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A NEW OLIGOCENE RODENT GENUS FROM PATAGONIA

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INTRODUCTION

The earliest known South American rodents are from the Lower Oligocene (Deseadan). Until recently all of the available material has been very fragmentary, consisting of isolated teeth, or fragmentary jaws, or, at best, of nearly complete lower jaws or palates with upper dentitions (cf. Loomis, 1914, p. 186; Wood and Patterson, in press). The discovery of two nearly complete and largely articulated rodent skeletons and of one partial one by the American Museum Scarritt Expedition in 1934 was therefore of very great interest. One of these specimens, A.M.N.H. No. 29600, is nearly complete, almost all parts of the skeleton being preserved, though the interpretation of some of them is difficult or impossible. The specimens are preserved in a thinly laminated bentonite, which compacted after deposition, with resulting compression of the specimens. For this reason it has been impossible to prepare the specimens as much as would otherwise have been desirable.

Since the Deseado is the earliest horizon in South America from which rodents have been found, these specimens are of great importance in connection with the recurrent problems of the origin of the South American rodents and their relationships, if any, to the Old World hystricomorphs.

The description of this material has been delayed until now by

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preparation and by the war. I wish to express my great appreciation to Dr. G. G. Simpson for lending these three specimens to me for study and description, and for arranging for the publication of the manuscript by the American Museum. This work was assisted by grants from the March Fund of the National Academy of Sciences.

Comparisons have been made with several other groups of rodents, listed below:

- 1. The contemporary and later (particularly Santacrucian and Recent) South American hystricomorphs, which are the forms, if any, descended from this type. For these comparisons I have drawn heavily on Tullberg (1899) and Scott (1905) and have not attempted to give them credit at every place where I have used their works.
- 2. The Eocene North American representatives of the Paramyidae and Sciuravidae, and such relatively little modified descendants as the Eocene and Oligocene Ischyromyidae. The author is engaged in an extensive study of the Paramyidae, from which it has already appeared that *Reithroparamys* is one of the more primitive of the better known members of the family, and hence many comparisons are made with that form. Comparisons with *Paramys delicatus* are based on the excellent skeleton (A.M.N.H. No. 12506) described by Matthew (1910). As far as can be told at present, the Paleocene or lower Eocene paramyids or sciuravids were most probably ancestral to the South American rodents.
- 3. The Theridomyidae and such other Old World forms as have been suggested in the past as possible ancestors of the South American hystricomorphs. For this section I have drawn on notes made in 1934 while visiting the European collections as Cutting Traveling Fellow in Columbia University, as well as on various published sources.
- 4. Such other rodents as seem to show certain habitus or heritage characters in common with the present material.

The forms actually used anywhere in this paper, for comparisons of any type, include those listed below, with their classification as based on the present scheme.

Suborder Protrogomorpha
Superfamily Ischyromyoidea
Family Paramyidae
Paramys, Reithroparamys, Ischyrotomus

Family Sciuravidae

Sciuravus, Tillomys, Mysops, Pauromys, Taxymys

Family Ischyromyidae

Ischyromys, Pareumys, Titanotheriomys

Superfamily Aplodontoidea

Family Aplodontidae

A plodontia

Suborder Sciuromorpha

Superfamily Sciuroidea

Family Sciuridae

Sciurus, Cynomys, Marmota

Superfamily Castoroidea

Family Castoridea

Castor

Superfamily Geomyoidea

Family Geomyidae

Family Heteromyidae

Heliscomys, Perognathus, Cupidinimus, Dipodomys, Heteromys, Liomys, Microdipodops

Suborder Myomorpha

Superfamily Muroidea

Family Cricetidae

Neotoma, Ondatra

Suborder Hystricomorpha

Superfamily Hystricoidea

Family Hystricidae

Hystrix

Superfamily Erethizontoidea

Family Erethizontidae

Coendu, Erethizon, Steiromys

Superfamily Cavioidea

Family Eocardiidae

Eocardia, Schistomys

Family Caviidae

Cavia, Dolichotis, Prodolichotis, Paradolichotis

Family Hydrochoeridae

Hydrochoerus, Prothydrochoerus

Family Dasyproctidae

Cuniculus, Dasyprocta

Superfamily Chinchilloidea

Family Chinchillidae

Chinchilla, Lagidium, Lagostomus, Perimys

Family Acaremyidae

Acaremys, Asteromys, Platypittamys, Sciamys

Superfamily Octodontoidea

Family Capromyidae

Myocastor, Neoreomys, Scleromys

Family Echimyidae

Echimys, Kannabateomys, Stichomys

Hystricomorpha inc. sed. Family Thryonomyidae Thryonomys Family Petromyidae Petromys Rodentia inc. sed. Family Theridomyidae Theridomys, Trechomys Family Bathyergidae Bathyergoides, Georychus, Bathyergus Family Pedetidae Parabedetes, Pedetes Family Ctenodactylidae Ctenodactylus Inc. sed. Phiomys

In addition to these general comparisons, interpretations of the myology have been greatly assisted by a study of the situation as illustrated by A. B. Howell in his "Anatomy of the wood rat" (1926). The cusp terminology used for the teeth is that of Wood and Wilson (1936).

DESCRIPTION OF MATERIAL

FAMILY ACAREMYIDAE, NEW FAMILY

Small, ground-living, New World hystricomorphs, retaining a dental pattern clearly showing four subequal transverse lophs on both upper and lower molars. Infraorbital foramen enlarged, progressively transmitting the masseter. Temporalis small. Skeleton initially scampering, with tendencies towards cursorial adaptations. Feet pentadactyl, with first digit reduced. Tibia and fibula separate.

GENERA: *Platypittamys*, described below, and *Asteromys* from the Deseadan; *Protacaremys* and *Acaremys* from the Colhuehuapian; and *Sciamys*, *Acaremys*, and *Palmiramys* from the Santacrucian.

This family is a natural group of Oligocene and Miocene South American rodents. They may be characterized as being small, light-bodied, scampering to subcursorial, "hystricomorph" rodents, with relatively primitive, though progressively hypsodont, cheek teeth whose pattern is based on four transverse crests. This pattern appears to be basic for the South American hystricomorphs. The general structure, that of a small, pentadactyl, scampering rodent, also seems basic for this group.

The Acaremyidae have usually been considered a subfamily of the Erethizontidae, the Acaremyinae. As pointed out by Scott (1905, p. 421), the similarities to the Erethizontidae are very slight, other than in the dentition. This probably means that both groups have retained the basic South American hystricomorph tooth pattern. It seems probable, on the basis of the present study, that there is really nothing in particular that the Acaremyidae have in common with the erethizontids, other than this retention of the ancestral tooth pattern, which probably merely means that they have common Eocene ancestors. Therefore, since the acaremyids do not show sufficient similarity to any other family to justify their transfer to it, it would appear necessary to raise them to the status of a family.

The erethizontids appear to have followed a rather different evolutionary direction, at least since the Miocene, being much stockier, more slowly moving forms, largely arboreal, and presumably already having developed quills. Structurally they appear to be widely separated from the other South American rodents. In some respects the South American rodents seem to show a basic dichotomy into the erethizontids and the others, with the erethizontids having retained something like the primitive tooth pattern but having diverged in their other characters. this is true, the Acaremyidae could very well represent the basic stock from which the other groups have been derived. This would seem to be a correct expression of the present state of knowledge of the subject. Since, however, it is still impossible to establish any direct phyletic relationships to the other groups of South American rodents, it seems best not to include the Acaremyidae in any of the superfamilies into which Simpson (1945) divided the hystricomorphs, but to consider them as representing a basic stock ancestral to the Cavioidea, Chinchilloidea, and Octodontoidea.

PLATYPITTAMYS, 1 NEW GENUS

GENOTYPE: Platypittamys brachyodon, new species.

DIAGNOSIS: An acaremyid with low-crowned cheek teeth and

¹ In view of the extreme crushing of the specimens on which this genus is based, I referred to it during the study as "pancake-mouse." I wish to express my appreciation to Professor and Mrs. C. H. Morgan of Amherst College for helping me in finding an approach to a Greek name for pancake. Unfortunately this seems to be one item for which the Greeks have no name, so the name of this genus is compounded from "pitta," a cake, and "platy," flat.

non-molariform premolars in which, apparently, the masseter had not yet begun to pass through the infraorbital foramen.

RANGE: Lower Oligocene (Deseadan) of the Scarritt Pocket, Patagonia.

Platypittamys brachyodon, new species

HOLOTYPE: A.M.N.H. No. 29600, a skeleton with skull, jaws, and most of the other bones, badly compressed. The skull is dorsoventrally flattened.

REFERRED SPECIMENS: A.M.N.H. No. 29601, a partial skeleton with the skull transversely flattened; and A.M.N.H. No. 29602, a partial skeleton without skull.

As mentioned above, these specimens were so badly crushed that their preparation, which was very skillfully done by the late Mr. Albert Thomson, was very difficult. In connection with the study of the specimens, only slight additional preparation was required. Where two bones lie on top of each other, it is completely impossible to separate them. For example, a humerus and a scapula are plastered over the palate of the holotype and are molded into the contours of the skull in such a way as to be completely inseparable from it, being essentially two-dimensional, and yet they completely conceal the structure of the ventral surface of the skull. In all the bones, this crushing and flattening It has been necessary, therefore, to restore all the bones to what is hoped is an approach to their original condition. both in the individual drawings and in the restoration (fig. 8). Only where restorations have been made of parts that are completely absent are they indicated by broken lines.

SKULL

The skull is preserved in two specimens, A.M.N.H. Nos. 29600 and 29601. In the former it is crushed dorsoventrally, the roof being exposed on one side and the lower jaws and palate on the other, the whole being only about 1 mm. thick. In A.M.N.H. No. 29601, the skull is flattened laterally and is slightly thicker. Because of the great crushing of both specimens, there is a considerable amount of guesswork in the restoration of the skull. It is frequently exceedingly difficult to distinguish sutures from the myriad cracks that criss-cross the bones. It is believed, however, that the statements that follow are substantially correct.

The skull as a whole was apparently rather slender, perhaps most nearly having the proportions of that of a rat or ground squirrel. Although there are similarities to the skull of *Sciuravus* (Matthew, 1910, fig. 13), the skull seems to have been less arched than in that form, and the jaw to have been proportionately larger. The antorbital region is about a third the length of the skull, as in other acaremyids and in *Ischyromys*, being appreciably longer than in *Paramys*, *Reithroparamys*, or *Sciuravus*, and the region behind the anterior end of the glenoid fossa is about a quarter the length, as in other acaremyids and in the paramyids and *Sciuravus*. As in most primitive rodents, the basicranial axis is nearly straight.

The skull, as is usual in small rodents, seems to have had an inflated braincase, with little or no trace of crests, and a generally fairly flat dorsal surface, with a slight arch in the frontal and parietal regions as in Reithroparamys and the ischyromyids. likewise appears to have been true in Acaremys and Sciamys (Scott, 1905, pl. 66, fig. 11; pl. 67, figs. 1, 4, 9, 10), although in the former there is a slight sagittal crest. Paramys and Reithroparamys, both being larger, show clearly marked ridges around the temporal fossa. *Sciuravus* does not. The snout presumably was essentially tubular in dorsal view and was rather similar in shape to that of *Sciuravus*. This tubular character does not seem to be present in later acaremyids. The breadth of the occipital region of *Platybittamys* may be exaggerated in figure 1. It seems especially likely that the external auditory meatus was not visible from the dorsum, but it is so visible in A.M.N.H. No. 29600 and is hence restored that way. It was not visible in *Reithroparamys*. Sciuravus, or Sciamys. There appears to have been no postorbital constriction, agreeing with the Hystricomorpha in general and the other acaremyids in particular and in contrast to *Paramys*, Reithroparamys, and ischyromyids. This would indicate a relatively larger brain, which may merely be correlated with the difference in size, although since the larger hystricomorphs agree with Platypittamys and since the small Sciuravus agrees in this respect with the paramyids, it probably indicates an increase in size of the frontal part of the brain in Platypittamys. The eyes were fairly large, and looked forward and outward as in Acaremys, Sciamys, Reithroparamys, Sciuravus, and squirrels, rather than upward as in Paramys, Ischyromys, Aplodontia, and many other rodents. The size of the bullae and the upward orientation of the meatus

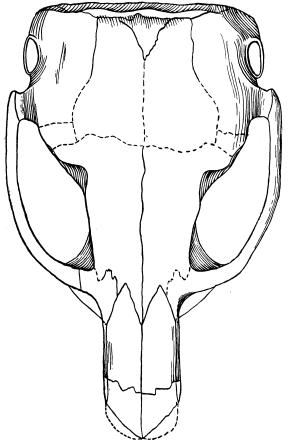


Fig. 1. Platypittamys brachyodon. Top view of skull, based largely on A.M.N.H. No. 29600, with additions from A.M.N.H. No. 29601. \times 3.

are quite suggestive of Acaremys, Ischyromys, Titanotheriomys, and Chinchilla. They are proportionately larger than in Reithroparamys and are not preserved in Paramys or Sciuravus, suggesting either that they were not ossified in these forms or that the ectotympanic had not yet established firm relationships with the skull.

The nasals (figs. 1, 2A) are long and slender, forming a tubular extension, which reaches forward of the anterior face of the incisor, very similar to the conditions in Reithroparamys and Sciuravus. There seems to have been a deep notch between the nasals and the premaxillaries in lateral view. This resembles the condition in Reithroparamys and differs from that in Sciuravus and Ischyrotomus and in all the Santacrucian forms except perhaps in some species of Sciamys (Scott, 1905, pl. 66, fig. 10), where, however, it is merely suggested. No such condition is seen in Acaremys (*ibid.*, pl. 66, fig. 11; pl. 67, figs. 4, 10). Among Recent hystricomorphs, the anterior extension of the nasals is seen in *Echimus* and to a lesser extent in Dasyprocta, Cuniculus, and Petromys. For most of their length, the nasals are of nearly uniform width, seen from above, as in Sciuravus, Ischyrotomus, Cuniculus, and Titanotheriomys, and do not taper gradually caudad as in Paramys, Ischyromys, Acaremys, Sciamys, Cavia, Chinchilla, Myocastor, and Echimys, nor do they narrow mesially as in Reithroparamys. Each nasal ends posteriorly in a point at the middle of the bone, separated by a wedge of the frontals. Only Sciamys latidens, of all the Santacrucian forms (Scott, 1905, pl. 67, fig. 1), shows even a suggestion of this character. This separation is perhaps suggested in Reithroparamys, but in general in that form the posterior end of the nasals forms nearly a straight line, as is also In Paramys, conditions are similar to those the case in *Sciuravus*. in *Platypittamys*, but the wedge of the frontals is much narrower. Lagidium is the only living form that has been compared with Platypittamys in which such a condition is seen. The posterior margin of the nasals lies just behind the anterior margin of the dorsal root of the zygoma, as in Acaremys, Reithroparamys, Paramys hians, and Ischyromys, not reaching as far as in Sciamys, Paramys delicatus, Ischyrotomus, Sciuravus, or Titanotheriomys. The present form agrees essentially with most of the other Santacrucian forms in this respect. Among modern hystricomorphs, the situation is modified by the retreat of the dorsal root of the zygoma owing to the enlargement of the anterior deep masseter.

However, *Chinchilla* and *Hystrix* agree in this respect with *Platypittamys*, although the conditions in *Hystrix* are only superficially similar. The adjacent sutures are slightly doubtful, but it appears that the nasal extends well posteriad of the premaxilla and not quite so far as the maxilla. This condition, while unusual, occurs in *Cuniculus* and to a minor extent in *Stichomys* (Scott, 1905, pl. 65, fig. 16).

The premaxilla sends a long slender process towards the dorsum of the skull, which ends slightly in front of the anterior end of the zygoma (fig. 2A). The exact rearward end of the ascending process is uncertain, but appears certainly to have been anteriad of the posterior tip of the nasal, and to have been appreciably shorter than in *Reithroparamys*, but about as long, relative to the position of the zygoma, as in *Paramys* and *Cavia*. On the lateral surface (A.M.N.H. No. 29601) it has been impossible to locate the suture between the premaxilla and the maxilla, and it has been drawn on the restoration about where it is in related forms.

The sutures bordering the frontal are very difficult to distin-However, it would appear that the frontal is fairly long, apparently being slightly longer than the parietal, as in Paramys, instead of being much longer, as in Reithroparamys. This would appear to be an agreement also with the other fossil and Recent hystricomorphs, except the erethizontids, in which the frontals are shorter than the parietals. Anteriorly, the frontals extend forward between the nasals, and the suture between the frontals can be traced clearly backward from here. At what is interpreted as the rear end of the bone, there appears to be a suture extending in a broad curve, posterolaterad from the median suture. direction of this suture is similar to that in Paramys, but very different from conditions in Reithroparamys. This presumed suture reaches the lateral margin of the top of the skull shortly posteriad of the small postorbital process. This process appears rather similar to that in such Recent forms as Lagostomus or Cuniculus and such Santacrucian forms as Steiromys, Neoreomys, Scleromys, Acaremys, Sciamys, and Perimys. In view of its prevalence among the Santacrucian and Recent forms, as well as its presence in *Platypittamys*, it is quite possible that such a postorbital process is a primitive character among the South American hystricomorphs. No indication of such a process is seen in the Paramyidae, Sciuravidae, Ischyromyidae, Bathyergidae, Hystrix, Thryonomys, or Petromys. The postorbital process in the Sciuri-

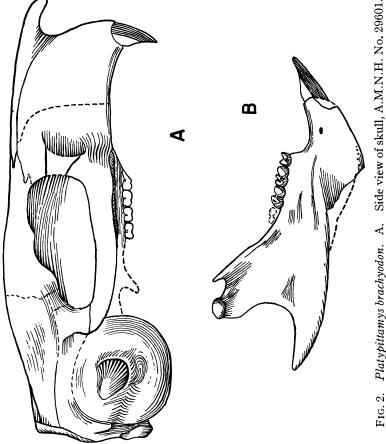


Fig. 2. Platypittamys brachyodon. A. Side view of skull, A.M.N.H. No. 29601. B. Lateral view, right jaw, A.M.N.H. No. 29601, with restorations based on lingual surface of jaw of A.M.N.H. No. 29600. Both \times 3.

dae is very different in shape and relationships and is surely a parallel development. There is also a roof over the central part of the orbit, formed by the lateral edge of the frontal. The posterior end of this roof marks the point where the temporalis muscle passed to the dorsum of the skull. The extent of this passage is limited posteriorly by the glenoid fossa and shows that the muscle was quite small. The Santacrucian acaremyids and *Chinchilla* show the same conditions as does *Platypittamys*. In *Sciuravus*, *Paramys*, and *Reithroparamys*, conditions are very different, indicating a much larger temporalis. The dorsal surface of the frontals was probably nearly flat, with no indication of any frontal sinuses. Nothing can be told in regard to the extent of the frontal within the orbit since it is impossible to distinguish the cracks from the sutures in this area, and since most of it is not visible in either specimen.

The parietal shows no trace of a sagittal crest and appears to have been flat or gently curved in cross section. The posterior margin reaches the front of the weak lambdoid crest, and the lateral margin seems to reach about halfway to the lateral margin of the dorsum of the skull. Although it is impossible to be certain, it seems probable that the dorsal limit of the temporal fossa was near the lateral margin of the parietals. This again would indicate a much weaker temporalis than in *Sciuravus*, *Paramys*, or *Reithroparamys*, where it reached nearly or quite to the midline of the skull. Again, *Platypittamys* is very similar to *Acaremys* and *Sciamys* in this respect.

One of the few sutures that is clearly visible on the skull (A.M. N.H. No. 29600) is that bounding the interparietal (fig. 1). This is a fairly large bone, with a broad, triangular outline. In no other hystricomorphs does the bone appear to have any particular resemblance to that in the present form, though it appears to be unknown in *Acaremys* and *Sciamys*. It is rather larger and more triangular than in *Reithroparamys* and *Titanotheriomys*, but is rather similar in proportions to the interparietal of *Sciuravus* and *Ischyromys*, although it is somewhat smaller than that of *Sciuravus*.

The squamosal is badly damaged in both specimens, and its relationships are very questionable. There does not, however, appear to have been a temporal foramen as in the ischyromyids, paramyids, *Aplodontia*, and many other rodents. According to Scott's figures (1905), such a foramen is present in *Steiromys* and

Perimys but is absent in Neoreomys, Sciamys, Schistomys, and Eocardia. The squamosal laps around the bulla, to hold it in place, as in Reithroparamys and Acaremys. There is a fairly strong mastoid process at the rear of the bulla. The zygomatic process extends out as a narrow shelf above the glenoid fossa, with its anterior and posterior edges nearly parallel, instead of having the posterior face sloping anterolaterad as in paramyids and Sciuravus. This is associated with the enlargement of the bulla in Platypittamys.

The masseter apparently was limited to the ventral surface of the zygoma, as in paramyids, sciuravids, and Ischyromys. least, if it had begun to grow up within the orbit, no trace of its presence can be found on the specimens, and it seems certain that it did not penetrate through the infraorbital foramen. This is a sharp distinction from Acaremys and Sciamys, where the typical hystricomorph conditions obtained. The compression of the skulls has made the determination of the exact size, shape, and position of the foramen somewhat questionable, but it seems to have occupied a position about as shown (fig. 2A), and to be somewhat larger and slightly higher on the face than in the protrogomorphs (paramyids, sciuravids, ischyromyids, etc.) and to be much smaller than in any other hystricomorphs. This material seems to establish that an enlargement of the infraorbital foramen definitely preceded the increase in the size of the masseter. The maxillary portion of the zygoma is fairly slender, but its position and alignment indicate that the zygoma arched quite widely from the skull as in Acaremys, Sciamys, Paramys, Sciuravus, Ischyromys, and most Recent South American hystricomorphs, instead of being essentially parallel to the skull as in Reithroparamys, Hystrix, Thryonomys, and Petromys. There is no suggestion of the forward migration of the zygoma, lateral to the infraorbital foramen, which is seen in the theridomyids. suture between the maxillary and malar could not be identified. The malar forms the lateral limits of the glenoid fossa as in Paramys, Reithroparamys, ischyromyids, and many other rodents. including particularly the modern hystricomorphs.

The bulla is large and round, completely ossified, and firmly held into the rest of the skull. It extends considerably higher on the skull than in *Reithroparamys*, and is more globular. It is somewhat larger than in ischyromyids, but seems to be quite similar to that of *Acaremys* (Scott, 1905, pl. 67, fig. 9) and *Chin*-

chilla. The meatus, situated near the middle of the lateral surface, is large and directed posterodorsad. There is essentially no meatal tube, the meatus lying only slightly above the surface of the bone. There is a slight lip along the anterior side of the meatus, as in *Ischyromys*. These conditions are identical with those in *Reithroparamys* and seem to be only slightly more primitive than in *Acaremys*. A groove running just below the meatus divides the bulla into dorsal and ventral portions, ending just below the tip of the mastoid process. This seems to have been true also in *Acaremys*. The size of the bulla suggests an animal with an acute sense of hearing.

It is impossible to interpret the ventral surface of the skull. In A.M.N.H. No. 29600, the atlas, the right scapula, right mandible, right humerus, and some ribs are plastered over the palate so that it is impossible to recognize the relationships of any of the palatal bones. A.M.N.H. No. 29601 is flattened in such a manner that the palate is not visible. The occiput is also not visible in either specimen, but it appears to have been fairly broad and certainly was not inflated. The lambdoid crest was weak. The foramen magnum seems to have been a dorsoventrally compressed oval.

The mandible (fig. 2B) is long and slender with, apparently, at least a slight inflection of the angle, which extends well to the rear, below the bulla, as in Trechomys, Cavia, Chinchilla, Coendu, Myocastor, and Thryonomys, but quite different from what is seen in Hystrix. Owing to the flattening of both specimens, the amount of inflection cannot be established with certainty but appears to have been considerable. In lateral view the angle appears to have been very similar to that of Erethizon, the inflected portion of which is invisible laterally. In the paramyids there is no inflection, but the ventral border is thickened mesially. In ischyromyids there is a slight inflection of the angle. Since this area serves for the insertion of the pterygoideus internus (Howell, 1926, fig. 24c), it presumably means that the importance of this muscle had increased in *Platypittamys* when compared with paramyids or ischyromyids. As in both Santacrucian erethizontids and all Recent South American hystricomorphs, there is an expansion of the ascending process of the mandible immediately posteroventral to the condyle, not found in Hystricidae, Petromys, or Thryonomys. This seems to indicate an increase in the size of the pterygoideus externus over conditions in the paramyids. The coronoid is quite small and separated from the condyle by a narrow furrow, being very different from what is seen in the paramyids, where the coronoid is large, but agreeing with later hystricomorphs. The mandible thus agrees with the skull in suggesting that the temporalis was small and weak. masseteric fossa has no distinct upper limits, differing in this from Tillomys (Wilson, 1938, fig. 11), but its ventral margin is marked by a ridge which slopes forward and upward, leaving the ventral margin of the mandible about beneath M₃, and ending under the rear of P₄, about as in theridomyids. This ridge marks the abrupt lower limit of the fossa. The fossa appears to extend considerably farther forward and to be much less definitely bounded dorsally than in Acaremys and Sciamys. It also extends farther forward than in Mysops, where it ends beneath M2 (Wilson, 1938, p. 208). In these respects, the present form is less like Tillomys, Mysops, Reithroparamys, and Paramys than are the later Acaremyidae, but all of them are rather distinct from the Eocene forms. This condition is interpreted as meaning that the masseter lateralis was beginning to spread out anteroposteriorly in *Platypittamys*, but that it was still relatively small. There is no tubercle for the anterior deep masseter, suggesting that it had not yet been differentiated. There is a small mental process of the mandible at the posterior end of the symphysis, rather similar to that in Sciamys (Scott, 1905, pl. 66, fig. 10), and larger than that of Reithroparamys or Paramys. There are a number of nutritive foramina in the extreme posteroventral portion of this process as in Paramys. These are not present in Reithroparamys. The mental foramen is fairly high on the mandible and at about the middle of the diastema. In this it agrees with Reithroparamys, ischyromyids, and with Sciamys and Neoreomys, and differs from the other Santacrucian rodents and from Tillomys, in which it is lower on the mandible. The symphyseal region is fairly large and is quite markedly corrugated, indicating a fairly firm union of the two mandibles. There presumably was no transversus mandibulae muscle. The pit for the geniohyal muscle is rather small and high on the mandible.

DENTITION

The teeth are generally similar to those of Asteromys but differ in a number of ways, chiefly in being much lower crowned. The unilateral hypsodonty that characterizes Asteromys has begun

to be developed, but it has only just appeared. There are also some differences in the patterns of the teeth. As far as can be told from the available material of *Asteromys*, *Platypittamys* is structurally ancestral to it, and is sufficiently more primitive to warrant generic separation.

In distinction from the paramyids, sciuravids, and ischyromyids, there is no trace of P³. This tooth, which is very small in those forms, is absent in most rodents, including all of the hystricomorphs.

P4 is much simpler than in any other known hystricomorph (fig. 3A, B). It clearly is a long way from having attained a molariform pattern and is much less advanced than that of Asteromys (Wood and Patterson, in press). There is a considerable difference in the anteroposterior diameter of the tooth in the two specimens of *Platypittamys*. This tooth is elongate transversely, though the wear surface is not so wide as are the lower parts of There are an undivided buccal amphicone and a the crown. lingual protocone, connected by a crest. From the protocone, an anteroloph curves across nearly the entire front face of the tooth. From the posterior side of the protocone, a posteroloph extends around the posterior margin of the tooth. At its lingual margin this is somewhat thickened into what is probably not sufficiently advanced to be called a hypocone. This latter is separated from the protocone by a faint groove in the lingual face of the tooth. There is a similar slight swelling of the anteroloph, likewise separated from the protocone by a faint furrow. This tooth is extremely interesting. It appears to be in a very primitive stage of evolution. If its simplicity is indicative of primitiveness and not of secondary simplification, it is necessary to go far back towards the basic stock of the rodents to find a form that could be ancestral to this genus. No member of the Paramyidae whose upper teeth are known has so simple a P⁴ as this. The Sciuravidae likewise do not show such a primitive pattern, the nearest approach to it being in Mysops (Wilson, 1938, fig. 5), where, however, the amphicone has divided and there is a clearly marked metaloph, considerably higher than the posteroloph. It is possible that P4 of Pauromys was in this stage of development, but upper teeth of this form are unknown. There are no other forms with which I am familiar that have a P4 anywhere near as simple as that of Platypittamys. Therefore, if the condition of this tooth is primitive, as it appears to be, no rodent whose upper

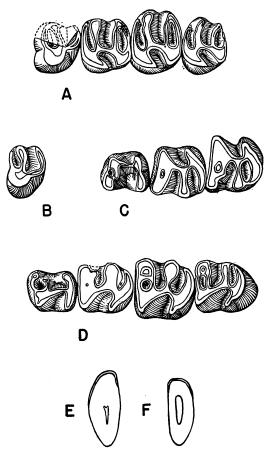


Fig. 3. Platypittamys brachyodon. A. LP⁴–M³, A.M.N.H. No. 29601, with P⁴ restored from A.M.N.H. No. 29600. B. LP⁴, A.M.N.H. No. 29600, anterior face to the right. C. LP₄–M₂, A.M.N.H. No. 29601. D. RP₄–M₃, A.M.N.H. No. 29600. E. RI¹, anterior view, A.M.N.H. No. 29601. F. RI₁, anterior view, A.M.N.H. No. 29601. All \times 10.

dentition has been described could be ancestral to *Platypittamys*. On the basis of our general knowledge of paleogeography and of rodent paleontology, it would seem almost certain that this form could only be descended from a Paleocene or lower Eocene northern form. It is suggested that it may be closer to the Sciuravidae than to the Paramyidae, the only two families known from the lower Eocene. It should be pointed out that this is not the only case where P⁴ of a middle Tertiary group does not seem capable

of being derived from that of any known Eccene rodent. The same is true of the heteromyids and geomyids (Wood, 1935, fig. 6; 1936, fig. 17).

Both upper and lower molars show fundamentally the same pattern as is found in the Ischyromyidae, namely, four transverse crests. The individual cusps, however, are not so distinct as in the ischyromyids. The upper molars are strikingly different from those of theridomyids in the absence of a mesoloph. In the lower teeth, however, the theridomyids likewise have four transverse crests (fig. 7).

M¹ (fig. 3A) is quite similar to that of Asteromys (Wood and Patterson, in press), differing in the lesser development of the lophs and the trace which still remains of the separate cusps in the protoloph and metaloph. The paracone is a distinct cuspule, which seems also to be the case in Asteromys, though it is smaller in that form. The metacone is very clearly marked as a round Both protoconule and metaconule seem to be indicated, although they are very faint, the teeth being apparently in transition to the uniform, lophate condition of Asteromys. The protoloph and metaloph are well developed and are connected by a mure, apparently representing the anterior arm of the hypocone. The anterior and posterior cingula bound the tooth, uniting with or coming close to the paracone and metacone. There is no trace of a mesostyle or a mesoloph. Indeed, none seems ever to be present in the South American hystricomorphs. This general idea has previously been expressed, with different wording, by Winge (1887, p. 128), who considered that the teeth of the ancestral South American hystricomorphs had four more or less complete transverse enamel folds. This point does not seem to have been stressed by subsequent authors. This basic tooth characteristic is a sharp distinction from the theridomyids (fig. 7) where the mesoloph is characteristically very well developed. Many figures of theridomyids suggest that there are only four transverse crests, but actually there are five in all forms, the valley between the anteroloph and protoloph being very shallow, so that it is quickly destroyed with wear. The figure of cf. Phiomys andrewsi from the lower Miocene of Southwest Africa (Stromer, 1926, pl. 42, fig. 24) also shows a mesoloph. Although, in general, none is present in the paramyids, there seems to be a tendency towards the development of such a crest in this family, whereas it is completely absent in Mysops and Taxymys (Wilson, 1938, figs. 5–9, 13–15).

As in Asteromys, M² is larger than M¹. This is in agreement with conditions in Sciuravus, but the reverse of the situation in Mysops. In general this tooth is very similar to M^1 . Here again the paracone and metacone are quite clearly shown, and the conules appear to be indicated by slight swellings of the lophs. As in many other rodents in this stage of evolution, distinct conules are visible only on unworn or nearly unworn teeth. The protocone has grown back along the lingual face of the tooth, both in this tooth and in M1, as in Asteromys, but it does not appear to have made as much progress in this direction as in the latter form. The separation of the protocone and hypocone is a distinct advance over the paramyids and some sciuravids, but these cusps are nearly as distinct in Sciuravus and Taxymys (Wilson, 1938). No trace of the posterior migration of the protocone is seen in sciuravids, and very little is shown by the theridomyids. This tooth is much more advanced than that of the Uintan ischyromid Pareumys (Burke, 1935, fig. 4), where the separation of the hypocone from the protocone has just begun.

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF UPPER TEETH

	A.M.N.H. No. 29601		A.M.N.H.
	Left	Right	No. 29600 Left
P4			
Anteroposterior	<u>.</u>	1.20	0.95
Width anterior			ca. 1.33
Width posterior		_	$ca.\ 1.31$
M^1			
Anteroposterior	1.30	1.31	1.33
Width protoloph	1.41		
Width metaloph	1.27		
M^2			
Anteroposterior	1.30	1.33	· —
Width protoloph	1.66		
Width metaloph	1.49		
M^3			
Anteroposterior	1.15	1.24	
Width protoloph	1.49	1.51	-
Width metaloph	1.16	1.10	
I¹			
Anteroposterior	. —	1.93	
Transverse		0.85	

M³ is similar to the two anterior molars but somewhat smaller (table 1), as in Asteromys, ischyromyids, and Mysops, instead of being of equal size, as in other sciuravids and paramyids. The protocone seems to form a larger part of the lingual surface of the tooth than in Asteromys. The posterior cingulum does not unite solidly with the metacone until after a fair amount of wear. The metacone is slightly farther to the rear than in the anterior molars, suggestive of the conditions in paramyids, but showing a trend towards the pattern of the anterior two molars.

P₄ is much the smallest of the lower teeth (fig. 3C, D) and is quite distinctive in its pattern. There are anterior and posterior crests, each formed of two cusps. These crests are united near the center of the tooth. In these respects this form is somewhat reminiscent of Pareumys (Burke, 1935, figs. 2-4). A short crest, perhaps an anterior cingulum, connects the metaconid and protoconid at the anterior end of the tooth. This is larger than in Pareumys. A spur from the protoconid extends towards the metaconid, damming off a small basin between it and the anterior The free end of this spur is somewhat expanded into a small cuspule. The metaconid is slightly anteriad of the protoconid, also as in *Pareumys*. The ectolophid lies near, but not at, the center of the tooth, running slightly diagonally. There is a very faint expansion near its middle, which could not be called a mesoconid but suggests the initial stage in its development. The hypoconid and entoconid form a continuous wall along the posterior border of the tooth, with no indication that both hypolophid and posterolophid are present or ever were present. more suggestive of a hypolophid than of a posterolophid. Pareumys both hypolophid and posterolophid are present. Except for Pareumys, this tooth is distinct from that of any other form with which it has been compared. On the one hand it is considerably simpler than the corresponding tooth of Asteromys (Ameghino, 1906, fig. 287), but could perhaps be the structural type from which the latter was derived. In Asteromys the talonid is approaching a molariform pattern, whereas in Platypittamys there is nothing suggestive of the molar pattern in the premolar. As in the case of the upper premolar, this tooth would seem clearly to establish the fact that no member of the Theridomyidae could possibly be ancestral to this form (fig. 7). The early members of the Paramyidae, some sciuravids (such as Sciuravus and Pauromys), or a form related to Pareumys could have given rise to a

tooth such as is present here, but they are all sufficiently distinct so that there is no evidence that they did. The movement of the ectolophid towards the middle of the tooth that characterizes *Platypittamys* has already gotten well under way in *Reithroparamys* and in sciuravids.

 M_2 is the largest of the lower molars, with M_1 and M_3 subequal. Each tooth is composed of four cross crests, the metalophid and hypolophid together with the anterolophid and posterolophid. The anterolophid unites with the metaconid after very little wear, thus surrounding a lake in the trigonid. This is true of all the molars of both specimens. Although all teeth are somewhat worn, it appears that the metaconid is connected to the protoconid primarily through the anterior cingulum and only secondarily through a direct crest. This is also the situation in Reithroparamys, Paramys, Mysops fraternus (Wilson, 1938, fig. 9), and in Pareumys. In addition Platybittamys agrees with these forms in the shortness of the metalophulid II. At least sometimes, a secondary bar connects the two crests through the trigonid basin, forming two small lakes (fig. 3D). M₂ seems somewhat more advanced than M₁, in that the union of the two posterior crests has occurred on that tooth in A.M.N.H. No. 29601, whereas they are still separate on M_1 . The hypolophulid I unites with the ectolophid, the entoconid being anterior to the hypoconid. The posterolophid is as large as the hypolophulid, but shows no trace of separate cusps. The central valley of all three molars opens widely on the lingual side, the valley draining freely, in contradistinction to Asteromys, where all the lingual valleys are closed by dams, and where the connection between the posterolophid and the entoconid appears weaker than that between the entoconid and the metaconid (Ameghino, 1906, fig. 287).

The incisors are laterally compressed, their transverse diameter being much less than their anteroposterior one (fig. 3E, F). This does not appear to be more than a generic character, there being great variation in this condition in many groups of rodents. In the paramyids, compressed incisors occur in *Reithroparamys*, and wide ones in most other genera. Among the theridomyids, *Trechomys* has compressed incisors, whereas in the more primitive *Theridomys* they are in the form of equilateral triangles. In *Sciamys* they are compressed; in *Acaremys*, broad and convex.

The upper incisors (fig. 3E) are slender and seem to have been

TABLE 2						
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH						

	A.M.N.H. No. 29601 Right	A.M.N.H. No. 29600	
		Right	Left
P ₄ -M ₃	·	6.20	6.36
P_4			
Anteroposterior	1.23	1.24	1.25
Width metalophid	0.93		ca. 1.06
Width hypolophid	1.02		ca. 1.03
$\mathbf{M_1}$			
Anteroposterior	1.46	1.49	1.46
Width metalophid	1.23		ca. 1.21
Width hypolophid	1.34		ca. 1.29
\mathbf{M}_2			
Anteroposterior	1.47	1.48	1.53
Width metalophid	1.43	_	ca. 1.54
Width hypolophid	1.41		ca. 1.52
M_3			
Anteroposterior		1.70	1.64
Width metalophid			ca. 1.33
Width hypolophid			ca. 1.28
I_1			
Anteroposterior	1.72		1.55
Transverse	0.68		0.88

nearly oval in cross section, as in *Reithroparamys*. The median face is flat, and the lateral face rounded, the diameter tapering both anteriorly and posteriorly. There was a very faint groove on the anterior face, just laterad of the middle of the tooth, similar to that in *Reithroparamys*, but too small to show on the figures. The pulp cavity is elongate and narrow, with a suggestion of an anterior expansion. The enamel is exceedingly thin and apparently extends from the middle of the lateral side, well around the anterior face onto the median surface, about as in *Reithroparamys*. The exact limits of the enamel-covered area are uncertain.

The lower incisors are somewhat more clearly preserved than the uppers (fig. 3F). The lateral and mesial sides are more nearly parallel than in the upper incisors. The essential relationships appear to be about as indicated for the uppers, with the enamel reaching about halfway around the lateral face of the tooth and almost a third of the way along the median surface. The anterior face of the lower incisors is slightly flatter than in the uppers,

and there is no trace of a sulcus. The pulp cavity is long and narrow, being almost a straight line. In all these respects the similarities to *Sciamys* and *Reithroparamys* are marked.

POSTCRANIAL SKELETON

Although all three specimens are fairly complete and contain a considerable number of vertebrae, it is not possible to determine the vertebral formula with certainty. There were presumably seven cervicals. Probably there were 13 thoracic vertebrae, of which the ninth is the anticlinal, and six lumbars. There seem to have been one sacral and two pseudosacrals and about 25 caudal vertebrae. These figures are approximately the same as those in Scott's figure of Neoreomys (Scott, 1905, pl. 70), which, in turn, is restored, using Myocastor as a guide. These figures also agree with the vertebral formula of Aplodontia and differ from that of Ischyromys, Sciurus, Cynomys, or Paramys in having one more thoracic and one fewer lumbar vertebrae than these forms (Wood, 1937, p. 179). The presence of 19 thoracic and lumbar vertebrae seems to be widespread among the rodents (Flower, 1876, p. 50) and is presumably primitive for rodents. The tail is apparently somewhat shorter than in most of these forms, but was nearly half the length of the entire vertebral column.

Most of the cervicals are covered by other bones or are in part squeezed into them. The neck, however, seems to have been rather shorter than in *Paramys* or *Ischyromys* and definitely shorter than in *Neoreomys*. The atlas lies immediately beneath the occiput in A.M.N.H. No. 29600 and shows the ventral surface. It is broad transversely and short anteroposteriorly, with little or no hypopophysis. The vertebrarterial foramen is small as in *Cynomys*, instead of being large as in *Ischyromys*. The transverse processes extend forward, reaching anteriad of the lateral surfaces of the occipital condyles but do not appear to have extended behind the main part of the atlas. In these respects the bone is completely different from that of *Ischyromys*. They are larger anteroposteriorly than in *Paramys*. The other cervicals are not visible.

The thoracic vertebrae increase in size from front to rear, and this increase continues about to the fourth lumbar as in *Paramys*. The spines of the anterior thoracic vertebrae were not very long, being completely covered by the scapula in A.M.N.H. No. 29600.

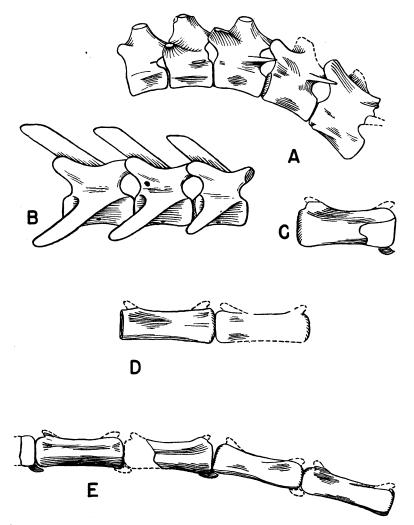


Fig. 4. Platypittamys brachyodon. A. Left side of ninth to thirteenth thoracic vertebrae, A.M.N.H. No. 29600. B. Left side of the fourth to sixth lumbar vertebrae, A.M.N.H. No. 29600, partially restored. C. Right side of eighth (?) caudal vertebrae, A.M.N.H. No. 29602. D. Right side of tenth (?) and eleventh (?) caudal vertebrae, A.M.N.H. No. 29602. E. Right side of twelfth (?) to fifteenth (?) caudal vertebrae, A.M.N.H. No. 29602. All × 3.

They appear to have been shorter than in *Sciamys*. The ninth to thirteenth thoracic vertebrae are visible. The spines are short, and all behind the ninth slope slightly anteriad. The bones as

preserved form an arch, which is probably the natural position (fig. 4A). The diapophyses are not distinguishable, nor are the facets for the heads of the ribs. The metapophyses progressively increase in size caudad. Large anapophyses are present on the last three thoracics, and a small one is present on the tenth. There is a suggestion on the last thoracic of a small diapophysis, although there seems to have been a rib for this vertebra.

The lumbar vertebrae are fairly large, with long, forwardly directed neural spines, which reach as far as the middle of the vertebra in front, and long diapophyses (fig. 4B). The latter decrease in length on the last two lumbar vertebrae. spines are longer than in *Neoreomys*, which otherwise appears to have been rather similar, and are very much longer than in the paramyids and ischyromyids. A very similar condition in regard to the length of the neural spines and diapophyses occurs in all saltatorial rodents (Hatt, 1932, p. 673) and is foreshadowed in the subricochetal Cupidinimus (Wood, 1935, p. 130, fig. 50). Median ventral foramina appear in the centra as in *Paramys*. Dipodomys, and Microdipodops, which are absent in Cupidinimus. As in *Paramys*, there appears to be no trace of the keeling on the ventral surface of the lumbars which is seen in *Ischyromys*. Paramys and Neoreomys, the metapophyses do not rise appreciably above the prezygapophyses. The most significant feature of the lumbars is the length of the neural spines and diapophyses. pointed out by Hatt (1932, p. 673), the increase in the length of the neural spines of richochetal forms is correlated with an increase in the size "of the Mm. multifidus spinae which support the fore end of the body during bipedal progression." They also serve for the insertion of the pars lumborum of the semispinalis, which is also used to hold up the front end of the animal in leaping (Howell, 1932, pp. 426-428). The long diapophyses are also characteristic of ricochetal forms but occur as well in quadrupedal leapers and cursorial forms. These are related to the longissimus dorsi, quadratus lumborum, and psoas major muscles (Hatt, 1932, p. 684).

The sacrum preserved in A.M.N.H. No. 29600 apparently consists of a single sacral vertebra and two pseudosacrals. The transverse processes of the sacral and first pseudosacral are fused, an advance over the situation in *Paramys* where the fusion is incomplete, and the processes of the sacral extend forward on each side of the last lumbar, as far as its middle. These are longer

than in *Paramys*. Only the single sacral seems to have articulated with the ilium, as in *Paramys*. This is more primitive than the condition in *Sciamys*, where there are two sacrals articulating with the ilium and two pseudosacrals (Scott, 1905, pp. 422–423).

The anterior portion of the caudal series is preserved in A.M. N.H. No. 29602. These seem to represent the first five caudals. The first four bones are of almost uniform size, and the fifth is appreciably longer. There are median ventral foramina. transverse processes are massive, anteroposteriorly expanded, and are nearly continuous for the entire length of the centra. Paramys this is true of the first two caudals, which lie within the basket of the pelvis, but does not characterize the more posterior This expansion of the transverse processes indicates fairly large extrinsic tail muscles, of the sort found in Pedetes (Hatt, 1932, p. 685) and quite different from the conditions found in all slender-tailed rodents. There is no suggestion of the large, elongated, transverse processes found in *Erethizon*. The similarities to Myocastor (Scott, 1905, pl. 70) seem to be very striking, particularly when it is realized that two additional caudals have moved into the pseudosacral region in the modern genus. The processes are wider and considerably shorter than those of Paramys delica-That is, there must have been muscles passing into the anterior portion of the tail of *Platypittamys*, but they were not so heavy as in the porcupine, beaver, or *Paramys*.

The posterior caudals seem to be nearly uniform rods (fig. 4D, E). There is still an appreciable, though interrupted, neural arch on what seems to be the eighth caudal, but behind this the vertebrae are essentially block shaped with a slight median constriction closely resembling those of *Myocastor*. There is no indication of the marked hourglass constriction seen in *Paramys delicatus*. The chevrons, which are preserved only in the posterior caudals, appear not to be paired but to be shaped like spherical triangles, filling the spaces between the vertebrae and resting on the anterior end of the posterior of each pair of vertebrae. They show considerable similarity to those of small-tailed ricochetal rodents and of *Myocastor* and are quite different from those of such fleshytailed rodents as *Pedetes*.

The lumbar vertebrae, then, show interesting similarities in structure to what is seen in ricochetal rodents, but these similarities are not found in the rest of the skeleton. This is interpreted as meaning that *Platypittamys* possessed strong back muscles, probably used to assist the animal in sitting up on its haunches. The structure of the caudal vertebrae indicates a slender tail, with muscles extending only into the proximal portion and with the distal part largely tendinous.

There seem to have been 13 ribs, increasing gradually in size to the ninth or tenth, after which they are progressively shorter. In all cases where they could be studied, the tuberosities are quite low and poorly marked, and the neck is but little, if any, constricted.

The scapula is considerably more elongate than is that of Erethizon, having a long, slender, tapering neck region (fig. 5A), about as in *Neoreomys*. The posterior side is essentially straight, whereas the cranial border curves somewhat anteriad, though it does not have the pronounced cranial expansion of that of Myocastor or Neoreomys (Scott, 1905, pl. 70), being more like that of Ischyromys, Echimys, or Thryonomys in this respect. dorsal borders of both scapulae of A.M.N.H. No. 29600 are too broken to permit adequate discussion. The central half of the spine appears to have been quite high, indicating fairly large supraspinous and infraspinous muscles. Ventrally, the spine ends well up on the side of the scapula, being continued in a long, slender, acromion process, which extends well beyond the glenoid fossa. The scapular notch is nearly a third of the way up the spine, but the spine is continued almost to the glenoid as a faint ridge. These features are very different from what is found in paramyids and ischyromyids and suggest the conditions in Neoreomys, Chinchilla, Myocastor, Echimys, and Kannabateomys or, to a lesser degree, Dasyprocta, Coendu, Georychus, Petromys, or Thryonomys. There is a small metacromion process, considerably smaller than that of any of the living hystricomorphs. details of the glenoid region cannot be determined.

The left clavicle is preserved in A.M.N.H. No. 29600 and shows very few diagnostic features. It is long and slender and only slightly curved. The two ends are but slightly expanded.

The humerus is represented only in A.M.N.H. No. 29600, by a nearly complete left humerus and a fragmentary right one (fig. 5B). Only the lateral surface is visible. It appears to be unusually thick for its length, but partly, at least, this is due to crushing, as may be told by comparison with the humerus of *Paramys*, to which this is quite similar. Particularly, the deltoid crest seems

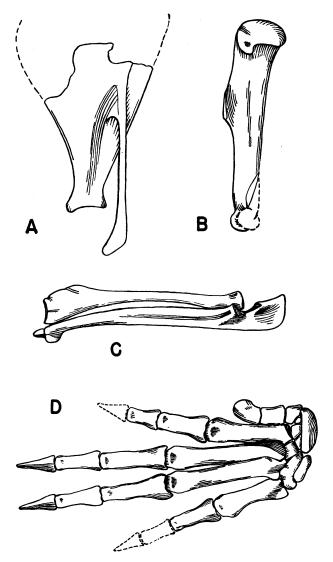


Fig. 5. Platypittamys brachyodon. A. Lateral surface of left scapula A.M.N.H. No. 29600, with restorations based on right scapula. \times 3. B. Lateral view of left humerus, A.M.N.H. No. 29600. \times 3. C. Lateral oblique view of left radius and ulna, A.M.N.H. No. 29600. \times 3. D. Dorsal view of left manus, A.M.N.H. No. 29600, with assistance from right manus and from A.M.N.H. No. 29601. \times 6. Dotted bones purely hypothetical.

to have been squeezed laterally so that it lies in the plane of the lateral margin of the bone. But even so the bone seems to have been proportionately quite stout. The head is less globular than that of Paramys or Ischyromys, not extending so far down the posterior face of the bone, indicating less freedom of movement at the shoulder. The greater tuberosity is large and is separated by a shallow groove from the head, as in *Paramys* and *Ischyromys*. On the lateral surface there is a pronounced notch between the tuberosity and the head, which is only slightly indicated in Paramys or Neotoma but which is equally well developed in Ischyromys The deltoid crest has a broad outer surface, which seems to have risen to a uniform height for about 2 mm., more suggestive of conditions in cricetids than in paramyids or Ischyromys, and which is perhaps somewhat suggestive of Theridomys. Proximally the crest tapers gradually towards the greater tuberosity as in Paramys, but there appears to have been a more distinct deltoid process. Distally there is a considerably more abrupt termination of the process than in Paramys where it tapers gradually into the shaft. There appears to have been a considerable thickening of the top of the crest, only slightly suggested in Paramys. In all these respects, this form differs even more from Neoreomys (Scott, 1905, pl. 70) and Ischvromys than from Paramys. The ectepicondylar ridge is broken, but it appears to have formed a wide flange, curving down to the ectepicondyle as in Paramys. The capitulum is broken off, but the median half of the distal end is preserved. There is a deep supratrochlear fossa on the anterior face of the bone, just proximal of the condyle, perhaps even larger than in *Ischvromvs*. Although this bone is somewhat broken here, this fossa is unquestionably very deep and seems to have penetrated all the way through the bone, as in Sciamys, Neoreomys, Trechomys, and Theridomys. There is an entepicondylar foramen as in Trechomys and Theridomys, though it seems to have been quite small, as in Paramys, Ischyromys, and Sciamys. It is absent in Neoreomys.

At least parts of both ulnas are present in A.M.N.H. Nos. 29600 and 29601. The only complete one is the right ulna of No. 29601, though two of the others are nearly complete. Unfortunately all three of the more complete bones are so preserved as to show only the median side. The shaft tapers very little distally, even less than is shown in figure 5C, in which the bone is slightly twisted so as to expose its narrow face. The shaft is

slightly bent as in *Ischyromys*, but without the sigmoid curve as in Paramys. Distally the ulna makes up about a third of the carpal articulation, as in Paramys and Reithroparamys. There is no suggestion of the distal flaring of the ulna seen in Ischyromys. The general appearance of the bone is rather similar to that of *Neotoma*. The olecranon is large, and the top is expanded at its free end, curving up towards the humerus, increasing the leverage of the triceps. This feature has not been seen in any of the forms with which these specimens have been compared except in Ischyromys. There is a deep tricipital fossa, on the main part of the olecranon, as in *Neoreomys*. It is deeper than that in *Paramys* but not so rugose. The coronoid process slopes off fairly gently into the shaft, as in Paramys, presumably serving as the origin of the flexor digitorum sublimis. Just distad of the coronoid is a deep fossa with an overhanging ventral margin, marking the insertion of the brachialis, also very pronounced in Paramys and Ischvromvs. This fossa continues distally as a shallow groove running most of the length of the bone, whereas in Paramys it is quite short. In Ischyromys it runs about a third the length of the ulna. Distally there is no indication in any of the available material of a fossa for the pronatus quadratus, which seems to have been very strong in Paramys and Reithroparamys. This may be due to the positions of the bones as preserved in Platypittamys, but more probably indicates that this animal was beginning to be limited to fore-and-aft motion of the forearm. The styloid process is fairly large.

The shaft of the radius is somewhat more curved than is that of the ulna. As in *Reithroparamys* and *Ischyromys*, the radius is considerably larger distally than the ulna, being especially wide just proximad of the distal end, where there is a marked lateral expansion presumably fitting close against the ulna. The bicipital tuberosity is fairly prominent. The head seems to have been transversely elongate, as in *Ischyromys* and *Paramys*.

The manus is preserved on both sides of the holotype. In A.M.N.H. No. 29601, one manus is preserved showing the ventral surface, largely concealed by sesamoids, and the other is completely flattened and obscured by other bones. The manus is pentadactyl (fig. 5D), with the thumb considerably reduced in size but apparently still functional. The whole first digit is longer than metacarpal V, but shorter than metacarpals II, III, and IV. The third and fourth digits are the longest and are

about the same size, with the second and fifth shorter and subequal. This suggests artiodactylate trends and is probably a cursorial adaptation. It is very suggestive of the arrangement in *Chinchilla*, *Dolichotis*, and *Myocastor* and is a marked contrast to *Sciamys*, where, according to Scott (1905, p. 423), the second and third metacarpals are subequal and the fourth is shorter. The manus is about half the length of the pes as in *Paramys*, *Reithroparamys*, *Marmota*, and *Erethizon*.

The scapholunar is large, extending across the entire radial surface. It is convex proximally to fit the radius and is slightly concave distally. As in *Reithroparamys*, there is no suggestion of any separation into scaphoid and lunar. In this respect *Platypittamys* agrees with most rodents and is more advanced than *Paramys*, *Ischyrotomus*, or *Ctenodactylus*. At the median side there is what seems to be a very large and elongate radial sesamoid, as large as the pisiform would be expected to be, and apparently much larger than it was in this particular animal, since the pisiform has not been certainly identified.

The cuneiform is very much smaller than the scapholunar and seems to have been placed somewhat diagonally, with its lateral margin farther distad than the mesial margin, fitting against the styloid process of the ulna. In life it must have been in contact with the scapholunar. This bone resembles that of *Reithroparamys* in its general shape, but differs from that both of that genus and of *Paramys* and *Ischyrotomus* in being very much smaller.

There was a rather large centrale, triangular in shape, with its base fitting against the scapholunar. The trapezium is a fairly large bone, supporting the pollex. It is convex proximally, where it fits against the scapholunar. Probably in life there was only a small area of this bone visible, and the reconstruction of the manus has been made in this manner. It abutted against the broad mesial face of the trapezoid.

The trapezoid has the shape of a trapezium, its proximal and distal faces being essentially parallel. The mesial slope is nearly at right angles to this, fitting against the trapezium. Laterally the slope is much more oblique, running from the short distal face to the long proximal one and ending almost at the lateral margin of the scapholunar. Its surface exposure is much greater than is that of *Reithroparamys*.

The magnum is essentially square or diamond shaped, with one of the angles directed proximally, wedged between the trapezoid

and unciform, and nearly, but not quite, reaching the scapholunar, being separated from it by the centrale. The two distal facets of the bone articulate with the second and third metacarpals. Its relationships are about as in *Reithroparamys*, *Myocastor*, and *Chinchilla*.

The unciform shares with the scapholunar the position of largest bone in the manus. It is an irregularly shaped bone, concave proximally and convex distally when viewed from the dorsal surface, although the proximal surface itself is convex. A long process extends proximo-mesially and makes contact with the lateral corner of the scapholunar. The cuneiform fits against its proximal surface. The general shape and relationships of the unciform appear to be about as in *Reithroparamys*, *Myocastor*, and *Chinchilla*, and quite different from what is found in *Paramys* and *Ischyrotomus*, where it is more rectangular. In *Platypittamys*, however, the unciform is considerably larger than in *Reithroparamys*.

Metacarpal I is very short, being actually shorter than either of the phalanges. Although the digit is unknown in *Reithroparamys*, it seems to have been more slender in that form, apparently undergoing a different type of reduction. The ungual phalanx of the pollex is broad distally and appears to have borne a hoof-like claw. This digit appears to have been slightly divergent but certainly was not opposable. The other four metacarpals expand distally, having quite slender shafts. The fifth is somewhat divergent on the best-preserved hand, but this was probably not true in life, and the manus is restored with a greater parallelism of the digits than was the case in any of the paramyids. All the ungual phalanges appear to be somewhat broadened and to have carried hooflets rather than claws. This was also true of *Sciamys* (Scott, 1905, p. 424).

Parts of both pelves are preserved in the holotype, and part of the right pelvis in A.M.N.H. No. 29601. The pelvis is long and slender (fig. 6A), as in *Sciamys*, being much less massive than in *Neoreomys* (Scott, 1905, pl. 70) and showing essentially no similarities to that of *Ischyromys*. The ilium is definitely trihedral, with a prominent external crest which, as in *Neoreomys* and *Paramys*, is far down towards the ventral side of the bone, although it is not so low as in *Hystrix* and erethizontids. The superior gluteal fossa is considerably larger than the inferior and is a broad, gently basined surface. The tubercle is a large, oval

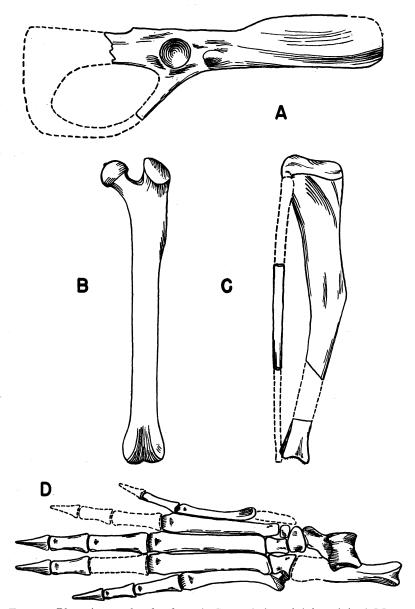


Fig. 6. Platypittamys brachyodon. A. Lateral view of right pelvis, A.M.N.H. No. 29600, with some additions from left pelvis. B. Anterior view of left femur, A.M.N.H. No. 29600. C. Mesial view of left tibia and fibula, A.M.N.H. No. 29600, with additions from right tibia. D. Dorsal view of left pes, A.M.N.H. No. 29601, with assistance from right pes and from A.M.N.H. No. 29602. Dotted outlines purely hypothetical. All \times 3.

prominence, slightly below the line of the posterior end of the gluteal crest, as in Paramys and Cavia, instead of being a continuation of it as in Neoreomys, Chinchilla, Myocastor, and Dasyprocta. The tubercle ends posteriorly in a rounded curve as in Cavia, Chinchilla, Dasyprocta, and Myocaster, not being continued posteriorly towards the acetabulum. In Paramys the tubercle grades into the anterior margin of the acetabulum as in erethizontids. The ligament of the rectus femoris had a broad origin over the entire surface of the tubercle as in Paramys. The ilium was attached with its long axis essentially parallel to the vertebral column, again as in Paramys. This, plus the length of the ilium, gave a strong anteroposterior component to the pull of the rectus femoris anticus and the tensor fasciae latae. notch marking the posterior end of the sacral articulation is well forward of the tubercle as in Cavia, Chinchilla, Myocastor, and Dasyprocta, instead of being just in front of it as in Paramys and Hystrix, or above it as in Neoreomys and erethizontids. This does not indicate a proportionately weaker articulation but rather results from the proportionately greater length of the ilium. ventral border of the acetabulum is concealed by the femur in both specimens, so that it may not be complete in this area. As far as is visible, however, it is complete. The main axis of the ilium is continued in the ischium, of which only the anterior part is preserved. There is a small but pronounced sciatic notch, which is completely absent in Neoreomys, Sciamys, Chinchilla, Myocastor, and Dasyprocta, but is present in Paramys, Cavia, Echimys, and the erethizontics. The anterior part of the pubis is preserved, sloping posteroventrad, whereas in Paramys there is little or no posterior slope. The anterior end of the obturator foramen is sharply rounded, like the small end of an egg. While the ilium is thus rather similar to that of *Paramys*, the posterior part of the pelvis differs from it in almost every respect. Unfortunately the pelvis of *Reithroparamys* is unknown. There are no very close similarities to the pelves of living hystricomorphs.

Both femora are preserved in the holotype, and the distal ends are present in A.M.N.H. No. 29601. They are, of course, flattened so that the width is considerably distorted, and it is impossible to prepare them so that all parts can be seen. Most of the bone, however, can be studied. The femur has an over-all length of about 26.5 mm., about 50 per cent longer than the humerus, and appears to have been essentially straight. The

greater trochanter extends slightly proximad of the head as in Reithroparamys, Paramys, and Ischyromys (fig. 6B). The head is at right angles to the neck as in paramyids and the Santacrucian hystricomorphs. The neck is at an angle of about 45° with the long axis of the bone, also as in paramyids. None of the available material shows the lesser trochanter or the trochanteric fossa. The femur appears to be of uniform width throughout, as is that of Reithroparamys, of Paramys, and of Ischyromys. The third trochanter may have been absent, but probably there was a very minute one, a notable distinction from Reithroparamys, where it is fairly large, or from *Paramys* and *Trechomys*, where it is both large and far down the shaft of the femur. In the small size of the third trochanter, *Platypittamys* anticipates *Eocardia*, Schistomys, Prodolichotis, and Sciamys of the Santacrucian (Scott, 1905), and Parapedetes (Stromer, 1926), where it is absent. Distally the two condyles appear to extend equally far, although this region is considerably damaged in all the available material. In the paramyids the medial condyle extends somewhat distad of the lateral. There is a deep patellar groove, and the patella is a narrow oval, like that of *Ischyromys* and *Paramys*.

Parts of the tibia and fibula are preserved from both sides of the holotype. They are all damaged distally, so that the exact length cannot be determined. The tibia, however, was at least 26 mm. long and probably a little longer. The tibia and fibula were separate throughout their entire length (fig. 6C) and appear to have been somewhat more divergent than in Sciamys (Scott, 1905, pl. 67, fig. 2) or *Neoreomys* (*ibid.*, pl. 70), and less so than in Titanotheriomys, resembling Paramys and Reithroparamys in this respect. There is no trace of the close appression of the two bones seen in *Sciamys*. The cnemial crest of the tibia was strong and forms a pronounced prominence about the middle of the shaft of the tibia. There seems to have been a slight mesial overhang of the crest. The posterior face of the tibia is arched. In all these respects the bone shows great similarities to that of Reithroparamys and of Titanotheriomys. The tibia of Paramys differs chiefly in that the cnemial crest is not pronounced and has no overhang. The distal end of the tibia does not seem to have been so deeply grooved as in Paramys, being more similar to that of Reithroparamys in this respect. This is, of course, related to the smaller size of the astragalar keels. The distal part of the fibula is round in cross section, and the proximal part is oval, about as in *Reithroparamys*. The bone seems to have been nearly straight, in contrast to the bowing of the tibia, again suggesting conditions in *Reithroparamys*. The head of the fibula does not seem to have been so expanded as in *Paramys*, *Reithroparamys*, and *Titanotheriomys*.

The pes is long and markedly compressed, with all the digits essentially parallel (fig. 6D). Like the manus, it seems to indicate a much greater amount of cursorial adaptation than is seen in the paramyids. As in the manus, there are some artiodactylate tendencies, with the axis of the foot passing between the third and fourth digits, which are of equal size. The second and fifth are also of about equal size, while the hallux is both shorter and more slender. The closest similarities to this foot shape that have been noted in Recent hystricomorphs are in *Chinchilla*. There are numerous similarities to the pes of *Parapedetes* (Stromer, 1926, pl. 42, fig. 11), except for the absence of the hallux in the latter, but they are probably in part retention of primitive features and in part similar adaptations. In many details the two are widely different, and there is no suggestion of close relationship.

The astragalus is preserved in all three specimens, but it is clearly shown only in A.M.N.H. No. 29602. The two keels are of nearly equal length, the lateral being only slightly longer than the mesial. They are aligned parallel to the long axis of the foot. In these respects the bone resembles that of Sciamys and of Lagostomus, Dolichotis, and Coendu among Recent hystricomorphs. It differs from the astragalus of Paramys, Reithroparamys, and Ischyromys, as well as from that of Neoreomys, Dasyprocta, Hystrix, Thryonomys, and many other hystricomorphs, in which the lateral keel is considerably longer than the mesial, and the axes of the keels are at an appreciable angle to the axis of the pes. In Cuniculus and Parapedetes the axes are parallel to the long axis of the foot, but the lateral keel is much longer than the mesial. As in Riethroparamys, the keels are distinctly lower than those of Paramys. The neck is inclined sharply mesiad, so that the center of the head is in line with the mesial keel as in Paramys, Reithroparamys, Dolichotis, Myocastor, and Coendu, in contradistinction to conditions in Sciamys and Parapedetes and many other hystricomorphs. The neck is fairly wide and, distally, expands mesiad. The navicular facet extends nearly straight across the width of the head but, when viewed from either the dorsal or ventral aspects, does not extend onto the median side of the bone as in

Sciamys. Unfortunately it is impossible to free the bone completely from the matrix, but it seems probable that the articulation was only distal. In this, Platybittamys differs markedly from Paramys and Reithroparamys, where the distal end of the astragalus is curved, with the facet extending the entire width, or from Neoreomys and Erethizon, where the articular surface continues onto the mesial side. There is no suggestion of the mesial sesamoids in this region that characterize the erethizontids. mesiad direction of the neck is, however, very similar to conditions in all of these genera and is quite different from its more anteroposterior direction in many Recent South American forms, such as Dasyprocta, Lagostomus, and Cuniculus. The plantar surface is more like conditions in Reithroparamys and Titanotheriomys than in any other forms with which it has been compared. ectal facet is elongate and, if projected onto a plane, would be a flattened hexagon, with long medial and lateral faces. hexagonal shape is rather different from that in Paramys. Reithroparamys, and Titanotheriomys, and is very distinct from the shape in *Erethizon*, where the facet is very broad and irregular. The facet is much less oblique than in Neoreomys or Paramys, resembling Reithroparamys and Erethizon in this respect. The ental facet appears to be an oval, elongate anteroposteriorly, as in Reithroparamys, Titanotheriomys, and Neoreomys, and not to broaden distally as in Paramys and, to a lesser extent, in It is impossible to be certain of this, however, owing to the impossibility of freeing the bone from the matrix. groove between the two facets is rather similar to that in Reithroparamys and Titanotheriomys and is much deeper than in Marmota. It is, however, very much shallower than in Erethizon, and there is no trace of an overhang of the groove by the facets as in the latter genus. It appears to be narrower than in Neoreomys. In general arrangement the groove is not too distinct from conditions in *Paramys*, but it lacks the numerous nutritive foramina found in the groove of the latter genus, which are also present in Erethizon. It seems possible that these may be associated with the larger size of the two latter genera. There do not appear to be any particular resemblances between the astragalus of Platypittamys and of Eocardia (Scott, 1905, p. 469). As indicated above, the astragalus of Platypittamys shows some general similarities to that of various of the later South American hystricomorphs, though no very striking similarities to any particular members of the group. There are quite notable differences from the astragali of most of the Santacrucian genera, particularly of *Steiromys*, *Eocardia*, and *Sciamys*.

One calcaneum is preserved in each of A.M.N.H. Nos. 29601 The former is lying on its side and is somewhat The latter is lying with its plantar surface exposed, and the upper surface is not available for study. The tuber is fairly long, quite slender, and of uniform width throughout. It is expanded slightly, dorsoventrally, at its posterior end. groove for the tendon of Achilles is not very deep or bounded by In these respects the bone is quite similar to that in Reithroparamys and Paramys, being perhaps somewhat more like the latter genus. It is also quite similar to that of Sciamys (Scott, 1905, p. 424, pl. 67, fig. 3). The process for the lateral ligament was much smaller than in Paramys, Ischyromys, or Aplodontia, being quite similar to the condition in Reithroparamys and Parapedetes. The exact situation in Platypittamys is not entirely clear, since there has been some breakage in this region in A.M.N.H. No. 29602. The lateral side of the distal end of the bone extends quite far forward, on the plantar surface at least, so that the cuboidal articulation, from this aspect, is diagonal. places the ental facet far posteriad. The dorsal surface apparently does not show this displacement, to judge from the character of the cuboid. The calcaneum extends distally about to the middle of the navicular, forming a calcaneo-navicular contact as in Cupidinimus (Wood, 1935, p. 227, fig. 153), instead of the calcaneum and astragalus having their distal ends about even, as in Paramys and Reithroparamys. Scott's description of conditions in *Neoreomys* (1905, p. 398) seems guite similar to the present form, whereas *Eocardia* (*ibid.*, p. 469) would appear to be very different. There is absolutely no similarity to the calcaneum of erethizontids, Steiromys (ibid., pl. 66, fig. 9) and Erethizon being equally divergent from the present form. Sciamys shows considerable similarity to *Platybittamys*. The closest similarity that has been noted, however, is with the Bridgerian Reithroparamys.

The cuboid is well preserved only in A.M.N.H. No. 29602, where it is seen from the dorsal aspect. It is narrower distally than proximally and has the proximal face inclined to the long axis of the foot. Essentially the same condition is found in Paramys delicatus, Ischyromys, Dasyprocta, Cuniculus, and Chinchilla. In Reithroparamys, as in Aplodontia, Dolichotis, Lagosto-

mus, Cavia, Myocastor, and Pedetes, the bone is rectangular, with the mesial and lateral faces subparallel. In all other forms with which it has been compared, the bone is trapezoidal or, in the Erethizontidae, essentially triangular. There is only a single proximal facet, that for the calcaneum. As far as could be told there is no naviculo-cuboid facet, although the two bones are very close together, and one may have been present. In the relationships of these bones, Platypittamys differs from Paramys delicatus and Reithroparamys as well as from Sciamys, Eocardia, Hystrix, Coendu, Steiromys, and Chinchilla, where there is neither an astragalo-cuboid nor a naviculo-calcaneal articulation, and from Ischyromys, where there is an astragalar-cuboidal articulation. It resembles such forms as Myocastor, Cuniculus, Dasyprocta, Cavia, and Parapedetes, where there is a marked naviculo-calcaneal articulation. Dolichotis and Lagostomus show a proportionate increase in the length of the calcaneum, the latter having a calcaneo-ectocuneiform articulation (Tullberg, 1899, pl. 35, fig. 6). The calcaneal facet slopes proximoventrad, forming an angle of but little more than 45° with the dorsal face of the bone, instead of being nearly ventrical as in Reithroparamys, Paramys, and Erethizon. There is a strong ventrolateral process as in Paramys robustus, but it is somewhat larger in the present form. It is more lateral than in Reithroparamys, where it is barely visible from the dorsum. The cuboid appears to be distinct from that of all forms with which it has been compared. It is perhaps most nearly like that of *Paramys delicatus*, but seems to have advanced, in a direction of its own, some distance from such a stage.

The navicular has about half the anteroposterior diameter of the cuboid and is thus appreciably larger proportionately than in Reithroparamys, Paramys, and most hystricomorphs, and more nearly resembles in this respect that of Ischyromys and the erethizontids. In the latter group, at least, this is due to the marked reduction of the cuboid, rather than to an enlargement of the navicular, as seems to have been the case in Platypittamys. There is no trace of the dorsomedian process which characterizes Reithroparamys and is suggested in Paramys. As in Reithroparamys, the bone does not widen towards the plantar surface. The lateral halves of the proximal and distal edges are essentially parallel, when viewed from above, while the bone tapers mesially from its center. In Paramys, the navicular has a nearly uniform

anteroposterior diameter, while in *Reithroparamys* its dorsal surface is constricted in the middle of the bone, so that neither of these forms resembles the conditions in *Platypittamys*.

The ectocuneiform is a large quadrate bone with its greatest diameter anteroposterior. In this it resembles that of Reithroparamys and of Paramys and is also rather similar to that of Cuniculus, Dasyprocta, Chinchilla, Dolichotis, Sciamys, and Parapedetes. It shows no particular resemblances to the bone in erithizontids, Hystrix, Lagostomus, or Cavia.

The mesocuneiform is also quadrate in dorsal aspect, but it is only about half the width and two-fifths the length of the ecto-cuneiform. Its greatest width is transverse. It is proportionately considerably smaller than in *Paramys*. This bone is not known in *Reithroparamys*. It appears closest to that of *Cuniculus* among living hystricomorphs.

The ectocuneiform is not preserved in any of the available material, but from the position of metatarsal I of A.M.N.H. No. 29601 it seems clear that it was considerably elongate, anteroposteriorly, extending quite far down the side of the second metatarsal. A similar elongation is seen in *Myocastor* and various hystricomorphs in which the hallux is vestigial. In *Paramys*, the ectocuneiform is long, but nowhere near so long as in *Platypittamys*.

There are five toes present, which are closely appressed, forming a long, narrow foot. Metatarsals III and IV are of essentially the same length and are equally massive. Metatarsal II is about the same length and thickness, but it extends farther proximad, so that its distal end does not reach to the ends of the other two metatarsals, about as in Sciamys. Metatarsal V is slightly more slender than the others and is slightly shorter than metatarsal It also extends distad in a long, olecranon-like process, well past the middle of the cuboid, where it either articulates with, or comes very close to, the lateral process of the cuboid. also true of Sciamys. The first metatarsal is buried on A.M.N.H. No. 29602 beneath the others. But on A.M.N.H. No. 29601 it may be seen to be a much shorter bone than any of the other metatarsals, being only about two-thirds their length, and much more slender, again suggesting the conditions in Sciamys. These characteristics of the metatarsals are very similar to the situation in Paramys, and are quite different from what is seen in Reithroparamys.

The general shape of the foot, with long, narrow, closely appressed metatarsals, all extending nearly the same distance distad and with no suggestions of proximal divergence, is suggestive of such hystricomorphs as *Dasyprocta*, *Dolichotis*, *Chinchilla*, and *Lagostomus*, although there has been no digital reduction as in these genera. The bones are much more elongate than in *Neoreomys* or *Eocardia*. The foot as a whole has no resemblance to that of *Sciamys*. There is no suggestion, either in *Paramys* or in *Reithroparamys*, of such an adaptation.

The digits are long and slender and are tipped with heavy, hoof-like claws, suggestive of those of *Sciamys*, *Myocastor*, *Cuniculus*, and *Cavia*. They are not so compressed as in *Paramys* and *Reithroparamys*. They do not appear to be so heavy as in *Steiromys* and *Coendu*.

Although it is impossible to present absolutely accurate limb ratios, they can be approximated. The hind limbs are roughly 50 per cent longer than the front, though, since no tibia is complete, it is impossible to be certain. The intermembral index, as calculated, comes to 67.6 or less. This is very similar to that in Sciurus and Paramys and is also quite close to the scampering heteromyids, Perognathus, Liomys, and Heteromys (Wood, 1935, table 5). The ratios computed from Scott's restorations of Neoreomys (Scott, 1905, pl. 70) and Eocardia (ibid., pl. 71) are 71.6 and 67.9, respectively, which do not differ significantly from the other forms. These two Santacrucian genera, however, differ from Platypittamys, and from the others listed, in that the radius is considerably shorter than the humerus. This same condition holds in *Ischyromys* (Wood, 1937, pl. 25, figs. 3, 4), where, however, the intermembral index is considerably higher. In Paramys, also this condition of a short radius holds true. The humerus of *Reithroparamys* is not known, so its ratio cannot be determined. These ratios are considerably lower than those of Dolichotis (87.5) and Paradolichotis (81.7) based on measurements given by Kraglievich (1930); or Hydrochoerus (78.3) and Prothydrochoerus (73.1) as given by Kraglievich (1940). The front limbs seem to have been more nearly equal in length to the hind limbs than in Sciamys (Scott, 1905, p. 423).

On the basis of the intermembral index (table 5), which has proved to be a useful guide to the habits of rodents, *Platypittamys* is close to *Eocardia*, *Neoreomys*, *Perognathus*, *Heteromys*, *Paramys*, and *Sciurus*. The ricochetal forms (*Dipodomys*) have a greatly

reduced intermembral index, and the fossorial (Cynomys, Ischyromys?) and cursorial (Dolichotis, Paradolichotis, Hydrochoerus) forms show an increased one. The intersegmental index for the hind limb is close to that of Paramys, Reithroparamys, Neoreomys, Eocardia, and Marmota. For the front limb, the scampering heteromyids Perognathus, Heteromys, and Liomys, and Ondatra and Prothydrochoerus are the closest. This does not lead to a very clear picture of the function of the limbs in Platypittamys.

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF LIMB BONES

	Humerus	Radius	Femur	Tibia
Platypittamys	18.2	17.5	26.5	26.8
Neoreomys (after Scott, 1905)	38.5	29.5	48.5	46.5
Eocardia (after Scott, 1905)	42	32	53	56
Dolichotis (av. of 3)	115	146	131	166
Paradolichotis	71	75	77	102
Hydrochoerus	250	269	303	360
Prothydrochoerus	171	127	209	196
Dipodomys ordii (after Wood, 1935,				
table 3)	15.2	17.0	28.5	38.5

TABLE 4
INTERSEGMENTAL INDICES

	Humerus/ Radius	Femur/ Tibia
Platypittamys	1.04	0.99
Neoreomys	1.30	1.04
Eocardia	1.31	0.95
Dolichotis	0.79	0.79
Paradolichotis	0.95	0.76
Hydrochoerus	0.93	0.84
Prothydrochoerus	1.35	1.07
Ischyromys	1.32	1.13
Heteromys	1.10	0.88
Liomys	0.97	0.88
Perognathus flavus	0.97	0.84
Paramys delicatus	1.29	1.04
Marmota	0.85	1.00
Ondatra	0.98	0.72
Reithroparamys		0.94

TABLE 5
INTERMEMBRAL INDEX $\frac{R + H}{100}$

Platypittamys	67.6	Dipodomys	44.4-50.1
Neoreomys	71.6	Heteromys	64.0
Eocardia	67.9	Paramys	68.4
Dolichotis	87.5	Sciurus	68.5
Paradolichotis	81.7	Ischyromys	78.6
Hydrochoerus	78.3	A p lodontia	75.3
Prothydrochoerus	73.1	Cynomys	80.8
Perognathus	64.5 - 78.0		



Fig. 7. Theridomys aquatilis. A. LP^4 – M^3 , Brit. Mus. No. 27756b. Upper Stampian, Cournon, Auvergne. B. LP_4 – M_3 , Brit. Mus. No. 27756a. Upper Stampian, Cournon, Auvergne. Both \times 5.

In view of these rather diverse suggestions, it seems probable that *Platypittamys* was not well adapted for saltatorial, amphibious, climbing, or burrowing locomotion, and that, in view of the parallelism of the digits, it was probably a scampering ground dweller, passing through the initial modifications for a cursorial adaptation but still retaining a fairly strong posterior dorsal musculature, used in sitting up on its haunches, perhaps to feed.

RELATIONSHIPS OF PLATYPITTAMYS TO OTHER RODENTS

There are three main problems in connection with the relationships of *Platypittamys*: (1) its relationship to the other South American hystricomorphs; (2) what forms seem most likely to have been its ancestors; and (3) what its relationship is, if any, to some of the other rodents that have been suggested as having relationships with the South American hystricomorphs. To a

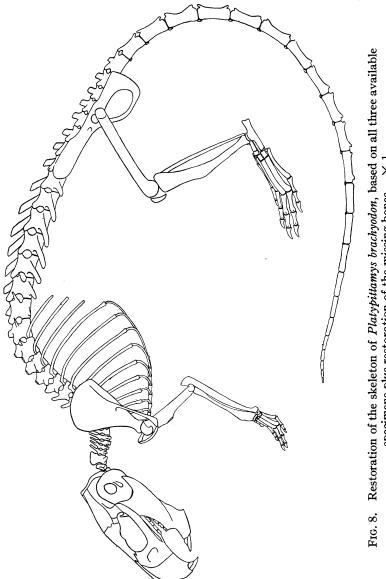


Fig. 8. Restoration of the skeleton of *Platypittamys brachyodon*, based on all three available specimens plus restoration of the missing bones. \times 1.

considerable extent these points have been considered in connection with the morphological description, but it would be worth while to pull all the loose strings together and summarize the relationships here.

It seems clear that *Platypittamys* is a member of the Acaremyidae and reasonably closely related to the other members of the family. Even if it were not too late in time, it does not appear that it would be possible for it to have been the direct ancestor of *Sciamys* and *Acaremys*, because of various points, particularly in the structure of the limbs, that suggest that *Platypittamys* was developing locomotor habits different from those of the other members of the family. Its dentition shows, however, that it is close to being the structural ancestor of the other members of the family in this respect. *Platypittamys* appears to be the most primitive Deseadan rodent known, which may indicate that the Scarritt Pocket local fauna is slightly older than the typical Deseadan fauna.

As was indicated earlier, the acaremyids and the erethizontids agree in possessing a tooth pattern that seems to be close to the primitive pattern for the South American hystricomorphs, and one from which the dental patterns of all the other forms could have been derived. In all the other characteristics studied. Platybittamys shows no resemblance to the conditions in the erethizontids, except for the fact that they are both hystricomorphs, and it seems certain that the acaremyids could be neither ancestral to, nor descended from, the erethizontids. Although nothing is known of the Deseado erethizontids other than their teeth, by the Santacrucian this family had already acquired essentially its modern locomotor adaptations, and very possibly they had already started in this direction by the Deseado. On the other hand, there does not seem to be any very valid reason why the Acaremyidae could not have been ancestral to the Chinchilloidea, Cavioidea, and Octodontoidea (excepting the African families that Simpson included in this superfamily). locomotor adaptations, Platypittamys seems to foreshadow a considerable number of the later South American groups, and could be either an actual ancestor to some of them or merely a short. sterile offshoot of the common ancestral stock, which had begun to develop cursorial specializations.

The closest structural similarities of *Platypittamys*, among the later Hystricomorpha, appear to be with *Chinchilla*, but there are

many points of similarity to other forms, and *Platypittamys* does not show enough resemblances to the chinchillids to justify its being grouped with them. If a superfamilial allocation for the acaremyids is required, however, it would probably be best to place them in the Chinchilloidea, although it is felt that this would obscure their relationships to other groups.

The two sources that have been commonly suggested as the origin of the hystricomorphs are the paramyids and sciuravids on the one hand and the theridomyids on the other. The paramyids are known from Europe and North America, from the uppermost Paleocene to the Oligocene. The sciuravids are known only from the Eocene of North America, and the theridomyids (excluding those forms that are frequently but almost certainly incorrectly referred to this family) only from the Upper Eocene and Oligocene of Europe. The temporal and geographic relationships would make it almost impossible that the theridomyids could be ancestral to *Platypittamys*, but the pattern of the teeth clinches the argument, by making it structurally impossible as The complete absence of the mesoloph and mesolophid in Platypittamys in particular and the South American hystricomorphs in general would seem to indicate that it cannot be descended from the theridomyids, where at least the former of these structures is well developed. This point of view is strengthened by the structure of the premolars and by the other comparisons that have been made. As has been shown, there are numerous similarities to various paramyids and sciuravids, particularly to Reithroparamys. If skeletal material of sciuravids were available. there could well be close similarities to some members of that family. In spite of this, there are important differences from all known members of both the Paramvidae and Sciuravidae. Many of these differences seem to indicate merely that the South American hystricomorphs had already become South American hystricomorphs by the Deseadan, and hence would be no insurmountable obstacle to their derivation from the paramyids or sciuravids. However, the structure of P_4^4 does not fit with their derivation from any known sciuravid or paramyid, unless there has been a marked simplification of the tooth pattern, followed by a respecialization, which does not seem reasonable. However, Eocene sciuravids are known from a very limited geographic area (Wyoming, northern Utah, and Colorado) and Eocene paramyids only from France, Wyoming, California, Utah, Colorado,

New Mexico, and British Columbia. It seems axiomatic that there must have been a considerable number of other forms of both of these families, living in other regions, and that they must have differed structurally from the forms that we know. ancestral South American hystricomorphs must have reached that continent, probably over a chain of islands, either along the line of Central America or of the West Indies, and must therefore have been derived from forms living not in Wyoming but in Mexico or the southeastern United States. Therefore, while it is impossible to derive Platypittamys from any known paramyid or sciuravid, it seems certain that its middle Eocene ancestors would have been forms which, when they are discovered, will fit either into the Paramyidae or the Sciuravidae. If the skeletons of members of the latter family were known, it seems certain that we could now tell to which family such an ancestor would have belonged.

There remains the problem of the relationships of the Acaremyidae to various other forms. The similarities to the Ischyromyidae, while certainly real, seem to be due merely to the fact that they are both early Oligocene groups, both descended from Eocene Paramyidae or Sciuravidae, and that neither has diverged to any very great extent from the ancestral conditions. *Pareumys*, in particular, shows certain similarities to *Platypittamys*, which may indicate that both the acaremyids and the ischyromyids came from the same group, perhaps of sciuravids (Burke, 1935, p. 9). *Phiomys* and its relatives show no more similarities to *Platypittamys* than do most other small, brachyodont, relatively unspecialized rodents. Until they become known from better material than at present, it may be impossible to determine their correct relationships.

Several other Old World families might be considered in this connection—the Hystricidae, Bathyergidae, Pedetidae, Thryonomyidae, and Petromyidae. As pointed out above, there are certain similarities in the foot and leg between *Platypittamys* and *Parapedetes*. In most of the rest of the skeleton, however, there are no suggestions of relationships. As far as can be told with the present lack of knowledge of the ancestry of the pedetids, there is no basis for suggesting relationships between the pedetids and the acaremyids.

The bathyergids, when first known in the lower Miocene, have already lost their premolars, so that they obviously cannot be

ancestral to the South American forms. As far as can be told from their morphology, they are very different throughout. Only one fossil form certainly referable to the Thryonomyidae is known, and the Petromyidae are unknown as fossils. Any interpretations of the relationships of these families must therefore be based on the Recent forms. These do not, however, show any very significant relationships to the acaremyids. More fossil hystricids are known, being represented in Europe as far back as the Oligocene. The published figures, however, do not seem adequate to permit an accurate interpretation of the tooth anatomy. There certainly seems to be no particular relationship between the hystricids and the acaremyids.

At present it does not seem possible to prove that none of these Old World forms is related to the South American ones, although for paleogeographic reasons any such relationship seems essentially impossible, and it is equally impossible to establish any particular relationship with the South American forms that would fit with what is known of rodent paleontology. It would seem that the conclusion that there is no special relationship between the South American and the Old World hystricomorphs is inescapable, the only connection between the two groups being that of common descent from paramyids or sciuravids, which would presumably be true for all the other rodents as well. That is, it would appear that it will shortly be necessary to revise the classification of rodents thoroughly in order to bring the grouping of families closer to what seems to be the true phylogenetic relationships within the order. As suggested by Simpson (1945, p. 210), it will probably be necessary to separate the hystricomorphs into three distinct groups, but it does not appear advisable to do this until it can be combined with a review of the rest of the order. This would involve an extended series of studies. some of which are already under way.

If the classification needs revision, it would be worth while to look into the matter of the basis of the present arrangement. Fundamentally, most classifications of the order are based on the structure of the masseter muscle and its relationships to the infraorbital foramen. In general, authors have considered, either tacitly or explicitly, that each of the various zygomasseteric struc-

¹ Friant (1935) has figured unworn teeth of *Hystrix* and *Atherura*. These show a crown pattern dominated by a confusion of tubercles. There are, however, clearly five crests in both the upper and the lower molars.

tures was acquired only once during the course of rodent evolution, and therefore that each type of zygomasseteric pattern represents a natural subdivision of the order. In spite of the well-known danger in basing a classification on a single character, this was considered justifiable because such structures were thought too complex to have been likely to have arisen on several different occasions. Up to the present time, so little is known of rodent phylogeny that it has been impossible either to prove or to disprove this assumption. In fact, with the exception of one family in which the zygomasseteric region has remained in its primitive condition (the Aplodontidae), there are no modern families that can be shown to have been derived from any specific ancestral families outside the limits of their own superfamilies. not meant to imply that the Paramyidae and Sciuravidae do not probably represent the Eocene or Paleocene source of most of the modern rodents, but merely that, until the transitional stages are found and studied, this presumed fact cannot be held to be demonstrated. To cite an analogous case, the situation is rather similar to what we would find in regard to carnivore phylogeny if the Miacidae were unknown.

Changes will probably have to be introduced into the concept of the uniqueness of each type of zygomasseteric variant. The earliest (and hence, presumably, the most primitive) known rodents all had small masseters, limited to the ventral surface of the zygoma. They also all possessed rather large, circular, infraorbital foramina, with no relationship to the masseter. Such are found in all the typically Eocene rodents, particularly in the Paramyidae and Sciuravidae, and in such later forms as the Ischyromyidae, Mylagaulidae, and Aplodontidae—that is, in the families that have been grouped elsewhere (Wood, 1937, 1947) as the Suborder Protrogomorpha. Incidentally, the use of this group as a fourth suborder of rodents makes the same implicit assumption of the uniqueness of each variant as do the other classifications.

Platypittamys shows a marked increase in the size of the infraorbital foramen, apparently without any corresponding enlargement of the masseter. Such an enlargement of the foramen should be, genetically, a simpler change to bring about than the enlargement of the masseter. It might well have developed independently in a number of distinct lines of rodents. It also seems probable that, once the enlargement of the foramen had occurred, an expansion of the masseter through such an opening could develop with great rapidity. On the other hand, the infraorbital foramen of the protrogomorphs is sufficiently large so that the masseter could spread through it without any previous increase in the size of the foramen. The fact that the infraorbital foramen is considerably larger in the South American hystricomorphs than in the Hystricidae may indicate a difference in the manner of development of the zygomasseteric structures in these two groups.

Initially, the rodents became separated from other mammals by the development of chisel-shaped incisors, used in gnawing. This requires a different usage of the jaw muscles from other types of chewing, and a number of modifications of the muscles, skull, and jaws took place. By the Eocene, these changes had already occurred, and the rodents became a successful and diversified group. However, the main muscle used by these forms was the temporalis, which would serve to close the jaw or to pull it backward. The masseter was much weaker and, although it would serve to pull the lower jaw forward, must have permitted only a lesser efficiency of gnawing and perhaps resulted in the limitation of the diet to relatively soft foods.

It would seem that in the Eocene the rodents had reached an evolutionary plateau, based on the gnawing of relatively soft materials, and that they underwent a wide adaptive radiation at This is borne out by the fact that the Eocene rodents had not developed hypsodont cheek teeth. Since the number of ecologic niches available to the rodents would be limited, and since it seems probable that they were very much more abundant than the existing collections would indicate, there must have been severe competition among the rodents, which would have developed a strong positive selective value for those mutations that caused an increase in the efficiency of the gnawing mechanism by an increase in the size of the masseter. This would have permitted the gnawing of a wider variety of harder foods, which would lead to the subsequent development of hypsodonty in the cheek teeth of many groups. All present information points towards the rather sudden development, near the close of the Eocene, and independently in a large number of separate groups of rodents, of modifications of the skull and jaws correlated with an increase in the size of the masseter. These changes do not seem to have been limited to any one area but appear to have occurred at least throughout the northern land mass, and may have developed only after the appropriate evolution of certain types of potential food plants.

At any rate, if the masseter of a paramyid or sciuravid were to increase in size, there would be only three ways in which it could enlarge its area of origin without interfering with the eyes: (1) an increase in the size of the zygoma; (2) expansion up the front of the zygoma, onto the face; (3) expansion up the inside of the zygoma, and eventually through the infraorbital foramen onto the side of the snout.

After such expansions took place, there undoubtedly followed other modifications of the infraorbital foramen and of the zygoma. The first of these three types of modifications has occurred in the Castoridae, in Cuniculus, and in other forms to a lesser extent. It is not known to have developed without one of the other types of modifications as well. The second type is the "sciuromorph" condition, found also in Titanotheriomys, and the third is the "hystricomorph" type. The "myomorphs" combine the second and third types. But, as has been pointed out, we are unable to show that any one of these suborders represents a natural group descended from a common ancestral stock. The "sciuromorph" zygomasseteric type is found in the Sciuridae, which possess many characteristics suggestive of direct derivation from paramyids; in Titanotheriomys, which as an ischyromyid is also derived from the paramyids or sciuravids but which cannot be closely related to the Sciuridae; in the Castoroidea, which show very few other characters suggesting relationships to the Sciuridae; and in the Geomyoidea, which appear in most respects to have more to do with the "Myomorpha" than with the "Sciuromorpha." As has already been indicated, it seems very probable that the "hystricomorph" construction arose independently two or more times. The inclusion of the Dipodoidea and perhaps of the Gliroidea in the "Myomorpha," as Simpson pointed out (1945, p. 205), is also open to some question.

If, as seems logical, the zygomasseteric structures have originated as has been suggested, there does not appear to be any reason why similar mutations should not have been selected in a similar manner by similar environmental conditions in distantly related forms, in different parts of the world. If this is the case, a classification based on such characters would prove to be unnatural, and the whole of rodent subordinal classification would have to be restudied. This, of course, would require extensive

investigations of a large number of groups entirely beyond the scope of the present work.

If this interpretation of the evolutionary changes involving the masseter and the infraorbital foramen is correct, and it seems increasingly probable that it is, it will be necessary to revise completely our present concepts of the superfamilial or subordinal relationships of the rodents. Such a revision could solve many of the paleogeographic problems presented by our present knowledge of rodent classification and distribution. When such a revision is made, it might result in bringing the Sciuridae and the Paramyidae close together; uniting the Cricetidae, Muridae, Eomyidae, and perhaps the geomyoids; separating the Castoroidea from all other "sciuromorphs"; and presenting an arrangement of the "Hystricomorpha" that would fit the Tertiary isolation of South America from the rest of the world.

CONCLUSIONS

In summary, it seems clear that *Platypittamys* represents the most primitive South American rodent known up to the present time. While it cannot be ancestral to all the other South American forms, because it is too late in time, it suggests very strongly that the family to which it belongs, the Acaremyidae, is structurally ancestral to all the South American hystricomorphs except the Erethizontidae, which appear to have diverged early from the other forms. Platypittamys had already begun to develop cursorial adaptations, although it was still primarily a scampering form. The masseter muscle apparently had not yet invaded the infraorbital foramen, although the foramen had enlarged considerably over the conditions found in the primitive rodents. The cheek teeth of *Platypittamys*, while more primitive than those of any other South American hystricomorph in the lowness of their crowns and the lack of any accessory complications, show the basic pattern from which all the later forms could have been derived, although the structure of the premolars suggests that this genus is on a definite sideline.

Platypittamys apparently is a descendant of the North American Eocene Paramyidae or Sciuravidae, although it cannot be a descendant of any form known as yet. Reithroparamys apparently is the most closely related form. There are no indications of relationships between Platypittamys and any Old World forms, particularly none with the Theridomyidae.

On the basis of this and other considerations, it is suggested that the principal types of zygomasseteric structure, which have served as the basis for the separation of the specialized rodents into three suborders, the Sciuromorpha, Myomorpha, and Hystricomorpha, all derived from a more primitive group, the Protrogomorpha, may not represent single derivations but may have developed independently several times, in which case a thorough revision of rodent classification will be necessary.

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