59.14,85,7:9,32(7)

Article XXVIII.— THE AUDITORY OSSICLES OF AMERICAN RODENTS.

By T. D. A. Cockerell, Lewis I. Miller and Morris Printz.

In the course of some work on the classification and relationships of rodents, our attention was attracted to the auditory ossicles as being likely to afford significant characters. A very moderate amount of experience convinced us that these structures were indeed of considerable value for taxonomic purposes, and we accordingly followed up the subject as far as circumstances permitted. In addition to such specimens as we could collect in the vicinity of Boulder, we were permitted the use of numerous skulls of Rocky Mountain species in the University Museum, through the kindness of Professor J. Henderson. Our outlook was then greatly extended by the loan of a series of South American skulls from the American Museum of Natural History, through Dr. J. A. Allen; while the U. S. National Museum kindly loaned skulls of a number of African species. Quite recently the U. S. National Museum, through Mr. G. S. Miller, has loaned skulls of three Old World species of true Cricetinæ. We could not have made even a preliminary survey of the field without the kind assistance of the persons and institutions mentioned. The African skulls have been treated in a short separate paper, which has been sent to the 'Zoologischer Anzeiger'. The American genera are discussed herewith; and for purposes of comparison, the three genera of Old World Cricetinæ. We also include genera introduced or domesticated in America. It is obvious that the investigation could be greatly extended with advantage, but we think we have carried it far enough to bring out some of the leading facts, and indicate some of the lines along which further progress may be made.

The great classical work on ear-bones is of course that of A. H. G. Doran, 'Morphology of the Mammalian Ossicula Auditus,' Trans. Linnean Society, ser. 2, Zool., Vol. I, pp. 371–497, plates 58–64. We have referred to this throughout as "Doran." The number of species treated by this author is astonishing, and includes many which are rare or difficult to obtain. The descriptions are usually sufficient, and the figures, though rather small, are good.

Although Doran's work is excellent, caution is needed in its interpretation, and indeed in the use of any work on this subject. The conformation of the ossicles is such that they present difficulties analogous to those found by students of the genitalia of insects. That is, they have so many processes

and angles, curves and hollows, that their appearance is greatly altered by even a little change of orientation. A naïve examination of Doran's figures or our own might thus lead to quite mistaken conclusions. Sometimes, after making a drawing, we have found it quite difficult to rediscover the precise position which gave the outline presented. In addition, these small objects have to be studied under a low power of the compound microscope, and frequently some conspicuous feature will not be in focus in a view which best illustrates some other one. Hence the final drawings come to represent the use of several different foci, supplemented by the hand lens. In some cases the lateral processes of the malleus project directly toward the observer, and practically defy all attempts to clearly indicate their nature in a drawing.

The difficulties described are still further augmented by the effects of age and of individual variation, the latter in some cases being quite large. Nevertheless, in spite of all complications, the salient facts appear to be reasonably clear.

Doran has minutely described the human ossicles, comparing their features with those of various animals. It will be sufficient here to briefly enumerate the named parts of the bones, indicating their positions.

Malleus. The largest of the three bones, is more or less hammer-like, as the name indicates. The large upper part, or *head*, presents a broad articular surface for the incus. In rodent mallei the part below the head is usually much constricted, and is called by us the *cephalic peduncle.* From the side of the head arises the cephalic process or *processus cephalicus*, obliquely (or even vertically) directed downwards, and frequently bounding above and without a large thin plate or *lamina.* The lower side of the lamina is bounded by the *processus gracilis*, which is usually slender, evanescent apically, and arises from the more or less swollen region between the cephalic peduncle and the base of the manubrium. The *manubrium* or handle extends downwards, and is a more or less flattened structure, like a dagger or knife-blade, usually with thickened margins (when it is said to be bimarginate), with a thin lamina between. The outer edge, attached to the tympanic membrane, is usually broadened and spatulate at the lower end (though sharply pointed in lateral view), and ends above in a sort of heel-like process, the *processus brevis.* On the side of the manubrium opposite to the processus brevis, sometimes half-way down the manubrial margin, but often above the manubrial base, is usually seen the *processus muscularis*, for the attachment of the tensor tympani. There still remains a process, to which we attach considerable importance; the *orbicular apophysis.* This is usually formed like the end of a finger, and extends outward from the root of the manubrium, at right angles to the manubrial blade, and to the processi muscularis and brevis.

Incus. Consists of a body, articulated with the malleus; from this proceeds outward a *processus brevis;* and downward a long process, the *stapedial process* (or processus longus), which articulates with the head of the stapes. At the end of the stapedial process, actually attached to the head of the stapes, is usually seen a button-like object, the *sylvian apophysis.*

Stapes. This stirrup-shaped ossicle consists of a head, from which descend two crura, to a transverse base, the last consisting of a thickened margin, surrounding a foot-plate, which in certain genera is strongly convex. At the side of the head is often seen a distinct process, the *stapedial process*, for the insertion of the stapedius muscle. Between the crura, in most groups, a blood-vessel runs, and frequently this is enclosed in a bony *intercrural canal.*

We have had constantly before us the question whether the auditory ossicles might throw any light on the origin of the Rodentia. Broom (Bull. Amer. Mus. Nat. Hist., XXXIII, p. 131) remarks, after discussing *Polymastodon:* "We have altogether in rodents quite a number of resemblances to characters found in *Polymastodon.* Most likely they are all due to convergence, though the suggestion has been made by Ameghino that the Rodents have sprung from the Multituberculates, and one would like to hesitate before denying the possibility."[1] We have no evidence concerning the auditory ossicles of the Multituberculata, but perhaps some indirect indications may be obtained by comparison with the line leading through the series Monotremata, Marsupialia, Insectivora, Chiroptera, etc. Gregory (Bull. Amer. Mus. Nat. Hist., XXVII, p. 467) represents the Rodentia as springing from some undiscovered placental type at the very base of the placental series, but nearest to the stem leading to Insectivora, Chiroptera and Primates. On p. 332 of the same work, Gregory concludes that "it seems not improbable that the stem forms of the Rodentia were Mesosoic Placentals, allied to the ancestors of the modern Insectivora and possibly to the contemporary ancestors of one or more of the Paratherian or Edentate orders."

While we cannot pretend to do anything more than indicate a few suggestive facts, these may not be without weight when considered in relation to the general structure of the animals.

(1.) The well developed orbicular apophysis of the malleus in the Myomorpha parallels the condition found in Chiroptera (as we have seen in a study of the ossicles of bats now in progress) and in Insectivora. We find, however, that the orbicular apophysis is absent in the Arvicolidæ and in the true (Old-World) Cricetinæ. The question arises, whether we are to con-

[1] Any connection between Rodents and Multituberculates is quite untenable if the characters and relationships of *Paramys* are taken into consideration. This genus is the oldest known rodent and represents approximately the primary type of the Simplicidentate families. The progressive specialization of each group can be traced more or less exactly from this primary type. The characters on which Ameghino and Broom rely in comparing rodents with Multituberculates are without exception secondary specializations. There are none of them present in *Paramys* save for the "diprotodont" specializations, which are present in several other unrelated phyla. Comparison of the skull or skeleton of Multituberculates with *Paramys* (which is contemporary with the last of them) shows not the least suggestion of relationship.— W. D. MATTHEW.

sider that the primitive Myomorpha possessed the apophysis, and that the Arvicolidæ and Cricetinæ have (apparently quite independently) lost it; or that the ancestors of the group had no apophysis, and those which still lack it are to that extent more primitive. Of these alternatives, the first is surely the more probable; but on similar grounds we must believe that the Myomorpha have not descended from close relatives of any of the other rodent groups. This idea is supported by Matthew, who (Bull. Amer. Mus. N. Hist., XXVIII, p. 67) represents the Myomorpha as arising *independently* from the Ischyromyids during the Eocene. The supposition would then be that those Eocene Ischyromyids possessed the apophysis, and it may not be going too far to suppose that the common ancestor of these and of the Insectivora-Chiroptera stem, somewhere in the later Mesozoic, also possessed this structure.

(2.) When we think of the human malleus as the type of that ossicle, the bone in the Myomorphous rodents, with its great cephalic process and lamina, seems very highly specialized. Upon comparison with Doran's plates, however, it is seen that this type of structure is frequent, and apparently of very ancient origin. Doran remarks that the Myomorpha and Insectivora, which agree in possessing an orbicular apophysis, also have the laminated malleus; hence we seem to find new and additional reason for connecting the ancestors of the Myomorpha with those of the Insectivora, and for holding the Myomorphan malleus to be really primitive among the rodents, although our first natural supposition was that it must be highly specialized.

(3.) Doran remarks (with good illustrations) that "in the shrews, the Mylogalidæ, Talpidæ, Centetidæ, and Hedgehogs proper one common feature exists — a malleus with a wide lamina and a processus gracilis united to the tympanic ring after the fashion of the Marsupials — in short, a low type of malleus." Comparison may be made with the malleus of the opossum. Here we directly connect the structures observed in the Myomorpha, through those of the Insectivora, with those of the Marsupials and ultimately the Monotremes. It seems to amount to a demonstration that the cephalic process and broad lamina are ancient, not new structures; and that when they are absent or scarcely developed, they have been lost.[1]

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[1] The Myomorpha retain several primitive characters in the osteology lost by the other groups. Prominent among these is the uninflected angle of the jaw, much more like that of *Paramys* and its allies.

If we interpret the loss of orbicular apophysis of the malleus as progressive, it would naturally be absent in the Arvicolines, the most progressive, recent, and modernized group, and in the higher (Palæarctic) members of the Cricetines, the group from which the Arvicolines are derived. The Arvicolines may be deserving of family separation; they certainly

I. ARVICOLIDÆ AND MURIDÆ.

By T. D. A. Cockerell and Morris Printz.

Text Figures 1–55, pp. 360–364.

As stated above, two groups of Muridæ (sens. lat.) lack the orbicular apophysis. One of these, commonly known as Microtinæ, we have ventured to separate as a family, for reasons given below, which might be supported by other anatomical characters, the discussion of which is outside the scope of this paper. A noteworthy feature in the skull is the usually prominent postorbital angle or process; evidently a typical character of the group, though evanescent in some of the smaller forms.

The case of the Cricetinæ is apparently a more or less parallel one. We were led to enquire into the matter by Doran's remark (without any figure) that in *Cricetus* "there is no orbicular apophysis." This seemed an astonishing statement, since this process is so well developed in all the American so-called Cricetinæ seen by us, as well as in the true Muridæ of the Old World. The examination of three species, representing as many genera, of true Cricetinæ has confirmed the absence of the orbicular apophysis, and taken with other characters, has seemed to abundantly justify the restriction of the group Cricetinæ to the old world genera related to *Cricetus*, leaving the American so-called Cricetines in a separate subfamily, for which Thomas has already furnished a name Sigmodontinæ.

We figure the mallei and incudes of the Cricetine genera examined, and would call attention to some of the more remarkable features.

Cricetus cricetus. (Near Magdeburg, Germany.)

Malleus. Head high and rounded; cephalic peduncle rather thick; articular surface large; lamina extensive; process gracilis very thin; processus muscularis large, at base of manubrium, which is slender and bimarginate.

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form a very distinct sub-family. I doubt the propriety of Sigmodontinæ as distinct from Cricetinæ.

The connection of the rodents with the insectivores and of these with the marsupials is supported by a whole series of osteological features, although for the most part they probably consist in the retention of primitive characters. Nevertheless the Simplicidentate rodents are a very clearly defined group osteologically in the Lower Eocene, when they first appear. The earliest tertiary Insectivora include a number of groups of quite remote relationship, definable only by possessing various primitive characters, and lacking the characteristic specializations of the other placental orders.

The position of the Lagomorpha is a difficult problem. Gidley thinks they have nothing to do with the rest of the Rodents and should be separated as a distinct order. Palæontology throws no particular light on this question. The earliest Lagomorphs are from the Lower Oligocene of U. S. (Leporidæ) and uppermost Eocene of Europe (Ochotonidæ) and are very close to the modern genera showing no notable approach to the Simplicidentates. They are certainly not derivable from *Paramys* or anything near it. The evidence here given does not confirm Gidley's view, although I should hesitate to say that it is clearly against it.— W. D. Matthew.

Incus. Curiously formed, with a very short truncate processus brevis; stapedial process long, ending in a cup-shaped sylvian apophysis, which has a very slender peduncle.

Cricetulus griseus. (Yu-Ling, China.)

Malleus. Head much less elevated and massive; lamina very extensive; processus muscularis rounded, well developed; manubrium bimarginate.

Incus. A small bone, with a massive but rather short processus brevis, and a slender straight stapedial process.

Phodopus bedfordiæ (Yuting-fu, China.)

Malleus. Head elevated, with a deep articular surface; lamina extensive; processus muscularis small and rounded; manubrium slender.

Incus. Articular surface broad and deep, saddle-like; processus brevis large, obtusely pointed; stapedial process rather short, with a large sylvian apophysis.

ARVICOLIDÆ.

Fiber zibethicus cinnamominus Hollister.

East of Boulder, Colorado (U. of Colorado Museum).

Malleus. Cephalic peduncle with a double curve, passing without much enlargement into the head proper, whence proceeds the long processus cephalicus, which is very stout basally, and gradually tapers, slightly curving as it approaches the exceedingly thin processus gracilis, the two enclosing a broad expanse of bony lamina. Orbicular apophysis absent. Manubrium bimarginate, with a flattened spoon-like distal end, in the manner of *Epimys;* processus muscularis at base of manubrium, as in *Mus.* This malleus is remarkable for the great development of the cephalic process. The figure does not show the manubrium.

Incus. Processus brevis rather poorly developed, short, rapidly tapering to a point, from which proceeds a ligament; stapedial process well developed, curving at its end, where it terminates in a well-developed sylvian apophysis. Articular surface for malleus exceedingly large, shallow, quadrilateral.

Stapes. Large, with symmetrical crura, which are long, slender, and not very divergent; head prominent; stapedial process small but distinct; foot-plate decidedly convex, surrounded by a symmetrical elliptical bony margin. Bony intercrural canal present. The base of the stapes has a diameter of about 1408 μ.

Microtus mordax (Merriam).

Pickwick Mine, Magnolia, Colorado (*J. D. Blanchard;* U. of Colorado Museum).

Microtus nanus (Merriam).

East of Boulder, Colorado (U. of Colorado Museum).

Malleus. This bone in *Microtus* is not unlike that of *Fiber,* and agrees with it in lacking the orbicular apophysis. Cephalic peduncle running straight up for some distance, then bulging to form part of the articular surface for the incus, passing

gradually into the thick head. Articular surface double and very shallow. Processus cephalicus well developed, sloping downward, rapidly tapering basally, and then continuing without much diminution of size. Processus gracilis slender, curved, long, with the cephalic process enclosing a subtriangular bony lamina. Manubrium bimarginate, broad, the distal end more distinctly spoon-shaped than in *Fiber;* processus muscularis basal as in *Fiber.*

Incus. Processus brevis short, pointed, with a ligament joining its extremity; stapedial process well developed, somewhat curved, ending in a very prominent sylvian apophysis. Articular surface large.

Stapes. Decidedly asymmetrical; crura rather short, divergent, one thicker than the other; foot plate broad, with a strong bony margin. A very large blood vessel passes between the crura, and in some cases a bony canal was present. Stapedial process distinct.

The two species of *Microtus* examined did not differ in any important character of their ossicles.

Doran examined the ossicles of *Arvicola amphibius, Microtus arvalis* and *Fiber zibethicus,* and remarks on the strong processus cephalicus of *Fiber.* Doran's figures of the mallei of *Arvicola* and *Fiber* suggest very different bones, but this is largely illusory, owing to the malleus of *Arvicola* having been drawn in such a position that the cephalic process, lamina and processus gracilis are not visible. The ossicles of *Arvicola* do not appear to differ materially from those of *Microtus.*

The Microtinæ differ from the true Muridæ in appearance, conspicuously in their teeth, and are peculiar for lacking the orbicular apophysis of the malleus. They seem to represent an ancient group, worthy of family rank. In Osborn's 'Age of Mammals,' p. 537, the Cricetinæ are included in the Microtinæ, but probably by an accident, as on p. 536 the Cricetinæ are given as a distinct subfamily. Matthew, Bull. Amer. Mus. N. Hist., XXVIII, p. 67, derives the Microtinæ (*Microtus* and *Fiber*) hypothetically from a common stem taking its origin in the Oligocene *Eumys,* a North American group. The American Cricetinæ are also supposed to be derived from *Eumys,* by another branch.

Following Miller in recognizing *Arvicola* as a distinct genus, we are able to recognize Gray's proposed name for the family, and the arrangement becomes:

Arvicolidæ Gray 1821. (*Microtidæ* Cope 1891.)
Subf. *Lemminæ.* (*Lemmi* Miller 1896.)
Subf. *Arvicolinæ.* (*Microti* Miller 1896.)
Subf. *Myotalpinæ* Miller 1896. (*Ellobii* Miller 1912.) Doran describes the ossicles of *Ellobius.*

MURIDÆ.

NEOTOMINÆ.

Neotoma mexicanaofallax (Merriam).

Boulder Cañon, Colo. (*J. D. Blanchard*).

Neotoma (Teonoma) Ocinerea rolestes (Merriam).

Gregory Cañon, near Boulder, Colo. (*Printz and Miller*); Marchioness tunnel Boulder Cañon, Colo. (*Henderson and Blanchard*).

Malleus. Manubrium bimarginate, with no processus muscularis, but a distinct tubercle present above the orbicular apophysis; whether this tubercle receives the tensor tympani was not ascertained. Orbicular apophysis large. Cephalic peduncle elongated, terminating in a relatively small head, with the articular surface for the incus much less than in the Arvicolidæ. Bony lamina extensive; processus gracilis long.

In animals of the same size, the malleus of *orolestes* was distinctly longer than that of *fallax*. In *orolestes* the cephalic peduncle has a distinct angular bend, whereas in *fallax* it is gently and more regularly curved. The orbicular apophysis in *fallax* lies almost in the same plane as the lamina, but in *orolestes* it is directed somewhat backward, out of that plane. The articular surface on the head of the malleus is higher and narrower in *fallax* than in *orolestes*.

Incus. Processus brevis thick and short; stapedial process long, with a distinct and well-developed sylvian apophysis, which is more easily separated from the stapes in *fallax* than in *orolestes*. Around the inner margin of the articular surface is a distinct broad groove. The whole inner side of the incus presents a concavity or groove, which is however variable in extent; it may be absolutely continuous with the articular surface. The incudes of the two species examined do not differ nearly so much in size as do the stapedes; there is also rather noteworthy variation in size between individuals of the same species.

Stapes. A stout bony intercrural canal is present.

The size of the ossicle differs in the two species, and this difference is not in proportion to the size of the skull, or to the size of the other ossicles. Thus: Skulls: *orolestes*, 4.5 cm. long; *fallax*, 4.3 cm.; ratio 100:95. Height of stapes: *orolestes* 985 μ; *fallax*, 848; ratio 100:86. Breadth of base of stapes: *orolestes*, 848 μ; *fallax*, 672; ratio 100:79.2. The crura of *fallax* are more divergent and less arched than those of *orolestes*, but in both one crus is shorter and straighter than the other, making the ossicle asymmetrical, this being especially marked in *orolestes*. In *fallax* the foot-plate is more convex than in *orolestes*. Individuals of *fallax* showed some remarkable variation in the processes of the stapes. In one example there was a distinct process on the inner surface of each crus, presumably connected with the intercrural canal. In this individual there was no stapedial process (for the stapedius muscle), but another individual of *fallax* had the stapedial process well developed. No stapedial process was found in *orolestes*.

Murinæ.

Epimys norvegicus (Erxleben).

Boulder, Colorado (*Printz and Miller*); Bloomington, Indiana (*Max M. Ellis*).

Malleus. Lamina well developed, with subtriangular outline; processus gracilis thin; cephalic peduncle scarcely curved, gradually passing into the head, which has a short articular surface as in Neotominæ (thus quite different from Arvicolidæ); articular surface deep, its margins presenting two conspicuous projections; cephalic process heavy, gradually tapering, its base much broader than in *Neotoma;* orbicular apophysis well developed, but much smaller in proportion to the rest of the ossicle than that of *Mus.* Manubrium bimarginate, its distal end flattened, spatulate, heel or processus brevis distinct. The processus muscularis exists as a tubercle near the upper side of the base of the orbicular apophysis, evidently corresponding to a similarly placed tubercle in *Neotoma.*

Incus. Heavy and compact, with the stapedial process very stout, with a narrow curved concavity running down its inner surface; articulating surface double, very broad; processus brevis short, pointed. Sylvian apophysis developed.

Stapes. Strongly asymmetrical, one crus being much shorter and straighter than the other; stapedial process small but distinct, at the junction of the head with the crus; foot-plate flat. No intercrural bony canal was found, but a blood-vessel passes between the crura.

Mus musculus L.

Boulder, Colorado.

Malleus. Readily distinguished from that of *Epimys norvegicus;* lamina with a subquadrate outline; processus gracilis quite heavy; cephalic peduncle with an angular bend (compare *Neotoma orolestes*); articular surface low and rather wide; orbicular apophysis large and prominent; processus brevis distinct; manubrium bimarginate, the inner margin very thin.

Incus. Difficult to separate from the malleus. Processus brevis prominent, and much thicker than the stapedial process, which it nearly equals in length. Sylvian apophysis present.

Stapes. Even more asymmetrical than that of *Epimys*; one crus practically straight, the other strongly arched; stapedial process obtuse but distinct; head large, foot-plate distinctly convex. A blood vessel, but no bony canal, passes between the crura.

Doran figures and describes the ossicles of the Australian *Conilurus mitchelli,* and it is evident that they differ only a little from those of *Epimys.* The incus has the same very thick stapedial process; the stapes seems to be more symmetrical; the orbicular apophysis is less robust. Doran says that the manubrium is rather shorter than in *Mus,* but his figure represents it as longer.

SIGMODONTINÆ.

(*Sigmodontinæ* Thomas, Proc. Zool. Soc. Lond. for 1896 (1897), p. 1019.)

Peromyscus nasutus (Allen).

Gregory Cañon, Boulder, Colorado (*Printz and Miller*).

Peromyscus truei (Shufeldt).

Rito de los Frijoles, New Mexico (*J. Henderson and W. W. Robbins*).

Malleus. Orbicular apophysis long and narrow, at right angles to the manubrium (it forms an acute angle with the manubrium in *Nectomys*, *Melanomys*, &c); cephalic peduncle thick basally, abruptly bending almost at a right angle, the portion between the bend and the head very thin; articular surface small and short, bounded externally by a considerable elevation; cephalic process very thin, oblique, with an outward slope; lamina broad and extensive; processus gracilis exceedingly thin; processus muscularis a large tubercle in the neck region, at the base of the orbicular apophysis; processus brevis obsolete; manubrium long, bimarginate, the distal end not spatulate.

Incus. Processus brevis thick, with a blunt apex, to which a ligament is attached; stapedial process moderately long, but thin, with a well developed sylvian apophysis.

Stapes. Head broad; crura thick and little divergent; stapedial process well developed; foot-plate slightly concave; intercrural canal present.

The two species examined presented no important differences. In the figure of *P. truei* the orbicular apophysis appears to have a different direction from that of *P. nasutus*, but this is owing to the position of the ossicle.

Oryzomys pectoralis Allen.

Cauca, Colombia; Popayan, ♂ ♀ (A. M. N. H. 32557, 32559).

Malleus. Orbicular apophysis relatively short; cephalic peduncle with an almost rectangular bend; articular surface small, its outer border less elevated than in allied genera; cephalic process thin, directed somewhat inward (thus different from *Peromyscus*, but not unlike that of *Melanomys*, in which it is vertical); processus gracilis thick basally, tapering to the apex; processus muscularis a prominent tubercle near base of manubrium; processus brevis obsolete; manubrium bimarginate.

Incus. Processus brevis rather long and narrow, distinctly curved; articular surface broad and double; stapedial process thin and moderately long, with a sylvian apophysis. In *Oryzomys* and *Peromyscus* the stapedial process of the incus reaches about or nearly as far as the bend in the cephalic peduncle of the malleus.

Melanomys chrysomelas (Allen).

Guerre, Costa Rica, ♀ (A. M. N. H. 9074/10775); Chontales, Nicaragua, ♀ (A. M. N. H. 29556).

Malleus. Orbicular apophysis thick, about as long as broad, with a transverse constriction; cephalic peduncle slender, the abrupt rectangular bend near the base; articular surface small, its outer margin elevated; cephalic process vertical; lamina large, subquadrate; processus muscularis large; processus brevis obsolete; manubrium bimarginate, not spatulate at end.

Incus. Cephalic portion long, forming an obtuse angle with stapedial process; processus brevis small and pointed, with a slight curve; stapedial process thickened distally, with a fairly large sylvian apophysis.

Nectomys palmipes Allen and Chapman.

Princestown, Trinidad. ♂ (A. M. N. H. 4667).

Malleus. Resembles in many ways that of *Mus;* orbicular apophysis very large, directed obliquely downward, forming an acute angle with the manubrium; cephalic peduncle thick, with a rectangular bend; head rather large, with a saddle-shaped articular surface, the outer margin strongly elevated; cephalic process thick; processus gracilis thick at base, tapering apically; lamina oblong; manubrium bimarginate, the margins quite heavy, and the processus brevis obsolete. A small tubercle above the base of the manubrium appears to represent the processus muscularis.

Incus. The most peculiar Sigmodontine incus seen. Processus brevis ill-developed, short and broad, obtuse; head large, with a broad articular surface, grooved to fit the saddle of the malleus; stapedial processes heavy, with a rectangular curve before the end, which has a very well developed sylvian apophysis.

Sigmodon sanctæ-martæ Bangs.

Onaca, Colombia (A. M. N. H. 15252).

Malleus. Orbicular apophysis longer than broad; cephalic peduncle curved, not abruptly bent as in the genera described above; head very thick and heavy, with a broad shallow articular surface, its outer surface strongly convex; processus gracilis large, laminate beneath; processus muscularis long and well developed, near the base of the manubrium; processus brevis obsolete; manubrium bimarginate, poorly developed or imperfect in our material.

Incus. Processus brevis rather small, thick at base, rapidly tapering to a pointed end; stapedial process heavy but not very long; a large pedunculated sylvian apophysis.

Akodon tolimæ Allen.

Rio Toché, Cauca, Colombia, ♀ (A. M. N. H. 32995).

Malleus. Orbicular apophysis short and heavy, as broad as long; cephalic peduncle thick basally, bent, but not to a right angle; head slight, with a prominent point bordering the articular surface on the inner side, but none on the outer; cephalic process moderately oblique, sloping outward, not strongly differentiated from the head; lamina large; manubrium with distal end spatulate.

Incus. Processus brevis small, pointed; stapedial process rather long, somewhat twisted, longitudinally ridged; sylvian apophysis circular, flattened, at right angles to the stapedial process.

There is a bony canal between the crura of the stapes.

When working with this animal we noted that it appeared doubtfully congeneric with *A. teguina* (Alston) from Guatemala, the teeth being noticeably different and the incisive foramina very much longer in *A. tolimæ.* (In the oldest known supposed

ancestors of the whole group, *Paramys*, the incisive foramina are comparatively very small and short.) Dr. J. A. Allen kindly informs us that Oldfield Thomas, Ann. Mag. Nat. Hist., (8). xi, p. 408 (April 1913), made *A. teguina* the type of a distinct genus *Scotinomys*. *A. tolimæ* is a typical *Akodon*.

Ichthyomys hydrobates Thomas.

Merida, Venezuela, ♀ (A. M. N. H. 24355).

Malleus. Orbicular apophysis small; cephalic peduncle thick, without the bend seen in the other genera, passing gradually into the thick head, the distal end of which (bounding the articular surface) is much produced; processus gracilis thin; manubrium bimarginate.

Incus. Processus brevis rather short, pointed, and with a small lateral projection; articular surface very broad; stapedial process rather long, thin, ridged externally; sylvian apophysis circular, pedunculated.

Phyllotis boliviensis (Waterhouse).

San Antonio, Peru, ♀ (A. M. N. H. 16494).

Malleus. Exceedingly large, being much larger than that of *Sigmodon sanctæmartæ*, the skull of which exceeds that of *P. boliviensis* in size; the transverse diameter, from level of end of orbicular apophysis to level of outer wall of head, is 1920 μ, the corresponding measurement in the *Sigmodon* being 1700 μ; the vertical distance from level of end of orbicular apophysis to level of end of cephalic crest is 800 μ, the corresponding distance in the *Sigmodon* 720 μ. Orbicular apophysis long, with a somewhat constricted neck; base of cephalic peduncle very heavy, somewhat convex or humped on outer side, passing obliquely to the very abrupt though not rectangular bend; head with a saddle-like articular surface, the outer side of which is greatly elevated; cephalic process thin, almost vertical; processus gracilis thin, flattened; manubrium very long, longer than the malleus is broad, bimarginate, with a sharp apex. The processus muscularis is found at the base of the manubrium, as it runs into the neck, but at the base of the orbicular apophysis is a two-horned process, from which (Fig. 44) a short ligament passes to a long slender process of bone arising from the wall of the tympanum.

Incus. Processus brevis thick, conical, pointed, with a ligament attached to its end; articular surface double; stapedial process thick, longitudinally ridged, with a circular broad sylvian apophysis.

Stapes. Broad, rather short, distinctly asymmetrical; foot-plate convex; stapedial process very minute.

The following key will probably be found valid for the separation of the above genera, but it remains to be tested by the examination of a larger number of species. It is based on the malleus.

Orbicular apophysis very small, its length less than half diameter of articular surface; cephalic peduncle with no angular bend (Tribe Ichthyomyini) *Ichthyomys* Thomas.[1]

[1] Thomas states that the cœcum of this aquatic genus is nearly absent, and contrasts this with the large cœcum of terrestrial (vegetarian) Muridæ. In *Fiber zibethicus cinnamominus*, which is aquatic but also largely vegetarian, we find an enormous cœcum, resembling in general that of *Neotoma orolestes*, and proportionately longer than in *Mus*, *Peromyscus*, *Onychomys*, *Perodipus*, etc.

Orbicular apophysis much larger ..... 1.

1. Outer border of articular surface not elevated, but inner border strongly elevated (Tribe Akodontini) ..... *Akodon* Meyen.
   Outer border of articular surface strongly elevated, or (*Oryzomys*) moderately so ..... 2.
2. Cephalic peduncle without an abrupt bend; head massive (Tribe Sigmodontini) *Sigmodon* Say & Ord.
   Cephalic peduncle with an abrupt bend (Tribe Peromyscini) ..... 3.
3. Processus cephalicus vertical or even sloping inward ..... 4.
   Processus cephalicus conspicuously sloping outward ..... 5.
4. Bend of cephalic peduncle very abrupt, rectangular. (Incus with short processus brevis) ..... *Melanomys* Thomas.
   Bend of cephalic peduncle less abrupt, not rectangular. (Incus with a long processus brevis) ..... *Oryzomys* Baird.
5. Bend of cephalic peduncle forming a very obtuse angle; orbicular apophysis with a constricted neck ..... *Phyllotis* Waterhouse.
   Bend of cephalic peduncle forming a right angle or almost ..... 6.
6. Orbicular apophysis forming practically a right angle with manubrium *Peromyscus* Gloger.
   Orbicular apophysis forming an acute angle with manubrium. (Incus peculiar; see fig. 35.) ..... *Nectomys* Peters.

Phyllotis antedates *Peromyscus*, but it is not necessary to form the tribal name from the oldest generic name. *Phyllotis* is rather aberrant in the group.

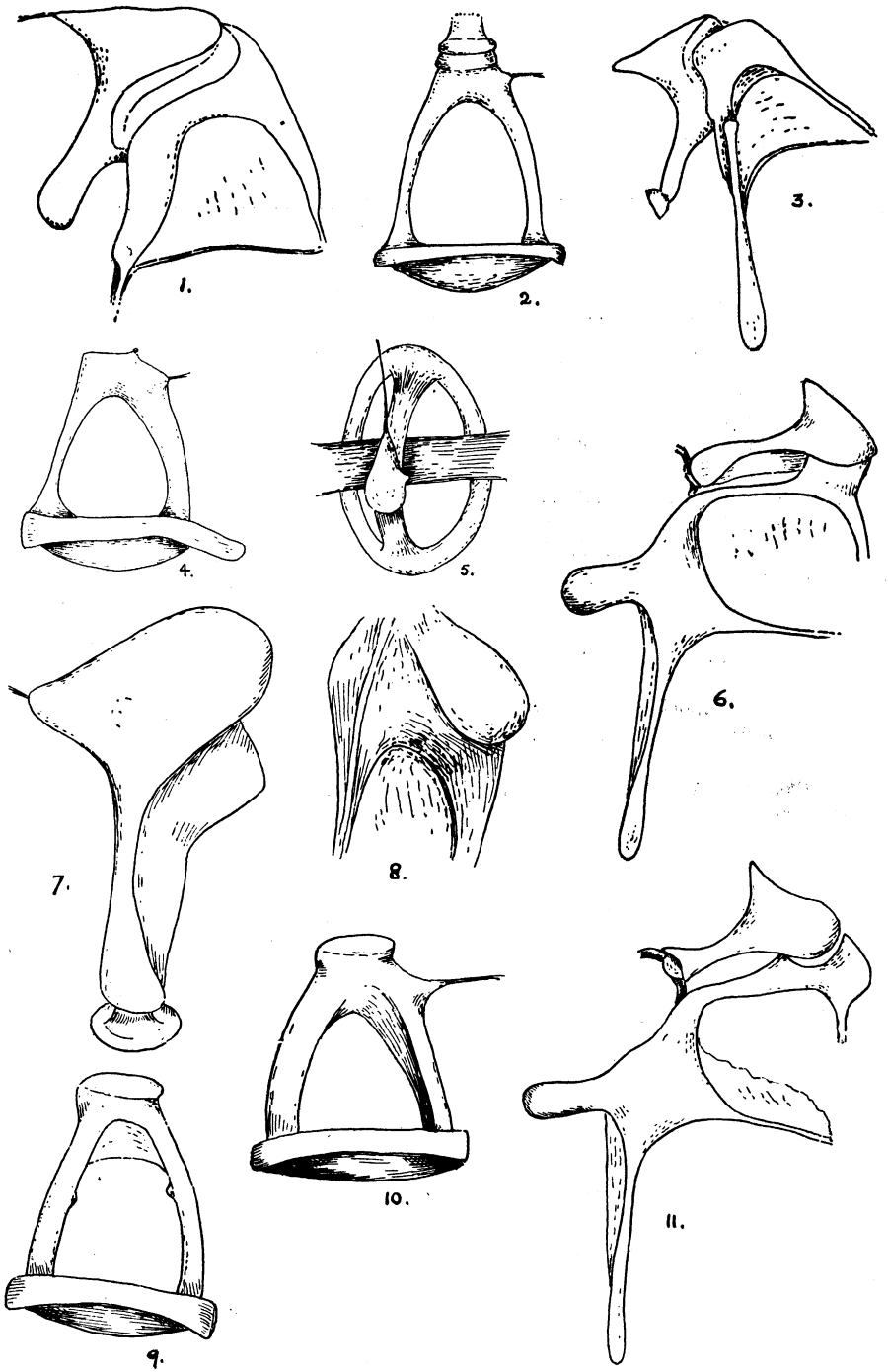

Fig. 1. *Fiber zibethicus cinnamominus.* Malleus and Incus.
Fig. 2. *Fiber zibethicus cinnamominus.* Stapes, with attached sylvian apophysis.
Fig. 3. *Microtus mordax.* Malleus and Incus.
Fig. 4. *Microtus nanus.* Stapes, lateral view.
Fig. 5. *Microtus nanus.* Stapes, from above.
Fig. 6. *Neotoma mexicana fallax.* Malleus and Incus.
Fig. 7. *Meotoma mexicana fallax.* Incus.
Fig. 8. *Neotoma mexicana fallax.* Base of manubrium.
Fig. 9. *Neotoma mexicana fallax.* Stapes.
Fig. 10. *Neotoma mexicana fallax.* Stapes.
Fig. 11. *Neotoma cinerea orolestes.* Malleus and Incus.

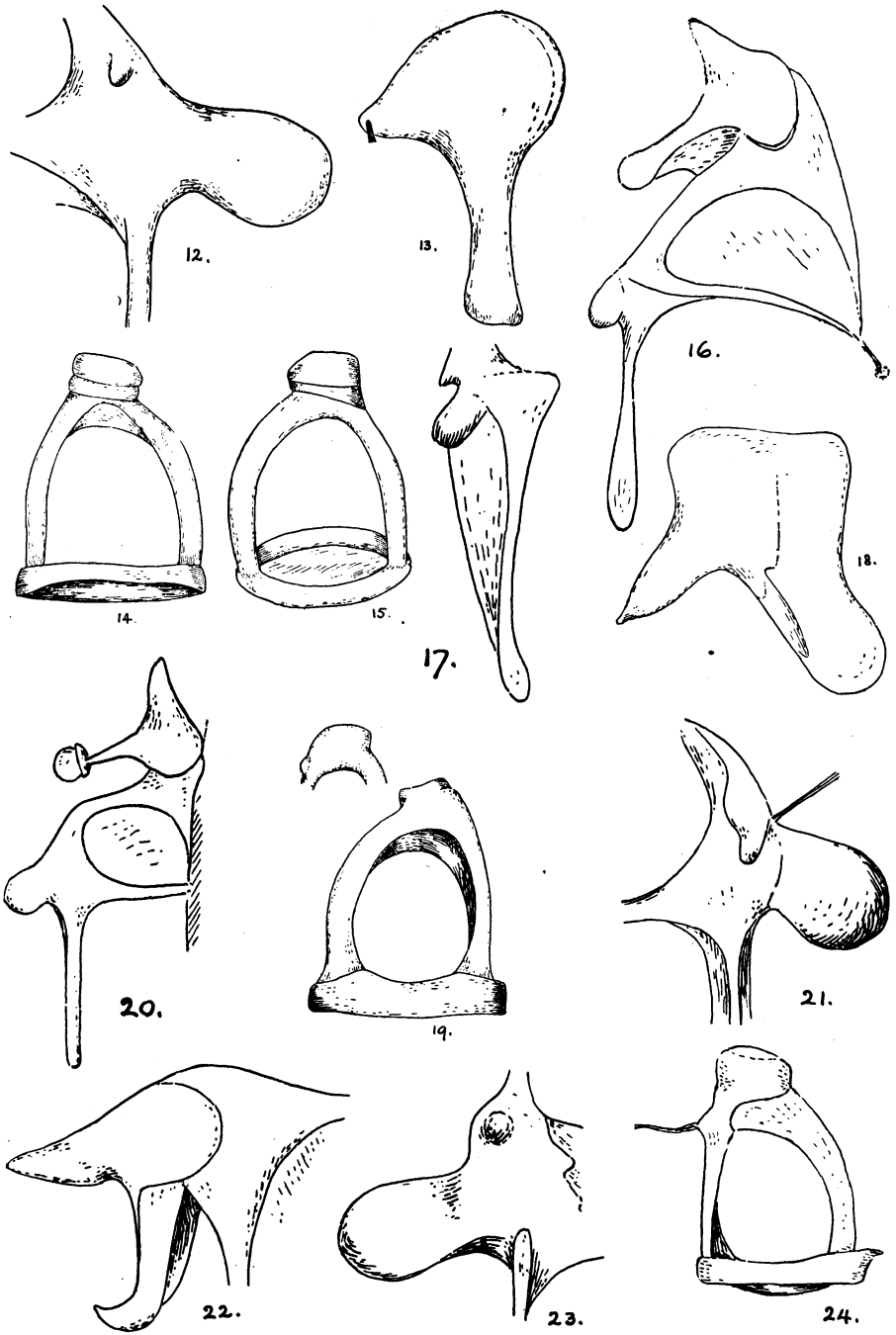

Fig. 12. *Neotoma cinerea orolestes.* Orbicular apophysis and adjacent parts.
Fig. 13. *Neotoma cinerea orolestes.* Incus.
Fig. 14. *Neotoma cinerea orolestes.* Stapes.
Fig. 15. *Neotoma cinerea orolestes.* Stapes.
Fig. 16. *Epimys norvegicus.* (Bloomington, Ind.) Malleus and Incus.
Fig. 17. *Epimys norvegicus.* (Bloomington, Ind.) Manubrium.
Fig. 18. *Epimys norvegicus.* (Boulder, Colo.) Incus.
Fig. 19. *Epimys norvegicus.* (Boulder, Colo.) Stapes.
Fig. 20. *Mus musculus.* Malleus and Incus.
Fig. 21. *Mus musculus.* Orbicular apophysis and adjacent parts.
Fig. 22. *Mus musculus.* Incus and part of Malleus.
Fig. 23. *Mus musculus.* Orbicular apophysis, Processus brevis, etc.
Fig. 24. *Mus musculus.* Stapes.

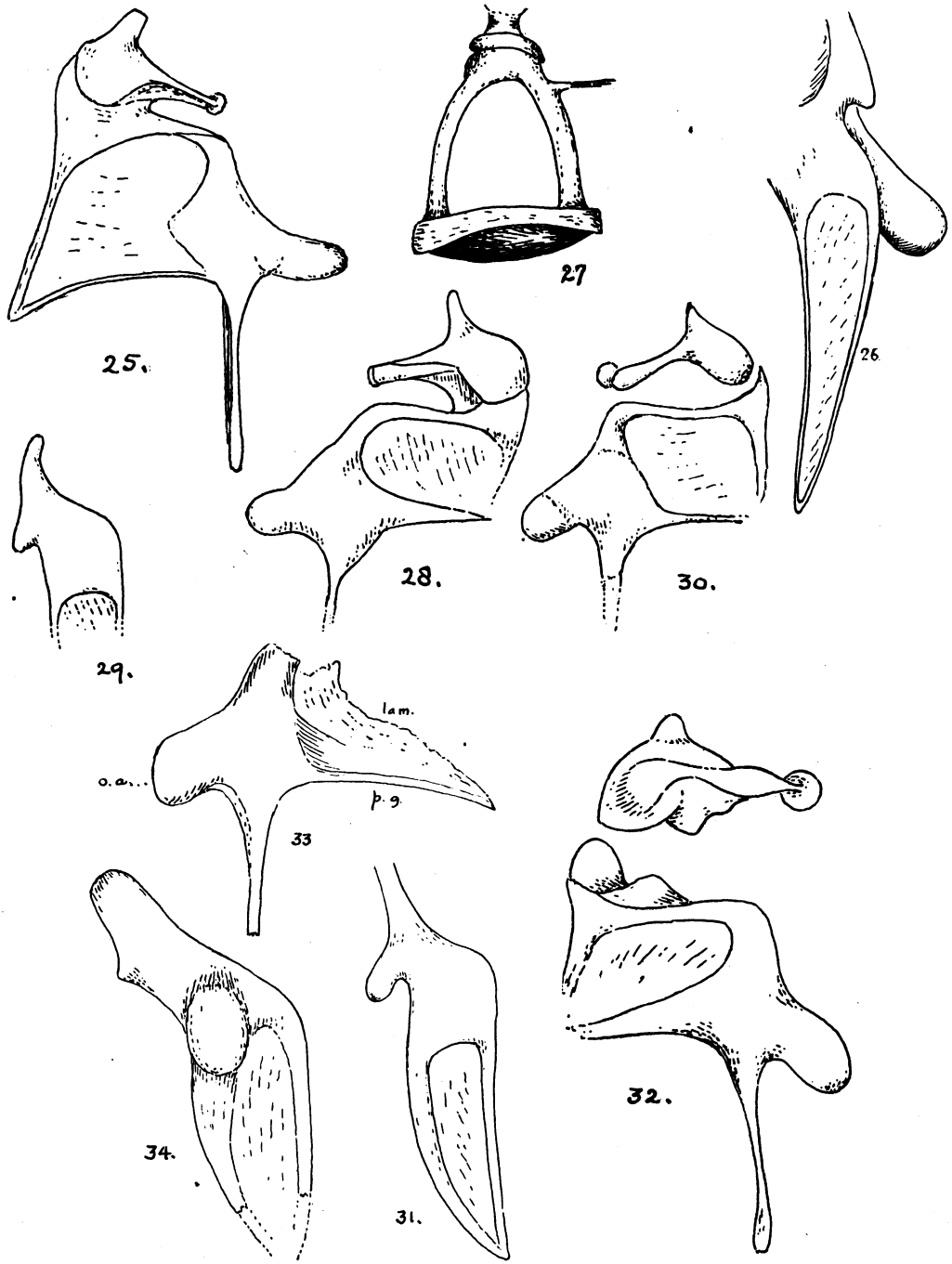

Fig. 25. *Peromyscus nasutus.* Malleus and Incus.
Fig. 26. *Peromyscus truei.* Manubrium.
Fig. 27. *Peromyscus truei.* Stapes.
Fig. 28. *Oryzomys pectoralis.* Malleus and Incus.
Fig. 29. *Oryzomys pectoralis.* Base of Manubrium.
Fig. 30. *Melanomys chrysomelas.* Malleus and Incus.
Fig. 31. *Melanomys chrysomelas.* Manubrium.
Fig. 32. *Nectomys palmipes.* Malleus and Incus.
Fig. 33. *Nectomys palmipes* Orbicular apophysis, Processus gracilis, etc.
Fig. 34. *Nectomys palmipes.* Manubrium.

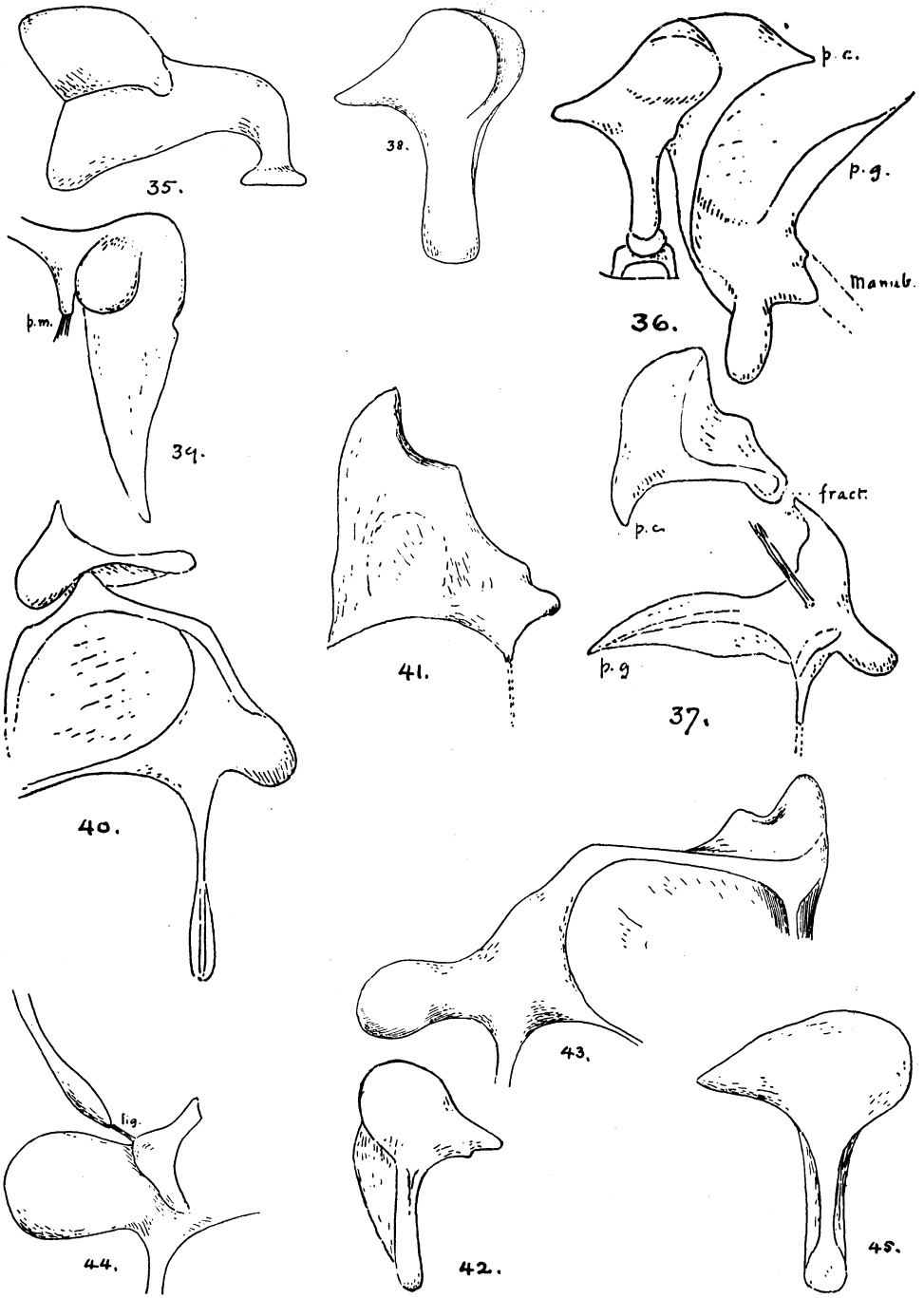

Fig. 35. *Nectomys palmipes.* Incus.
Fig. 36. *Sigmodon sanctæ-martæ.* Malleus and Incus.
Fig. 37. *Sigmodon sanctæ-martæ.* Malleus.
Fig. 38. *Sigmodon sanctæ-martæ.* Incus.
Fig. 39. *Sigmodon sanctæ-martæ.* Manubrium and Processus muscularis (p. m.).
Fig. 40. *Akodon tolimæ.* Malleus and Incus.
Fig. 41. *Ichthyomys hydrobates.* Malleus.
Fig. 42. *Ichthyomys hydrobates.* Incus.
Fig. 43. *Phyllotis boliviensis.* Malleus.
Fig. 44. *Phyllotis boliviensis.* Orbicular apophysis and adjacent parts.
Fig. 45. *Phyllotis boliviensis.* Incus.

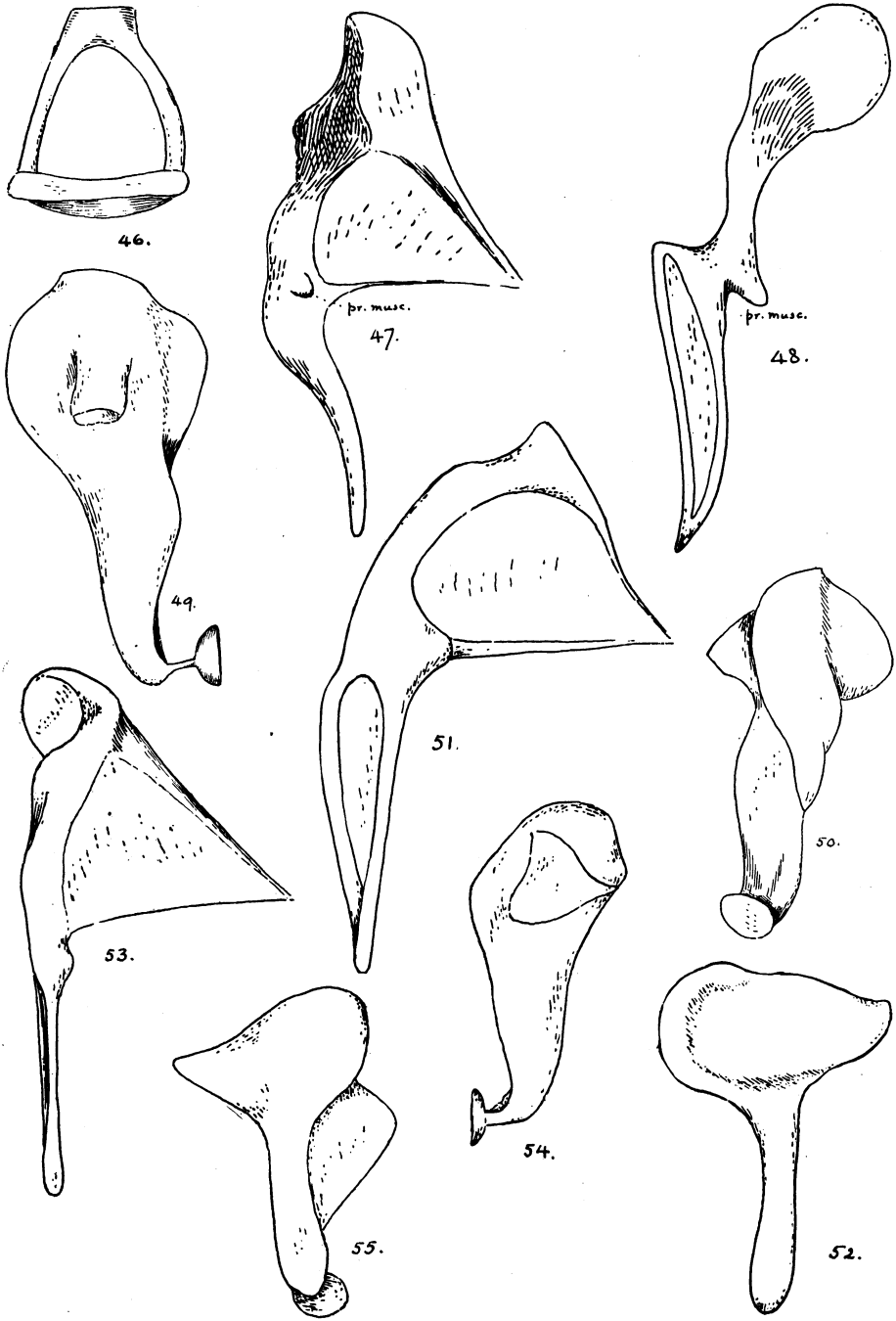

Fig. 46. *Phyllotis boliviensis.* Stapes.

Fig. 47. *Cricetus cricetus.* Malleus. Near Magdeburg. Germany: U. S. N. M. 153383.

Fig. 48. *Cricetus cricetus.* Malleus. Near Magdeburg, Germany: U. S. N. M. 153383

Fig. 49. *Cricetus cricetus.* Incus. Near Magdeburg, Germany: U. S. N. M. 153383

Fig. 50. *Cricetus cricetus.* Incus. Near Magdeburg, Germany: U. S. N. M. 153383

Fig. 51. *Cricetulus griseus.* Malleus. Shensi, Yu-Ling, China; A. de C. Sowerby, U. S. N. M. 155017.

Fig. 52. *Cricetulus griseus.* Incus. Shensi, Yu-Ling, China; A. de C. Sowerby, U. S. N. M. 155017.

Fig. 53. *Phodopus bedfordiæ.* Malleus. Shensi, Yuting-fu, China; A. de C. Sowerby, U. S. N. M. 155040.

Fig. 54. *Phodopus bedfordiæ.* Incus. Shensi, Yuting-fu, China; A. de C. Sowerby, U. S. N. M. 155040.

Fig. 55. *Phodopus bedfordiæ.* Incus. Shensi, Yuting-fu, China; A. de C. Sowerby, U. S. N. M. 155040.

II. FAMILIES OTHER THAN ARVICOLIDÆ AND MURIDÆ.

By T. D. A. Cockerell and Lewis I. Miller.

Text Figures 61–124, pp. 374–378.

LEPORIDÆ.

Oryctolagus cuniculus (L.).

Boulder, Colorado (domesticated.) "Belgian Hare."

Malleus. Head moderate, the rounded apex rising little above the articular surface; cephalic process directed laterad, short and pointed, but stout; a rudimentary lamina, extending from the processus cephalicus to the neck; processus gracilis quite rudimentary; articular surface rather deep; manubrium long, bimarginate, curved, sharply pointed as seen in lateral view, with a prominent heel (processus brevis); seen from the outer side the manubrium appears broad, parallel sided, rounded at either end; processus muscularis not clearly defined in our material, though Doran figures it as well developed.

Incus. Subquadrate, with the processus brevis short and rounded; stapedial process long, stout and curved, with a well developed elliptical sylvian apophysis. The incus has a strong general resemblance to that of the Sciuridæ.

Stapes. Thick, with a relatively small aperture between the crura; no stapedial process. We found no intercrural canal or bood vessel.

Sylvilagus auduboni minor (Mearns).

Mesilla Park, New Mexico.

Malleus. Head slightly more developed than in *Oryctolagus*, with the cephalic process oblique, and the lamina better developed.

Incus. Quadrate, and even more massive than that of *Oryctolagus*, but of the same general type. The ridge dividing the articular surface has a double curve, instead of being regularly concave as in *Oryctolagus*. The processes also differ in detail from those of the other genus; the processus brevis is truncate, while the stapedial process is larger and nearly straight. The stapedial process in *Sylvilagus* has a lateral bony lamina, absent from *Oryctolagus*.

Doran examined the ossicles of *Lepus europæus occidentalis* deWinton, and states that they are identical in form with those of *Oryctolagus cuniculus*.

OCHOTONIDÆ.

Ochotona saxatilis figginsi Allen.

Trappers' Lake, Garfield Co., Colorado (*A. H. Felger*).

The wall of the middle ear is thick, composed of cancellous bone, which in the lower part of the bulla has a thickness of fully 2 mm., greatly reducing

the tympanic space. There is nothing of this sort in the Leporidæ; but a similar condition, though less extreme, occurs in *Thomomys* and *Perognathus*, the latter having this feature least, though still well developed. The cochlea has a high spine.

Malleus. Similar in general to that of the Leporidæ, but still with very distinct features. Head not elevated above the articular surface; cephalic process directed laterad as in *Oryctolagus*, pointed; manubrium bimarginate, dagger-shaped, not curved, the outer margin narrower than in *Oryctolagus*, and spatulate apically; the upper part of the manubrium is divided by a very prominent partition, which isolates a deep cavity or excavation invading the lower part of the head, a feature apparently peculiar to *Ochotona*.

Incus. Elongated, with a triple articular surface; stapedial process very long, even longer than the body, having a lateral groove, but without a true sylvian apophysis, being merely broadened out at end, with a slight median depression; processus brevis very poorly developed, much smaller than in Leporidæ.

Stapes. Of the same general type as that of *Oryctolagus*, but broadened basally, so as to become more triangular in outline; intercrural aperture small, broad-oval; stapedial process evident. No intercrural canal.

The auditory ossicles merely support the opinion, previously based on many other good characters, that the Ochotonidæ constitute an exceptionally distinct family. We should like to know the physiological significance of the extraordinary condition of the tympanic walls, which we have determined to be perfectly normal by the examination of several skulls.

SCIURIDÆ.

Marmota flaviventer warreni Howell.

Between Meeker and Axial, Colorado (*A. H. Felger*).

Malleus. The sides are flatter than in *Sciurus*, and the head rises into a conspicuous blunt point high above the articular surface, which is deep and narrow; the manubrium is much broader at the base than in any true squirrel, though otherwise of the same type, with the extremity spatulate and the inner border angular; there is hardly a trace of a processus brevis. The elongated processus cephalicus, directed laterad and somewhat downward, is of the same general type as in other Sciuridæ.

Incus. Body wide, with the articular surface deeply cut; processus brevis pointed, rather short, more slender than in *Cynomys;* stapedial process very long and thick, broadened out at the end, but without a true sylvian apophysis. The processes are nearly at right angles to one another.

Stapes. Proportionately a very large ossicle, with a bony intercrural canal.

Doran's figure of the malleus of *Marmota marmota* (L.) looks quite unlike ours, being taken in a quite different position, but his description is applica-

ble, and has been partly repeated in the above account. From Doran's account the end of the manubrium is much less spatulate in *M. marmota* than in our animal. It is also evident that the stapedial process of the incus is longer in *M. warreni* than in *M. marmota.*

Cynomys leucurus Merriam.

Between Meeker and Axial, Colorado (*A. H. Felger*).

Malleus. Head large, rising in a rounded eminence well above the articular surface, but somewhat flattened laterally; articular surface double and deeply cut. Manubrium thick anteriorly and thin posteriorly, the end feebly spatulate, with a well-developed processus muscularis near the middle of the side. Very distinct from *Marmota* by the form of the head and manubrium.

Incus. Body subquadrate, with a wide but shallow articular surface; processus brevis massive, pointed; stapedial process not very long, broadening at end, but without a sylvian apophysis.

Stapes. Similar to that of *Citellus grammurus* in most respects, but (at least in *C. gunnisoni*) the foot-plate is quite flat, and there is no stapedial process. There is a bony intercrural canal.

Cynomys gunnisoni (Baird).

Florissant, Colorado (*T. D. A. Cockerell*).

In a specimen examined, the ossicles were slighter, and the stapedial process of the incus noticeably more slender. This may be due to immaturity. Some years ago the senior author borrowed Mr. E. R. Warren's collection of *Cynomys* skulls, to determine whether any specific characters could be found which could be recognized in semifossil specimens. He found some rather conspicuous differences in the skulls, but they appeared to represent individual variations, and he was quite unable to detect definite cranial characters to separate *C. gunnisoni, C. leucurus* and *C. ludovicianus.* According to Baird's figure, the accessory palatine foramina are mesad of the last molars (instead of caudad of them) in *C. gunnisoni,* but this appears to be an error. An apparently fossil specimen from the Arroyo Pecos, Las Vegas, New Mexico (*M. Benedict*), appeared to differ from *C. ludovicianus* by having the nasals about 22 mm. long in a skull 61 mm. long (20 mm. in skull 62 mm. in *ludovicianus*); least breadth of palate 5 (instead of 6) mm.; parietals narrower, not over 7 mm. broad at middle (instead of 8); but the study of a series of *ludovicianus* showed that these were not valid characters. The living species are nevertheless quite distinct on characters of pelage, and thus we find that in dealing with fossils we should be equally in danger of confusing different species, and of distinguishing supposed species on fallacious characters.

Citellus grammurus (Say).

Howard's Ranch, near Sugar Loaf, Colorado (*Frank Goddard*).

Malleus. Head wider and less elongated than in *Sciurus fremonti;* articular surface deeply cut; a ridge extends downwards from the articular area and terminates in a projection on the neck; manubrium long, flattened, spatulate apically, with a sharp processus muscularis (for the tensor tympani) near the middle; near the margin of the manubrium, on the opposite side from the processus muscularis, is an elongated groove, apparently representing the thin area which occupies the whole of the middle of the manubrium in various other rodents.

Incus. Body subquadrate; articular surface double, but one of the surfaces is divided by a ridge; processus brevis rather short, stout, pointed; stapedial process stout, with a lateral bony lamina; no sylvian apophysis.

Stapes. Large, with very long but stout crura, both slightly curved; stapedial process very prominent. A prominent bony intercrural canal.

Citellus elegans (Kennicott).

Near Buford, Colorado (*A. H. Felger*).

The ossicles are almost identical in size and form with those of *C. grammurus.* The ossicles of the European *Citellus citellus* (L.) are figured by Doran, who says that the malleus is in general like that of *Sciurus vulgaris,* but has a more distinct trace of a processus brevis; while the incus is of the *Tamias* form. Doran's figure of the malleus represents that ossicle in a position not shown in our figures; but when the malleus of *C. grammurus* is placed so as to give the same view as Doran's figure, it appears that the processus cephalicus and attending lamina in our animal are much longer, and the processus muscularis is much further down the side of the manubrium. The incus of *C. grammurus,* compared with Doran's figure, has the stapedial process much stouter distally. It is to be remarked that *C. citellus* belongs to typical *Citellus,* whereas *C. grammurus* is the type of *Otospermophilus* Brandt, regarded by Mearns as a distinct genus. The two do not differ greatly in cranial or dental characters, but the interorbital breadth of *C. grammurus* is much greater than in the European animal. *C. elegans,* which does not belong to *Otospermophilus,* has ossicles like those of *grammurus.*

Eutamias operarius (Merriam).

Boulder Cañon, Colorado (*Miller and Printz*).

Malleus. The most delicate of the Sciuridæ examined; articular surface deeply cut; processus cephalicus, as in *Citellus grammurus,* becoming thin and fragile distally; a small projection below the articular surface, as in *C. grammurus;* manubrium slender, broadly spatulate apically.

Incus. Formed practically as in *Sciurus fremonti,* with a long stapedial process.

Stapes. Rather small, with a very well developed stapedial process.

E. quadrivittatus (Say) presented no difference in the ossicles worthy of note.

Callospermophilus lateralis (Say).

Marvine Lodge, Rio Blanco Co., Colorado (*A. H. Felger*).

Malleus. Much more like that of *Sciurus* than *Eutamias;* head long, elevated apically; manubrium long and thin, spatulate apically.

Incus. Considerably smaller than in *Sciurus* or *Citellus grammurus.* No sylvian apophysis.

Stapes. Smaller than in *Sciurus* or *Citellus grammurus;* stapedial process rudimentary. A well-developed bony intercrural canal.

Sciurus fremonti Audubon and Bachman.

North Boulder Creek, Colorado (*F. W. Rohwer*).

Malleus. Head comparatively long and narrow; manubrium spatulate apically.

Incus. Processus brevis rather more slender than in *Callospermophilus;* stapedial process long, sharply bent at the end.

Stapes. Larger and heavier than in *Callospermophilus.*

Doran has described the ossicles of *Sciurus* at considerable length, and figures those of *S. maximus.* His figure of the malleus looks much more like ours of *Eutamias* than *Sciurus;* but on examining a series of *S. fremonti* and *S. aberti* (which does not materially differ in the ossicles) we find that the thin laminar continuation of the processus cephalicus (as in *Eutamias* and *Otospermophilus*) is much elongated in good specimens, even more than in Doran's figure. The general conclusion is that the ossicles of *Sciurus,* sens. lat., are very uniform in type.

The Sciuridæ in general are distinguished by the character of the manubrium, which is a solid structure, instead of being thin with a thickened margin, as in other groups.

Among the Sciurid genera we have studied, *Marmota* stands entirely apart by the high curved crest-like pointed process on the head of the malleus. The ossicles of all the other genera are so much alike that it seems impracticable to construct a satisfactory key for their separation. In the classification given in Osborn's 'Age of Mammals,' the family Sciuridæ is divided into five subfamilies, of which the Sciurinæ contain *Sciurus* and *Tamias,* while the Arctomyinæ consist of *Palæarctomys, Spermophilus* (*Citellus*), *Arctomys* (*Marmota*) and *Cynomys.* However, judging from the ear bones, and also from the cranial characters (cf. the parallel rows of molariform teeth, the flattened dorsal surface of the skull, the structure of the posterior part of the mandible in *Marmota*) the marmots constitute a valid subfamily MARMOTINÆ (Arctomyinæ), while the genera *Cynomys* and *Citellus* are Sciurine. The fossil *Palæarctomys* evidently belongs to Marmotinæ, although the molars distinctly converge posteriorly.

CASTORIDÆ.

Castor canadensis Kuhl. History unknown.

Malleus. Head large, obtusely rounded above, the apex well above the articular surface; articular surface very wide; cephalic process rudimentary; manubrium slender, curved, very strongly bimarginate, very little expanded apically. The difference between our figures and Doran's of the European beaver are partly due to the position of the ossicle, but the head in ours is certainly more rounded, less angular, and the plane of the manubrium appears to be different.

Incus. Robust, with a large body, a small pointed processus brevis, and a large, thick stapedial process, having a sort of spiral twist near the end.

The stapes of *Castor* is well figured and described by Doran. He states that there is no bony intercrural canal, such as exists in the Sciuridæ.

The Castoridæ are at once distinguished from the Sciuridæ by the strongly bimarginate manubrium.

HETEROMYIDÆ.

Perognathus penicillatus Woodhouse.

Fort Mohave, Arizona (*J. Henderson*).

The bullæ are little inflated, but in the dry skull the whole region of the ear appears chalky white, the wall of the middle ear being composed of cancellous bone, of which there is a rather thin layer below, but a very thick one above. The inner posterior cells of this cancellous area are very large, but the others are small. The cancellous bone is finer (with smaller cells) than in *Ochotona,* and does not reach the cochlea on both sides as it does in that genus; in fact the open cavity beneath the cochlea is very large.

Malleus. The malleus and incus are firmly attached together, the junction being marked by a line which is scarcely impressed. Head large and obtusely rounded, well elevated above the articular surface; no processus cephalicus, but a delicate and short processus gracilis, bounding a rather small lamina; manubrium dagger-shaped, bimarginate, with a minute angular processus brevis and a basal processus muscularis.

Incus. Body large and rounded, the processes diverging at right angles; processus brevis fully two-thirds length of stapedial process. No sylvian apophysis.

Stapes. Ordinary in form, except that the foot plate is strongly convex and bullate below, approaching the condition of the Geomyidæ. There is no stapedial process. There is a very delicate, slightly ossified intercrural canal.

Perodipus montanus (Baird).

Hooper, Colorado (*E. R. Warren*).

The tympanic cavity is greatly inflated, and its upper part is divided by thin vertical walls, suggestive of the mesenteries of an actinian. The

number of these walls varies on each side from about 8 to 11. This condition is very different from that of *Perognathus*, though there are some points of similarity. The various cranial and dental differences, together with the peculiar auditory ossicles (especially the incus), almost suggest the propriety of raising the Dipodomyinæ to family rank.

Malleus. Relatively large; head not elevated above the articular surface to any great extent, but broad and rounded above; articular surface deep, strongly margined; cephalic process not developed, but the stout processus gracilis bounds a well-defined lamina; manubrium very thin, bimarginate. In our figure the manubrium appears narrower than it actually is, because the ossicle was placed in such a position as to exhibit the processus gracilis above.

Incus. A very remarkable bone, saddle-shaped above, with a long body and relatively short processes. There is no sylvian apophysis.

Stapes. Rather narrow, with a large wide head; crura not strongly divergent; foot plate strongly bullate, though not nearly so much so as in *Thomomys*.

GEOMYIDÆ.

Thomomys clusius Coues.

East of Boulder, Colorado (*Norman de Witt Betts*).

Malleus. Head not very broad, scarcely at all elevated above the articular surface; processus cephalicus angular; no distinct processus gracilis; manubrium bimarginate, its outer side broadened, subspatulate apically; processus brevis a distinct angular projection.

Incus. Elongate, with a broad but rather short processus brevis, and a long stapedial process, which is bifurcate at the end. There is no sylvian apophysis.

Stapes. With an enormous bullate foot-plate as shown in the figure. There is an intercrural canal, as shown in one of our figures.

Doran figures and describes the ossicles of *Geomys bursarius* (Shaw). He says of the stapes: "On its base there projects toward the vestibule a very large bulla, better developed than in *Mustela* or *Hyrax*, and rivalling the same condition already described by Hyrtl as existing in *Phalangista cookii*." This bulla, as shown by Doran's figure, is about as in *Perodipus*, and not nearly so extreme as that of *Thomomys*. In *Phalangista cookii*, however, the bulla is fully as convex as in *Thomomys*. The incus of *Thomomys* is not at all like that of *Perodipus* or *Perognathus*, and judging from Doran's figure is not much like that of *Geomys*. The malleus of *Thomomys* is rather suggestive of that of the rabbit.

ZAPODIDÆ.

Zapus princeps Allen.

Five miles east of Boulder, Colorado (*D. M. Andrews*).

Malleus. A large more or less discoid body above the manubrium, from which arises the slender arched cephalic peduncle, and also a rather short processus gracilis, which enters the middle of the broad lamina; at the base of the processus gracilis is a well developed processus muscularis, shaped like the end of a finger, standing out almost at right angles to it (this is not shown in our figure, being on the wrong side); the head is relatively slight, with a small articular surface, and the well developed processus cephalicus is directed downwards, bounding the lamina; manubrium dagger-shaped, bimarginate, the margin seen from without broad but extremely thin, the inner margin slender.

Incus. Very small, with a short low-conical processus brevis, and a longer stapedial process. There appears to be a small sylvian apophysis.

Stapes. Crura subparallel, one of them strongly angular above on the outer side, for the insertion of the stapedius muscle; foot-plate convex.

There is a delicate intercrural canal. There is a curious general resemblance between the malleus of *Zapus* and that of *Plecotus*, as figured by Doran. The large rounded and compressed swelling above the base of the manubrium, well shown in our figure, can only be regarded as an orbicular apophysis, although its form is peculiar.

OCTODONTIDÆ.

Proechimys semispinosus (Tomes).

Colombia (*Leo. E. Miller;* A. M. N. H.).

The malleus and incus were found to be separable.

Malleus. Head transversely elongated, rounded, of the same general type as that of *Dasyprocta, Aulacodus, Capromys, Chinchilla* and *Dolichotis;* manubrium bimarginate, dagger-like, the outer border broadened and spatulate, the heel or processus brevis well developed.

Incus. The two processes subequal, the stapedial one thick, the other tapering.

Stapes. Triangular, with a high head and very broad base. There is a delicate bony intercrural canal.

Doran figures and describes the ossicles in an *Octodon cumingii* six weeks old. The figures represent the ossicles as curiously different from the rest of the Hystricomorpha (which are otherwise, on the whole, surprisingly uniform in general type), and we are led to wonder whether this is due to the youth of the animal, or is normal for *Octodon;* or whether, possibly, there is some error in identification. The ossicles figured strike one as being very Sciurine in type.

DASYPROCTIDÆ.

Dasyprocta sp.

Central Park Menagerie, New York; ♀ (in captivity). (A. M. N. H., 23082.)
The malleus and incus could not be separated.

Malleus. Head transversely elongated, flattened above, rounded at the abincal end; from beneath, the rounded extension of the head appears subtriangular, with a deep pit on the under side, below which is the rudimentary but stout processus gracilis; manubrium broad and short, bimarginate.

Incus. Head rather long; processus brevis conical, stout; stapedial process longer, curved at the end, with a small button-like sylvian apophysis, without a narrowed peduncle.

We were unable to study the stapes, but it is figured by Doran. It is entirely of the same type as that of *Proechimys.*

CAVIIDÆ.

Cavia; Domesticated Guinea-Pig.

Bloomington, Indiana (*Max M. Ellis*).
The incus could not be separated from the malleus.

Malleus. Head transversely elongated, flattened above, the abincal extremity variably lobulated; processus gracilis scarcely indicated; manubrium a short stout triangular process of bone, variably bifid at end, and with an extremely large processus brevis. The actual size of the combined malleus and incus is hardly less than that of *Dasyprocta,* although the skull of the latter is so very much larger.

Incus. Very much as in *Dasyprocta;* stapedial process longest.

Stapes. Large in proportion; crura thick; base broad; stapedial process short and obtuse. There is considerable variation, as shown in our figures. We found no intercrural canal; Doran states that one is sometimes present.

Cavia, though so familiar, is really a remarkable animal, with cranial characters very distinct from those of *Dasyprocta,* etc. The auditory ossicles seem to be very variable, and no doubt the whole animal, as it exists in a domesticated state, is in a condition of instability.

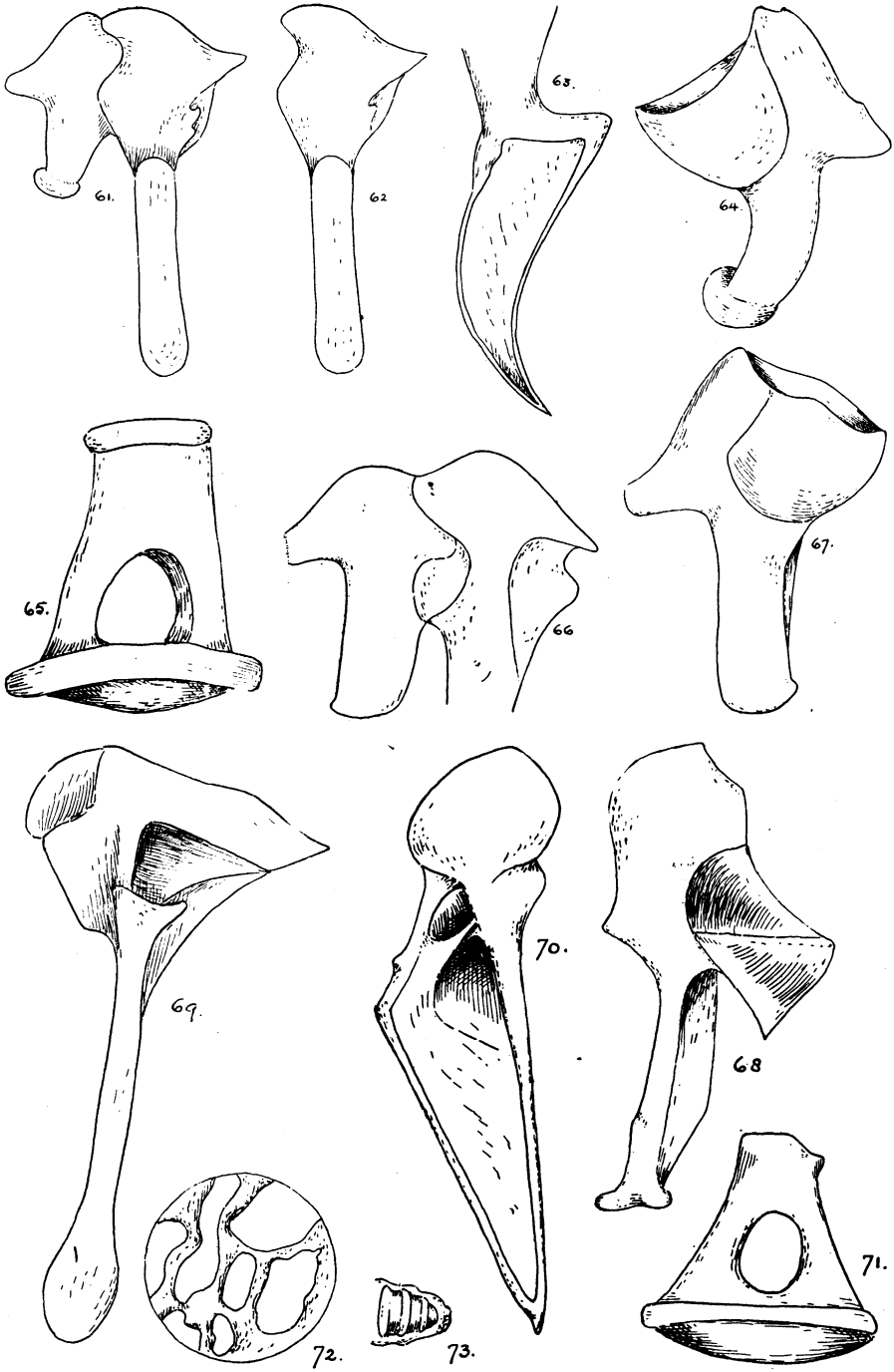

Fig. 61. *Oryctolagus cuniculus.* Malleus and Incus.
Fig. 62. *Oryctolagus cuniculus.* Malleus of another specimen.
Fig. 63. *Oryctolagus cuniculus.* Manubrium.
Fig. 64. *Oryctolagus cuniculus.* Incus.
Fig. 65. *Oryctolagus cuniculus.* Stapes.
Fig. 66. *Sylvilagus auduboni minor.* Malleus and Incus.
Fig. 67. *Sylvilagus auduboni minor.* Incus.
Fig. 68. *Ochotona saxatilis figginsi.* Incus.
Fig. 69. *Ochotona saxatilis figginsi.* Malleus.
Fig. 70. *Ochotona saxatilis figginsi.* Malleus, showing manubrium.
Fig. 71. *Ochotona saxatilis figginsi.* Stapes.
Fig. 72. *Ochotona saxatilis figginsi.* Portion of tympanic wall, much magnified.
Fig. 73. *Ochotona saxatilis figginsi.* Cochlea.

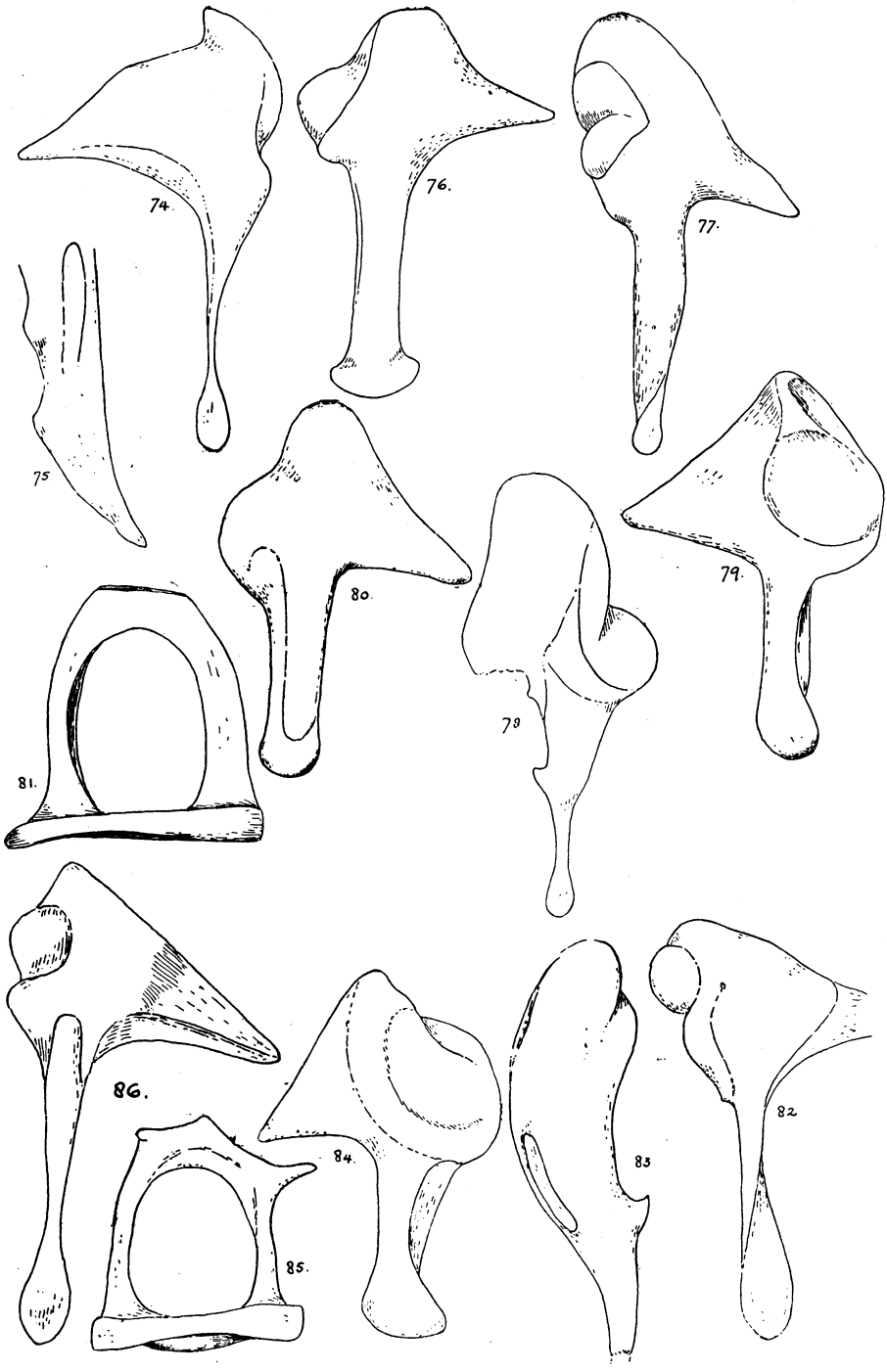

Fig. 74. *Marmota flaviventer warreni.* Malleus.
Fig. 75. *Marmota flaviventer warreni.* Manubrium.
Fig. 76. *Marmota flaviventer warreni.* Incus.
Fig. 77. *Cynomys leucurus.* Malleus.
Fig. 78. *Cynomys leucurus.* Malleus.
Fig. 79. *Cynomys leucurus.* Incus.
Fig. 80. *Cynomys leucurus.* Incus.
Fig. 81. *Cynomys gunnisoni.* Stapes.
Fig. 82. *Citellus grammurus.* Malleus.
Fig. 83. *Citellus grammurus.* Malleus, showing manubrium. The foreshortened processus cephalicus and adjacent parts are not shown.
Fig. 84. *Citellus grammurus.* Incus.
Fig. [illegible] Stapes.

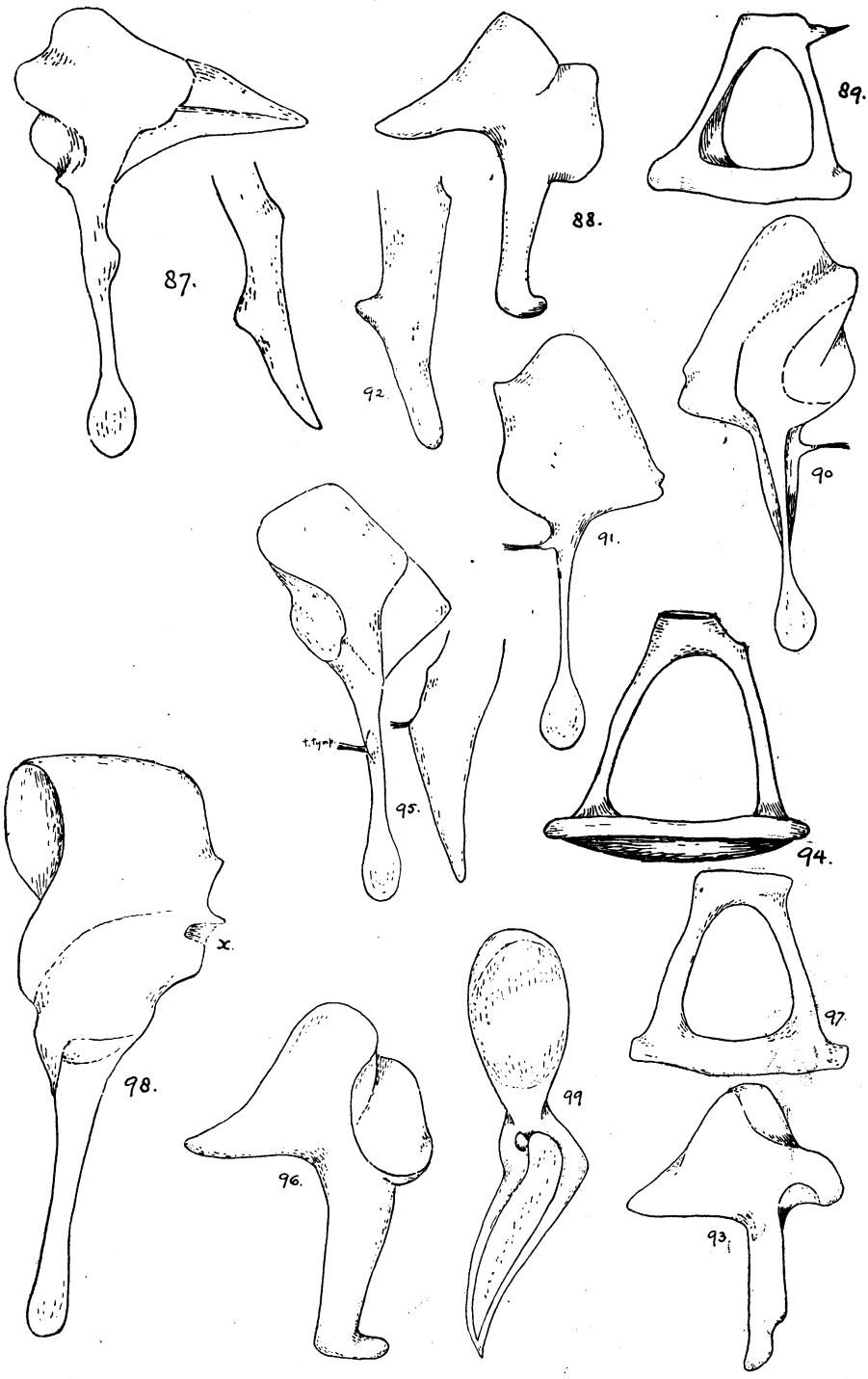

Fig. 87. *Eutamias operarius.* Malleus, and side view of manubrium.
Fig. 88. *Eutamias operarius.* Incus.
Fig. 89. *Eutamias operarius.* Stapes.
Fig. 90. *Callospermophilus lateralis.* Malleus.
Fig. 91. *Callospermophilus lateralis.* Malleus.
Fig. 92. *Callospermophilus lateralis.* Manubrium.
Fig. 93. *Callospermophilus lateralis.* Incus.
Fig. 94. *Callospermophilus lateralis.* Stapes.
Fig. 95. *Sciurus fremonti.* Malleus, and side view of manubrium.
Fig. 96. *Sciurus fremonti.* Incus.
Fig. 97. *Sciurus fremonti.* Stapes.
Fig. 98. *Castor canadensis.* Malleus. At place marked x, injured by Anthrenus.

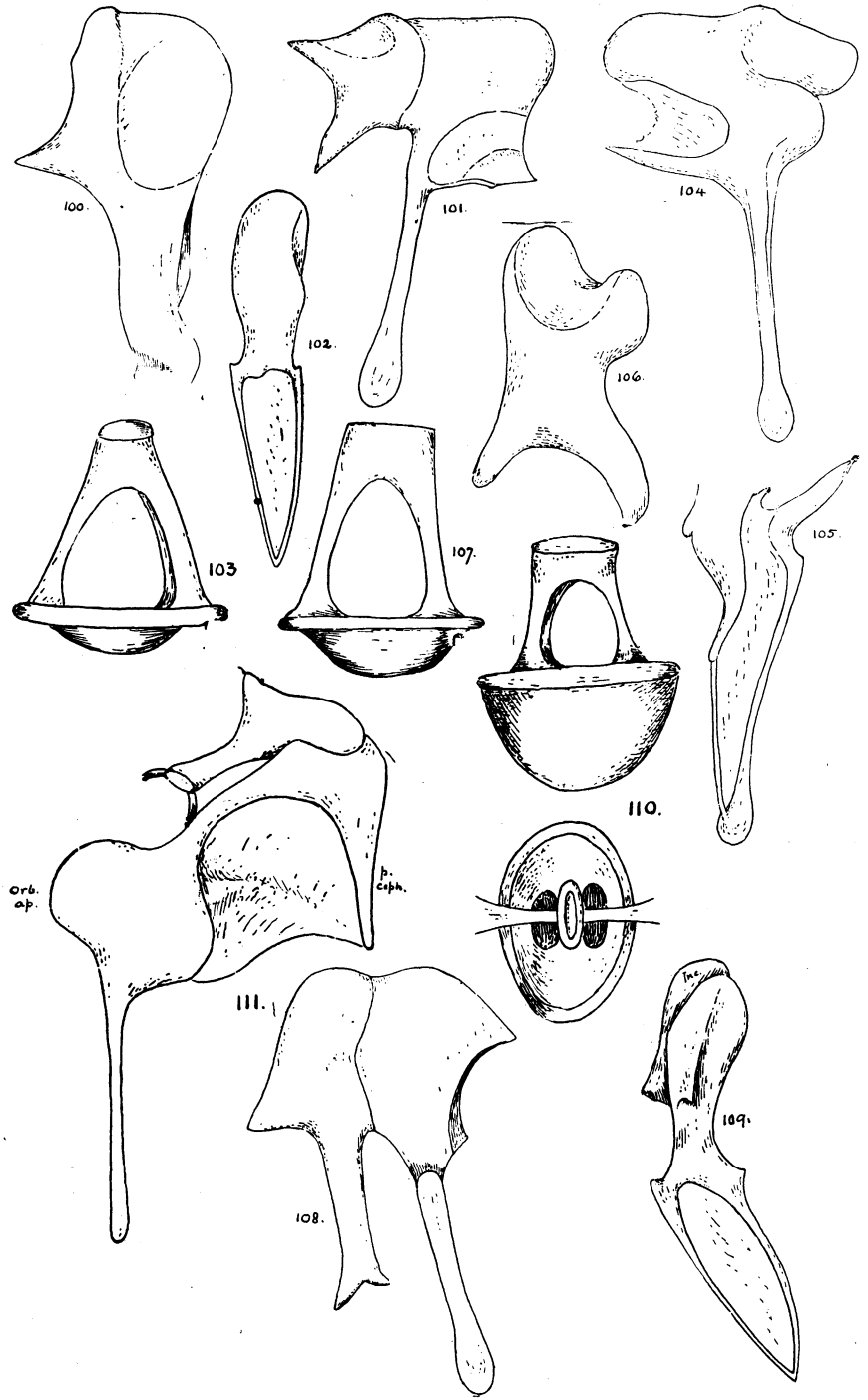

Fig. 100. *Castor canadensis.* Incus.
Fig. 101. *Perognathus penicillatus.* Malleus and Incus.
Fig. 102. *Perognathus penicillatus.* Malleus, showing manubrium.
Fig. 103. *Perognathus penicillatus.* Stapes.
Fig. 104. *Perodipus montanus.* Malleus.
Fig. 105. *Perodipus montanus.* Manubrium.
Fig. 106. *Perodipus montanus.* Incus.
Fig. 107. *Perodipus montanus.* Stapes.
Fig. 108. *Thomomys clusius.* Malleus and Incus.
Fig. 109. *Thomomys clusius.* Melleus, showing manubrium.
Fig. 110. *Thomomys clusius.* Stapes, views from side and above.
Fig. 111. *Zapus princeps.* Malleus and Incus.

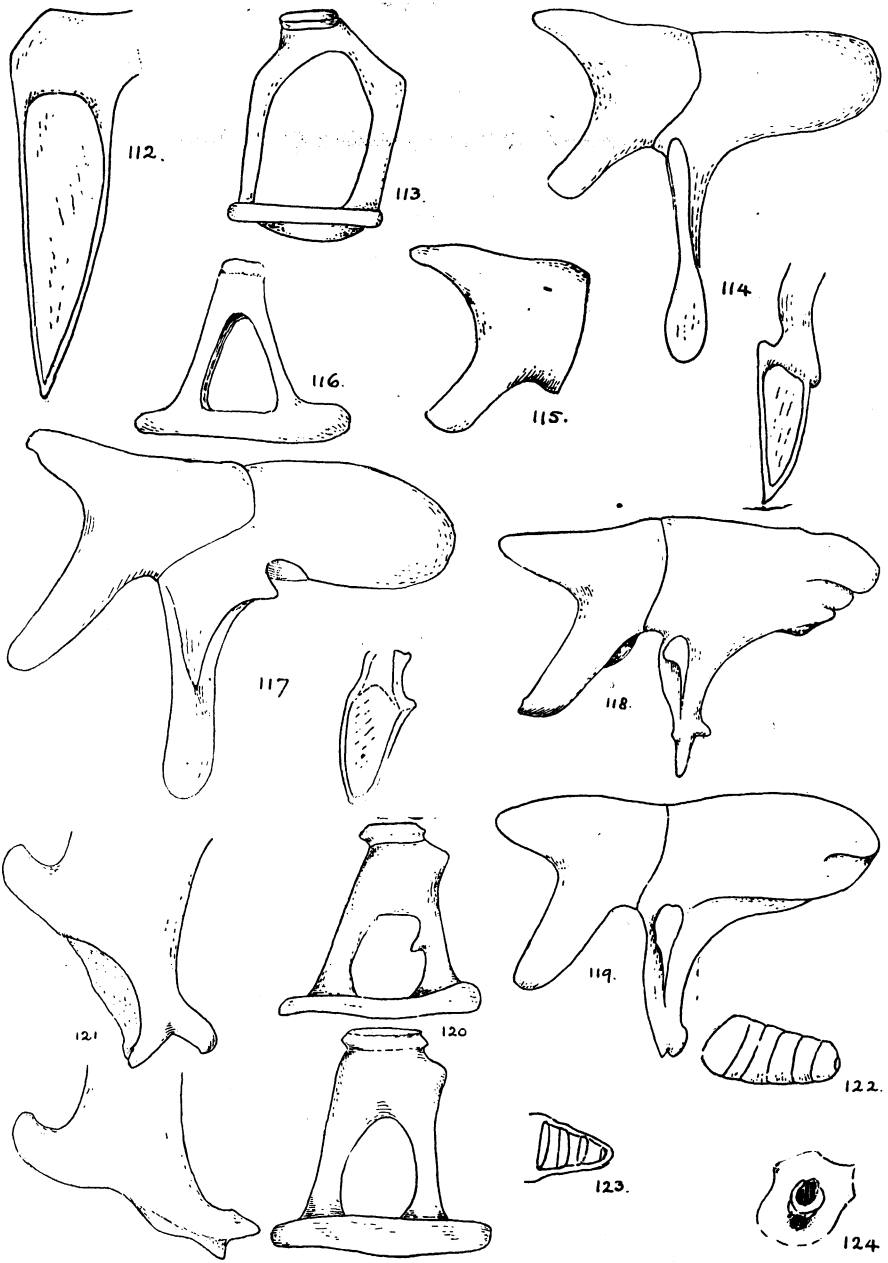

Fig. 112. *Zapus princeps.* Manubrium.
Fig. 113. *Zapus princeps.* Stapes.
Fig. 114. *Proechimys semispinosus.* Malleus and Incus, and side view of manubrium.
Fig. 115. *Proechimys semispinosus.* Incus.
Fig. 116. *Proechimys semispinosus.* Stapes.
Fig. 117. *Dasyprocta.* Malleus and Incus, and side view of manubrium.
Fig. 118. *Cavia.* Malleus and Incus.
Fig. 119. *Cavia.* Malleus and Incus, showing variation.
Fig. 120. *Cavia.* Stapes, showing variation.
Fig. 121. *Cavia.* Manubrium, showing variation.
Fig. 122. *Cavia.* Cochlea, from without.
Fig. 123. *Cavia.* Cochlea, section.
Fig. 124. *Cavia.* Double external auditory meatus. In *Dasyprocta* the lower orifice is very small, and is connected with the large upper one. In *Proechimys* there is a minute foramen below the large meatus, separated from it but emerging through a groove on its lower inner face. This foramen or incision appears to represent the auricular fissure, for the auricular branch of the pneumogastric nerve; but it is not readily apparent why there should be a large orifice, leading into the tympanum, in *Cavia.*

1–5, DACLYTOMYS DACTYLINUS.
6–10, THRINACODUS APOLINARI.

APPENDIX.[1]

The characters of the auditory ossicles may supply taxonomic evidence of the greatest importance, especially in so puzzling a group as the Rodents. They would supply an independent series of differentiations to act as a check on the differentiations of teeth skull and skeleton. They may afford the clue to unravel some of the puzzles which parallelism and convergence have brought about in the systematic position and relations of different groups.

Nevertheless, I think their evidence should be used with great caution, and rather to discover clues and confirm other evidence than as an independent basis of taxonomy. The reason for such caution is this:

(1) The great difficulty in classifying rodents by osteologic and dental characters lies in the frequent parallelism and convergence in these characters. To some extent the adaptive value and correlation of these characters can be seen and interpreted. So far as this is possible, we can determine whether characters are to be interpreted as due to similar adaptation or to fundamental relationship. This is our guide for the solution of problems and harmonizing of conflicting evidence.

(2) I cannot question that the characters and evolution of the ear-bones are subject to parallelism and convergence quite as much as the more obvious mechanism of the teeth and skeleton parts. But the adaptive relationship is so obscure and recondite that the mechanical reasons for their form are not apparent. Whether the resemblances in the ear-bones of two rodents are controlled by heredity or by similar adaptation (similar as respects the parts concerned) we cannot tell. Until we know the significance of the resemblances and differences we have no way of using them as a secure basis of classification; we have to solve the apparently conflicting evidence by arbitrary assumptions that one feature is due to parallelism, another to affinity.

This same criticism holds true with regard to other characters of more or less obscure relation to the adaptive environment, when used in classification. The use of the genitalia, of brain or other characters of soft anatomy has been advocated as of fundamental value in taxonomy because, it is said, they are not in direct contact with the environment and hence less subject or not at all subject to the deceptive results of parallelism. I do not think this is true at all. Every character of an animal as I see it is a product of its heredity and environment; every character is moulded by the adaptation. The characters of the soft anatomy are often controlled by a different set of adaptive circumstances, altered by circumstances that do not affect the osteology, or left unchanged by others that do. For that reason they are of great taxonomic value, as they often show clearly relationships that have been obscured or hidden in the osteology by adaptive divergences, or primary divergences that have been concealed by convergent evolution in the osteology. But they are more apt to lead us astray because we cannot so readily interpret their adaptive value. Resemblances due to parallelism are not so obviously superficial. It is not so easy to see what the primitive conditions must have been. And, above all, we lack the

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[1] In response to request from the authors, for comment and criticism of the foregoing paper, the following comment and suggestions have been offered by Dr. Matthew and Dr. Gregory.— EDITOR.

evidence of palæontology to show us beyond question what the primitive conditions in each group actually were, and what the historic facts are as to the course of its evolution.

This last is an incurable defect. Where we cannot check our inferences and interpretations by their correspondence with the facts of the geologic record, their taxonomic evidence cannot be of equal weight with evidence that is so supported. It may be of great supplementary value indeed. But if used as fundamental it is very apt to be misleading. Instance Tullberg's monograph of the Rodents, a treatise beyond criticism as to thoroughness and method of handling the anatomical evidence. But having no sufficient data as to the fossil rodents, he is entirely astray in his conclusions as to their phylogeny and consequently as to their taxonomy. The later discoveries of skulls and skeletons of Eocene and Oligocene rodents show that the primary type was not *Bathyergus* as he supposed, and that the Hystricomorphs are a specialized, not a primitive group.

I do not mean to minimize the importance of this class of characters in taxonomic work, but only to emphasize the need for caution in their use.—W. D. MATTHEW.

In response to the request of the authors for "comment or criticism" I can only call attention to a few of the problems and conclusions which their admirable studies offer for further development.

(1) The resemblances of the ossicles of the Myomorpha to those of the Shrews and other Insectivores, in relation to the origin of the Rodents.

(2) The taxonomic value of the ossicles in the Arvicolidæ, Muridæ, Sciuridæ, Hystricomorpha etc.

(3) Are the Heteromyidæ related to the Geomyidæ?

(4) Are the Zapodidæ Myomorpha?

(5) Are the Lagomorpha an entirely distinct order (Gidley) or do their ossicles connect them with other rodents?

(6) Do highly specialized life habits (as in the Spalacidæ, Pedetidæ, *Sciuropterus*) have any clearly discernible relation to the form of the ossicles?

W. K. G.