the pollex, presence of radial sesamoid, characteristic form of astragalus etc.

The varying construction of all modern rodents in teeth, skull and skeleton can readily be derived in all details from the Eocene Ischyromyid type. They have undergone a great variety of parallel and divergent changes of reduction and specialization of parts, in adaptation to their various terrestrial, cursorial, fossorial or amphibious habits. The adaptations in the masseter muscle and its attachments offer an obvious case of parallelism with analogous structural changes in the several groups. The perfecting of the

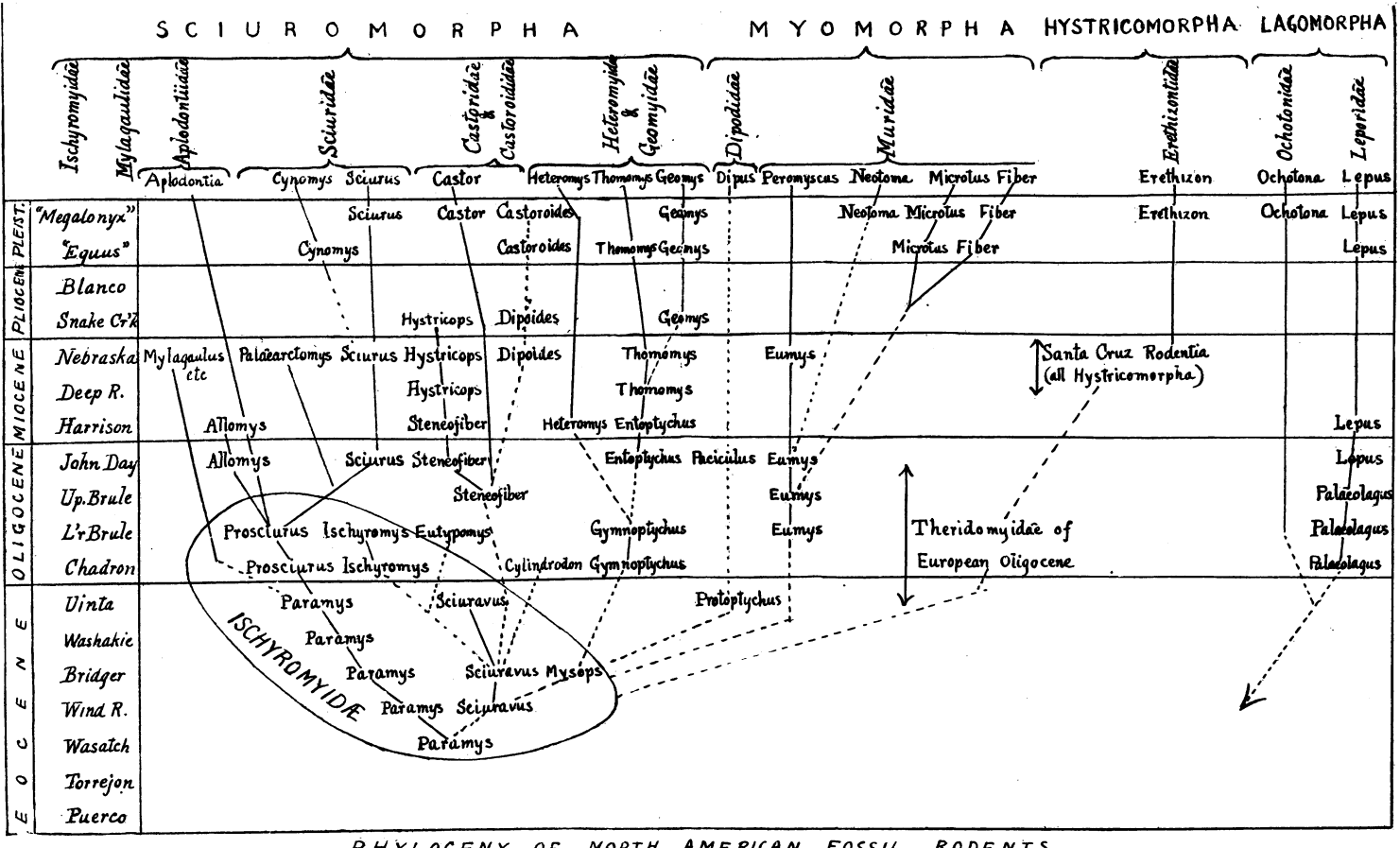
bulla, its peculiar specializations in certain groups, the increase in brain capacity, with consequent broadening of the cranium, reduction of sagittal crest, widening of postorbital constriction, change in the position and direction of the paroccipital, and numerous minor changes in the skull, afford instances of much closer parallelism, with homologous structural changes in the several groups.

The teeth of modern rodents show a great variety of both parallel and divergent evolution as compared with Ischyromyidæ. In the Hystricomorphs p^3 is lost and the crowns of the teeth are lengthened to a varying extent, and their pattern complicated in various ways. In the Myomorpha p^3 is always and $p\frac{4}{4}$ usually lost, and in the higher groups the crowns are lengthened and their pattern complicated. In the Castorids p^3 is lost and the crowns lengthened and complicated, in the Geomyids and Heteromyids p^3 is lost and the crowns much elongate, but the pattern becomes simpler. The Sciurids and Aplodontiidæ retain the primitive dental formula, the former retaining more nearly the brachyodont teeth, especially in the Sciurinæ.

The limbs and feet in the Hystricomorphs show a great variety of reductions and specializations, but the group appears to have been primarily characterized by short limbs and short broad feet with a tendency to tridactylism. The Myomorphs have one peculiar progressive feature, the consolidation of tibia and fibula, but are mostly conservative in foot structure. The Sciuromorphs include some very primitive types, and others that are highly specialized. Fossorial, cursorial and saltatorial adaptations appear in each group, and afford instances of fairly close parallelism.

It will be observed that the most primitive rodents, except in the features conditioned by brain evolution, are the arboreal types. This is wholly in accord with the evidence from other groups, in supporting the theory which I advanced some years ago that all mammals are derived from arboreal ancestry.

The most primitive European rodents, the Theridomyidæ and Pseudosciuridæ, although imperfectly known, approach very nearly to the Ischyromyidæ, but appear to be transitional in several respects between this family and the Hystricomorpha. The antorbital region agrees with Ischyromyidæ except for the somewhat larger size of the infra-orbital foramen, which also faces forward instead of partly downward, so that it could, and according to Zittel (1893) did transmit a branch of the masseter, as in Myomorphs and Hystricomorphs. They agree with Hystricomorpha in dental formula, and several of the Theridomyidæ show a marked approach in tooth pattern toward certain Hystricomorph families, and also a very noticeable prominence of the antero-inferior border of the masseteric fossa, the jaw being otherwise constructed as in Ischyromyidæ. This feature may



PHYLOGENY OF NORTH AMERICAN FOSSIL RODENTS

Showing the Geological and Phylogenetic Relationships of the Ischyromyidæ.

Fig. 19.

fairly be interpreted as prophetic of the Hystricomorph construction of the angle.

It is, however, open to very serious question whether the differences of these two groups from the Ischyromyidæ are any greater than may be found among different members of some of the modern families of the Rodentia, and their retention as distinct families should be regarded rather as a matter of convenience in classification than as indicating any very wide structural differences.

Classification.

The Ischyromyidæ are included in the Sciuromorpha by definition, as the infraorbital foramen does not transmit any portion of the masseter, and they are undoubtedly most nearly allied in nearly all structural features to the modern Sciuridæ. They are sharply separated however from the Sciuridæ, Castoridæ, Castoroididæ, Geomyidæ and Heteromyidæ by the primitive construction of the antorbital region, agreeing with the Aplodontiidæ and Mylagaulidæ in this respect. This distinction was sharply marked as far back as the Oligocene, for the Upper Oligocene *Sciuri* (*S. ballovianus, feignouxi, chalaniati*), and the Oligocene genera *Eutypomys* and *Steneofiber* (Castoridæ), *Gymnoptychus* (Heteromyidæ), and *Entoptychus* and *Pleurolicus* (Geomyidæ), are completely modernized in their antorbital construction, and no intermediate forms are at present known.[1] In view of the importance which the characters of this region assume in the classification of rodents, and of the antiquity of this distinction among the Sciuromorpha I think it should be the primary basis of division in this group of the order.

The Theridomyidæ and Pseudosciuridæ, on the other hand, although so closely resembling Ischyromyidæ as hardly to merit family distinction, must be referred to the Hystricomorphs (if we include the Anomaluridæ in this group) by definition, and the first family at least, apparently has true Hystricomorph affinities, and must be regarded as approximately ancestral to the group, despite the serious difficulties in accounting for the geological and geographical distribution of the known members of Theridomyidæ and Hystricomorpha.

The interesting Uinta genus *Protoptychus* appears to be, as shown by Scott, of Myomorph affinities, but far from typical, related and possibly ancestral to the Dipodidæ, but with marked indications of affinity to the Geomyidæ and Heteromyidæ as well. It is perhaps an annectant form between Sciuromorpha and Myomorpha. *Eumys* of the Middle and Upper Oligocene is unmistakeably and typically Myomorph and quite nearly

[1] *Sciurus ballovianus* and *Ischyromys veterior* (see p. 63 supra) are possible exceptions to this statement.

related to the Cricetinæ, with which it agrees well in skull structure as well as in dentition. True Hystricomorpha are unknown in North America until the Pleistocene, the nearest possible approach being *Cylindrodon*, whose provisional position in the Ischyromyidæ is rather a matter of convenience in classification than of actual affinity. Typical Myomorpha first appear here in the Middle Oligocene, while the typical Sciuromorpha have developed and differentiated out of the primitive group by the beginning of the Oligocene.

The Sciuromorph families may be defined as follows:

Sciuromorpha Brandt: Infraorbital foramen small, not traversed by masseter. Antero-inferior border of masseteric fossa little or not at all crested. Dentition $\frac{1.0.2\text{-}1.3\text{-}2}{1.0.1.\ 3\text{-}2}$.

A. *Aplodontoidea* Gill, 1872: Infraorbital foramen moderately small, sub-circular, close to lower margin of orbit, origin of masseter wholly behind and below it, and not extended forward upon the side of the muzzle.

1. *Ischyromyidæ* Alston, 1876. Teeth $\frac{1.0.2.3}{1.0.1.3}$, short-crowned. Skull of moderate width, no postorbital process, zygomatic arch moderately deep, angle uninflected. Arboreal and terrestrial, Lower Eocene to Oligocene. Genera *Ischyromys, Paramys, Sciuravus, Mysops, Prosciurus.*

2. *Mylagaulidæ* Cope, 1881. Teeth $\frac{1.0.1.2}{1.0.1.2}$, premolar enlarged, hypsodont; molars reduced and caducous, $m\frac{1}{1}$ absent except in milk dentition. A postorbital process on frontal; zygomatic arch deep; skull wide posteriorly, posterior border of angle greatly inflected and posterior end everted. Nasals with or without bony horncores. Fossorial, Middle Miocene to Lower Pliocene. Genera *Mylagaulus, Ceratogaulus, Epigaulus, Mesogaulus.*

3. *Aplodontiidæ* Thomas, 1897. Teeth $\frac{1.0.2.3}{1.0.1.3}$, progressively hypsodont, with prominent mesostyles and metastylids. No postorbital process; zygomatic arch slender; skull wide posteriorly; postero-inferior portion of angle greatly inflected, posterior end everted. Fossorial, Oligocene to recent. Genera, *Aplodontia, Meniscomys, Mylagaulodon.*

B. *Sciuroidea* s. l.: Infraorbital foramen small, compressed, anterior in position; origin of masseter extended forward upon the side of the muzzle above and behind the infraorbital foramen, limited superiorly by a prominent crest extending forward and upward from the anterior margin of the orbit. Includes three groups regarded as superfamilies by most modern systematists.

1. *Sciuridæ.* Teeth $\frac{1.0.2\text{-}1.3}{1.0.1.3}$, short crowned and tubercular. Postorbital processes on frontals; skull of moderate width, arches slender to moderate, posteroinferior border of angle moderately inflected. Mastoid not inflated, auditory meatus short. Arboreal, terrestrial and fossorial. Oligocene to recent. Genera, *Sciurus, Palæarctomys, Arctomys, Cynomys, Pteromys, Sciuropterus, Tamias, Spermophilus,* and many others.
2. *Castoridæ* (and *Castoroididæ*). Teeth $\frac{1.0.1.3}{1.0.1.3}$, progressively hypsodont, with transverse enamel inflections (typically three external and one internal above, reversed below). No postorbital process; zygomatic arch deep; mastoid not inflated, auditory meatus long. Fossorial and amphibious, Oligocene to recent. Genera, *Castor, Steneofiber, Chalicomys, Trogontherium, Dipoides* (syn. *Sigmogomphius* and *Eucastor*), *Castoroides,* ? *Eutypomys.*[1]
3. *Geomyidæ* (and *Heteromyidæ*). Teeth $\frac{1.0.1.3}{1.0.1.3}$, progressively hypsodont with one, finally no transverse inflection. No postorbital process. Mastoid inflated, meatus long. Fossorial (Geomyidæ) and saltatorial (Heteromyidæ), Oligocene to recent. Genera, *Geomys, Thomomys, Entoptychus, Heteromys, Gymnoptychus, Heliscomys, Dipodomys, Perognathus,* etc.

The geological distribution of the North American fossil rodents is given in the following table, so far as known to me:

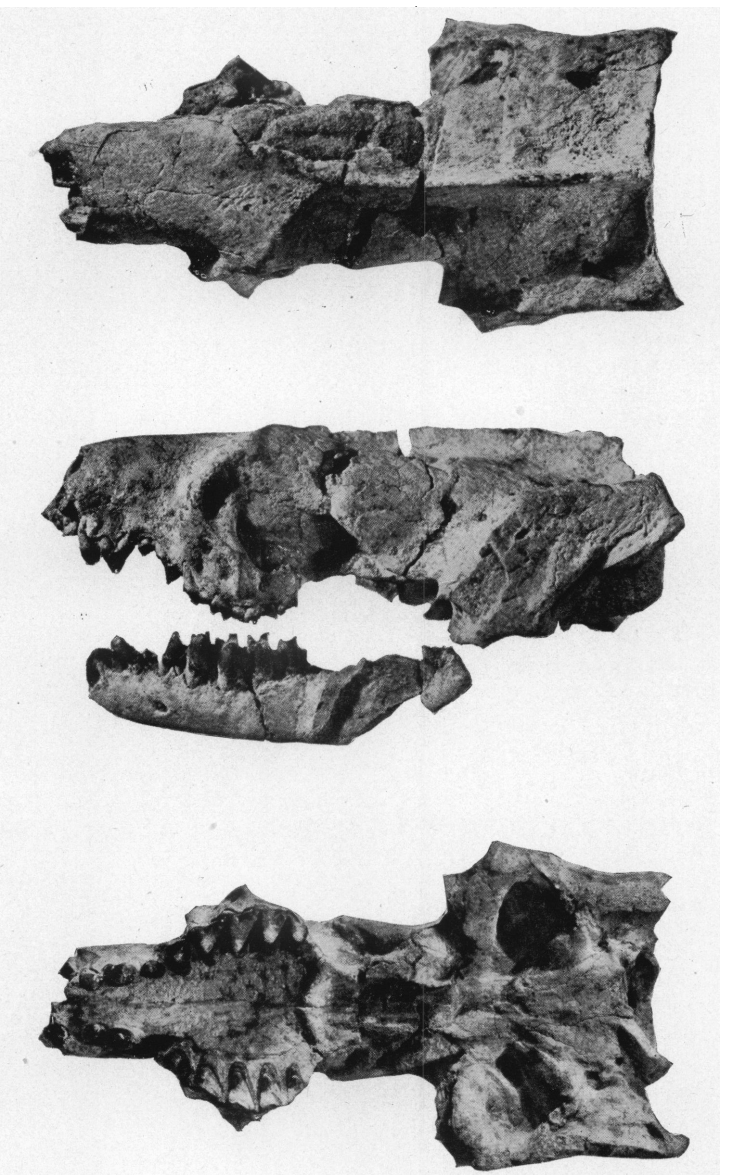
[1] Sciurid by definition in several respects, but apparently of Castorid affinities.

Geological Distribution of North American Fossil Rodents.

Sciuromorpha	Eocene								Oligocene				Miocene			Plio-cene		Pleis-to-cene		Modern
	Puerco	Torrejon	Wasatch	Wind R.	L. Bridger	U. Bridger	U. Washakie	U. Uinta	Titanoth'm	Oreodon	Protoceras	John Day	Harrison	Deep R.	Nebraska	Snake Creek	Blanco	Equus	Megalonyx	
ISCHYROMYIDÆ																				
Paramys			×	×	×	×	×	×												
Sciuravus				×	×	×		×												
Mysops					×															
Ischyromys									×	×										
Prosciurus									×	×		×								
?*Cylindrodon*									×											
APLODONTIIDÆ																				
Allomys												×	×							
Mylagaulodon												×								
Aplodontia																			×	×
MYLAGAULIDÆ																				
Mesogaulus														×						
Mylagaulus													×	×	×	×				
Ceratogaulus														×						
Epigaulus															×					
SCIURIDÆ																				
Sciurus												×		×	×			×	×	×
Palæarctomys															×					
Arctomys															×			×	×	×
Cynomys															?			×	×	×
Tamias, Spermophilus etc.																			×	×
CASTORIDÆ																				
Eutypomys									×	×										
Steneofiber											×	×	×		?					
Euhapsis													×							
Eucastor															×	×				
Hystricops															×	×				
Castoroides																		×	×	
HETEROMYIDÆ																				
Gymnoptychus									×	×										
Heliscomys										×										
Heteromys													?							
Perognathus, Dipodomys etc.																			×	×

(*Geological Distribution, continued.*)

	Eocene								Oligocene				Miocene			Plio-cene		Pleis-to-cene		
	Puerco.	Torrejon	Wasatch	Wind R.	L. Bridger	U. Bridger	U. Washakie	U. Uinta	Titanoth'm	Oreodon	Protoceras	John Day	Harrison	Deep R.	Nebraska	Snake Creek	Blanco	Equus	Megalonyx	
GEOMYIDÆ																				
Entoptychus and *Pleurolicus*												×	×							
Thomomys														×	×			×	×	×
Geomys															×	×		×	×	×
Myomorpha																				
DIPODIDÆ																				
?*Protoptychus*								×												
?*Paciculus*												×								
MURIDÆ																				
Eumys										×	×		×							
Peromyscus												×			×				×	×
Neotoma, Reithrodontomys																			×	×
Fiber, Microtus																		×	×	×
Hystricomorpha																				
ERETHIZONTIDÆ																				
Erethizon																			×	×
Lagomorpha																				
LEPORIDÆ																				
Palæolagus									×	×	×									
Lepus												×	×		?	?		×	×	×
LAGOMYIDÆ (= Ochotonidæ)																				
Lagomys																			×	×



Apternodus mediævus. Skull, enlarged to three diameters; top, side and under views. Lower Oligocene, Wyoming.