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Eupetaurus and the Living Petauristine Sciurids

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INTRODUCTION

In Stehlin and Schaub's (1951) abundantly illustrated monograph on the morphology of rodent teeth, the poorly known Recent flying squirrel genera *Eupetaurus* and *Iomys* were removed from the Sciuridae, in which these living genera universally have been placed. On the basis of supposed dental evidence, *Eupetaurus* was compared with the African "cane rat" *Thryonomys* and with the South American echimyid *Carterodon* and closely related forms. Drawings of a dentition of *Eupetaurus* based on earlier drawings of Jentink (1890a) were published. *Iomys* was compared with the American Oligocene ischyromyids *Ischyromys* and *Titanotheriomys*. Actual references to these groups were not formally made, but relationships were implied.

Two years after the appearance of Stehlin and Schaub's monograph, Schaub (1953) proposed a classification for all the rodents that he believed to possess a basic five-crested, cheek-tooth pattern like that of the middle Tertiary genus *Theridomys*. These he proposed to call a new suborder, Pentalophodonta. The Pentalophodonta were divided into two infra-

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orders, Palaeotrogomorpha and Nototrogomorpha. The infraorder Nototrogomorpha is the same as Wood and Patterson's (in Wood, 1955) suborder Caviomorpha. The infraorder Palaeotrogomorpha contained three superfamilies (the Theridomyoidea, Hystricoidea, and Castoroidea), plus six *familiae incertae sedis*: Thryonomyidae, Eupetauridae (created for *Eupetaurus* alone), Petromyidae, Bathyergidae, Spalacidae, and Rhizomyidae.

There appears to have been no further explicit comment in the literature on the affinities of *Iomys*. The genus was not listed as an ischyromyid by Wood (1955, p. 171), but Wood did state that his Sciuridae (*ibid.*, p. 172) is the same as the Sciuridae of Simpson (1945), plus four genera. *Iomys* was therefore indirectly reaffirmed as a sciurid.

The Eupetauridae were treated as a valid rodent family in two current monographic treatises on Recent and fossil mammals. Grassé and Dekeyser (1955, p. 1496) simply followed Schaub (1953), listing the family as valid and reprinting Stehlin and Schaub's figure of the upper dentition. Schaub himself (1958) reiterated his comments and figure of 1951 and 1953, though he added a new extinct family, the Pellegriniidae, to the list of Palaeotrogomorpha, *familiae incertae sedis*. Although no new information has been added, these listings of the family in important monographs suggest that the family is now considered valid. The family Eupetauridae thus seems to be well on its way to becoming an accepted family of living rodents, the only such family named since the naming of the Seleviniidae in 1939. The only demurrer thus far voiced was a comment by Wood (1955, p. 172) in which he stated that it seemed drastic to separate *Eupetaurus* from the Sciuridae. Wood stated, however, that he had no opinion about the relationships of the genus.

Eupetaurus and *Iomys* are known from skins, skulls, and, in the case of *Iomys*, even specimens preserved in alcohol. *Iomys* is common in some museum collections, but *Eupetaurus* is presently known from only three skulls and a few skins. *Iomys* can be assigned to the Petauristinae almost by inspection, and no extensive arguments for its return to that subfamily are elaborated here. *Eupetaurus*, on the other hand, has been thought to have a non-petauristine dentition similar to the dentitions of certain African and South American rodents which are taxonomically as well as geographically far removed from the flying squirrels. Dental similarities can be misleading if overemphasized at the expense of other anatomical features. In the case of *Eupetaurus*, a whole galaxy of characters of the skull, jaw, patagium, ecology, and geographic occurrences was ignored and taxonomic assignment was based only on interpretation of the dentition. A left lower cheek-tooth series of *Eupetaurus* was mistaken for

a right one through reference to a misleading figure instead of to an actual specimen.

The purpose of the present paper is to develop arguments for the return of *Eupetaurus* to the sciurid subfamily Petauristinae. The principal task attempted here is to reconcile the superficially non-petauristine dentition of *Eupetaurus* with that of *Petaurista*. Success in that attempt would remove the only serious stumbling block now threatening the recognition of *Eupetaurus* as a petauristine squirrel.

I am indebted to Dr. Joseph Curtis Moore for pointing out this problem, for valuable discussion of Recent sciurid systematics, for the opportunity to study skulls and jaws on loan to him of all the Recent petauristine sciurid genera except *Pteromyscus* and *Petaurillus*, and for the opportunity to study G. H. H. Tate's photographs of specimens of these latter two genera. Specimens on loan to Dr. Moore were generously provided by the Museum of Comparative Zoölogy, Harvard University, the United States National Museum, and the Bombay Natural History Society. Mr. Humayun Abdulali of the Bombay Natural History Society is especially to be thanked for the loan of one of the three known skulls of *Eupetaurus*, thereby permitting a detailed first-hand analysis to be made here in New York. I also wish to thank Drs. Richard G. Van Gelder, Karl Koopman, Craig Black, Joseph Curtis Moore, and Edwin H. Colbert for critical readings of the manuscript. A list of the petauristine skulls and jaws studied is given at the end of the paper.

The measurements of the skull and jaws of *Eupetaurus* (B.N.H.S. No. M.1856) are taken from Moore's notes, and the discussion of skull characters is almost wholly based on Moore's written comments to the author.

With the exception of figures 1, 6, and 7, the illustrations were prepared by Mr. Chester Tarka.

ABBREVIATIONS

- A.M.N.H., the American Museum of Natural History, Department of Mammalogy
- A.M.N.H.:A., the American Museum of Natural History, Department of Mammalogy, Archbold Collections
- B.M.N.H., British Museum (Natural History)
- B.N.H.S., Bombay Natural History Society
- C.N.H.M., Chicago Natural History Museum
- I.M., Indian Museum, Calcutta
- M.C.Z., Museum of Comparative Zoölogy, Harvard University
- U.S.N.M., United States National Museum

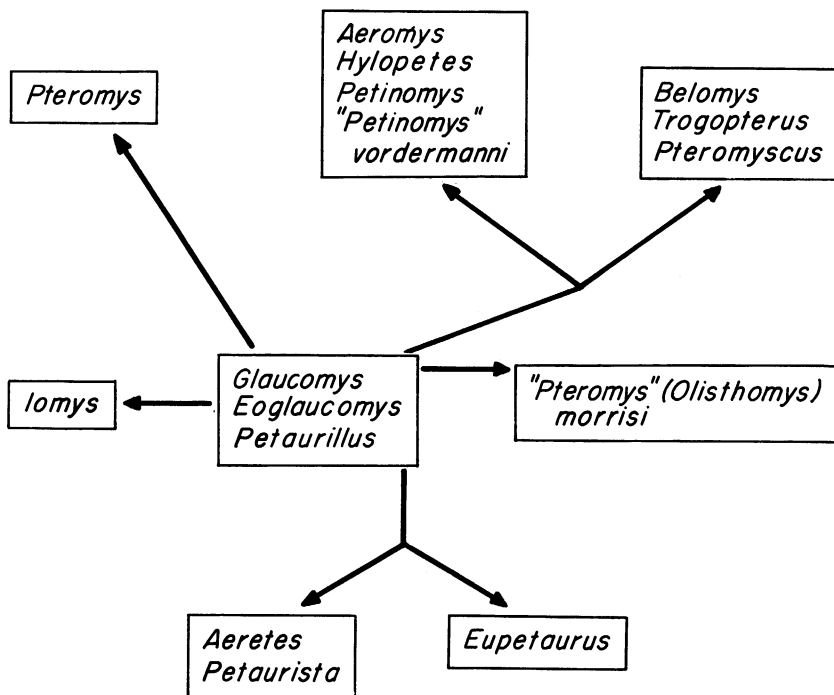


FIG. 1. Diagrammatic representation of suggested interrelationships of the living petauristine sciurids, based principally on the dentition, ear region, and baculum.

OUTLINE OF THE MAJOR GROUPS OF RECENT PETAURISTINE SQUIRRELS

Figure 1

In order to determine the affinities of *Eupetaurus* it has been necessary to review the characters of all available genera of living petauristine sciurids. *Petaurillus* and *Pteromyscus* were not seen, but were studied from unpublished photographs of British Museum types made by G. H. H. Tate. The characters of these last two genera were discussed by Thomas (1908) and Ellerman (1940), and those descriptions are accepted here. The greatest emphasis has been placed on the dentition, particularly the upper dentition, following the examples of Forsyth Major (1893) and Thomas (1908), but information concerning the baculum provided by Pocock (1923) has been incorporated where possible. The extent to which individual variation of the specimens has influenced Pocock's

conclusions is not known and cannot be determined in this study. Moore (1959) has argued for the use of bullar septa in sciurine systematics. The characters of the bullar septa are apparently even more useful in petauristine systematics. All the information gathered here seems to be in general agreement, although many gaps in knowledge remain to be filled.

The living petauristine sciurids appear to fall into five major groups which might be classified as tribes, which would bring the method of classification of this subfamily into general accord with the current practice of dividing the Sciurinae into tribes. It is of course possible to propose tribes, subtribes, subgenera, and so on, but such is not the purpose of this paper, for the analysis given here is not adequate for that. An attempt has been made to keep the following outline as "natural" as possible, so that diagnoses will be biologically meaningful as well as convenient short-cuts to identification. Major divisions of the outline¹ attempt to designate major functional differences of morphology. Further work is needed before formal subdivision of the Petauristinae should be attempted. A study of possible Tertiary members of the subfamily would be especially valuable.

- A. Check teeth without much crenulation or highly cuspidate crown pattern (*Pteromys* approaches the other groups in that the lower teeth possess low crests of the type seen in *Petaurista* and *Petinomys*).
- I. Pattern of upper cheek teeth simple, resembling that of *Sciurus*. Hypocone either absent, fused into posterior wall of protocone, or otherwise indistinct. P⁴ generally small. P³ present, large. Bullae with two ventral septa except in an undescribed new genus [*"Pteromys"* (*Olisthomys*) *morrisoni* Carter, 1942], which possesses six. The undescribed genus is therefore possibly related to the *Trogopterus* and *Petinomys* groups. Further study will probably show that *Olisthomys* should be elevated to generic rank. Pocock (1923) did not examine bacula of *Pteromys*, the undescribed genus, or *Petaurillus*. Those of *Glaucomyss* and the otherwise closely similar genus *Eoglaucomyss* are widely disparate. . . . *Glaucomyss* group
 - a. Metaconule semi-isolated, connected only to anterolingual corner of metacone. Diagonal cross crest from posterolingual border of metacone to posterior cingulum. Lower cheek teeth with various crests in the talonid basin, somewhat as in *Petinomys* and the *Petaurista* group.
 *Pteromys*
 - b. Metaconule incorporated in metaloph; connected, in some cases weakly, to the protocone. No diagonal cross crest from metacone to posterior cingulum. Lower cheek teeth generally with smooth talonid floors.
 - 1. Size of animal medium. Bullae with half a dozen ventral septa, the posterior ones of the multiple anastomosing type. Baculum not known

¹ I wish to emphasize that what follows is not a dichotomous key for the purpose of identifying unknown specimens.

- ... Undescribed new genus [*"Pteromys"* (*Olisthomys*) *morrisi* Carter, 1942]
2. Size of animal medium. Baculum elongate, straight, without spiniform processes on left side. *Glaucomys*
 3. Size of animal large. Baculum short, curved, with spiniform processes on left side. *Eoglaucomys*
 - c. "Pygmy flying squirrels, rather sharply differentiated from the other genera by the simpler cheekteeth and the relative size of the upper teeth. P⁴ is noticeably smaller than M¹; but P³ is quite well developed, so that the three anterior teeth decrease evenly in size from M¹ forwards. The cheekteeth with low ridges, the pattern not distinct, though evidently much as in normal Sciuridae. P⁴ . . . noticeably reduced; cusps of lower teeth low. Zygomatic plate a little higher and broader than is usual. Bullae large. Size very small" (Ellerman, 1940, p. 302). "Orbit . . . not extremely lengthened, averaging less than one-third of occipitonasal length . . ." (Ellerman, 1949, p. 5) *Petaurillus*
 - II. Hypocone enlarged. P³ absent. Bullae with one ventral septum. Baculum undescribed. *Iomys* group, *Iomys*
 - B. Occlusal surface of cheek teeth crenulate to highly cuspidate. Hypocone distinct except in forms (*Hylopetes*) transitional to the *Glaucomys* group.
 - I. Cheek-tooth pattern highly crenulate. Hypocone indistinct. Bullae with two (*Hylopetes*), three incomplete (*Aeromys*), or "honeycomb" (*Petinomys*, "*Petinomys*" *vordermanni*) septa. *Petinomys* group
 - a. No mesostyle. Molars with lingual cingulum. Crenulation of protoloph, metaloph, and cingula extreme. Size of animal large. Bullae with three incomplete septa. Baculum unknown. Tail rounded and narrow. . . *Aeromys*
 - b. Strong mesostyle. Distinct mesoloph. Crenulation at a minimum for the group. No lingual cingulum on molars. Size of animal medium. Baculum with "a supplementary crest behind the main crest, which is entirely ventral; apex spatulate" (Pocock, 1923, p. 246). Bullae with complex "honeycomb" septa. *Petinomys*
 - c. Mesoloph indistinct or absent. No lingual cingulum. Crenulation extreme. Size of animal very small. Bullae with complex "honeycomb" septa. Baculum not known.
 - ... Undescribed new genus [*"Petinomys*" *vordermanni* (Jentink, 1890b)]¹
 - d. Mesostyle incorporated in buccal portion of mesoloph. In many specimens a shallow indentation may be found posterior to the hypocone, which suggests a possible origin of the flexus in this position in the *Petaurista* group. No lingual cingulum. Size small to medium. Bullae with but two ventral septa. Baculum with "a single crest curving distally up on to the left side of the bone to the apex, which is simple, not spatulate" (Pocock, 1923, p. 246). *Hylopetes*
 - II. Molars squared. Hypocones large, lingual, especially on M¹ and M². Ectolophs with prominent, angular styles. P⁴ elongate, tending to become enlarged, and with double parastyle. Individual cheek-tooth cusps still recognizable, high, and forming a complex, file-like surface when

¹ Ellerman (1949, p. 14) suggested that this is a subspecies of *Petinomys setosus*. I have seen only one specimen and do not know whether the whole *setosus* group (*sensu* Ellerman) is generically separable from *Petinomys*.

- truncated by wear. Bullae with multiple anastomosing or complex "honeycomb" septa. *Trogopterus* group
- a. P⁴ not enlarged. P³ bicuspsate. Trace of a lingual cingulum. Crown pattern slightly less complex than that of *Trogopterus* and with much lower cusps than those of the latter. Bullae with complex "honeycomb" septa. "Distal end of baculum abruptly upturned and ending in a two-headed or hammer-shaped lamina" (Pocock, 1923, p. 246). *Belomys*
 - b. P⁴ enlarged. P³ with single cusp. No lingual cingulum on molars, but protocone crenulate. Cusps high, truncated early by wear to produce one long, gently undulating, rough surface from P⁴ to M³. Bullae with multiple anastomosing septa. Baculum not known. *Trogopterus*
 - c. "Much like *Belomys*, but with P³ vestigial, and P⁴ not conspicuously larger than M¹; also differing in details of the pattern of the upper teeth, and with the bullae very much enlarged. The teeth when worn appear to present a rather more normal, less wrinkled appearance, but in younger skulls the complexity of the molars is great. The external projection in the upper molars is less marked than in *Belomys*, and apparently there are only two inner cusps present, the small anterior one being barely traceable. The lower teeth are more or less as in *Belomys*; M₃ considerably elongated. Externally like *Belomys*, but ear smaller and without tufts" (Ellerman, 1940, pp. 280-281). *Pteromyscus*
- III. Size of animal large. Cheek teeth ranging from brachydont and simple to lophodont and moderately complex. In high-crowned species cross lochs interconnect the principal crests. The resulting fossettes and fossettids fill with vegetable matter, not cement (A.M.N.H. No. 32643, *Petaurista inornata*, is a rare exception to this rule). The occlusal surfaces of the cheek teeth tend to wear nearly flat in high-crowned forms. In the upper cheek teeth a long and deep median valley (or flexus) separates the protoloph from the metaloph. Mesoloph absent. P⁴ may possess a small mesostyle at the buccal end of the median valley; on the molars the mesostyle is generally absent or, if present, tiny. Anterior cingulum elevated to an anteroloph on high-crowned species. Posterior cingulum elevated to a posteroloph (except frequently on M³) on high-crowned species. Sharp reëntrant fold (or flexus) runs anterobuccally from a point immediately posterobuccal to the hypocone. This feature is invariably present, is not to be confused with the hypoflexus separating the protocone and hypocone of such forms as *Belomys* and *Trogopterus*, and is absent in all other known members of the Petauristinae, though its origin was possibly from a shallow fold similar to that of some specimens of *Hylopetes*. When present, the cross lochs of the upper cheek teeth develop between the anteroloph and the protoconule and between the metaloph conules and the posteroloph. Lower cheek-tooth pattern basically similar to but an embellishment of that of *Pteromys volans*. The lower cheek-tooth pattern of *Petinomys* is also similar, though clearly related more closely to the patterns of *Hylopetes* and "*Petinomys*" *vordermanni*. *Petaurista* group
- a. Incisors broad, grooved. Cheek-tooth pattern the same as in *Petaurista*. The enamel walls vertically corrugated, resulting in a vermiform cross section of the cusp walls, but this can occur in *Petaurista* (e.g., *P. elegans*,

A.M.N.H. No. 102468; *P. petaurista yunanensis*, A.M.N.H. No. 114894).
 Bullae with three septa. *Aeretes*

- b. Incisors not so broad as in *Aeretes* nor grooved as in that weakly separable genus. Crown pattern ranging from low and simple (e.g., *Petaurista leucogenys*) to high and moderately complex (especially *P. xanthotis*). P^4 generally smaller than M^1 (exception: the *Eupetaurus*-like species *P. xanthotis*). Upper molar protocones linguallly fluted in high-crowned species. Bullae generally with two ventral septa, but septa may be single or absent (e.g., *P. philippensis*, A.M.N.H. No. 163097; *P. elegans*, A.M.N.H. No. 102468), or the posterior of the two septa may branch (e.g., *P. punctatus*, M.C.Z. No. 36580; *P. petaurista yunanensis*, A.M.N.H. No. 114894). "Apex of baculum hollowed, irregularly spatulate, with small accessory processes" (Pocock, 1923, p. 246). *Petaurista*
- c. Incisors not grooved and relatively rather small. Cheek teeth very high-crowned, P_4 technically hypsodont; when the animal is fully adult the enamel does not extend more than about 0.5 mm. into the alveolus and thins abruptly as it enters the alveolus. The roots may be seen easily in buccal view. The cheek teeth are very high-crowned and take a long time to erupt, during which time they are nevertheless in use and are worn. The cheek-tooth pattern is, aside from being high-crowned, rather simple and free from minor plications. The peculiarity of the pattern is caused principally by the increased extent of the postero-lingual diagonal flexus in the upper teeth and hypertrophy of the buccal end of the anterolophid in the lowers. P^4 is considerably larger than M^1 . The upper molar protocones and hypocones have completely merged, their original separation being indicated only by a shallow vertical groove on the lingual wall of P^4 (note that the "sciurid hypocone" does not lie posterior to the very prominent diagonal flexus in these teeth). A strong cross loph connects the protoloph with the anteroloph, isolating a fossette. The metaloph has been displaced at its lingual attachment to the protocone by the enlarged post-hypoconal diagonal flexus; it now connects to the protoloph at a point just lingual to the paracone. A second, non-subdivided (in contrast to most high-crowned specimens of *Petaurista*) fossette is enclosed by the metaloph and postero-
 loph, except on M^3 in early stages of wear. The lower cheek teeth possess the same basic plan as that of *Petaurista*, but the crown is higher and the pattern less complicated by secondary plication of primary features. A lingual diagonal flexid dominates the central area of the crown, extending diagonally anterolabial from the posterolingual part of the crown in all the cheek teeth. A simple, nearly round remnant of the talonid basin lies posterior to the lingual diagonal flexid. Anterior to the latter there is an anterior fossettid on the molars. There may be two such structures on P_4 . The method of chewing is mainly by antero-posterior trituration. For this purpose the occlusal surfaces of the cheek teeth wear nearly flat, as in most advanced rodents. The triturating surface of the upper cheek-tooth series is anteroposteriorly somewhat convex; that of the lower series is somewhat concave. The lower jaw possesses a weak coronoid process which does not rise above the condyle. Below this a prominent fossa is present on the buccal side of the ascending

ramus. The condyle is compound, a portion of the ascending ramus having extended to a point posterior to the original condyle and there converted to a posterior extension of the condylar surface. The hamular processes of the pterygoids are quite short, and the pterygoid fossae possess three diagonally elongate pits for the origin of powerful pterygoid musculature. The caudal opening of the sphenopterygoid canal (see Hill, 1935) is divided by a wide and powerful bony bridge. All these adaptations are apparently related to increased efficiency in anteroposterior trituration. Two bullar septa. Baculum unknown. Claws relatively blunt
.....*Eupetaurus*

As a first approximation, the various Recent petauristine genera may be grouped as follows, based primarily on a study of the characters of the dentition, auditory region, and baculum (data from literature), but with attention to other features as well. Studies of skull and pelage characters, a thorough analysis of geographic distribution, and, above all, the study of potential Tertiary petauristine ancestors are needed to confirm or modify these groupings. Further work may show that the groups listed here can be classified as tribes, paralleling current classification of the subfamily Sciurinae.

PETAURISTINAE

- Glaucomys* group
 - Eoglaucomys*
 - Glaucomys*
 - Pteromys*
 - Undescribed genus [“*Pteromys*” (*Olisthomys*) *morrissi*]
 - Petaurillus*
- Iomys* group
 - Iomys*
- Petinomys* group
 - Aeromys*
 - Petinomys*
 - Undescribed genus (“*Petinomys*” *vordermanni*)
 - Hylopetes*
- Trogopterus* group
 - Pteromyscus*
 - Belomys*
 - Trogopterus*
- Petaurista* group
 - Aeretes*
 - Petaurista*
 - Eupetaurus*

ORDER RODENTIA BOWDICH, 1821

SUBORDER SCIUROMORPHA BRANDT, 1855

SUPERFAMILY SCIUROIDEA GILL, 1872

FAMILY SCIURIDAE GRAY, 1821 (INCLUDING EUPETAURIDAE
SCHAUB, 1953)

SUBFAMILY PETAURISTINAE SIMPSON, 1945

EUPETAURUS THOMAS, 1888*Eupetaurus cinereus* Thomas, 1888

LECTOTYPE¹: I.M. No. 9492, skin and skull, from an animal collected alive at an altitude of 6000 feet above sea level in the Kafiristan-Chitral area and taken to G. M. Giles at Gilgit, northern Pakistan. Described and figured by Thomas.

REFERRED SPECIMENS: Several skins in the British Museum were mentioned by Thomas. One of them (B.M.N.H. No. 88.9.29.1, cotype) possesses a fragmentary snout, but the rest of the skull is missing. Another skull in the Leiden Museum was discussed and figured by Jentink (1890a). An additional skull, discussed and figured in the present paper, is in the collections of the Bombay Natural History Society (B.N.H.S. No. M.1856).

RANGE: Kashmir area, Himalaya Mountains. Exact range unknown. A specimen has been taken at 6000 feet above sea level. Thomas supposed, probably correctly, that the animal frequents rocks and precipices and lives largely on lichens, mosses, and other rock-loving plants.

SKULL

Figures 2 and 3

The skull demonstrates that *Eupetaurus* is sciuiromorph; the jaw, that it is sciurognath. Except for modifications related to feeding, the skull and jaw are only slightly modified from those of various species of *Petaurista*, to which *Eupetaurus* is quite evidently related. Some of the most striking ways in which the skull and jaws differ from those of *Petaurista* are the constricted base of the snout, the anterior convergence of the upper cheek-tooth row, the very high placement of the posteriorly open glenoid fossa in order to allow anteroposterior motion of the lower jaw, the lowering of the mandibular coronoid process to achieve the same end, and minor modification of some of the pterygoid muscle attachments.

¹ Apparently chosen by Jentink (1890a, p. 144) from Thomas' two cotypes.



FIG. 2. *Eupetaurus cinereus* Thomas, 1888, skull, B.N.H.S. No. M.1856. Top: Dorsal view. Middle: Side view. Bottom: Occlusal view. All $\times 1$.

All these are surely related to the incipient hypsodonty of *Eupetaurus*.

Dr. Joseph Curtis Moore has very kindly provided his notes on the skull of *Eupetaurus cinereus*, based on B.N.H.S. No. M.1856. The list of characters given below has been selected from them. Moore's choice of

characters is based on his work on the living Sciurinae (Moore, 1959), and therefore many of the attributes listed here characterize other sciurids as well. In view of the fact that the sciurid nature of *Eupetaurus* has been denied, a large selection of sciurid characters is given.

Nasals wider than premaxillae on dorsum of skull

Base of rostrum constricted (to 12.7 mm. compared to 16.0 mm. farther forward)

Temporal crests quite prominent and making sagittal crest 7 mm. long



FIG. 3. *Eupetaurus cinereus* Thomas, 1888, B.N.H.S. No. M.1856. Above: Right and left lower jaws, occlusal view. Below: Right lower jaw, side view. Both $\times 1$.

Frontals sending wedges 2 mm. long between maxillae and premaxillae, and sending wedges 3 mm. long between premaxillae and nasals

Interorbital breadth not approximating length of frontal

Squamosals very high (reaching as high as base of postorbital process of frontal bones but about 5 mm. posterior to them)

Frontoparietal suture not closed

Parieto-interparietal sutures ankylosed

Sagittal suture open between nasals and between 5 mm. of frontals, but the rest completely ankylosed

Length of infraorbital canal less (12.7 mm.) than that of maxillary tooth row (21.0 mm.)

Diameter of infraorbital foramen normal, not fenestroid

Upper extremity of lip of infraorbital foramen making contact with maxillo-premaxillary suture
Dorso-anterior process of premaxillary well developed, meeting corner of nasal
Origin of masseter muscle extending onto premaxillary and even to a point higher than lacrimal
Masseteric tubercles present and projecting precisely laterad, not ventrad
Masseteric tubercles moderately thick and protrusive
Area on side of rostrum from which masseter muscle originates considerably exceeding area anterior to it
Palate intruding on pterygoid fossa by about 1 mm. posterior to M³
Supraorbital foramen a notch in this specimen but nearly a foramen in type specimen
Sphenopalatine foramen minute or possibly absent
Masticatory and buccinator foramina united
Ectopterygoid ridge of alisphenoid poorly developed
Maxillo-lacrimal contact not greatly exceeding lacrimo-jugal contact in length
Greatest width of lacrimal bone not greater than twice its distance from pre-maxillary
Orbit not apparently circular
Zygomatic process of squamosal extending forward to a point even with post-orbital process of frontal
Zygomatic process of squamosal with a very high base (12 mm. above occlusal plane)
Ridge crossing face of alisphenoid from anterior base of squamosal zygomatic process not present
Superior process on jugal low
Transbullar septa, two
Postglenoid foramina, one small (1 mm. in diameter) foramen very close to posterior edge of base of zygomatic process of squamosal
Temporal foramina present, fairly prominent, and multiple
Third upper premolar present, peg-like, and spreading
Upper incisors mildly opisthodont, small; enamel pale yellow, not orange
Masseteric fossa not very deep
Coronoid process of mandible reduced

The measurements (in mm.) of B.N.H.S. No. M.1856, taken by Moore, are:

| | |
|---|------|
| Occipitonasal length. | 77.5 |
| Condylobasal length. | 72.5 |
| Length of right orbit. | 27.5 |
| Length of right suborbit | 23.7 |
| Condyllo-premolar length. | 52.4 |
| Greatest length of auditory bulla | 15.0 |
| Diastema length. | 15.5 |
| Mastoid breadth | 30.0 |
| Zygomatic breadth | 46.5 |
| Interorbital breadth. | 19.0 |
| Span of postorbital processes | 35.3 |
| Postorbital constriction. | 16.6 |

| | |
|---|------|
| Isthmus of zygomatic process of squamosal | 6.5 |
| Palatal length. | 41.7 |
| Greatest length of nasal | 27.5 |
| Greatest breadth of one nasal. | 10.8 |
| Midsagittal length of frontals. | 30.7 |
| Midsagittal length of parietals (and unseen interparietals) | 23.9 |
| Greatest height of zygomatic arch at superior process. | 5.6 |
| Least height of zygomatic arch | 3.3 |
| Least height of rostrum on incisive foramina. | 16.0 |
| Least distance between high points of squamosals | 17.1 |
| Span of masseteric tubercles | 18.5 |
| Greatest span of premaxillary on dorsum. | 14.8 |
| Least span of nasals on dorsum | 7.7 |
| Greatest breadth of condyle on condylar process of mandible | 4.6 |
| Greatest length of condyle on condylar process of mandible. | 6.1 |
| Greatest anterior and posterior span of condylo-coronary process. | 17.9 |
| Coronoid process to lowest point on angular process | 33.5 |
| Condylar process to lowest point on angular process | 36.1 |
| Anteriormost bone to angular process | 49.7 |
| Incisor tip to angular process. | 55.0 |
| Incisor tip to condylar process | 58.1 |
| Anterior end of symphysis to condylar process. | 55.5 |
| Alveolar length of mandibular tooth row. | 22.3 |
| Crown length of mandibular tooth row. | 21.0 |

DENTAL NOMENCLATURE

The dental nomenclature used in this paper is principally that of Wood and Wilson (1936), with certain additional terms derived from Stirton's (1935) terminology of beaver cheek teeth and Black and Wood's (1956) slightly modified mylagaulid terminology. There are myriad patterns of rodent teeth, many of which defy analysis at the present time. Sometimes the cusps can be correctly identified; sometimes not. In high-crowned rodents the upper and lower cheek-tooth cusps cease to interlock, and the patterns are no longer subject to such rigorous selection as formerly, when occlusal relations had to be complied with. In general, various new plications of the crown pattern are acquired, and cusps and valleys may connect in new ways. These modifications are advantageous for the animal, chiefly because such complications both strengthen the tooth and increase the roughness of the occlusal surface. Such teeth are both longer lasting and more efficient. But once a rodent lineage frees itself from interlocking occlusion, the homologous relations of the pattern become more and more difficult to recognize as time goes on and the line evolves away from its generally tritubercular ancestry. This is one of several major reasons for our ignorance concerning rodent interrelationships.

Eupetaurus is demonstrably a petauristine sciurid on the basis of a large number of characters other than the dentition. For these reasons it is especially interesting that many homologies of the superficially indecipherable dental pattern of *Eupetaurus* are fairly readily determined. Dentally, *Eupetaurus* is merely a very high-crowned flying squirrel. Many of the dental features found in other squirrels and dentally squirrel-like rodents also occur in *Eupetaurus*, but in greatly modified form as the result of the very high-crowned nature of *Eupetaurus* teeth. The problems of recognizing the homologies of these features are similar to the problems of determining the homologies of beaver or mylagaulid tooth cusps and valleys, but certainly are no more difficult.

The general nomenclature of Wood and Wilson (1936) is extensively employed here. Stirton (1935) utilized certain additional terms for valleys between cusps in beaver teeth. These valleys are frequently homologous with those of other rodents or even non-rodents. Where believed to be homologous, Wood and Wilson's and Stirton's terms (slightly modified by Black and Wood, 1956) are used here. Where there is doubt, as with Stirton's paraflexed/fossettid and paraconid, the term has been avoided and a descriptive phrase is applied. Fields (1957) has taken a different approach with certain caviomorph rodents, applying the beaver terminology without the implication of homology. Topographic position and convenience were the principal criteria of application. In the long run, a terminology based on homology seems preferable. Non-homologous structures can always be given new names, such as the caviomorph neoloph and neolophid of Wood and Patterson (1959, p. 288).

DENTITION OF *Eupetaurus*

Figures 4 and 5

The incisors of *Eupetaurus* are much smaller than those of *Petaurista*. The curvature is about the same, but the incisors are not so deep and present a triangular rather than an elongate-oval cross section. The upper incisors do not project so far ventrad as in *Petaurista*. The enamel band of each incisor is a pale yellow color. Clearly, some of the functions of the incisors are either no longer necessary to the animal or have been supplanted by the increased triturating efficiency of the cheek-tooth system.

P³ is a peg-like tooth, differing little in structure from P³ of other genera. The apex consists of one cusp which is horizontally planed off flat by wear. In low-crowned petauristines the anterior face of the trigonid of P₄ wears a sloping facet on P³.

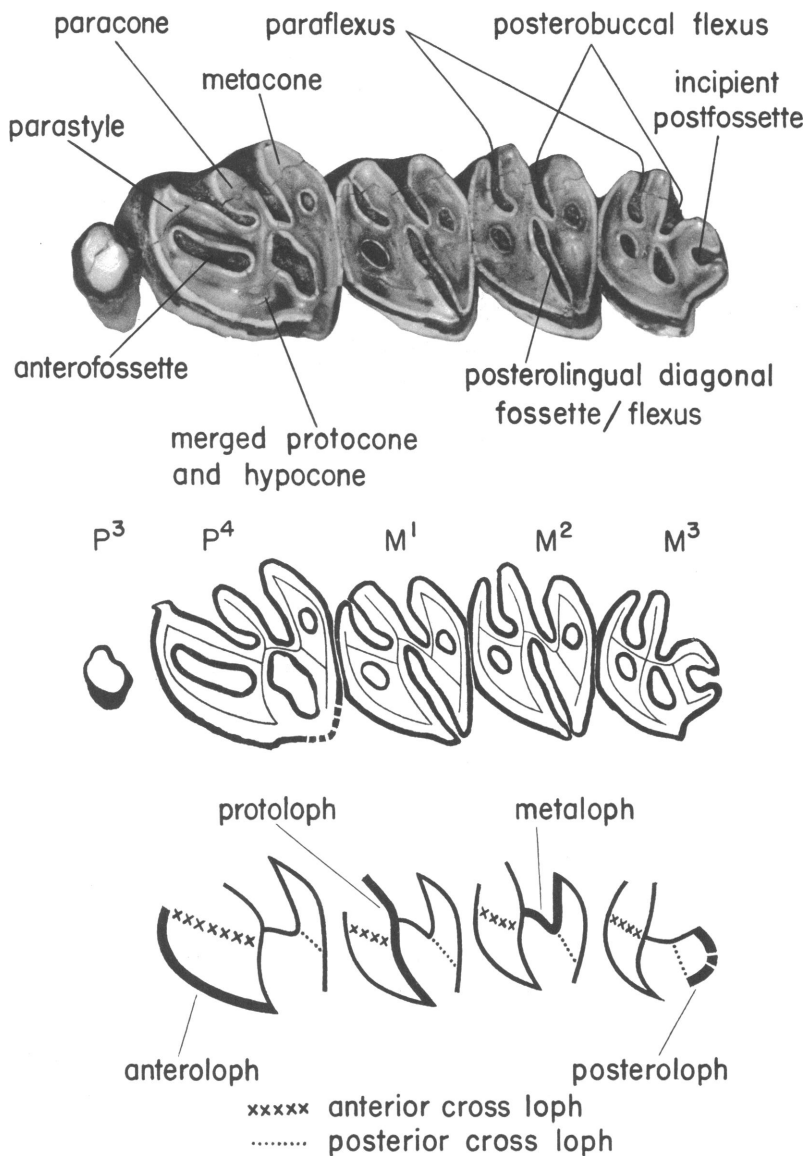


FIG. 4. Left upper cheek teeth of *Eupetaurus cinereus* Thomas, 1888, B.N.H.S. No. M.1856. *Top*: Unretouched photograph. *Middle*: Pattern, with positions of major lophes marked by thin lines. *Bottom*: Abstract of major lophes, named lophes emphasized. All $\times 4$.

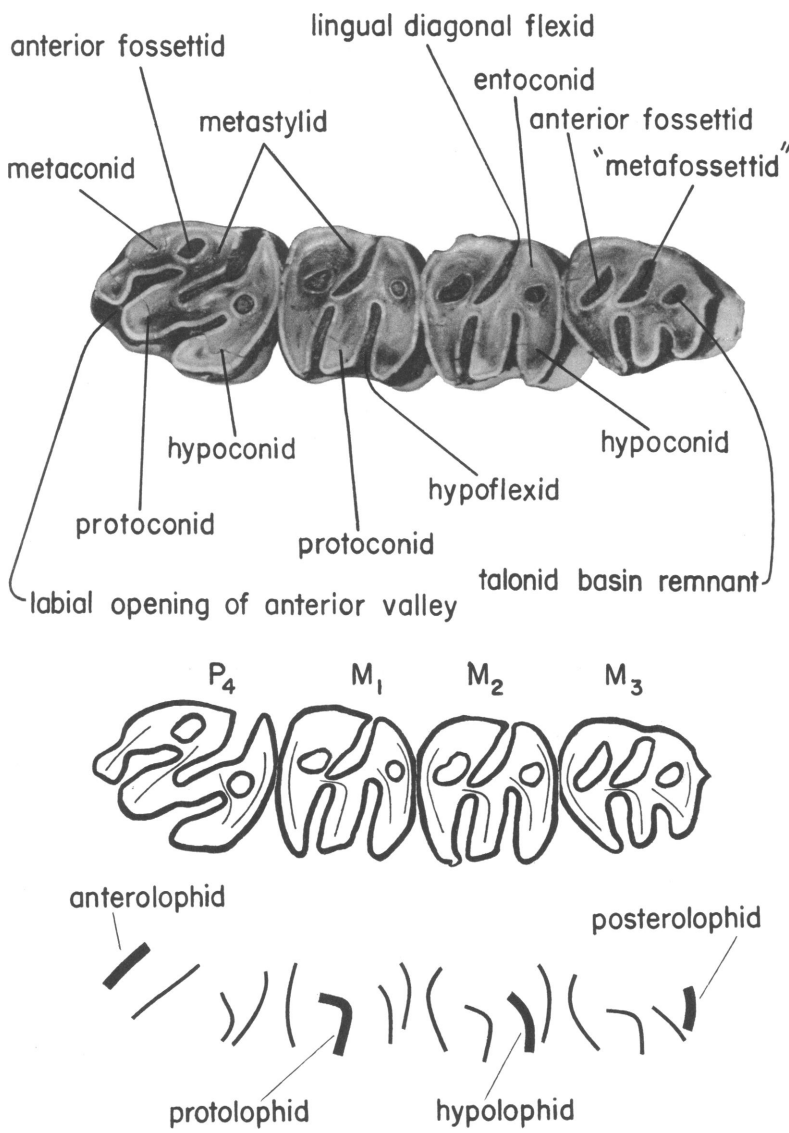


FIG. 5. Left lower cheek teeth of *Eupetaurus cinereus* Thomas, 1888, B.N.H.S. No. M.1856. *Top:* Unretouched photograph. *Middle:* Pattern, with positions of major lophids marked by thin lines. *Bottom:* Abstract of major lophids, named lophids emphasized. All $\times 4$.

P⁴ is the largest tooth in the jaw. M¹ and M² are smaller and approximately equal in size. M³ is the smallest posterior cheek tooth. Like the molars which follow it, P⁴ is a high-crowned tooth in which the cusps and their interconnecting ridges have combined into lophs and cross lophs. What were once minor basins and flexa between cusps have become important structures which complicate the cross-sectional pattern of the tooth, at once increasing the roughness of the occlusal surface and strengthening the tooth by the strategic placement of resistant enamel plates. This method of increasing the efficiency and useful life of the tooth has been adopted by almost all high-crowned mammals, the desmostylians being notable exceptions. Almost certainly P⁴, and possibly even the molars, technically are hypsodont for a short time during the youth of each individual, but emplacement of the cheek-tooth series is terminated at a definite point fairly early in adulthood. If Jentink's figure of the Leiden specimen may be relied on, P⁴ of that specimen was not fully emplaced when the animal prematurely died. The molars of the Leiden specimen are more worn than P⁴ and presumably were completely in place at the time. If one adds the height of the crown of the Leiden P⁴ ventral to the mouth of the posterolingual diagonal flexus to the height of the crown from the roots to the present occlusal surface of P⁴ in the Indian Museum and Bombay specimens, a minimum figure for crown height of a hypothetically complete, unworn, *Eupetaurus* P⁴ is obtained. Such a tooth would be prismatic, would not be able to be formed or emplaced all at one time, and would therefore fulfill for a time the definition of hypsodonty. But the fully adult *Eupetaurus*, as represented by the Indian Museum and Bombay specimens, is no longer technically hypsodont. The roots have closed, and the crown of P⁴ extends only a very short distance into the alveolus, presumably in order to affect somewhat more solid implantation than is usual in squirrels. *Eupetaurus* has therefore stopped short of horses, beavers, and the like, in the adults of which extensive modifications of the maxillary have been needed in order to house the unerupted portion of each upper cheek-tooth crown. Nor are the various fossettes and flexa of *Eupetaurus* filled with true cement. Instead, a mixture of vegetable matter and "tartar" occupies the fossettes dorsal to the level of wear, contributing to the strength of the tooth to a limited degree. The advantages of this inferior method of increasing strength must be largely offset by an increased tendency to develop infections.

P⁴ possesses three major buccal cusps, the parastyle, paracone, and metacone. These are homologous with the same cusps in *Petaurista*. On the almost unworn left P⁴ of the Leiden specimen, the parastyle is followed

by a secondary buccal fold, but this is a buccal development from the anterior cross loph, not part of a double parastyle. When unworn, the left P⁴ of the Bombay specimen apparently possessed a similar secondary fold. Between the parastyle and paracone lies a broadly open paraflexus. The paraflexus takes a nearly anteroposterior course within the tooth and is nearly parallel with the long axis of the anteroflexus/fossette. The paracone consists of an anterobuccally trending vertical pillar at about the middle of the buccal wall of the tooth. Posterior to the paracone a posterobuccal flexus indents the crown. As there is no mesostyle, this flexus is neither a mesoflexus nor a metaflexus, but may be thought of as a combination of both. Posterior to the posterobuccal flexus the metacone juts out buccally. Its root is housed in a swelling of the maxillary which is continuous with the posteroventral border of the maxillary zygomatic process.

The lingual face of P⁴ consists of one major cusp representing the protocone. The hypocone has long since fused to the protocone as in most other sciurids. The anterior cingulum has become elevated and is therefore properly regarded as an anteroloph. The anteroloph arcs forward and labiad to terminate at the parastyle. Posterior to the merged protocone and hypocone is the posterolingual diagonal flexus/fossette. In an early stage of wear, at about the time the tooth becomes fully implanted, the flexus becomes isolated as a fossette. This flexus/fossette is a much more important structure than in *Petaurista* and has extended to the central part of the crown, anterobuccally displacing the metaloph to an almost unrecognizable but nevertheless topologically acceptable position. As P⁴ wears, the cross section of the metaloph becomes more and more displaced. Jentink's illustration of the Leiden specimen shows the nearly unworn metaloph condition. The posterolingual diagonal flexus/fossette is medially constricted. The posterior cingulum has become elevated and may be regarded as a posteroloph. It runs from the metacone to the posterolingual corner of the crown. Two cross lophs complete the framework of the tooth. An anterior cross loph, foreshadowed in many species of *Petaurista*, runs from the protoconule region to the parastyle, thereby isolating the anterofossette from the paraflexus. A posterior cross loph, present in virtually all species of *Petaurista*, runs from the metaloph to the posteroloph, isolating the postfossette. In early wear the anterofossette opens forward, lingual to the parastyle (Leiden specimen). It is isolated by the time P⁴ is fully implanted. The postfossette is not invaded by a crest, as might have been expected in view of the double metaconule so common in *Petaurista*.

The upper molars of *Eupetaurus* possess almost exactly the same major

features of the pattern of P^4 but are smaller, less prismatic, more antero-posteriorly compressed, and have less room to form within the maxillary above them. The parastyle projects labiad beyond the junction of the anterior cross loph. The latter is not plicated. The anterofossette is small and may never have opened forward as a flexus. The posterolingual diagonal flexus of M^1 and M^2 remains open for a time after that of P^4 and M^3 has been converted to a fossette by wear. The postfossette of M^3 is the last fossette to be isolated by wear.

The lower cheek teeth of *Eupetaurus* are not obviously those of a sciurid and seem at first sight to resemble no other rodent cheek teeth at all. Notably perplexing is the fact that there are two flexa on the buccal side of each cheek tooth and only one prominent flexus on the lingual side, at least at the stages of wear represented on the three known specimens of the genus. Most rodents with high-crowned teeth of this general type have exactly the reverse situation: there is a single buccal flexus and two or more lingual ones. Doubtless this is one reason why Stehlin and Schaub (1951) mistook Jentink's figure of the left lower dentition for a right one. Neither Thomas (1888) nor Jentink (1890a) labeled their figures adequately. There is a further complication, which may not have misled Stehlin and Schaub but which may mislead future workers unless elucidated. Thomas' original figure gives an occlusal view of a left lower cheek-tooth series, but the buccal view is of a right lower jaw. Tate's unpublished photographs of the same specimen show that the right lower jaw is considerably damaged, the incisor and M_2 being missing. If it be assumed that the damage was present in 1888, Thomas' figure of the right lower jaw is therefore either a reversed view of the left jaw or has been completed with reference to the left jaw. The occlusal view is not of the same side. Jentink's figure is an occlusal view of part of a left lower jaw, but comparison with Thomas' figure would lead one to think it to be a right one unless the facts were known. Reference to an actual specimen resolves these difficulties and establishes the true state of affairs.

P_4 offers the most clues concerning cusp homologies and is discussed in the greatest detail. An unworn P_4 is not available, but Jentink's figure of the Leiden specimen affords valuable data not clearly indicated on the other two specimens. P_4 may have worn for a time during implantation, but, if technically hypsodont, it must have been so for a shorter period than its upper counterpart. In the adult Bombay specimen the roots are visible on the lingual side. As in the upper teeth, the original anterior part of the crown takes up most of the tooth. There are four main

lophids: an anterolophid, short "protolophid,"¹ hypolophid, and posterolophid. The crest of the anterolophid is isolated from the rest of the tooth by a valley which runs from the anterobuccal base of the tooth irregularly posterodorsolingual to a high pass, drops down again to form the hollow of an anterior fossettid, and then emerges high on the lingual wall of the tooth. The lingual emergence of this valley is clearly seen in the Leiden and Indian Museum specimens. As the tooth wears, the lowest parts of this valley become isolated to form either one or two fossettids. Posterior to the lingual emergence of this valley lies the metastylid. Ventral to the level of the valley the metastylid base merges with the posterolingual base of the complex metaconid region, as can be seen at the stage of wear shown by the Bombay specimen. From the metaconid-metastylid a strong "protolophid" runs anterolabial to the protoconid. The protoconid is high and pillar-like and is separated from the hypoconid by the hypoflexid, which runs posterolingual almost to the remnant of the talonid basin. The mesoconid is represented by a bulge in the lingual wall of the hypoflexid and is best seen in the nearly unworn Leiden specimen. The hypoconid is continuous with the posterolophid, which in turn is continuous with the entoconid. Anterior to the posterolophid the hypolophid forms a second connection between the hypoconid and entoconid, thereby isolating part of the talonid basin as a fossettid. In a completely unworn tooth this remnant of the talonid basin would have been "drained" by the hypoflexid. This last character is a departure from the situation in *Petaurista*. Anterior to the entoconid the complex and variable lingual flexids of *Petaurista* have been stabilized as a single valley, the lingual diagonal flexid. After entering the crown the lingual diagonal flexid turns abruptly forward and runs toward the apex of the protoconid. This condition is possibly related morphogenetically to the anterolabial course of the posterolingual diagonal flexus/fossette of the upper cheek teeth. The great extent of the lingual diagonal flexid has anterolingually displaced the connection between the higher parts of the trigonid and talonid.

The lower molars are somewhat simpler than P_4 , but all the major features of P_4 have their counterparts. The molars decrease in size posteriorly, and the height of the crown appears to do likewise. How much of this crown height reduction is caused by wear is not known. The lingual

¹ This crest would be called a metalophid or metalophulid II by most students. In most mammals the term "protolophid" for a crest running from the protoconid to the metaconid region and the terms "metalophid" or "crista obliqua" for a crest running from the metaconid region to the hypoconid seem preferable. In rodents the homologies are in doubt. For this reason quotation marks have been placed here around "protolophid."

roots of all the molars are visible in the adult Bombay specimen. The principal difference from the pattern of P_4 is that the anterolophid and "protolophid" take a more transverse course on the molars, projecting buccally to form the first two of the three buccal folds of the crown. The same situation is incipiently present in *Petaurista*, in which the buccal end of the anterolophid is a much more important structure on the molars than on P_4 . In *Eupetaurus*, however, the trigonid has expanded at the expense of the talonid, and the buccal end of the anterolophid has hypertrophied. The lingual opening of the valley of which the anterior fossettid is the remnant is quite high on all the molars and is early obliterated by wear. Its former position can be seen on M_1 and M_2 of the Indian Museum specimen. The left M_3 of the Indian Museum specimen possesses a double anterior fossettid, marking two low points in the valley posterior to the anterolophid. On the same tooth the lingual end of the hypoflexid has become isolated to form a second fossettid buccal to the principal talonid basin remnant.

DISCUSSION

Figures 6 and 7

Stehlin and Schaub (1951) did not have a skull or jaw of *Eupetaurus* at hand, but relied instead on Jentink's (1890a) figure for details of the dental pattern. Unfortunately, the left lower dentition figured by Jentink was not labeled as such and was assumed to be a right one by Stehlin and Schaub. Stehlin and Schaub's interpretation of Jentink's figure of the upper dentition and their misinterpretation of Jentink's figure of the lower dentition led Schaub (1953) to propose a new family for *Eupetaurus*. In Schaub's (1953) view, the Eupetauridae are a *familia incertae sedis* within his palaeotrogomorph pentalophodonts. Quite evidently, Thomas' (1888) original figures of the skull and dentition and Thomas' colored plate of a hypothetical living animal based on the characters of the pelage were not consulted. Had Thomas' paper been consulted, Schaub surely would have preferred to reproduce Thomas' rather than Jentink's figures. Schaub's only references to the original Thomas (1888) paper were either author citations or a reference (Schaub, 1953, p. 398) derived from Ellerman (1940, p. 304). Had an actual specimen been consulted, it is difficult to see how *Eupetaurus* could have been placed anywhere but in the petauristine sciurids, in which the genus had previously rested.

Stehlin and Schaub were of the opinion that the dentition of *Eupetaurus* is similar to that of *Carterodon*, *Nelomys*, and *Thryonomys*. *Carterodon*

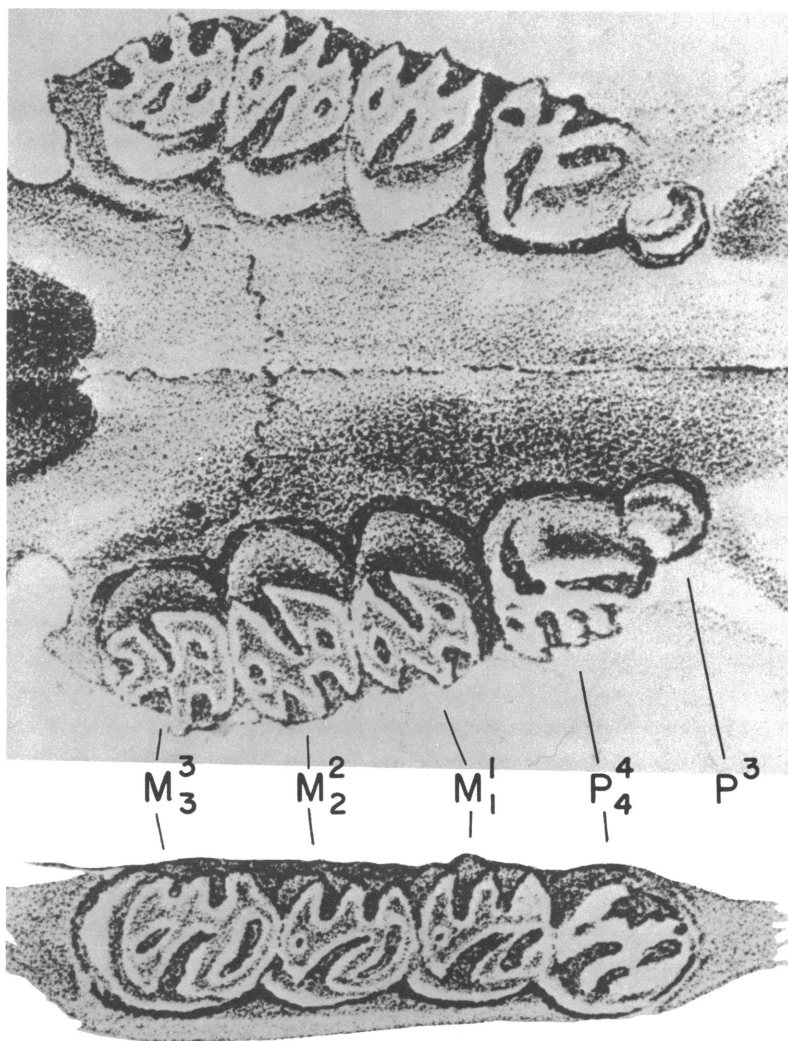


FIG. 6. Detail from Jentink's (1890, pl. 7, figs. 1, 2) drawings of the Leiden Museum specimen of *Eupetaurus cinereus*. *Above*: Cheek-tooth region of skull. *Below*: Lower left cheek teeth (anterior is to the right). The lower jaw has been silhouetted to remove background shown in Jentink's figure. Jentink gave neither measurements nor scale; the scale here is therefore approximately $\times 4$.

and *Nelomys* are living echimyd caviomorphs, restricted to South America. *Carterodon* is reported by Ellerman (1940, p. 107) to be rare and restricted to a part of Brazil. *Nelomys* is now considered a synonym of *Echimys*.

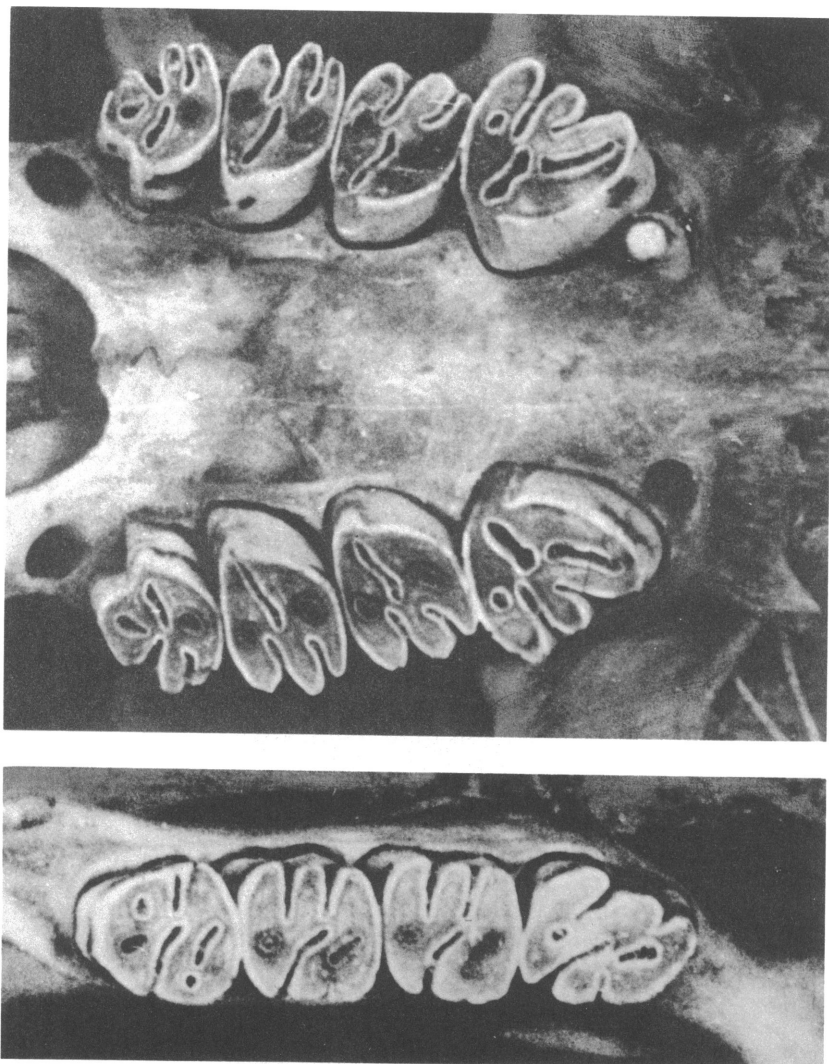


FIG. 7. Dentition of the type specimen of *Eupetaurus cinereus* Thomas (1888), I.M. No. 9492. Detail from photographs made by G. H. H. Tate. *Above*: Cheek-tooth region of skull. *Below*: Lower left cheek teeth (anterior is to the right). The scale has been determined as $\times 4$ by comparison with measurements given by Thomas. For tooth identifications, compare with figure 6.

Both *Carterodon* and *Echimys* are reported by Ellerman (*op. cit.*, p. 106) as externally more or less rat-like rodents, *Echimys* with coarse fur,

Carterodon with grooved incisors and softer fur. The interrelationships and phylogeny of the Echimyidae were discussed by Wood and Patterson (1959). They believed echimyids to be related to primitive members of the Octodontidae, in which they now place *Platypittamys*. Further work is now in progress by Patterson and Kraglievich that apparently will confirm this point. There is no question that these echimyids are caviomorphs.

The echimyid dentition has differentiated to a considerable degree in South America since the Oligocene (Wood and Patterson, 1959). *Carterodon* and *Echimyis* prove to have rather different dentitions when these are studied in detail. Nevertheless, there seems to be little reason to doubt that their common ancestry was near *Deseadomys* Wood and Patterson, 1959. In the upper dentition the first two molars of *Carterodon* (see Stehlin and Schaub, 1951, p. 51, fig. 51) retain some of the paramyid-like features of *Deseadomys* and in this respect resemble *Eupetaurus*. The lingual end of the paraflexus tends to become isolated as a fossette similar to the anterofossette of *Eupetaurus*. No postfossette appears at the stage of wear shown in the specimen illustrated by Stehlin and Schaub, but a very young individual might be expected to show this feature in early wear. *Deseadomys* possesses such a fossette (metafossette of Wood and Patterson). The hypoflexus of *Carterodon* is not homologous with the posterolingual diagonal flexus of *Eupetaurus*, because the former lies anterior to the hypocone and the latter posterior (as interpreted in the present paper). The third upper molar of *Carterodon* resembles its counterpart in *Eupetaurus* even less than do M^1 and M^2 . The deciduous upper fourth premolar is, of course, not comparable to the permanent P^4 of *Eupetaurus*. In the lower cheek teeth, the pattern of *Eupetaurus* would resemble that of *Carterodon* and such close allies (or synonymous forms?) as *Euryzygomatomys* and *Cercomys*, except that the fossettids of *Eupetaurus* are not found in the South American genera and the resemblance of the teeth is such that right lower cheek teeth of *Eupetaurus* resemble left ones of the echimyids and *vice versa*. This last argument is decisive. *Eupetaurus* is not significantly similar to *Carterodon*.

Echimyis itself (including *Nelomys*) has cheek teeth even more peculiarly specialized than those of *Carterodon* and its allies, retaining virtually no paramyid-like (therefore *Eupetaurus*-like) features. A detailed comparison seems unnecessary. The arguments just given above apply *a fortiori*.

Thryonomys, on the other hand, is something of a puzzle. *Thryonomys* is restricted to Africa at present. Hinton (1933) has described a supposed late Tertiary (Chinji) relative, *Paraulacodus*, from the Siwalik beds of Pakistan, but illustrations are not available. *Thryonomys* has been con-

sidered by most students to be a member of the Hystricomorpha, *sensu stricto*. Certainly it is both hystricognath in jaw structure and hystricomorph in masseter structure, but it appears that each of these characters can be acquired independently. Wood (1955, p. 184) was uncertain of the ancestry of the genus, although he placed it in the Hystricomorpha, *sensu stricto*. The dentition of *Thryonomys* is not similar to that of any member of the Theridomyidae or Hystricomorpha, *sensu stricto*, in that it lacks at least one loph on the upper cheek teeth. This loph appears to be the all-important mesoloph, a loph present in theridomyids, *Phiomys* and its allies,¹ eomyids, and hystricids, but absent in caviomorphs (Wood and Patterson, 1959) and many other rodents. The upper molars of *Thryonomys* seem to have only three lophs when worn (e.g., Ellerman, 1940, pp. 146, 147, figs. 26, 28; and various published figures after Ellerman's figures) but young individuals, such as A.M.N.H. No. 53955 (*Thryonomys harrisoni*), show rather clearly that the most posterior loph of each molar is a compound structure possibly combining the metaloph and posteroloph. The ancestors of *Thryonomys* probably possessed four-crested upper molars. The upper molar pattern of *Thryonomys* is thus much more similar to that of primitive echimyids than it is to that of hystricids or other Old World five-crested rodents. The permanent fourth premolars of *Thryonomys* are suppressed, dp_4^1 remaining in use throughout life as in advanced echimyids. In the maxilla the root of the incisor has extended to a point above dp_4^1 , leaving no room for P^4 to form, which suggests that the retention of dp_4^1 is merely convergent with the retention of dp_4^1 of echimyids. The lower molars of *Thryonomys* have two labial and three lingual pillars in worn teeth, but in completely unworn teeth there is a strong suggestion that this similarity to echimyids and various other rodents is also convergent. In unworn *Thryonomys* lower molars, such as M_2 of A.M.N.H. No. 53955 (*Thryonomys harrisoni*), there is a small crest from the anterior end of the protoconid which runs linguad a short distance anterior to the first major lophid. There is thus a strong possibility that the "protolophid" (metalophid of most recent authors) is retained in *Thryonomys*, in contrast to its loss in various echimyids. *Thryonomys* is thus viewed here as only superficially similar in lower molar pattern to echimyids, even though the upper molars are closely comparable and may even have homologous patterns.

¹ Wood (1955, p. 172) stated that phiomyids are four-crested, and he placed them in the Sciuromorpha. They are of course ultimately derived from that source, but both *Phiomys* and *Phthinylla* are here found to be five-crested, although the mesoloph is admittedly short. Wood's phiomyids are probably best placed in Wood's Theridomyomorpha, perhaps only as a theridomyid subfamily.

The upper molars of *Thryonomys* differ from those of *Eupetaurus* in the same way that those of certain echimyids do. The lower molars of *Thryonomys*, regardless of the homologies of the lophids, are similar to those of *Eupetaurus* only if right molars of one genus are compared with left ones of the other. The skulls are wholly dissimilar. The similarities of the dentition of *Eupetaurus* to those of certain echimyids and *Thryonomys* that have been adduced by previous authors as evidence of close relationship of these genera are thus viewed here as superficial. There are more than 600 genera of rodents, all of which appear to have differentiated from paramyid or paramyid-like ancestry (certain recent authors to the contrary notwithstanding). It should come as no surprise that many have acquired similar dental patterns, whether homologous or analogous. The paramyid pattern has often served as a basis for radiations of more advanced rodent tooth patterns. Only the sciurids retain it essentially unmodified today, yet even within the sciurids the flying squirrels have modified it greatly in such genera as *Trogopterus*, *Iomys*, *Petaurista*, and *Eupetaurus*.

The affinities of *Thryonomys* are still in doubt. The genus is not related to *Eupetaurus* or the caviomorphs, but its position within the Hystricomorpha, *sensu stricto*, is uncertain. There are similarities of the dentition to those of certain genera usually separated widely in classifications, such as *Apodecter* Hopwood (1929), *Neosciuromys* Stromer (1926), *Sayimys* Wood (1937a), and *Petromus* Smith (1831), but some of the similarities between these genera probably represent convergence. The subject has been discussed cautiously by Stromer (1926) and Bohlin (1946). The thryonomyids provisionally are regarded here as hystricomorphs (*sensu stricto*), *incertae sedis*, following the consensus.

ORIGIN OF THE DENTAL PATTERN OF *EUPETAURUS*

Figures 8 and 9

Among the various species of *Petaurista* and *Aeretes*, one in particular stands out as basically similar to *Eupetaurus* in dental plan: *Petaurista xanthotis*.¹ This species is found living from Tsing Hai (Koko Nor) and Kansu southeastward to Szechwan and Hupeh and southward to Yunnan. In Yunnan, specimens have been taken as high as 10,000–11,000 feet in the Likiang Range (Allen, 1940, p. 744). Milne-Edwards (1868–1874) believed that *Petaurista xanthotis* was possibly to be included in *Aeretes*

¹ Ellerman and Morrison-Scott (1951, p. 464) place this highly distinctive species in *Petaurista leucogenys* as a subspecies.

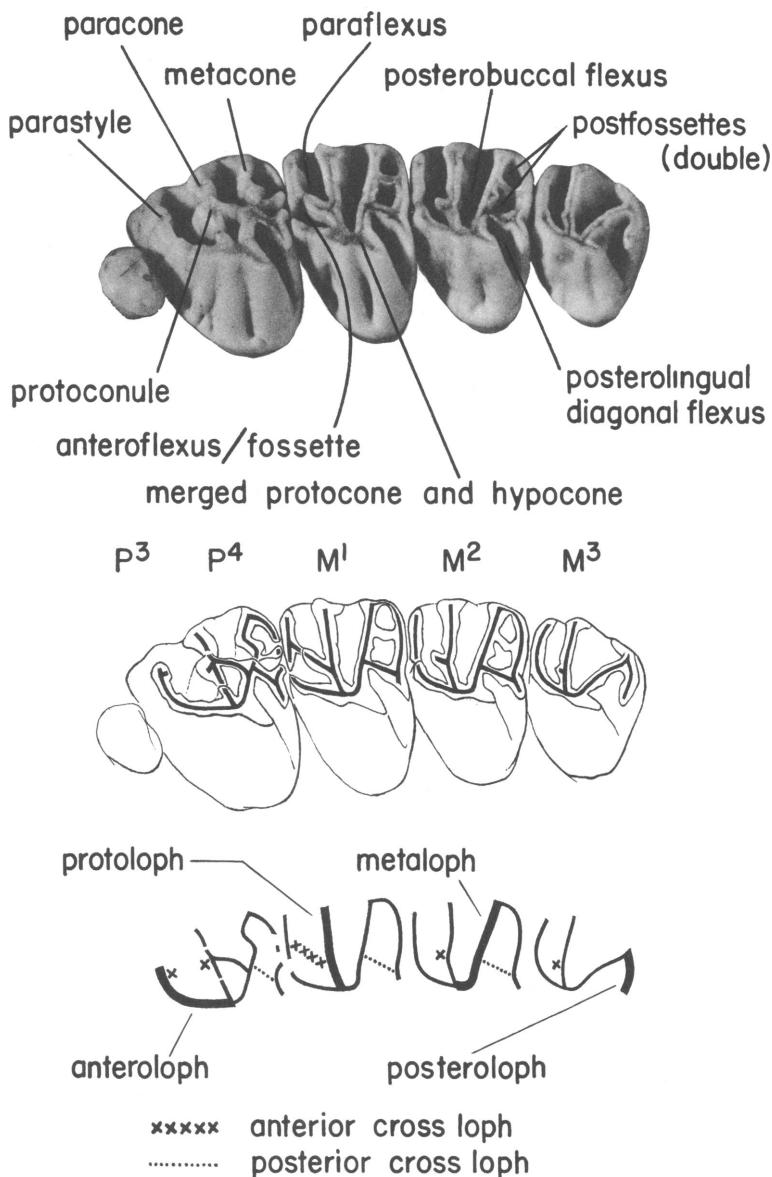


FIG. 8. Left upper cheek teeth of *Petaurista xanthotis* (Milne-Edwards, 1868–1874), M.C.Z. No. 23910. *Top*: Unretouched photograph. *Middle*: Pattern, with positions of major lophi marked by heavy lines. *Bottom*: Abstract of major lophi, named lophi emphasized. All $\times 4$.

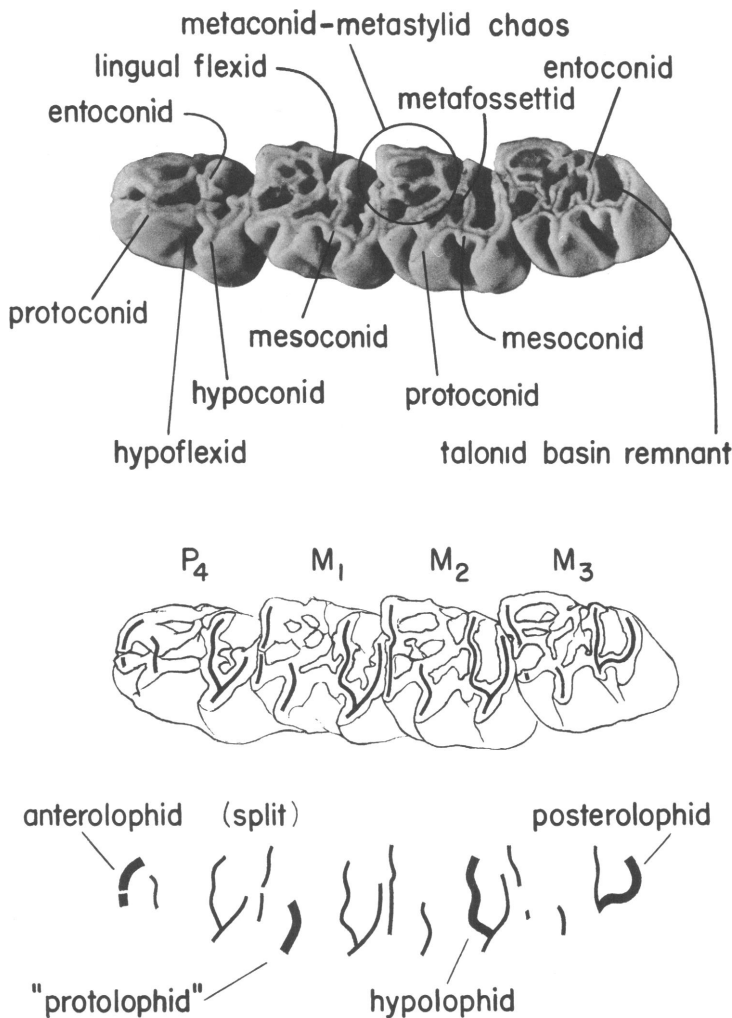


FIG. 9. Left lower cheek teeth of *Petaurista xanthotis* (Milne-Edwards, 1868–1874), M.C.Z. No. 23910. *Top*: Unretouched photograph. *Center*: Pattern, with positions of major lophids marked by heavy lines. *Bottom*: Abstract of major lophids, named lophids emphasized. All $\times 4$.

melanopterus (Milne-Edwards, 1867). It is at least a distinct species, however, and may deserve higher rank. Although *Petaurista xanthotis* differs as profoundly in the dentition from other species of the genus as does *Aeretes melanopterus*, the two species do so in quite different ways.

Petaurista xanthotis could be made the type of a new genus, but that step should be taken only after a more thorough analysis than is possible in this paper. *Eupetaurus* appears to have originated from *Petaurista xanthotis*-like stock.

Petaurista xanthotis is at present separated by the Himalaya Mountains and Tibetan Plateau from the range of *Eupetaurus* on the Kafiristan-Kashmir border south of the Hindu Kush. This barrier was elevated to great height during late Cenozoic time (Colbert, 1935, pp. 1-28, and references cited therein) and possibly has isolated *Eupetaurus* continuously for several million years. During this period the lineage leading to *Petaurista xanthotis* apparently changed little and that leading to *Eupetaurus cinereus* apparently modified the dentition and the masticatory musculature to a considerable degree. *Petaurista xanthotis* in itself is, of course, not ancestral to *Eupetaurus cinereus*, but in the following remarks the characteristics of its dentition (particularly the upper cheek teeth) are treated as, in general, structurally ancestral to those of *Eupetaurus*. The ancestors of *Eupetaurus* surely passed through a closely similar stage, even if it should be determined eventually that the dentition of *Petaurista xanthotis* is merely convergent with the dentition of such ancestors.

Petaurista xanthotis is the most high-crowned species of *Petaurista*, but the species is in no sense hypsodont. P⁴ is larger than the molars and presents a curved anterolingual wall comparable to that of *Eupetaurus*. The roots, however, can be seen. The dental pattern differs from that of P⁴ of *Eupetaurus* in several ways. The anterior cross loph has not yet connected the protoloph to the parastyle to isolate the anterofossette from the paraflexus. Instead, the connection between the protocone and the protoconule isolates a small fossette from the posterolingual end of the paraflexus. This fossette was evidently once part of the posterobuccal flexus but has become separated from the latter as the result of a cross crest between the conules. The anterior cross loph has, however, begun to project anterolabial from the lingual half of the protoloph of P⁴ in many other species of *Petaurista*. The metaloph of P⁴ is slightly displaced (see especially M.C.Z. No. 23907, an old individual) by the posterolingual diagonal flexus in *Petaurista xanthotis*. The region of the postfossette is quite complicated, but the principal difference is that the postfossette of *Petaurista xanthotis* (and other species) is basically double as the result of at least one cross loph labial to the posterior cross loph, whereas the valley between the metaloph and posteroloph has been reduced to a single tiny postfossette on the even higher-crowned P⁴ of *Eupetaurus*. The upper molars of *Petaurista xanthotis* differ from those of *Eupetaurus cinereus* in much the same manner as in P⁴, except that the anterofossette

may become isolated as in *Eupetaurus*, and the posterobuccal flexus passes anterior to the posterolingual diagonal flexus instead of running toward it as in P^4 or posterior to it as in P^4-M^2 of *Eupetaurus*. The anomalous condition in *Eupetaurus* is clearly the result of the anterolingual "headward erosion" of the posterolingual diagonal flexus. M^3 differs from that of *Eupetaurus* in that the anterior cross loph is variably present and the lingual part of the double postfossette may be connected with the posterolingual diagonal flexus in early stages of wear. The posterobuccal flexus reaches a more lingual point than in *Eupetaurus*.

In the process of elevating the crowns of P^4-M^3 to produce prismatic teeth, *Eupetaurus* has therefore gone beyond the stage represented by *Petaurista xanthotis*. The basic features of these teeth are the same, but the pattern has been modified by the stabilization of the anterofossette and postfossette. These have come to be vertical, enamel-walled tubes with smooth sides. The lack of plication of these structures is possibly related in part to their small size and in part to the need for reduction of surface area in a blind pocket filled with decaying vegetable matter. The elongation of the posterolingual diagonal flexus has also proceeded beyond the condition exhibited by *Petaurista xanthotis*. In the latter this flexus extends anterolabial a greater distance deep in the crown than it does near the apex. A continuation of this trend as the crown became higher resulted in the great anterolabial extent of the flexus seen in worn teeth of *Eupetaurus*. The deepest part of the posterolingual diagonal flexus has in effect tunneled "under" the posterobuccal flexus, forcing the latter to terminate behind it at a more labial point than before. In the process the cross section of the metaloph became contorted in the plane of occlusion, for the metaloph must pass lingual to the posterobuccal flexus and labial to the posterolingual diagonal flexus on its way from the metacone to the fused protocone and hypocone. This contortion is responsible for much of the difficulty in deciphering the dental plan of the upper cheek teeth of *Eupetaurus*, but once this is understood the homologies of other features of the dental plan are rapidly comprehended.

The lower dentition of *Eupetaurus* has stabilized the more complex and variable pattern of *Petaurista xanthotis* and has enlarged the buccal end of the anterolophid. The number of minor plications has been greatly reduced. In many essentials, however, the pattern of a moderately worn *Eupetaurus* tooth is a further development in a trend of pattern changes from moderately worn to well-worn teeth in *Petaurista xanthotis*. The small projection anterior to the protoconid on P_4 of *Petaurista xanthotis* has become the buccal end of the anterolophid. The "protolophid" and hypoconid are the same. The buccal end of the most posterior of the

principal lingual flexids on P_4 of *Petaurista xanthotis* has become isolated as a talonid basin remnant in early wear stages of *Eupetaurus*. When P_4 is relatively unworn in *Eupetaurus*, this fossette is "drained" by the hypoflexid, and no posterolingual connection to the edge of the tooth has been seen, though it may exist in completely unworn teeth. In early wear the lingual part of the most posterior lingual flexid has "captured" the metafossettid on the left P_4 of M.C.Z. No. 23911, a specimen of *Petaurista xanthotis*, but in the other three specimens of this species examined the metafossettid is either isolated or connected with the anteriormost of the two principal lingual flexids. Homologies are therefore in doubt in this region. On P_4 of *Eupetaurus* the hypolophid may well have been breached by the lingual diagonal flexid, as in the one specimen of *Petaurista xanthotis*. The complex metaconid-metastylid region is much simpler in *Eupetaurus* than in *Petaurista xanthotis*, and it is not clear exactly which plications are retained in *Eupetaurus*. The lower molars have been modified from a *Petaurista xanthotis*-like condition in much the same way as has P_4 . The buccal end of the anterolophid is as large as the other two buccal pillars; the talonid basin remnant has been modified into a small, enamel-lined tube; and the various fossettids that lie lingual to the protoconid in *Petaurista xanthotis* have been reduced to a single anterior fossettid. The lingual flexid has been stabilized. The mesoconid no longer wrinkles the hypoflexid.

The pattern of the lower cheek teeth of *Eupetaurus* was therefore derived from some *Petaurista xanthotis*-like ancestor. The principal differences are interpreted here as the result either of the increased height of crown of *Eupetaurus* or of a few minor changes in crown pattern acquired by *Petaurista xanthotis*.

CONCLUDING REMARKS

The recent removal of *Eupetaurus* and *Iomys* from the Sciuridae and their subsequent return to that family advocated in this paper have a broader bearing on rodent classification than might ordinarily result from such simple taxonomic adjustments. *Eupetaurus* and *Iomys* are animals, not dentitions. Failure to consider more than the dentition has resulted in what are regarded here as grave errors in classification. Surely it is more fundamental to realize that a squirrel can possess a highly modified feeding mechanism than to believe that the animal is not related to squirrels because of that one anomalous feature. But what was done was to ignore all but the dentition and then to seek out among all the thousands of different rodent tooth patterns those few that agree, classifying the bearers

together in one group. In the case of *Eupetaurus*, the group to which the genus was referred was itself an unnatural association of unrelated but convergent genera on opposite sides of the Atlantic Ocean. Differences in morphology and geographic occurrence from other supposedly related members of the group led to the creation of a separate family, the Eupetauridae, for *Eupetaurus* alone. Thus the most interesting and theoretically significant facts about *Eupetaurus* and *Iomys* were obscured by an analysis which made use of only a small part of the available body of data. These facts are that *Eupetaurus* and *Iomys* are merely flying squirrels which have modified their feeding mechanism, each in its own way. *Iomys* has changed little from the ancestral dental pattern, but *Eupetaurus* has changed its dental pattern sufficiently to require considerable analysis before the pattern can be interpreted. But interpreted it can be, and when analyzed it proves to be only a modification of the dentition of *Petaurista*. The skulls of *Iomys* and *Eupetaurus* can be determined to be sciurid almost at a glance. The question, then, can be asked: Is the amount of differentiation sufficient to require the separation of these dentally odd sciurid derivatives as distinct families or subfamilies? They are not raised to such high rank in this paper, though elevation to the rank of tribes within the Petauristinae may eventually prove useful when enough data are available to give a reasonably balanced account of their total morphology, ancestry, and geographic distribution. The dental differences from *Glaucomys*-like petauristines are not really very great in *Iomys*, and the differences from *Petaurista* exhibited by *Eupetaurus* are mainly the result of the high-crowned teeth of the latter. Once interlocking occlusion is abandoned, the dental pattern of either the upper or the lower cheek teeth is free to shift to a design that produces the greatest strength and resistance to infection combined with the necessary roughness of the tritulating surface. Such a pattern may be quite different from one that must also interlock with its opposite counterpart. The petauristine genus *Eupetaurus* has, indeed, made an important functional shift in the nature of its feeding mechanism, but at present it seems best to regard the genus as merely a highly modified petauristine sciurid rather than as the sole member of a monotypic family.

The adaptive shift of the *Eupetaurus* feeding mechanism is potentially of the sort that leads taxonomists to propose higher categories. In effect, *Eupetaurus* is presently observable at a point in time, the Recent, when it is potentially the ancestor of a higher category within the Rodentia, but as yet no taxonomic radiation into many genera, all with the same basic adaptation, has occurred.

The differentiation of the Recent genus *Eupetaurus* from a *Petaurista*-like sciurid provides a significant parallel to the derivation of various dentally

high-crowned rodents from sciuravid and paramyid stock in the early and middle Tertiary. The adaptive shift of the feeding mechanism is analogous to the shifts that led to the distinctive morphology of the dentition of beavers, mylagaulids, eutypomyids, and numerous other high-crowned rodents. The principal difference between the adaptive shift of *Eupe-
taurus* and that of the other high-crowned rodent groups is that in *Eupe-
taurus* the shift has not proceeded far and there has been no proliferation of genera. *Eupe-
taurus* is still basically a flying squirrel. When its habits become known, it may be expected that they will prove to be unusual, as Thomas long ago suggested.

MATERIAL STUDIED

With the exception of *Glaucomys* and *Petaurista*, a list of the skulls and jaws of various Recent petauristine genera that were studied in the course of preparation of this paper is given here, essentially with the same aim as that of Moore (1959, pp. 202–204) for the Recent Sciurinae. Many specimens representing numerous species and subspecies of *Petaurista* and *Glaucomys* were seen, but it would serve no particular purpose to list them all. In addition to the skeletal material, numerous skins not accompanied by skulls or jaws were studied. It should be emphasized that the following list in no way expresses a considered opinion as to the validity of the species and subspecies mentioned, which are merely accepted on the basis of the literature, but their placement in genera has been checked carefully.

Eoglaucomys fimbriatus: U.S.N.M. Nos. 35490, 35492, 35494, 35496, 63468, 173361–173368, 173370–173373, 174082, 201086

Glaucomys volans: Large sample in the American Museum of Natural History

Glaucomys sabrinus: Large sample in the American Museum of Natural History

Pteromys momonga: U.S.N.M. No. 14240; A.M.N.H. No. 184566

Pteromys volans aluco: A.M.N.H. Nos. 85466, 85487

Pteromys volans incanus: A.M.N.H. Nos. 19526, 19534

Pteromys (Olisthomys) morrisoni: A.M.N.H. No. 113031

Iomys horsfieldi: U.S.N.M. Nos. 151792, 252321, 292653, 292654; A.M.N.H. Nos. 185169, 185170; A.M.N.H.:A. No. 103313

Aeromys tephromelas: U.S.N.M. Nos. 283511, 291285

Aeromys bartelsi: U.S.N.M. No. 267398

Aeromys phaeomelas: U.S.N.M. Nos. 196743, 292649, 292650

Aeromys thomasi: U.S.N.M. No. 317237

Petinomys hageni: U.S.N.M. Nos. 143344, 143345

Petinomys maerens: A.M.N.H.:A. Nos. 103149–103151

Petinomys lugens: U.S.N.M. Nos. 252318–252320, 252322–252324, 252326, 252327

Petinomys vordermanni: U.S.N.M. No. 124986

- Petinomys layardi*: A.M.N.H. No. 150063
Petinomys crinitus: M.C.Z. No. 35232; C.N.H.M. Nos. 87438–87441
Hylopetes phayrei probus: A.M.N.H. Nos. 163552–163564
Hylopetes phayrei phayrei: U.S.N.M. Nos. 123941, 123932, 123933
Hylopetes phayrei anchises: M.C.Z. Nos. 35775, 35777, 35778
Hylopetes phayrei laotum: M.C.Z. Nos. 35780–35783, 35900; U.S.N.M. Nos. 253580, 260621–260624
Hylopetes alboniger: M.C.Z. Nos. 27833, 28087
Hylopetes alboniger orinus: A.M.N.H. Nos. 114884–114886
Hylopetes everetti: M.C.Z. No. 36378; U.S.N.M. Nos. 104625, 258237
Hylopetes belone: M.C.Z. No. 23792
Hylopetes nigripes: A.M.N.H. Nos. 29719–29723; C.N.H.M. Nos. 63030, 63031; U.S.N.M. No. 144959
*Hylopetes lepidus*¹: U.S.N.M. No. 38251; A.M.N.H. No. 54822
*Hylopetes electilis*²: A.M.N.H. Nos. 58158–58164, 58166–58168, 58171, 58172, 58175–58182
Hylopetes sp.?: U.S.N.M. Nos. 261082, 261083, 294887, 294888, 294893, 294895–294897, 296804
Belomys pearsoni: U.S.N.M. No. 257845; A.M.N.H. No. 114889
Belomys pearsoni blandus: M.C.Z. No. 38197; A.M.N.H. Nos. 87419, 87420
Belomys sp.: A.M.N.H. Nos. 167889, 167890
Trogopterus edithae: M.C.Z. Nos. 28083–28085; U.S.N.M. Nos. 241271, 258520
Trogopterus xanthipes: U.S.N.M. Nos. 258980, 268872; A.M.N.H. No. 111355
Aeretes melanopterus: M.C.Z. Nos. 19993, 19994, 21095; A.M.N.H. Nos. 45328, 56933
Petaurista: Numerous examples of more than a dozen species were investigated. *Petaurista* is quite common in collections. The most important specimens seen were M.C.Z. Nos. 23907, 23908, 23910, and 23911. These are all referable to *Petaurista xanthotis*, at once the most aberrant and *Eupetaurus*-like species presently referred to *Petaurista*.
Eupetaurus cinereus: B.N.H.S. No. M.1856

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¹ Ellerman and Morrison-Scott (1955, p. 31) have pointed out that the type specimen of *Hylopetes sagitta* belongs to a species of *Petinomys*. They have therefore revived *Hylopetes lepidus* (Horsfield).

² Ellerman (1940, p. 301) placed this species in *Petinomys*.

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