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PROTOPTYCHUS, A HYSTRICOMORPHOUS RODENT FROM THE LATE EOCENE OF NORTH AMERICA

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ABSTRACT. The North American late Eocene *Protoptychus* Scott possesses an enlarged infraorbital foramen, a depression on the side of the snout anterior to this foramen for the origin of the anterior part of the middle masseter, tetralophate P^4-M^3 , an enlarged incisive foramen, a deep pterygoid fossa, and apparently no stapedia foramen or carotid canal. These characters also occur in the Caviomorpha. With regard to the zygomatic structure and acquisition of an essentially molariform P^4 , *Protoptychus* is more advanced than both its possible North American ancestor, which may be either a paramyid or *Mysops*, and *Platypittamys*, the most primitive Deseadan (Oligocene) caviomorph. The Protoptychidae, on present evidence, cannot be related closely to any rodents other than these. Pending further knowledge, the family is retained in the Protrogomorpha, but the possibility exists that it may be a specialized offshoot from the North American caviomorph ancestry.

INTRODUCTION

In the course of studying the cranial foramina of North American protrogomorphous and sciurumorphous rodents, I examined the type skull of *Protoptychus* (Princeton University 11235) and a second, much damaged facial region (PU 11230). I was immediately struck by features that set this form completely apart from all others I had at hand. These were the unusual shape and great posterior extent of the incisive foramen, the large size of the infraorbital foramen, the flatness of the sides

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of the snout, and the depression of an area on the snout anterior and extending somewhat dorsal to the infraorbital foramen. I was led, finally, to conclude that *Protoptychus* is a primitive hystricomorphous rodent possibly allied to the ancestry of the South American Caviomorpha. The lower jaw is present in specimens that I have not seen which belong to the Field Museum of Natural History; Turnbull (personal communication) is in the process of preparing these for description.

TAXONOMIC HISTORY OF *Protoptychus*

The monotypic genus *Protoptychus* has had a checkered history in the literature of rodent taxonomy. Scott, in describing the skull of *Protoptychus hatcheri* from the Uinta deposits of Utah, stated: "That *Protoptychus* is an ancestral form of the *Dipodidae* seems abundantly clear." "It is not improbable that the *Heteromyidae* were derived from some form related to *Protoptychus*, though not from that genus itself" (1895: 280, 286). Matthew (1910: 68) followed Scott in associating the genus with the *Dipodidae*. Schlosser (1911: 427) created the subfamily *Protoptychinae* as one of two divisions of the family he termed *Geomyoidea*. Miller and Gidley (1918: 443) placed the subfamily back in the *Dipodidae*. Wood (1935: 239-240) stated that the tooth structure did not indicate close relationship to the *Geomyoidea*, and he noted that Schaub's studies on the jumping mice and dipodids eliminated them also as relatives of *Protoptychus*. He suggested that, instead, ". . . *Protoptychus* may represent an aberrant and sterile offshoot of the *Ischyromyidae*." Wood (1937: 261) formally raised the taxon to familial rank, *Protoptychidae*, as a division of the *Ischyromyoidea*. Simpson (1945: 78) and Wilson (1949: 99-100) followed Wood's familial designation and placement of the genus. A diagnosis of the family was published by Wood in 1955 (p. 171).

DENTITION

Figure 1, a and b

In most respects Scott's description of *Protoptychus hatcheri* (1895) is accurate, but there are a few points that require reconsideration. He failed to notice the presence of a minute, peglike third premolar, and the revised dental formula (as noted

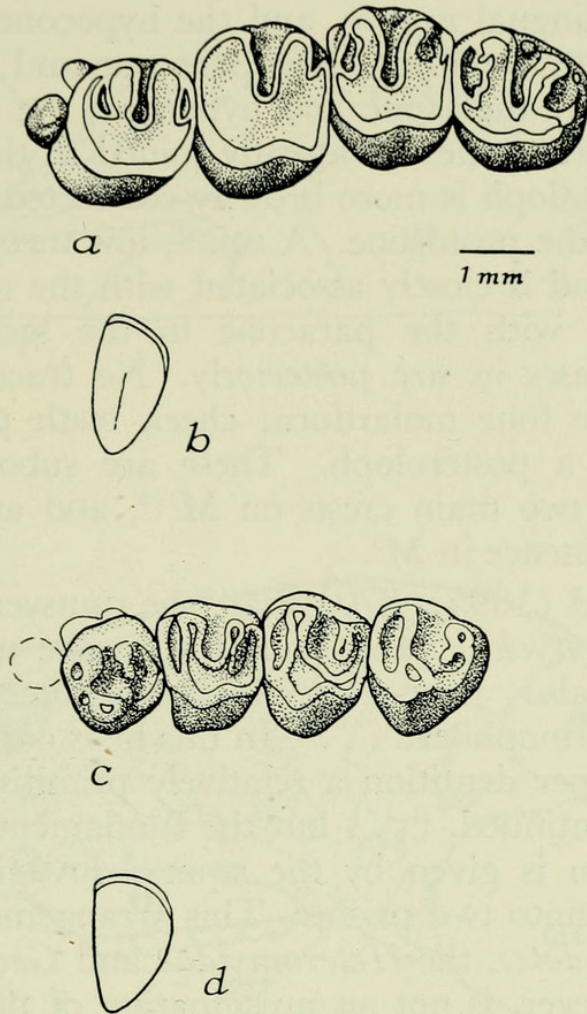


Figure 1. Dentition of *Protoptychus hatcheri* (PU 11235): a. left cheek teeth, view perpendicular to wear surface; b. left incisor, cross section. Dentition of *Mysops parvus* (USNM 18043): c. left cheek teeth, view perpendicular to wear surface; d. left incisor, cross section.

by Wilson, 1937: 450) is thus $I^1 C^0 P^2 M^3$. P^4-M^3 are brachyodont and notably higher crowned lingually than labially; although quite worn, they are clearly four-crested (Fig. 1a). The most conspicuous feature of the crown is a mesoflexus, which is broadest at the labial side and ends, at this stage of wear, near the middle of the tooth. The crowns of M^{1-3} are grooved in the middle of the lingual side, the groove fading away well before reaching the base of the enamel; P^4 possesses only a vague suggestion of this groove.

Although the four molariform cheek teeth are lophate, the cusps are still readily compared with those in paramyid teeth as figured by Wood (1962: 8, fig. 1A). On the labial side the paracone and metacone flank the mesoflexus. The protocone is

anterior to the lingual groove, and the hypocone, posterior; the crown is quadrate in outline. The paracone and protocone form the protoloph; the metacone and hypocone, the metaloph. The hypocone and protocone are already joined in the slightly worn M^3 , and the metaloph is more broadly connected with the hypocone than with the protocone. A small, low mesostyle is present on the molars and is closely associated with the metacone in the first molar and with the paracone in the second and third molars; it increases in size posteriorly. No trace of it is to be seen in P^4 . The four molariform cheek teeth possess both an anteroloph and a posteroloph. These are subordinate in importance to the two main crests on M^{1-2} , and are nearly equal to them in prominence in M^3 .

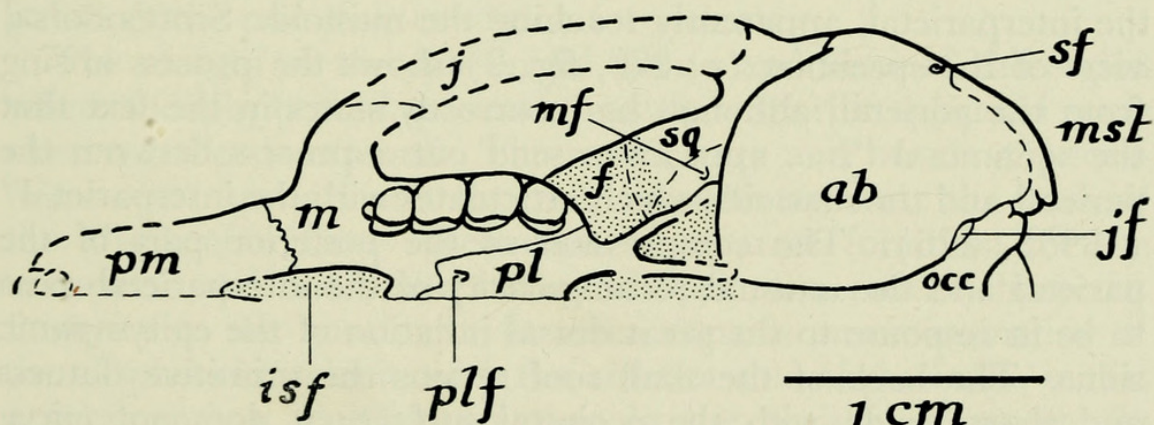
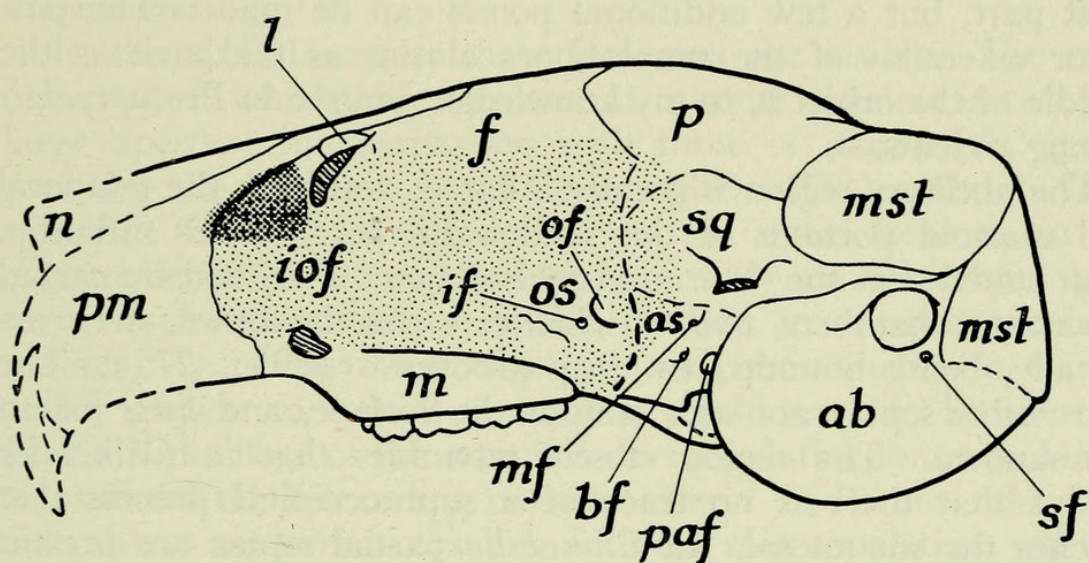
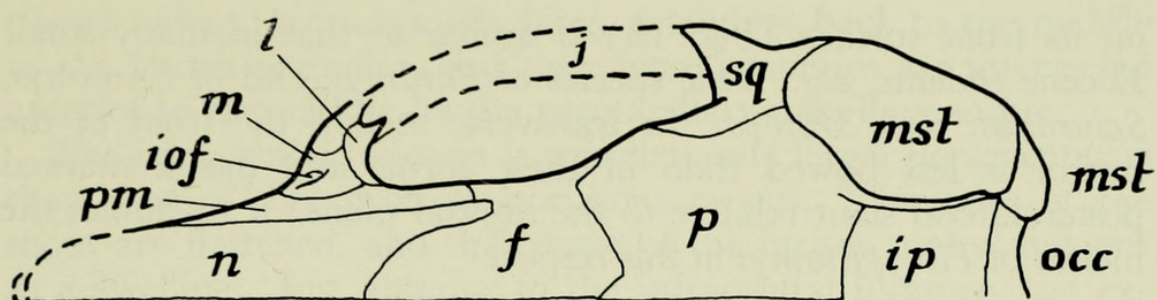
Scott remarked (1895: 270) that "the transverse crests visible on M^3 of *Protoptychus* (and doubtless in the unworn state of the other teeth, also) have a certain resemblance to the teeth of squirrels and spermophiles" In this he is correct because all retain in the upper dentition a relatively primitive arrangement of cusps. He continued, ". . . but the fundamental character of the tooth pattern is given by the enamel invaginations, which tend to divide it into two prisms. This arrangement is most like that found in *Pedetes*, the *Heteromyidae* and *Geomyidae*." The mesoflexus, however, is not an invagination of the enamel from the lingual side of the tooth, it is simply a valley in the enamel between two worn crests; the crown is not divided into two prisms.

The incisor enamel as seen in a peel from the transverse break appears to be pauciserial. Pauciserial and multiserial enamels are similar, and a transverse section is not ideal for distinguishing them; the enamel is certainly not uniserial. Scott did not figure the incisor in cross section; the distribution of enamel

Figure 2. Skull of *Protoptychus hatcheri* (PU 11235); dorsal, lateral, and ventral views; sutures diagrammatic.

Key: stippled areas: bone missing, crushed, or matrix covered; dark area on snout: site of origin of masseter medialis; hatched areas: cross section of bone; dashed lines: structure reconstructed.

Bones: *ab* — auditory bulla, *as* — alisphenoid, *f* — frontal, *ip* — interparietal, *j* — jugal, *l* — lachrymal, *m* — maxilla, *mst* — mastoid, *n* — nasal, *occ* — occipital, *os* — orbitosphenoid, *p* — parietal, *pl* — palatine, *pm* — premaxilla, *sq* — squamosal. Foramina: *bf* — buccinator, *if* — interorbital, *iof* — infraorbital, *isf* — incisive, *jf* — jugular, *mf* — masticatory, *of* — optic, *paf* — post-alar fissure, *plf* — palatine, *sf* — stylomastoid.



on its front surface (Fig. 1b) is similar to that in many small Eocene rodents, *e.g.*, some species of *Paramys*, and of *Franimys*, *Sciuravus*, and *Mysops*. In transverse section the front of the incisor is less bowed than in these forms and has a marked posterolateral slant relative to the sagittal plane; it resembles the incisor of *Platypittamys* in this respect.

SKULL

Figure 2

Scott's description of the skull is adequate and accurate for the most part, but a few additional points can be made. The posterior extension of the nasal bones almost as far back as the middle of the orbits is, to my knowledge, unique to *Protoptychus* among rodents.

The auditory region is greatly inflated, and both the temporal and mastoid portions of the skull participate in this inflation. Scott stated that the "... mastoid bulla ... is divided by partial septa into chambers, two of which are plainly shown, even externally, being bounded by deep grooves" (1895: 275). The two visible septae are seen only at the surface, and their extent is unknown. The region closely resembles that in *Chinchilla* except that there is no trace of a supraoccipital process that reaches the squamosal. In *Chinchilla* partial septae are present in the epitympanic sinus.

The parietal overlaps the dorsal epitympanic sinus laterally, and a narrow process of the parietal extends posteriorly beside the interparietal, apparently reaching the mastoid. Scott's dorsal view of the specimen (p. 270, fig. 2) shows the process arising from the parietal, although he incorrectly states in the text that the squamosal "... appears to send out a process between the parietal and the mastoid, which articulates with the interparietal" (1895: 276). The compression of the posterior part of the parietal and the unusual rectangularity of the interparietal seem to be in response to the great dorsal inflation of the epitympanic sinus. The back of the skull roof retains the primitive flatness and sharp angle with the occipital surface; it does not curve downward onto the occipital surface as it does in dipodids, heteromyids, and those caviomorphs in which the auditory region is also greatly inflated.

Many of the cranial foramina are preserved in the type specimen. The incisive foramina, unlike those of any protrogomor-

phous rodent, are unusually long, extending back to the middle of the fourth premolar, and their lateral margins are intersected anterior to the middle by the premaxillary-maxillary suture.

The infraorbital foramen is conspicuously larger dorsoventrally than that of any protrogomorphous rodent. The sides of the snout are flattened, and the course of the incisor root stands out as a swelling. Just anterior to the infraorbital foramen and extending somewhat dorsal to it is a depression on the side of the snout; this area appears to have been the site of origin of the anterior part of the medial masseter, which must have passed through the infraorbital foramen. *Protoptychus* was hystri-comorphous.

In the orbital region, three foramina are visible. The optic foramen, of which only the ventral margin remains, is clearly a large aperture in comparison with those of paramyids, and is probably the structure which Scott (1895: 278) called "a large sphenoid fissure." Anteroventral to the optic foramen in the orbitosphenoid is a small aperture, possibly an interorbital foramen. A foramen occurs in this position in various unrelated rodents, *e.g.*, *Ischyromys*, *Geomys*, and questionably in *Castor*, and I attach no special taxonomic significance to its presence here. In the floor of the orbit is a dorsal palatine foramen, which transmitted the descending palatine artery. In *Paramys* this foramen shares a common opening with the sphenopalatine, whereas in *Protoptychus*, as in *Sciuravus*, the foramen is in the orbital floor posterolateral to the sphenopalatine foramen. The posterior palatine foramen, the exit for the artery, is wholly within the palatine, the primitive condition for rodents.

The margin of the sphenoidal fissure and most of the region where the alisphenoid, parietal, frontal, and orbitosphenoid come close together is crushed. The masticatory and buccinator foramina open upward and forward, respectively, near the back of the alisphenoid bone. Retention of separate foramina for the masseteric and buccinator nerves is a primitive rodent character. Posterior to the buccinator foramen there is an emargination of the alisphenoid, which, with the anterior side of the bulla, makes a foramen. A multiple aperture in the position is present in *Reithroparamys*; there is no comparable foramen in other paramyid skulls or in *Sciuravus*.

The postglenoid and the temporal foramen are absent, probably because of the greatly inflated bullae. The stapedial foramen, carotid canal, and mastoid foramen appear to be absent,

but they (especially the last two) may have been obliterated by the slight lateral crushing which the specimen has suffered. The pterygoid fossa is very deep, and inadequately preserved for full description.

DISCUSSION

By the process of elimination it is possible to rule out relationship to any rodent group except the Paramyidae, the genus *Myosops*, and the Caviomorpha. Of the protrogomorphous rodents, all but the Paramyidae and *Myosops* are significantly different from *Protoptychus*.

In 1959 Wood (p. 359) thought that the Protoptychidae might have been derived from the Sciuravidae; sciuravids are primitive in most skull characters and in this respect could be ancestral. However, the cheek teeth and their incipient crests are not nearly so primitive. Unlike the condition in *Protoptychus* and paramyids, the medial valley of the crown is open lingually and blocked labially by the mesostyle. Wilson (1949: 91) noted this and other characteristics of the cheek teeth as being markedly different from those of most paramyids.

The cheek teeth of *Protoptychus* are advanced over those of paramyids in that the third premolar is greatly reduced, the fourth premolar and third molar are tetralophate, and the metaloph is more closely connected with the hypocone than with the protocone. The major cusps, however, are still readily identifiable, and the anteroloph and posteroloph are not quite equal in prominence to the crests formed by these cusps. The basic pattern is most nearly comparable to that of *Paramys* and *Reithroparamys*. Some reduction of the third premolar has already occurred in *Reithroparamys*. Wood (1962: 248) tentatively suggested derivation of *Protoptychus* from *Reithroparamys* but stated, "On the other hand there are some undescribed specimens (including skeletons) that seem to suggest other relationships for *Protoptychus*." These remain undescribed.

The cheek teeth of the Ischyromyidae (including only *Ischyromys* and *Titanotheriomys*) are very similar. However, the infraorbital foramen is much smaller, and the zygomatic plate is tilted, indicating a trend toward a sciuromorphic type of masticatory musculature¹. The dorsal palatine foramen is well inside

¹Having examined the evidence, I agree with Wood (1937: 195) rather than Black (1968: 275) on this point.

the sphenopalatine foramen; the pterygoid fossa, though well developed, is not nearly so deep; and there is a well-defined carotid canal in ischyromyids.

The cylindrodontids¹, specifically *Ardynomys*, which has four-crested cheek teeth, differ in detail. The dorsal palatine foramen is not separated from the sphenopalatine; the pterygoid fossa is shallow, and the carotid canal is present although small.

The Eocene rodent that most closely resembles *Protoptychus* is *Mysops*. There are three differences between the molariform teeth of the two genera (cf. Fig. 1c and d). In *Mysops* the anteroloph of P⁴ is not fully developed as a continuous crest; the metaloph is incomplete and does not meet the hypocone, though its trend is toward the anterior part of that cusp; and whereas in *Protoptychus* the cusp is prominent, in *Mysops* it is a very minor one. As seen in transverse section, the incisors of *Mysops* are very similar to those of *Protoptychus*, but the anterior surface is more bowed. The alveolus for P³ indicates that in *Mysops* the tooth was not reduced. A striking bit of evidence for relationship between the two genera is that in *Mysops* the length ratio of the incisive foramina to diastemal length exceeds .60, a ratio greater than that known for any protrogomorphous rodent (Wahlert, 1972). Although the foramina do not extend as far back as the first premolar, as in *Protoptychus*, their size suggests a stage intermediate between a paramyid or sciuravid and *Protoptychus*.

The Aplodontoidea, even the earliest ones, are so different in cusp pattern that close relationship to them can be ruled out. Prosciurids, which are most likely ancestral to aplodontoids, differ in the same regard. In them the pterygoid fossa is not deep, and there is a conspicuous stapelial foramen.

There is nothing about the dentition of *Protoptychus* that suggests relationship to the Hystricidae, which, to judge from their geologic record, may have been of Oriental origin (Wood and Patterson, 1970: 636).

The phiomyids, most notably *Metaphiomys*, bear some similarity to *Protoptychus* in that they are hystricomorphous and also have enlarged incisive foramina (Wood, 1968). The cheek

¹Wilson (e.g., 1949: 93) and Wood (personal communication), on the basis of dental similarity, place *Mysops* in the Cylindrodontidae. I hesitate to accept this assignment because, in the one partial skull of the genus (USNM 18043), the incisive foramina are considerably longer relative to the diastemal length than in *Cylindrodon*, *Pseudocylindrodon*, and *Ardynomys*.

teeth, however, are quite different; the crown pattern of *Protoptychus* is four-crested, whereas those of *Phiomys* and *Metaphiomys* are five-crested, the fifth crest being the mesoloph. Likewise the cheek teeth of the theridomyids differ in having five crests.

Myomorphous rodents can be excluded from possible relationship because the cheek tooth cusp pattern is essentially different. All sciuromorphic forms can be eliminated because of their zygomasseteric structure. Furthermore, the stapedial artery, which may well have been lacking in *Protoptychus*, is retained and its foramen is conspicuous in heteromyids and eomyids; in sciurids the foramen is present although less easily seen.

The remaining group for consideration is the Caviomorpha. The Caviomorpha are hystricomorphous; many of the early South American members of the group, e.g., the Deseadan *Cephalomys* (Wood and Patterson, 1959: 343, fig. 21), *Sallamys* and *Incamys* (Patterson and Wood, in preparation), and several Santacruzian genera illustrated in Scott (1905) have elongate incisive foramina. The living caviomorphs lack the tympanic portions of both the stapedial and internal carotid arteries (Guthrie, 1963: 478; Bugge, 1971: 532), as is quite possibly the case in *Protoptychus*. The pterygoid fossa is very deep in caviomorphs.

The cheek teeth of *Protoptychus* are lophate and are based on a series of four crests that are fully homologous with those of primitive caviomorphs. *Protoptychus* retains a small but distinct mesostyle on the molars which is lacking in caviomorphs, except *Branisamys luribayensis*, which has the cuspule on the second molar (Hoffstetter and Lavocat, 1970: 172 and fig.); it lacks the lingual valley, the hypoflexus, which is prominent in caviomorphs, but does have an indentation in that position. The fourth premolar of *Protoptychus* is molariform, unlike those of the more primitive Deseadan caviomorphs, *Deseadomys*, and *Platypittamys*, but shows some resemblance to one specimen of *Sallamys* (Patterson and Wood, in preparation).

The incisors, as noted above, appear to have pauciserial enamel. This is a plausible condition for a caviomorph relative, since multiserial enamel was surely derived from pauciserial (Korvenkontio, 1934; Wahlert, 1968: 13), and the two are not very different, bands of the inner enamel layer in each being several prisms wide.

The simplest taxonomic interpretation of *Protoptychus* is to

call it a hystricomorphous member of the Protrogomorpha. Structural details which are like those found in caviomorphs would be attributed either to convergence or to parallelism stemming from common ancestry within the Protrogomorpha. The consequence of this interpretation would be that the hystricomorphous condition of the masseter and infraorbital foramen arose more than once from the protrogomorphous condition, a conclusion in keeping with the similar multiple origin of sciuromorphic musculature, *e.g.*, independently in *Titanotheriomys*, and with its presence as a component of the myomorphous condition. *Mysops* may be a close relative of *Protoptychus*, but until a good skull of the genus is known this can be taken as no more than a possibility. The specialized characteristics of *Protoptychus*, especially those associated with the masseter and with the auditory region, confirm the need for a separate family to receive the genus.

Protoptychus could be a caviomorph, but, on the basis of the earliest forms known, a rather complicated explanation would be required. There are three anatomical barriers to placing *Protoptychus* in the Caviomorpha: its precociously molariform (*i.e.*, four-crested) fourth premolar, the lack of a distinct hypoflexus in the molars, and its hystricomorphous condition. According to Wood (1949) the most primitive Deseadan caviomorph¹, *Platypittamys*, has only a slightly enlarged infraorbital foramen, which did not transmit any part of the masseter, and a simpler fourth premolar than any paramyid known at the time of its description; whether the condition of the premolar was primitive or reduced could not be determined. On the basis of an undescribed Gray Bull paramyid, Wood and Patterson (1959: 296–297) were able to ascertain that the absence of a separate metaloph in the fourth premolar of *Platypittamys* and some other Deseadan caviomorphs is primitive. The Gray Bull paramyid, *Franimys*, was described by Wood in 1962 (pp. 139–147). The fourth premolar is comparable and also simple.

Although the cheek tooth patterns of *Protoptychus* are closer to those of *Paramys*, *Reithroparamys*, and *Mysops*, it is possible to derive them from that of *Franimys*. The direct ancestor of the South American Caviomorpha would then have been primi-

¹The caviomorphs described by Hoffstetter and Lavocat (1970) from the Deseadan of Bolivia are more advanced in that they already have enlarged infraorbital foramina and the posteroloph in some is divided into two parts (I do not agree that a mesoloph is present).

tive in comparison with its closely related North American contemporaries. Wood and Patterson (1959: 406) stated, "The South American rodents were not descended from immigrants from Wyoming, but rather from rodents that lived in some part of middle America or southeastern United States, regions from which the Eocene mammalian faunas are essentially unknown." The rarity of *Protoptychus* in fossil collections supports the possibility that it, too, is based in a stock evolving elsewhere than in the western United States.

Until the lower jaw of *Protoptychus* is described, however, retention of the hystricomorphous Protoptychidae in the Protrogomorpha seems advisable for the present, since a hystricomorphous skull can accompany a sciurognathus jaw (*e.g.*, *Pedetes*). The similarities to caviomorphs are very suggestive nevertheless. The future may reveal that *Protoptychus* was a precociously specialized offshoot of the northern group from which caviomorphs arose.

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ADDENDUM

Since this manuscript was submitted, W. D. Turnbull (personal communication) has provided me with a description of the lower jaw in a Field Museum specimen of *Protoptychus*; only the outside of the jaw has been prepared so far. Turnbull states, "The masseteric fossa of the lower jaw is distinct but shallow, and the angle is laterally offset and rather attenuated. From the offset angle and the appearance of the junction of the angle with the ramus, I'd say it had a well developed pars reflexa to the masseter, but I've not seen the medial side so know nothing about its area of insertion." He concludes that the jaw was probably quite hystricognathus. This evidence adds support to the hypothesis that *Protoptychus* is related to the caviomorph rodents through common ancestry either within the paramyids or within a Middle American caviomorph population that is as yet unknown.



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