BULLETIN OF THE PEABODY MUSEUM OF NATURAL HISTORY, YALE UNIVERSITY

The *Bulletin of the Peabody Museum of Natural History* was published as peer-reviewed monographs from inception in 1925 through 2004. Volumes reported on original research in the natural sciences based on the collections of the Peabody Museum of Natural History at Yale University, covering diverse topics that include evolution, phylogeny, taxonomy, systematics, biology, botany, zoology, invertebrate and vertebrate paleontology and paleoecology, paleobotany, and archaeology.

Beginning with Volume 47 (2006), the *Bulletin of the Peabody Museum of Natural History* was converted to a journal format.
Journal issues are available from BioOne Complete at https://bioone.org/.

The original monograph series incorporated the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication with Volume 19, Article 2 (1967). The *Postilla* series, which ceased publication with Number 232 (2004), was merged into the journal. These archives are available through EliScholar, a digital platform for scholarly publishing provided by Yale University Library at https://elischolar.library.yale.edu/.

This work is licensed under a Creative Commons Attribution-NonCommercial-ShareAlike 4.0 International License.
https://creativecommons.org/licenses/by-nc-sa/4.0/

Yale PEABODY MUSEUM OF NATURAL HISTORY

P.O. Box 208118 | New Haven CT 06520-8118 USA | peabody.yale.edu

PEABODY MUSEUM OF NATURAL HISTORY
YALE UNIVERSITY
BULLETIN 28

Early Cenozoic Mammalian Faunas
Fayum Province, Egypt

Part I
African Oligocene Mammals: Introduction, History of Study, and Faunal Succession

ELWYN L. SIMONS
Department of Geology and
Peabody Museum, Yale University
New Haven, Connecticut

Part II
The African Oligocene Rodentia

ALBERT E. WOOD
Department of Biology
Amherst College
Amherst, Massachusetts

New Haven, Connecticut
November 20, 1968

Bulletins published by the Peabody Museum of Natural History, Yale University, are numbered consecutively as independent monographs and appear at irregular intervals. Shorter papers are published at frequent intervals in the Peabody Museum *Postilla* series.

The *Peabody Museum Bulletin* incorporates the *Bulletin of the Bingham Oceanographic Collection,* which ceased independent publication after Vol. 19, Article 2 (1967).

Communications concerning purchase or exchange of publications should be addressed to the Publications Office, Peabody Museum of Natural History, Yale University, New Haven, Connecticut 06520, U.S.A.

Printed in the United States of America

CONTENTS

Part I African Oligocene Mammals: Introduction, History of Study, and Faunal Succession

Part II The African Oligocene Rodentia

FIGURES

Part I

Part II

TABLES

YALE UNIVERSITY, PEABODY MUSEUM OF NATURAL HISTORY BULLETIN 28
105 p., 18 figs., 1968

PART I. AFRICAN OLIGOCENE MAMMALS: INTRODUCTION, HISTORY OF STUDY, AND FAUNAL SUCCESSION

ELWYN L. SIMONS

1. INTRODUCTION

The vertebrate microfaunas described in this paper have been recovered as a result of six seasons of paleontological exploration in the upper Eocene and Oligocene badlands exposures of the Fayum Province, U.A.R., a project initiated and directed by E. L. Simons. The seasonal expeditions took place annually from the winter of 1961–62 up to the present (1967). This field research has been supported to date by grants G-18102, P-433, and GP-3547 in Geology, National Science Foundation; by Smithsonian Foreign Currency Program grants 5 and 23; by Higgins and Sheffield scientific funds from Yale University; the John T. Doneghy Fund, Peabody Museum, Yale University; the Boise Fund of Oxford University; and the Wenner-Gren Foundation of New York. This Bulletin has been published with the aid of a National Science Foundation Publication Grant, No. GN-528. Our expeditions have been greatly facilitated by personnel and equipment provided by the Ministry of Industry, U.A.R., (Department of Geological and Mineralogical Research, and through the Geological Museum, Cairo), and by the Department of Geology, Cairo University. Other field equipment and assistance has also been provided on occasion by the Pan American–U.A.R. Oil Company, Cairo, U.A.R.

Although the area to the northwest of Lake Qarun, from which these collections were secured, has been the object of several previous seasons of paleontological research (some of considerable duration), only a few specimens of smaller Mammalia were previously recovered. It had been supposed formerly that depositional conditions had not favored the preservation of small fossils. In general, early collectors, many of whom were not trained vertebrate paleontologists, appear to have focused their attention on recovery of the larger faunal elements, particularly specimens of such large, easily noticed continental and marine vertebrates as *Arsinoitherium, Palaeomastodon,* hyaenodont creodonts, anthracotheres, hyracoids, fossil whales and sea cows, crocodiles, turtles, and pristid and siluroid fishes. The more difficult search for smaller land mammals was not emphasized. Nevertheless a sufficient number of these smaller vertebrates were recovered to indicate that they were indeed preserved on occasion in this interbedded marine, deltaic, and continental sedimentary sequence. Although the bone-bearing sediments of the Jebel el Qatrani Formation are typically coarse sands or gravels, small, fragile mammal bones occasionally occur in fine sand lenses. For example, these rare finds included an extremely delicate frontal bone of an anthropoid primate discovered by Markgraf in 1908 (Simons, 1959). Of the twenty or so previously recovered specimens of small mammals, eight belonged to Primates and eight to rodents. Three other small specimens were referable to Macroscelididae, Carnivora, and Chiroptera. In 1959, when our project was initiated, it thus appeared that further fieldwork might yield more extensive microfaunal remains, and this has subsequently proved to be the case.

Abundant vertebrate fossils of microfaunal size have been recovered by the Yale expeditions through a combination of screening unconsolidated sands, quarrying of claygall-rich channel sands, and collecting from wind-eroding unconsolidated sands. Diligent search for new bone-bearing sites throughout the entire section of continental and near-shore sediments of the escarpments north of Birket Qarun has produced a very considerable enlargement of the known Fayum Oligocene microvertebrate faunas. Two indices of the scope of these new additions will suffice. Before 1961 only eight jaws of Rodentia were known from the early Oligocene Jebel el Qatrani Formation of the Fayum. Finds of mandibles and maxillae of members of this order made by the Yale expeditions now total more than 200. Of Primates from these beds, parts of five mandibles were previously known. These jaws included the type species of several much discussed genera of archaic Anthropoidea, *Propliopithecus, Moeripithecus, Apidium,* and *Parapithecus.* Our recent expeditions have secured dozens of additional primate jaws or jaw fragments (including the first known maxillae of any Old World Oligocene primate species) and much more than this number of isolated teeth. These finds, together with other materials of the smaller vertebrates recovered during the recent field seasons, allow for a new and more meaningful assessment of the environment and history of the North African Middle Tertiary.

Apart from the effort to secure better representation of the mammalian microfauna of these fluviatile and marine sediments, several other objectives motivated the field research reported here. These objectives were as follows:

1. To determine the exact stratigraphic position of earlier quarries and localities in the Oligocene lower fossil wood zone (lower portion of the Jebel el Qatrani Formation) which overlies the marine beds of the Eocene Qasr el-Sagha Formation. Almost all previously discovered sites were relocated and the entire fossil wood deposits surveyed for additional areas profitable for quarrying operations. During the course of this work, Yale Quarry E in the lower fossil wood zone was opened a few miles due east of the main region of excavation at or near Quarry A, which had been the main site of the expeditions of Beadnell (1898–1904), of the American Museum of Natural History (1906–07), and of the University of California, Berkeley (1947). An extensive Oligocene vertebrate fauna recorded from this new site included most of the previously known large mammal species together with a new small primate genus and species *Oligo-*

pithecus savagei (Simons, 1962) and a diversified series of rodents, proviverrids, and hyracoids, including several new species. Here also were found several silicified fruits or seedpods which appear to be referable to the family Araceae and to one of the genera *Epipremnum, Scindapsus,* or *Cyrtosperma.* Present species of these genera are marsh-dwelling or riparian plants. Fossil woods from these beds cannot be meaningfully identified. Elsewhere in the fossil wood zone a representative sample of Fayum Oligocene Mammalia was obtained, and north of American Museum Quarry A, mandibles of two new species of small proviverrids were secured.

2. To clarify the anatomy of such African Eocene mammals as *Moeritherium* and *Barytherium* by further collecting in the uppermost part of the primarily transitional marine section of the Qasr el-Sagha Formation at the Qasr el-Sagha escarpment, and, if possible, to add to knowledge of such terrestrial vertebrates of the North African Eocene as occasionally occur in these beds. Beds 16 and 17 of Beadnell (1905) in this escarpment were walked out over a total distance of about thirty-five miles. In both beds a deltaic depositional facies (Vondra, personal communication, 1966) is indicated and in them many additional archaeocete whales, sirenians, turtles, sea-snakes, gavials, and pristid and siluroid fishes were collected. Three important sites containing remains of the archaic proboscidean *Moeritherium* were discovered. The first of these sites, found in December 1961, on excavation revealed a partial skeleton of *Moeritherium* sp., unfortunately lacking all parts of the limb skeleton.

This material, taken together with numerous unassociated postcranial remains, particularly of the limbs and feet from a second site, Yale Quarry H, in bed 17, provides the first extensive materials for analysis of overall postcranial anatomy in these earliest proboscideans. Perhaps of significance are certain postcranial resemblances between *Moeritherium* and members of the exotic Miocene and Pliocene circum-Pacific order, Desmostylia. In the course of this phase of our paleontological exploration in the Qasr el-Sagha Formation a jaw, evidently of *Apterodon,* and calcanea of anthracotheres were recovered. These are the oldest well-preserved specimens of African Tertiary land mammals.

3. To recover more extensive vertebrate faunas from the poorly fossiliferous upper 500 feet of the Jebel el Qatrani Formation. Near the base of this part of the section, approximately 140 feet* above the main general level of fossil wood zone quarries (A, B, C, D, E, and F) a minor stream channel rich in fossils (Quarry G) was discovered. Together with a considerable series of other mammalian species, Quarry G has yielded to date about 20 partial upper and lower dentitions of the archaic catarrhine primate, *Apidium moustafai,* and a series of larger isolated teeth which appear to represent two species of *Propliopithecus, P. haeckeli* and *P. markgrafi.* Dozens of maxillae and mandibles of rodents were discovered in this quarry.

At a level about 150 feet above Quarry G, and at about the same distance be-

---

* It should be pointed out that these Oligocene fossil quarries are in irregularly deposited (lenticular) channel sands and gravels cut into other sands or flood-plain deposits. Thus, measurement of vertical distance between certain quarry levels varies from place to place. The fossil wood zones of early authors are actually broad complexes of fluviatile deposits consisting of sand and gravel channels cut into mainly unfossiliferous flood-plain deposits. The top of the lower fossil wood zone lies approximately 300 feet below the bottom of the upper fossil wood zone.

low the widespread basalt that caps the Oligocene Jebel el Qatrani Formation in the Fayum depression, an important new area (Yale Quarry I) yielding hundreds of vertebrate fossils was discovered in January 1963. In December 1963 Yale Quarry J was opened at the same level but farther east. These lie in the "upper level" or upper fossil wood zone of Osborn (1908, 1909). More recently a number of other sparingly fossiliferous localities at about this level have been found (localities or quarries K, L, M, N, O, P, Q, and R). Preliminary faunal analysis indicates that these sites contain new, later Oligocene species—most being different from any found at the lower quarries. Comparison with certain material collected by the American Museum in 1907 indicates that the upper fossil wood zone is the approximate stratigraphic horizon of recovery of a few species described by Osborn (1908, 1909) as having come from "upon the upper level." Osborn's species, based on type specimens collected in 1906–07 from this upper level, include *Apidium phiomense, Metaphiomys beadnelli,* and *Metasinopa fraasi.* The fauna from the upper fossil-bearing horizon of the Egyptian Oligocene is of particular interest because it is the latest occurring series of land vertebrates known, to date, from the Oligocene of the African continent and might be of Middle or Late Oligocene age. Direct comparison of materials from the level of Quarry I has shown that anthracotheres and primates from this horizon are smaller and more primitive than those of the early Miocene of Kenya. These faunal differences indicate that a considerable lapse of time must separate the East African and Egyptian Oligocene faunas, but Wood's studies of Fayum rodents reported here indicate definite evolutionary ties with the rodents of the East African Miocene. These in turn are currently under study by Lavocat in Paris.

During December and January 1963–66, excellent mandibular rami of several new primate species were recovered at Quarry I, thanks in large part to the able assistance of G. E. Meyer. Two of these, *Aegyptopithecus zeuxis* and *Aeolopithecus chirobates* were named in a previous paper (Simons, 1965). Finally, a K/Ar date recently calculated by G. Curtis, University of California, Berkeley, from a sample of the basalt flow that lies about 250 feet above the level of Quarry I, stands at approximately 24.7 million years. Richard Armstrong at Yale has recently dated another sample of this basalt at 27 ± 3 million years. These suggest rough concordance at about 25 million years; in other words, the basalt was apparently formed just at the beginning of the Miocene. Dates from sediments occurring lower in the Fayum Oligocene section may be forthcoming from Vondra's research.

ACKNOWLEDGMENTS

From the number of persons, far too large for me to enumerate accurately, who have been helpful in the furtherance of the project reported here, I should particularly like to thank Dr. Y. S. Moustafa, vertebrate paleontologist, without whom it would have been difficult to initiate our program in the field in Egypt. Thanks are due also to Dr. Riad S. Higazy, former director of the General Egyptian Organization for Geological Research and Mining, United Arab Republic, who initially welcomed the possibility of renewed paleontological field studies in the Fayum badlands, to the present director Dr. Rushdi Said, and to Dr. Osman

Moharam, director of the Geological Survey and his colleague Dr. Abdul El Al Fawzi, both of whom have been extremely considerate in furthering our cooperative scientific venture. Dr. Said was also helpful in discussing with us the possible location of new Cenozoic vertebrate sites in Egypt. Drs. A. Huzaiyin and Darwish el Farr, and Mr. Baher el Khashab of the Geological Survey and Geological Museum, Cairo, have also provided most useful services and facilities.

During the project's six seasons the writer has had many able coworkers and assistants in the field. In 1961–62 these were D. E. Savage, University of California, Berkeley; D. E. Russell, Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris; P. E. Lemke, Peabody Museum, Yale University; and Y. S. Moustafa, S. Moustafa, and a field crew varying from seven to nine, directed by F. S. Faheem, who were generously supplied by the Geological Survey of Egypt.

Most valuable contributions to our second season (1962–63) were made by A. D. Lewis of the Museum of Comparative Zoology, Harvard, and J. G. Mead from the Peabody Museum, Yale University. Services were also provided by Y. S. Moustafa as research associate; by S. Moustafa and E. M. Helmi as interpreters; and by M. A. Rahman and A. M. Ahmed as field assistants made available to our expedition by the General Egyptian Organization for Geological Research and Mining, U.A.R. Our third-season staff included Mr. and Mrs. G. E. Meyer and C. Seymour III from Yale; Y. S. Moustafa and S. Nagib, Cairo University; and U. Abdella, M. S. Ahmed, and A. L. Mohamed from the Geological Survey. During our fourth season, T. Walsh, G. E. Meyer, D. E. Pilbeam, and J. A. Smith from Yale University were assisted in the field by B. el Khashab, Cairo Museum, and by U. Adbella, M. S. Ahmed, M. B. Mahmoud, and I. L. Fadel, our previously trained field collectors.

The fifth-season party consisted of Dr. C. F. Vondra and B. E. Bowen, Iowa State University, Ames, Iowa; L. G. Tanner, University of Nebraska State Museum, Lincoln, Nebraska; G. E. Meyer from Yale; and B. el Khashab, U. A. Ibrahim, S. M. Osman, and M. M. Saber from the Geological Survey.

In our sixth season the party included G. E. Meyer and J. S. Boyer from Yale; L. G. Tanner, University of Nebraska State Museum; C. F. Vondra, B. E. Bowen, and D. W. Powers from Iowa State University; and B. el Khashab, U. A. Ibrahim, S. S. Osman, and H. H. Ahmed from the Survey.

Thanks are also due A. Huzaiyin, D. el Farr, and M. el Ramly of the Geological Museum, Cairo; K. D. Adam, Stuttgart, Germany; A. J. Sutcliffe, British Museum (Natural History); and M. C. McKenna, American Museum of Natural History; for making available collections of Fayum vertebrates in their respective institutions for research and study by the authors. Field collection data and photographs of specimens secured by the University of California (Berkeley) Pan-African Expedition of 1947 were also supplied through the courtesy of D. E. Savage. Drs. C. F. Vondra and M. C. McKenna kindly read and criticized the manuscript of Part I, and Dr. C. C. Black that of Part II.

The figures were prepared by A. E. Wood and the section is reproduced by courtesy of Scientific American, Inc.

2. HISTORY OF THE STUDY

The Fayum Province of Egypt lies in an approximately circular depression with its southern and eastern margins situated on an average about 10 miles to the west of the Beni Suef Province of the Nile valley. In the northwestern quadrant of this depression lies the brackish water Birket (Lake) Qarun, the "Lake Moeris" of Herodotus. This largest lake in North Africa, situated about 60 to 70 miles to the southwest of Cairo, has a main axis (approximately 20 miles long) trending east-west. The present lake surface lies about 147 feet below sea level. However, in late Pleistocene times and intermittently up to the end of the Ptolemaic period the surface stand of the lake was at a higher elevation, and the prehistoric lake clearly occupied a much larger area. The Fayum depression itself has an area of approximately 1200 square miles.

The localities of the celebrated Fayum vertebrate faunas are distributed mainly on a bench averaging about 3½ miles in width and about 40–50 miles long, situated immediately below a basalt and/or gravel-capped escarpment, Gebel Qatran or Jebel el Qatrani, trending from northeast to southwest on the north side of Lake Qarun. To the south this bench drops off toward the lake in a lower escarpment where the late Eocene Qasr el-Sagha Formation is exposed. Near the top of the latter series of cliffs species of the earliest known African continental vertebrates, *Moeritherium, Barytherium,* and possibly *Apterodon* and *Brachyodus* have been found.

Initial discovery of fossil vertebrates in the Fayum was made by the noted geologist and explorer, Georg Schweinfurth (1836–1925), who in 1877 undertook the first detailed geological study of the Eastern Desert of Egypt (Schweinfurth, 1886). During the course of geological explorations around Lake Qarun in 1879, he secured a series of invertebrate and vertebrate remains from an island near the center of Lake Qarun, Geziret el-Qorn. These materials included shark teeth and cetacean bones, which were turned over to the German paleontologist W. Dames for description in 1883. At that time he (Dames, 1883) identified the cetacean remains as belonging to a species of archeocete whale. In a later publication (1894), with further material supplied by Schweinfurth from localities in the Qasr el-Sagha escarpment, Dames diagnosed these materials as belonging to a new species *Dorudon (= Zeuglodon) osiris.*

Beginning in October 1898, further geological exploration of the Fayum depression was initiated by the Egyptian Geological Survey under the direction of H. J. L. Beadnell. Mapping and section measurement undertaken by Beadnell's group on the eastern edge of the depression near the village of Sela was carried northward during 1898 along the eastern margin of cultivated land and then westward across the north shore of Lake Qarun to the outlying hill, Gar el Gehannam,* which lies about 20 miles to the southwest of the western tip of Lake Qarun. Some localities investigated during this traverse of 1898 yielded bones of fossil vertebrates. Returning to these areas in April 1901, Beadnell's group, together with Dr. C. W. Andrews, then on a collecting expedition from the British Museum (Natural History) to secure Recent Egyptian mammals, made further and more significant discoveries. Remains of the sea-snake *Pterosphenus* were recovered by Andrews near the western end of the lake when these localities were revisited. A few days later, while making a descent of the Qasr el-Sagha escarpment at a point about two and a half miles northwest of Qasr el-Sagha, this group discovered an extensive new series of fossil vertebrates which were later to be described under the names of *Barytherium, Moeritherium, Eosiren,* and *Gigantophis.* During the course of a three weeks' intensive collecting campaign (1901) in this immediate vicinity a camelman brought in a strange tooth from a site lying higher in the section and several miles to the north. At this new site was found more of the dentition which became the type of *Palaeomastodon beadnelli* Andrews (1901a).

In the winters of 1901–04 the Egyptian Survey party under the direction of Beadnell concentrated primarily on this fossiliferous continental horizon which came to be known as the "fossil wood zone." It was during these seasons that the material upon which type species of the genera *Arsinoitherium, Phiomia, Saghatherium, Geniohyus,* and *Megalohyrax,* among others, was recovered from continental sediments overlying the marine beds in which the first finds of land mammals had been made.

The scientific interest aroused by Andrews' and Beadnell's reports of these discoveries can hardly be imagined today. The ancient and unique land-mammal faunas of the Dark Continent were at last being discovered, and although these events took place over 60 years ago, we still know almost nothing of the land vertebrates of the African Paleocene apart from what has been found in the Egyptian Fayum. Andrews and Beadnell promptly set about the task of reporting and describing their finds which in various ways involved them with the question of origin and radiation of numerous major categories of Mammalia, in particular the Orders Proboscidea, Cetacea, Sirenia, Hyracoidea, and Embrithopoda. Soon after their discovery some of these materials were published by Andrews (1901 a–e) whose papers included descriptions of the type species of the primitive Proboscidea, *Moeritherium* and *Palaeomastodon. Barytherium,* a gigantic mammal then of uncertain ordinal position, was also described at this time. Meanwhile, Beadnell (1902) described and illustrated the huge and bizarre four-horned ungulate *Arsinoitherium,* which was subsequently placed in a distinct order, Embrithopoda, by Andrews (1906). Together Andrews and Beadnell (1902) proposed a third ancient proboscidean genus, *Phiomia,* and described an ancient hyracoid *Saghatherium,* both from the early Oligocene fossil wood zone. Andrews (1903) established another genus of giant hyracoid, *Megalohyrax,* and in 1904 named a third member of this order, *Geniohyus.* In 1905, follow-

---

* Beadnell's spelling (1905). This hill is also referred to variously as Gar, Garet, Quaret, and Gabel Gehannam (or Gehennem).

ing these preliminary notes, Beadnell's monograph on the "Topography and geology of the Fayûm Province of Egypt" appeared, and in the following year Andrews' compendious study, "A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt," was published by the British Museum.

After these discoveries and contributions by British and Egyptian geologists and mammalogists, the Fayum localities were opened by the Egyptian Geological Survey to outside collectors, sometimes with and sometimes without the cooperation of the Survey; the intensity of collecting in the region increased in the years following.

In January 1906, Henry Fairfield Osborn sailed for Cairo with his assistants from the American Museum of Natural History, Walter Granger and George Olsen, armed with a letter of introduction to Lord Cromer and to the director of the Egyptian Geological Survey from no less a personage than President Theodore Roosevelt. By February 5 this expedition had set up their main camp in the center of the lower fossil wood zone and during the following weeks they enlarged the two main excavations started by Beadnell into American Museum Quarries A and B. For three weeks Osborn, accompanied by H. T. Farrier of the Survey, reconnoitered the area and made an extended collecting trip to "Zeuglodon" valley, 20 miles to the southwest of the western tip of Birket Qarun. He then departed leaving Walter Granger in charge.

For some time before the arrival of this expedition, Richard Markgraf, a German geologist and private collector, had been securing Fayum vertebrates primarily for Dr. Eberhard Fraas of Stuttgart but also for other institutions in Germany. Markgraf was employed by the American Museum to collect jointly with Granger's party and during the remainder of the field season, which lasted until June 14, 1906, he continued the work of exploration of the fossil wood zone, bringing in scattered materials, mainly from the northeast of Quarries A and B.

The German collector was the first to discover a method for locating the smaller land vertebrates in this region. Basically the method involves digging back far enough into those slopes where innocuous-looking, small bone-claygall-coprolitic layers are exposed so that comparatively unweathered portions of these thin beds or lenses can then be quarried or left for a while to be wind-eroded. To my knowledge nearly all the smaller Mammalia of the Egyptian Oligocene have been recovered from such horizons, and not from the major quarries such as A, B, C, and D, where stronger stream currents had locally washed together much larger bone fragments, such as femora, pelves, and partial skulls of *Arsinoitherium, Palaeomastodon,* etc. Markgraf's method of collecting is entirely adapted to the rather unusual conditions of sedimentation of the Jebel el Qatrani Formation and was described by Granger. By applying this method Markgraf personally recovered nearly all of the small Mammalia of the Fayum known to the early workers, including the types on which *Parapithecus, Apidium, Propliopithecus,* and *Moeripithecus* were based, and a primate frontal bone, fragments of small birds, chiropteran bones, and macroscelidid and rodent jaws. Markgraf continued to live at Senurus in the Fayum and to collect for various institutions.

The greater part of the season of 1906 was occupied in collecting large Mammalia in the Quarries A and B originally opened by Beadnell. The search for larger mammals conformed to Osborn's wishes in the matter. Primarily he appears to have wanted materials for exhibition, judging from his correspondence of the period and from passages such as the following: "The finding of the two heads of *Moeritherium* and *Palaeomastodon* was the chief object of our expedition from the purely museum standpoint." (Osborn, 1907, p. 827)

From the more than 500 specimens secured by the American Museum nearly all the new additions to the fauna came from scattered localities and not from the main quarries. Perhaps the primary contributions to paleontological knowledge made by this expedition were the recovery of the first rodents from the African Oligocene and the discovery of the upper fossil wood horizon. The latter "zone"—actually a complex of three or more superposed channel systems only 20 to 80 feet thick (where exposed)—is not as thick as the lower fossil wood zone of the Jebel el Qatrani Formation which ranges from approximately 120 to 180 feet. Both these "zones" are similar lithologically, consisting mainly of coarse, unconsolidated stream channel deposits separated by fine-grained mudstones, freshwater limestones, and other mainly unfossiliferous flood-plain deposits. From the upper fossil wood zone given by Osborn (1908, p. 270) as about 200 feet below the basalt on the bench "above" Quarries A and B, which are in the lower fossil wood zone, came the types of a rodent *Metaphiomys beadnelli,* a primate *Apidium phiomense,* and a creodont *Metasinopa fraasi.* New forms recovered in Quarry A included two species of creodonts *Pterodon leptognathus* and *Pterodon phiomensis* described by Osborn (1909), *Ptolemaia lyonsi* Osborn (1908) of uncertain ordinal position, and the rodent *Phiomys andrewsi.* Following Osborn's preliminary notes of 1908 and 1909, few additional studies of the American Museum Fayum collections were published—apart from Matsumoto's contributions of 1922, 1923, and 1924 on *Moeritherium, Palaeomastodon, Phiomia,* and in 1926 on hyracoids. Some further elaboration on the Fayum Proboscidea was included in Osborn's monograph of 1936.

The very large collection of vertebrates at the Natural History Museum in Stuttgart was assembled by Markgraf in the years before 1911. Professor E. Fraas, who was in charge of this material, assigned it for study and publication to Dr. Max Schlosser of Munich. The Stuttgart fossils included three new species of primates, as well as creodonts, rodents, and problematical insectivore and bat remains. These were described by Schlosser (1911), who also had available some specimens collected by Stromer and Markgraf for the Munich Paleontological-Geological Collections. A lower jaw of *Mixohyrax* from the Basel Museum and a skull of *Moeritherium* from the Frankfort Senkenberg Museum completed the material available to Schlosser. In 1913 Dr. Martin Schmidt completed a revision of the Fayum anthracotheres which was the last major contribution by European authors to the study of Egyptian Oligocene vertebrates.

In 1947, as part of the University of California Pan-African Expedition, further paleontological exploration and mapping was conducted in the Fayum badlands. Participants were Drs. R. H. Denison and H. B. S. Cooke and Professors P. E. P. Deraniyagala and V. L. vanderHoof. These workers opened several small quarries in the area of the American Museum Quarry A and secured a representative collection of anthracotheres, arsinoitheres, proboscideans, and hyaenodont creodonts.

Following this expedition little vertebrate fossil collecting was done in the Fayum until the arrival of the first Yale expedition in November 1961. However, in 1950, Y. S. Moustafa had discovered an interesting skull of *Prozeuglodon* which was figured and described by him (1954).

In 1958 a primate frontal bone was located in the American Museum collections and its significance as the only known part of a skull of an Old World Oligocene primate was recognized (Simons, 1959). At that time some doubts had been raised by Hürzeler (1956) and Piveteau (1957) as to whether *Apidium* and *Parapithecus* were truly Primates. The frontal clearly belonged to a member of Anthropoidea as it showed postorbital closure and other features (e.g., interfrontal fusion) not typical of prosimians. It was, however, of an appropriate size to belong with either *Apidium phiomense* or *Parapithecus fraasi* and thus indirectly reenforced the primate status of one or both of these species. It was speculated (Simons, 1959, p. 14) that this frontal might be of *Apidium.* Later partial confirmation of this possibility came from the discovery of an early Oligocene catarrhine primate skull from western Texas (found by Dr. J. A. Wilson in 1964) which he has named *Rooneyia* (Wilson, 1966). This has an extraordinarily similar frontal, except that postorbital closure has not developed. In 1963 a composite upper dentition of an *Apidium* species was published (Simons, 1963). Wilson (personal communication) agrees with the author that the upper dentition of *Rooneyia* is more like that of an *Apidium* species than of any other known primate. These resemblances between forms so greatly removed geographically from each other are interesting but, inasmuch as the Texas skull and the Fayum material of *Apidium* are the only published specimens of Oligocene primates with remains of upper teeth preserved, understanding the significance of their similarities will have to await fuller knowledge of Oligocene primates. Confirmation that the frontal is of *Apidium* came in the winter of 1966 when a probable association of *Apidium* teeth with an interorbital septum fragment like that of the frontal fragment described by Simons (1959) was found.

During Yale's first Fayum expedition, remains of two new primate species, *Apidium moustafai* and *Oligopithecus savagei,* were found and described (Simons, 1962). *Oligopithecus,* known only from a partial left lower jaw, has molar structure reminiscent of Eocene omomyid primates. It has been suggested (Simons, 1962, p. 9) that a slight molar bilophodonty might possibly make it pertain to an early stage in the differentiation of cercopithecoid monkeys. The materials of *Apidium moustafai* reported in the same paper showed that *Apidium* was definitely closely related to *Parapithecus fraasi* and was a member of Parapithecidae. Isolated upper molars reported at that time also suggested a phyletic relationship with the Pontian catarrhine *Oreopithecus.* This affinity proposed on the basis of lower molar homologies had earlier been pointed out (Simons, 1960).

Recently two new genera and species of primates from the upper levels of the Fayum badlands have been described (Simons, 1965). The smaller of these, *Aeolopithecus chirobates,* may be related to the gibbons. The larger, *Aegyptopithecus zeuxis,* is an excellent candidate for an ancestor of the fossil dryopithecine apes and ultimately of the living Great Apes and man.

3. FAUNAL SUCCESSION

The stratigraphy of rocks exposed on the north side of the Fayum depression was carefully described by Beadnell (1905), who published nearly a dozen detailed sections of transects of the region. However, this work is not generally available, having been published in a limited edition long out of print. Recently C. F. Vondra has gathered extensive biostratigraphic data for reinterpretation of the geologic history of the region. Consequently, the geology of the Fayum will be published separately by him when his field and laboratory studies have been completed. The names proposed by Beadnell as "Series" have precedence in American usage as "formations" and will be so referred to here. Although Said (1962, p. 101–6) mainly utilized Beadnell's terms for formations, which he redefined, he also introduced inadmissible contractions such as [Gebel] Qatrani Formation and [Wadi] Rayan, i.e. he used these formational names both with and without Gebel and Wadi. These usages are abandoned here. Said also proposed a new name, Gehannam Formation, for the "Ravine beds" discussed by Beadnell, but on present evidence this sequence cannot be sustained as lithologically different from the overlying Birket Qarun Formation. It is not the intent of the present introduction to alter the definitions of rock-stratigraphic units in the Fayum used by Beadnell except to substitute, in conformity with accepted modern American usage, the term "Formation" for his "Series,"* Rock-stratigraphic names used by Beadnell and utilized here are as follows:

Beadnell (1905)	This Paper
Basalt	Basalt
Jebel el Qatrani beds (="Fluviomarine" Series)	Jebel el Qatrani Formation
Qasr el-Sagha Series	Qasr el-Sagha Formation

The Yale expeditions have collected mainly from these two Formations of the Fayum region. Their depositional history and faunal content will be briefly considered below.

QASR EL-SAGHA FORMATION

The principal escarpment of the Fayum badlands is formed in the upper portions of the Qasr el-Sagha Formation and is well developed in the exposures

---

* Beadnell (1905) used the term "Series" in a rock-stratigraphic sense. In most instances he applied the term to mappable, lithologically homogeneous rock units, i.e. formations (Vondra, personal communication, 1967).

north of Lake Qarun. In the Fayum this Formation is composed primarily of deltaic and interdeltaic deposits. At Beadnell's type locality and section near Qasr el-Sagha temple, the Qasr el-Sagha Formation has a total thickness of 610 feet. Study of the marine invertebrate fauna from this Formation indicates that it is probably of late Bartonian age and correlative with the upper part of the Mokattam or with the overlying Maadi Formation of the Cairo region. In the Fayum, however, these late Eocene deposits are much thicker than at Maadi and differ lithologically, facts that can be related to their transitional deltaic origin. The more frequent occurrence of plant debris, land vertebrates, and distributary channel sands in the Qasr el-Sagha Formation attests to this hypothesis. Certain localities in Beadnell's beds 16 and 17 of this Formation are particularly indicative of a deltaic facies, being rich in silicified logs, in carbonaceous layers of plant material, and at some sites in proboscidean, hyaenodont, anthracothere, and chelonian remains. Northeast of the Qasr el-Sagha temple, massive cliffs of distributary channel sands indicate the presence of a large river in this area in late Eocene times.

Unpublished studies by Vondra suggest that the environment of deposition of the lower portion of this Formation at Qasr el-Sagha is interdelataic shallow marine and littoral. The upper beds are deltaic and interfinger with distributary channel sands. The foreset beds of the deltaic deposits dip, for the most part, in a northeasterly to northwesterly direction and these deposits are continuous for several miles.

The sand-sized fraction of the Qasr el-Sagha Formation is composed almost entirely of well-rounded quartz grains. The absence of feldspars indicates that the sandstones are mature—having been recycled several times or having undergone rigorous climatic (subtropical, humid) conditions in an area of low relief.

The following mammalian species have been recovered to date from the Qasr el-Sagha Formation north of Lake Qarun, Fayum Province, Egypt, U.A.R.

FOSSIL MAMMALIA FROM THE QASR EL-SAGHA FORMATION

ORDER Cetacea
SUBORDER Archaeoceti
FAMILY Dorudontidae

Dorudon elliotsmithi (Dart) 1923
Dorudon osiris (Dames) 1894
Dorudon sensitivus (Dart) 1923
Dorudon stromeri (Kellogg) 1928
Dorudon zitteli (Stromer) 1903

ORDER Proboscidea
SUBORDER Moeritherioidea
FAMILY Moeritheriidae

Moeritherium lyonsi Andrews 1901a
Moeritherium ancestrale Petronievics 1923
Moeritherium gracile Andrews 1902
Moeritherium trigodon Andrews 1904

SUBORDER Barytherioidea

FAMILY Barytheriidae

Barytherium grave (Andrews) 1901a

ORDER Sirenia

Eotheroides libycum (Andrews) 1902

ORDER Deltatheridia

SUBORDER Hyaenodontia

FAMILY Hyaenodontidae

?*Apterodon* sp. nov.

ORDER Artiodactyla

FAMILY Anthracotheriidae

?*Brachyodus* sp. nov.

JEBEL EL QATRANI FORMATION

At the top of the Qasr el-Sagha Formation, which is typically capped by a littoral coquinoidal sandstone, occurs a desert bench established as the Jebel el Qatrani Formation. In most areas to the north of the Qasr el-Sagha escarpment this lithologic unit is composed of variegated sands, gravels, and sandstones, with interbedded layers of siltstone and claystones. At infrequent intervals in the upper part of this Formation thin bands of lacustrine limestone occur, for example immediately above the Yale Quarry G.

In the basal unconsolidated sands of the Jebel el Qatrani Formation terrestrial vertebrates begin to occur in some abundance, generally associated with silicified logs and deposited in fluviatile cross-bedded quartz sand and gravel. Even though the sand and gravel grains are well-rounded, very delicate rodent jaws and other small vertebrate remains are often preserved intact, indicating that most of these fossils had not been transported far to their burial sites. Although Beadnell (1905) thought he had detected mixed "fluviomarine" molluscs in upper horizons of this Formation, he was in error; at any one locality the invertebrate fauna of the Formation is terrestrial. Thus the use by Osborn and Beadnell of the alternate term "Fluviomarine Series" for this unit in the Fayum section was a misnomer and was replaced by Beadnell's equivalent term, Jebel el Qatrani. In the lower and upper fossil wood zones deposition was entirely terrestrial, for reworked marine vertebrates and invertebrates are not present save for very rare fragments of dental batteries of rays and occasional shark teeth which are greatly outnumbered by lungfish tooth plates indicating freshwater deposition. It is far more likely that occasional elasmobranchs entered coastal fresh or brackish streams than that semimarine conditions existed at the times of deposition of the bulk of the Jebel el Qatrani sediments. Preliminary studies by C. F. Vondra (written communication, 1966) indicate that the Jebel el Qatrani Formation is entirely terrestrial in deposition. He believes this sequence could be subdivided into two members, each consisting of a channel flood-plain complex. Each such member would constitute a depositional cycle composed of: (1) fluvial aggradation first, restricted to the channel; (2) aggradation across a wide alluvial plain by a freely meandering stream, with no channeling evident at this stage; (3) development of ponds and lakes recorded by the deposition of fresh-water limestones.

Vondra reports further that: "The channel deposits consist of well-rounded quartz sandstones and quartz and chert pebble conglomerates. The flood-plain deposits are red to rust-yellow in color and contain a high admixture of red clay. Preliminary evidence suggests rigorous climatic conditions—probably humid, subtropical to tropical—in an area of low relief. Dense forests probably existed at least along the major streams; however, savannahs may have existed in interstream areas. Silicified logs are abundant in both the lower and upper channels [fossil wood zones]. Although the logs show varying degrees of abrasion, many possess roots and branches extending laterally from them, indicating that they were not transported any great distance before burial. There are virtually no other plant remains preserved in the Jebel el Qatrani Formation with the exception of occasional horizons of friable sandstone that contain thin root-like, calcareous, vertical, sand projections. However, this does not mean that abundant vegetation or forests did not exist during the Oliogocene. The upper portion of both members is characterized by several very calcareous, well-indurated sandstones which are incrusted with a druse of sand-calcite crystals. These may represent caliches which may have formed during brief intervals of aridity." (Vondra, written communication, 1966.)

The Jebel el Qatrani Formation conformably overlies the Qasr el-Sagha Formation, but unlike the underlying formations of the Fayum section it varies greatly in thickness laterally. According to Vondra (personal communication, 1967) this is the result of pre-Miocene erosion. Near the main fossil vertebrate localities, primarily to the south and southwest of the twin basalt-capped conical hills Widan el-Faras (ears of the mare), Vondra has measured a maximum thickness of 947 feet. Southwestward along the bench formed in the lower three-quarters of this formation, the lithology becomes increasingly uniform, with the occurrence of sands and sandstones predominating; the relief decreases until the minor escarpments in this area merge into the undulating, gravel-covered desert about 14 miles west of Gar el Gehannam. Earlier authors have speculated that the Jebel el Qatrani Formation represents the deposits of a major river, discussed as the "Urnil" by Blanckenhorn (1900, p. 458), which possibly was flowing from higher land containing exposures of the Nubian Sandstone to the southwest. This river or rivers had nothing to do with the present Nile.

The following is a list of all the species collected from this Formation.

FOSSIL MAMMALS FROM THE JEBEL EL QUATRANI FORMATION*

ORDER Insectivora

SUBORDER Macroscelidea

---

* The majority of these species are presumed to be from the lower fossil wood zone (level of Fayum quarries A, B, C, D, E, and F), but the localities of most early types are not known. If the species is known to occur in the upper levels in quarries G, I, J, M, or a level equivalent to one of these, the species entry concludes with the letter of the relevant quarry horizon.

Only the orders Rodentia, Primates, and the family Hyaenodontidae listed here reflect recent taxonomic revision pertinent to Oligocene Fayum mammals. Most of the taxa of other mammalian groups listed here need revision.

FAMILY Macroscelididae

Metoldobotes stromeri Schlosser 1910

ORDER Chiroptera

SUBORDER Microchiroptera

gen. et sp. nov.

FAMILY ?Phyllostomatidae

Vampyravus orientalis Schlosser 1910

CLASS Mammalia *incertae sedis*

Ptolemaia lyonsi Osborn 1908, A

ORDER Primates

SUPERFAMILY Cercopithecoidea

FAMILY Parapithecidae

Parapithecus fraasi Schlosser 1910
Parapithecus sp. nov., I
Apidium phiomense Osborn 1908, I, M
Apidium moustafai Simons 1962, G

SUPERFAMILY Hominoidea

FAMILY Pongidae

Propliopithecus haeckeli Schlosser 1910, G
Propliopithecus markgrafi (Schlosser) 1910
Propliopithecus sp. nov., I
Aegyptopithecus zeuxis Simons 1965, I, M
Aeolopithecus chirobates Simons 1965, I

FAMILY indet.

Oligopithecus savagei Simons 1962, E

ORDER Rodentia

FAMILY Phiomyidae

Phiomys andrewsi Osborn 1908
Metaphiomys beadnelli Osborn 1908
Phiomys paraphiomyoides Wood (described below, p. 41)
Phiomys lavocati Wood (described below, p. 45)
Paraphiomys simonsi Wood (described below, p. 49)
Metaphiomys schaubi Wood (described below, p. 58)
Gaudeamus aegyptius Wood (described below, p. 73)
Phiocricetomys minutus Wood (described below, p. 77), I

ORDER Deltatheridia

FAMILY Hyaenodontidae

Metasinopa aethiopica (Andrews) 1906
Metasinopa fraasi Osborn 1909, I
Apterodon altidens Schlosser 1910
Apterodon macrognathus (Andrews) 1904
Apterodon minutus Schlosser 1910

Pterodon africanus Andrews 1903
Pterodon leptognathus Osborn 1909
Pterodon phiomensis Osborn 1909
Hyaenodon brachycephalus Osborn 1909

FAMILY Proviverridae

gen. et sp. nov., G

ORDER Proboscidea
SUBORDER Moeritherioidea
FAMILY Moeritheriidae

Moeritherium andrewsi Schlosser 1911

SUBORDER Elephantoidea
FAMILY Palaeomastodontidae

Palaeomastodon beadnelli Andrews 1901a
Palaeomastodon barroisi Pontier 1907
Palaeomastodon intermedius Matsumoto 1922
Palaeomastodon parvus Andrews 1905
Phiomia serridens Andrews & Beadnell 1902
Phiomia minor (Andrews) 1904
Phiomia osborni Matsumoto 1922
Phiomia wintoni (Andrews) 1905

ORDER Embrithopoda
FAMILY Arsinoitheriidae

Arsinoitherium zitteli Beadnell 1902
Arsinoitherium andrewsi Lankester 1903

ORDER Hyracoidea
FAMILY Procaviidae

Pachyhyrax crassidentatus Schlosser 1910
Saghatherium antiquum Andrews & Beadnell 1902
Saghatherium annectens Matsumoto 1926
Saghatherium euryodon Matsumoto 1926
Saghatherium macrodon Matsumoto 1926
Saghatherium sobrina Matsumoto 1926

FAMILY Geniohyidae

Geniohyus mirus Andrews 1904
Geniohyus diphycus Matsumoto 1926
Geniohyus gigas Matsumoto 1926
Geniohyus magnus (Andrews) 1904
Geniohyus micrognathus (Schlosser) 1911
Geniohyus subgigas Matsumoto 1926
Bunohyrax fajumensis (Andrews) 1904
Bunohyrax affinis Matsumoto 1926

Bunohyrax major (Andrews) 1904
Megalohyrax eocaenus Andrews 1903
Megalohyrax minor Andrews 1904
Megalohyrax niloticus (Schlosser) 1910
Megalohyrax pygmaeus Matsumoto 1921
Megalohyrax suillus (Schlosser) 1910
Titanohyrax palaeotherioides (Schlosser) 1910
Titanohyrax andrewsi Matsumoto 1921
Titanohyrax schlosseri Matsumoto 1921
Titanohyrax ultimus Matsumoto 1921

ORDER Artiodactyla
SUBORDER Suiformes
FAMILY Cebochoeridae

Mixtotherium mezi Schmidt 1913

FAMILY Anthracotheriidae

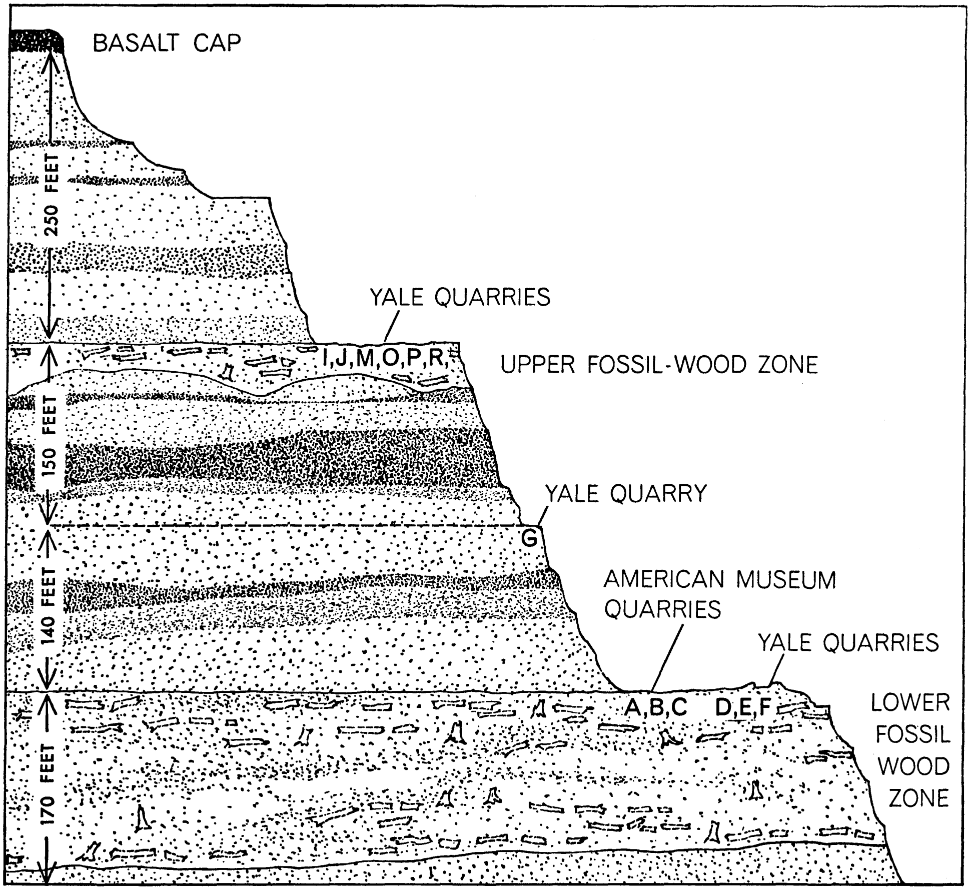
Rhagatherium aegyptiacum Andrews 1906
Brachyodus andrewsi Schmidt 1913
Brachyodus fraasi Schmidt 1913
Brachyodus gorringei (Andrews & Beadnell) 1902
Brachyodus parvus (Andrews) 1906
Brachyodus rugulosus Schmidt 1913

LOCALITIES

In a manner typical of the times, early collectors gave very little attention to recording the precise localities of land mammals from the lower fossil wood zone of the Jebel el Qatrani Formation. Consequently, most of the specimens of Egyptian Oligocene land mammals in the large collections at the Stuttgart Natural History Museum, the British Museum (Natural History), and the Geological Museum, Cairo, are recorded only as having been found "north of Birket Qarun." We now know that this Formation contains many faunal horizons spanning several million years of deposition. The poor locality records of early workers make it difficult to determine whether any of the land-mammal type specimens found before 1906 were collected in the fossiliferous stream channel deposits of the upper fossil wood zone which contains a different fauna and lies about 300 feet above the main collecting localities (Quarries A through F) of Beadnell and Andrews. There is a considerable probability, however, that none of the earlier finds was collected from the upper fossil wood zone. Osborn (1908, p. 265) considered that mammalian fossils in the upper sandstones (approximately the level of Yale Quarry I) had first been recovered by the American Museum party in the winter of 1906–07 and that this was one of the significant accomplishments of that season. Markgraf was then collecting for the American Museum expedition and prospected for new sites to the north of Quarry A. He might have found fossils in the upper beds earlier than this, but it seems unlikely.

Since distinguishing the age relationships of known Fayum species is of considerable importance in understanding their evolution, the restriction of genera and species to the middle level of Quarry G, and upper level Quarries J, I, and M (if known), has been indicated above (see p. 17). Apart from the types of *Apidium phiomense, Metaphiomys beadnelli,* and *Metasinopa fraasi,* none of the type specimens of Fayum species collected and described before the Yale expeditions can be shown by field records to have come from the upper fossil wood zone. Since fossil localities in this zone are very sparse and the American Museum group, including Markgraf, believed that they had been the first to find fossils in the upper zone, one can assume with some confidence that the ones described before 1906 were recovered from the lower fossil wood zone. In fact, during the course of the first two Yale expeditions, no significant fossil deposits were located in the upper zone in spite of diligent searching. Since January 1963 several sites yielding land vertebrates in abundance, i.e., Quarries I and J in 1964, and Quarries M and R in 1965–66, have been found in this zone. Preliminary surveys of the fauna from these upper localities show a faunal composition quite distinct from the lower zone. Many of the mammals studied so far are distinct at least at the species level from the fauna of Yale Quarry G. This faunal horizon in turn lies about equidistant stratigraphically between Quarries A and I and about 165 to 200 feet below Quarry I.

The American Museum expedition named their Quarries A, B, and C, and the great majority of their collections come from these three sites. As new quarry sites have been located during the course of the Yale expeditions, this alphabetical designation of quarries and localities has been continued. On the accompanying section the approximate vertical distances between the Yale and American Museum quarries are shown.



SECTION 1. Schematic cross-section of the Jebel el Qatrani Formation showing quarry locations. (Reprinted with permission. Copyright © 1967 by Scientific American, Inc. All rights reserved.)

THE AFRICAN OLIGOCENE RODENTIA

ALBERT E. WOOD

ABSTRACT

The large Yale collections of rodents from the Early Oligocene Jebel el Qatrani Formation of the Fayum, Egypt, permit a thorough study of this, the earliest rodent faunule from Africa. All belong to the African family, Phiomyidae. The genera *Phiomys* and *Metaphiomys* of Osborn are restudied and much more completely defined on the basis of the new material. Two new species of *Phiomys*, ***Ph. paraphiomyoides*** and ***Ph. lavocati,*** and one of *Metaphiomys*, ***M. schaubi,*** are described. There is a new species, ***P. simonsi,*** of *Paraphiomys*, a genus previously known only from the Miocene. Two new genera, ***Gaudeamus*** and ***Phiocricetomys,*** complete the rodent assemblage.

Within every species for which a series of specimens is available, there is a great deal of individual variation in tooth pattern, a probable indication that the phiomyid ancestors had reached Africa not long before Jebel el Qatrani times, in the very late Eocene.

The Fayum rodents are a closely related complex, structurally ancestral to the Miocene phiomyids of Africa, and, through them, to the modern *Petromus. Gaudeamus* clearly represents an ancestor of the modern *Thryonomys.* No decision is reached as to whether these rodents should be lumped in a single family (Thryonomyidae) or divided into two or three families (Thryonomyidae, Petromuridae, Phiomyidae) of the superfamily Thryonomyoidea. No relationships can be established between the Thryonomyoidea and any other group of Oligocene or later rodents.

Although there are certain similarities to the Theridomyidae, such differences as the presence of a hystricognathous angle of the lower jaw and of a third upper premolar (deciduous?) in the phiomyids, together with differences in detail of tooth pattern and differences in direction of evolution, seem to rule out a theridomyid ancestry for the phiomyids. Ancestry within Eocene members of the European family Pseudosciuridae is not excluded, since P^3 (or dP^3) is present in at least some of these forms. However, it is concluded that the phiomyid ancestor was probably a paramyid or a member of an unknown protrogomorph stock that invaded Africa from Asia.

All the Oligocene phiomyids are in process of losing their permanent premolars; in all but *Phiocricetomys* the deciduous premolar is retained throughout life, as in *Petromus* and *Thryonomys.* This retention occurs in a number of other rodents. It is suggested that if there were strong selection for molarization of the premolar area, retention of the already molariform deciduous teeth would be an effective way to bring this about.

Similarities between the Oligocene and Miocene history of rodents in South America and Africa are pointed out. It is concluded that the two areas were invaded in similar ways, by similar indirect routes, at about the same time, and that

the similarities between certain later caviomorphs of South America and certain thryonomyoids of Africa are pure parallelism.

DIE OLIGOZÄNEN NAGETIERE AFRIKAS

ALBERT E. WOOD

ÜBERSICHT

Die umfangreichen Sammlungen der Yale Universität von Nagetieren des frühen Oligozäns von der Djebel el Qatrani Formation im Fayum Gebiet Ägyptens macht ein eingehendes Studium dieser frühesten Nagetierfauna Afrikas möglich. Alle Exemplare der Sammlung gehören der afrikanischen Familie der Phiomyidae an. Osborn's Gattungen *Phiomys* und *Metaphiomys* wurden einer erneuten Untersuchung unterzogen und sind an Hand des neuen materials sehr viel eingehender definiert worden. Zwei neue Arten von *Phiomys*, ***Ph. paraphiomyoides*** und ***Ph. lavocati***, und eine neue Art von *Metaphiomys*, ***M. schaubi***, werden beschrieben. Es gibt eine neue Art, ***P. simonsi***, von *Paraphiomys*, eine Gattung das war bis jetzt nur aus dem Miozän bekannt. Zwei neue Gattungen, ***Gaudeamus*** und ***Phiocricetomys***, vervollständigen die Gruppe der Rodentia.

Jede der Arten, für die eine grössere Reihe von Exemplaren vorliegt, zeigt grosse Variationen in den morphologischen Merkmalen der Zähne; wahrscheinlich haben die Vorfahren der Phiomyidae Afrika nur kurz vor der Djebel-el-Qatrani Zeit, gegen das Ende des Eozäns, erreicht.

Die Fayum Rodentia sind ein eng verwandter Komplex, die morphologischen Vorfahren der afrikanischen Phiomyidae des Miozäns und, über diese letzteren, des neuzeitlichen *Petromus*. Der gegenwärtige *Thryonomys* stammt ohne Zweifel von *Gaudeamus* ab. Es ist noch nicht entscheidbar ob diese Rodentia in einer einzigen Familie (Thryonomyidae) zusammengefasst oder in zwei oder drei Familien (Thryonomyidae, Petromuridae, Phiomyidae) der Überfamilie Thryonomyoidea unterteilt werden sollten. Eine Verwandschaft zwischen Thryonomyoidea und irgend einer anderen Gruppe der oligozänen oder späteren Rodentia hat nicht nachgewiesen werden können.

Obwohl gewisse Ähnlichkeiten mit Theridomyidae bestehen, die Existenz eines histricognathen Angularfortsatzes des Unterkiefers und eines dritten oberen Prämolars (Milchzahn?) bei den Phiomyidae sowohl wie Unterschiede in Einzelheiten der Zahnmorphologie wie auch der Entwicklungsrichtung, scheinen eine Abkunft der Phiomyidae von Theridomyidae zu verneinen. Eine Abstammung innerhalb der eozänen Angehörigen der europäischen Familie der Pseudosciuridae kann nicht ausgeschlossen werden, da P^3 oder dp^3 in zumindestens einigen dieser Arten vorhanden ist. Man kommt jedoch zu dem Schluss dass der phiomyidische Vorfahre wahrscheinlich ein Paramyide oder Angehöriger eines unbekannten protrogomorphischen Urtyps war, der von Asien nach Afrika einwanderte.

Alle oligozänen Phiomyidae sind im Begriff ihre Prämolaren zu verlieren;

alle, ausser *Phiocricetomys,* behalten den Milchprämolaren während ihrer ganzen Lebenszeit, wie auch *Petromus* und *Thryonomys.* Dasselbe findet in einer Reihe anderer Nagetiere statt. Es wird angedeutet dass, im Falle einer ausgeprägten natürliche Zuchtwahl zur Entwicklung backenzahnformigen Prämolaren, die Konservierung des schon backenzahnähnliches Milchzahns ein wirksamer Weg zu diesem Zweck sein würde.

Es wird auf Ähnlichkeiten in der oligozänen und miozänen Geschichte der Nagetiere Südamerikas und Afrikas hingewiesen. Der Verfasser kommt zu der Schlussfolgerung dass eine Einwanderung in beide Gebiete über ähnlich indirekte Pfade zur ungefähr derselben Zeit stattfand und dass die Ähnlichkeiten zwischen gewissen späteren Caviomorphen Südamerikas und bestimmten Thryonomyoidea Afrikas ein reiner Parallelismus sind.

LES RONGEURS AFRICAINS DE L'OLIGOCÈNE

Albert E. Wood

Résumé

Les grands collections, de Yale, des rongeurs provenant de la Formation Jebel el Qatrani de l'Oligocène inférieur du Fayum, Egypte, permettent une étude complete de cette faunule, la plus ancien des rongeurs de l'Afrique. Tous appartiennent à la famille africaine Phiomyidae. Les genres *Phiomys* et *Metaphiomys* de Osborn sont étudiés de nouveau et définis beaucoup plus complètement sur la base du materiel nouveau. Deux espèces nouvelles de *Phiomys,* ***Ph. paraphiomyoides*** et ***Ph. lavocati,*** et une de *Metaphiomys,* ***M. schaubi,*** sont décrites. Il y a une espèce nouvelle, ***P. simonsi,*** de *Paraphiomys,* un genre préalablement connu dans le miocène seulement. Deux genres nouveaux, ***Gaudeamus*** et ***Phiocricetomys,*** complètent l'assemblage des rongeurs.

Dans chaque espèce, representée par une série de specimens, il y a beaucoup de variations individuelles dans la morphologie dentaire. C'est une indication que probablement les ancêtres des phiomyidés parvinrent en Afrique peu avant les temps Jebel el Qatrani, trés tard dans l'Eocène supérieure.

Les rongeurs du Fayum sont un complexe strictement lié; du point de vue structurel ce sont les ancêtres des phiomyidés africains du Miocène, et à travers eux, du *Petromus* actuel. *Gaudeamus* représente clairement l'ancêtre du *Thryonomys* actuel. A ce jour, il n'est pas possible de dire si ces rongeurs doivent être groupés dans une seule famille (Thryonomyidae) ou separés en deux ou trois familles (Thryonomyidae, Petromuridae, Phiomyidae) de la superfamille Thryonomyoidea. Il n'y a aucune indication d'un parenté entre les Thryonomyoidea et les autres groupes des rongeurs de l'Oligocène ou d'une époque ultérieure.

Bien qu'il y ait des ressemblances avec les theridomyidés, des différences, comme la présence d'un angle hystricognathe de la mandibule inférieure et d'une 3^{e} premolaire supérieure (de lait?) dans les phiomyidés, ainsi que des différences dans les détails du structure dentaire et dans la direction de l'évolution, semblent exclure la dérivation des phiomyidés d'ancêtres theridomyidés. Une

dérivation des membres de la famille européenne des pseudosciuridés n'est pas exclue, puisque P^3 (ou dP^3) est présent au moins dans quelques unes de ces formes. Cependant, on a conclu que les ancêtres phiomyidés étaient probablement des paramyidés ou des membres d'un souche protrogomorph inconnue qui venait d'Asie et envahit l'Afrique.

Tous les phiomyidés de l'Oligocène ont la tendance à perdre leurs prémolaires; autre que le *Phiocricetomys,* la prémolaire de lait est gardée toute la vie, comme en *Petromus* et *Thryonomys.* Cette retention est présent chez plusieurs autres rongeurs. On suggére que s'il y avait une forte sélection pour la molarisation de la zone premolaire, la rétention des dents de lait déjà molariformes pourrait être une façon effective de la réaliser.

Des ressemblances entre l'histoire des rongeurs de l'Oligocène et du Miocène en Amérique du sud et en Afrique sont indiquées. On a conclu que les deux continents ont été envahis d'une maniére semblable, à travers de semblable chemins indirects, pendant le meme temps et que les ressemblances parmi certains caviomorphs ultérieurs de l'Amérique méridionale et certains thryonomyoidés de l'Afrique sont pur parallélisme.

АФРИКАНСКИЕ ОЛИГОЦЕНОВЫЕ ГРЫЗУНЫ

АЛЬБЕРТ Э. ВУД

РЕЗЮМЕ

Большие йельские коллекции грызунов формации Джебель-эль-Катрани раннего олигоцена Фаюма, Египет, позволяют основательное изучение этой, самой ранней в Африке, небольшой грызуновой фауны. Все эти грызуны принадлежат африканскому семейству Phiomyidae. Осборновые роды *Phiomys* и *Metaphiomys* были снова изучены и определены с гораздо большей полнотой на основе нового материала. Описаны два новых вида рода *Phiomys* — *Ph. paraphiomyoides* и *Ph. lavocati,* и один вид рода *Metaphiomys* — *M. schaubi.* Тоже описан новый вид рода *Paraphiomys* — *P. simonsi;* этот род был прежде известен только в миоцене. Два новых рода, *Gaudeamus* и *Phiocricetomys* дополняют скопление грызунов.

Во всяком виде для которого располагаем рядом экземпляров, строение зубов изменяется в замечательной мере. Это вероятно значит, что предки фиомиидов достигли Африки незадолго до времён Джебель-эль-Катрани, в очень позднем эоцене.

Грызуны Фаюма являются близким родственным комплексом, структурными предками миоценовых фиомиид Африки и, посредством них, современного *Petromus. Gaudeamus* является очевидно предком современного *Thryonomys.* Не удалось решить надо ли этих грызунов объединить в одно семейство (Thryonomyidae), или разделить их на два или три семейства (Thryonomyidae, Petromuridae, Phiomyidae) надсемейства Thryonomyoidea. Определить родство между Thryonomyoidea и какой бы то ни было группой олигоценовых или более поздних грызунов, тоже не удалось.

Хотя есть некоторое сходство с Theridomyidae, кажется что такая разница как присутствие хистрикогнатового угла нижней челюсти и третьего верхнего премоляра (молочного?) у фиомиид, вместе с разницей в подробностях зубного узора и разницей в направлении эволюции исключают возможность теридомиидовых предков фиомиид. Происхождение от эоценовых членов европейского семейства Pseudosciuridae не исключается, так как P^3 (или dP^3) находится по крайней мере у некоторых из этих форм. Все таки заключается, что предок фиомиид был вероятно какой-то парамиид, или член какой-то неизвестной протрогоморфовой группы, который переселился в Африку из Азии.

Все олигоценовые фиомииды в процессе потери их премоляров; у всех кроме *Phiocricetomys* молочный премоляр удерживается в течение всей жизни, как у *Petromus* и *Thryonomys.* Это удержание происходит у множества других грызунов. Выдвигается гипотеза что если селекция совершается в пользу моляризации предкоренной области, удержание молочного премоляра, уже похожего на моляр, было бы пригодным для того способом.

Указывается на сходство между олигоценовой и миоценовой историей грызунов Южной Америки и Африки. Заключается что грызуны распространились в этих двух областях сходными образами, переселившись сходными косвенными путями приблизительно одновременно, и что сходства между некоторыми Caviomorpha Южной Америки и некоторыми Thryonomyoidea Африки являются чистым параллелизмом.

PART II. THE AFRICAN OLIGOCENE RODENTIA

ALBERT E. WOOD

1. INTRODUCTION

As indicated in the Introduction to Part I, the collections made by the Yale expeditions to the Fayum have greatly increased the number of rodent specimens from the Jebel el Qatrani Formation. These rodents are of great interest, since this is the earliest level from which any rodents are known from Africa. The various living rodent families of Africa have been among the most difficult to place, taxonomically, and anything that can be learned of their ancestry is very important to the student of rodent evolution. The present study shows that the ancestors of two of the modern genera, *Thryonomys,* and *Petromus,* are to be sought in the Oligocene of Egypt. The material is especially significant because of the importance placed by Lavocat (1962), in his studies of the Miocene rodents of Africa, on the Phiomyidae as the basal stock of the African rodent radiation. It is also of great interest because, as indicated below, we are apparently dealing here with the initial stages of an evolutionary explosion by the descendants of a recent rodent immigrant. The chance to study such an explosion in action is a very unusual opportunity.

The previously known material includes the four lower jaws of *Phiomys andrewsi* and one of *Metaphiomys beadnelli* described by Osborn (1908), and a maxilla and two lower jaws referred by Schlosser (1911, p. 90) to *Phiomys andrewsi,* an allocation which, as indicated below (p. 34), is not correct for at least his two figured specimens. In addition, three other specimens in the American Museum collections have been identified during the present study. The 135 rodent specimens in the new collections permit the addition of three genera (two new) and six new species to the previously known two monotypic genera. They also enable us to learn much about rodent dental variability within what are clearly contemporaneous and homogeneous populations. This variability, together with the structure of Miocene and later forms, permits an effort at determining the directions in which the Fayum rodents were evolving. There is now sufficient material to permit the identification of isolated cheek teeth and incisors in both the Yale and American Museum collections.

All the specimens, in both the Yale and American Museum collections, are from the Jebel el Qatrani Formation (see above, p. 17). The various American Museum and Yale quarries are distributed through about 350 feet, vertically, of sediments, as shown in the geologic section (p. 21). Apparently there was a sufficient time lapse to have permitted some evolution to have taken place, as indicated by the replacement of *Metaphiomys schaubi* by *M. beadnelli* in the upper beds, and by the significant size differences between the earlier population of *Phiomys paraphiomyoides* and the later one of *Ph.* aff. *paraphiomyoides.** It seems probable, however, that the time interval was short, the evolution rapid.

The author is deeply indebted to Dr. Elwyn Simons for permitting the study of this collection. Dr. Malcolm McKenna has lent the specimens in the American Museum collections. Some (but a relatively small part) of the Yale specimens were studied briefly by Dr. René Lavocat, who has very kindly allowed me to use his notes on them. I have unhesitatingly absorbed his ideas about these animals, both as to their identities and as to their relationships to the Miocene rodents of Africa, but must bear sole responsibility for the conclusions I have drawn. This study has been assisted by several grants to me from the Marsh Fund of the National Academy of Science; by grants GB 1977 and GB 6075 to me from the National Science Foundation; and by a National Science Foundation Senior Postdoctoral Fellowship that enabled me to study the rodents of the Naturhistorisches Museum in Basel during the year 1966–1967. The statistical analyses and editorial work have been performed by Frances W. Wood.

The abbreviations used in the text are as follows:

AMNH	American Museum of Natural History, New York
CM	Geological Museum, Cairo
YPM	Peabody Museum, Yale University, New Haven, Connecticut

---

* In this paper *Ph.* stands for *Phiomys* and *P.* for *Paraphiomys.*

2. SYSTEMATICS

Family PHIOMYIDAE Wood 1955

Diamantomyidae, Schaub, 1958, p. 786.

Referred Genera. *Phiomys, Metaphiomys, Gaudeamus, Paraphiomys, Phiocricetomys, Diamantomys, Phiomyoides, Pseudospalax, Apodecter, Phthynilla, Pomonomys, Bathyergoides* and *Neosciuromys.*

Distribution. Fayum Oligocene of Egypt, Miocene of South-West Africa, Morocco and Kenya.

Emended Diagnosis. Rodents in which the lower molars are fundamentally four- or five-crested, although progressively there are but three crests; upper cheek teeth range from six-crested to three-crested; dP_4 elongate; angle of jaw hystricognathous; infraorbital foramen hystricomorphous; dP_4^4 retained unusually long, and perhaps permanently in progressive forms; dental formula P_{0-1}^{0-2}, M_3^3.

Discussion. My former reference (1955, p. 172) of this family to the Protrogomorpha was clearly in error, since the structure of the angle and that of the infraorbital foramen in the Phiomyidae show obvious distinctions from those in the protrogomorphs. Similarly, since all the known theridomyoids are sciurognathous (Lavocat, 1955, p. 634; 1962, p. 289), it is not possible to place the phiomyids in or near to the Theridomyidae, as indicated by Schaub (1958, p. 705); to consider them closely related to that family, as shown by Viret (1955, p. 1551); or to consider them a family related to the theridomyids or even a subfamily of that family, as indicated by McKenna (1962, p. 26, footnote). As discussed below, the teeth of *Phiomys andrewsi* are quite variable and may be interpreted either as showing a transition from a four-crested to a five-crested pattern or vice versa. There is no direct evidence to choose between these two, so that their teeth could be derived from those of theridomyids. However, there is no evidence to support the idea that the thoroughly sciurognathous theridomyids could have changed to such extreme hystricognaths as the phiomyids. In view of the known extensive parallelism within the Rodentia, it is absolutely necessary to base a classification on all available lines of evidence, and not limit one's criteria to the teeth any more than to the structure of the infraorbital foramen or of the angle. It therefore seems best to place the phiomyids near some of the other Old World forms that are both hystricomorphous and hystricognathous, and that have cheek tooth patterns of the same general type as do the phiomyids. It is probable, as indicated below (fig. 17, p. 79), that the phiomyids were ancestral to the modern African genera *Thryonomys* and *Petromus,* each usually placed in a monotypic family. There are no suggestions of close relationships to any other groups of living African rodents, and in particular there is no evidence of relationship to the Hystricidae.

GENUS *Phiomys* Osborn 1908

GENOTYPE. *Ph. andrewsi* Osborn, 1908.

REFERRED SPECIES. ***Ph. paraphiomyoides,*** n. sp., and ***Ph. lavocati,*** n. sp.

DISTRIBUTION. Early Oligocene Jebel el Qatrani Formation, Fayum of Egypt.

DIAGNOSIS. Primitive phiomyid; lower molars varying from nearly five-crested, through clearly four-crested to a pattern reduced almost to three; upper molars, where known, approximate a four- or five-crested pattern; although teeth are crested, the constituent cusps are still clearly distinguishable; posterior half of dP_4 molariform, anterior half formed of two appressed cusps connected to talonid by an ectolophid; P_4 with non-molariform posterior half; deciduous tooth retained in some species until late in the animal's life, and perhaps persistent in others; cheek tooth pattern highly variable; jaw stocky or slender, but with a long, slender post-dental portion; coronoid process and condyle extend very little above occlusal surface of cheek teeth.

DESCRIPTION. No trace of any part of the skull is preserved in any specimen of this genus.

The lower jaw (figs. 1 A, 3 C and G) is slender to stocky, with a very pronounced angular process arising from the middle of the lateral side of the mandible and extending markedly laterad—a fully hystricognath angle. The ventral surface of the jaw is convex, following the course of the incisor, rather than being nearly flat as shown in Osborn's figure of the referred specimen, AMNH 13271 (Osborn, 1908, fig. 4). In this respect, his illustration of the holotype is much more accurate. The mental foramen is small and lies below the rear end of the short diastema. The ventral edge of the masseteric fossa is formed by the everted angle. There is little or no suggestion of a masseteric knob, although a groove at the anterior end of the masseteric fossa (see especially fig. 3 G) indicates that the anterior end of the masseter profundus was partly differentiated. The coronoid process slopes gently backward, passing the alveolar border by the rear of the last tooth, M_3 in adults (figs. 1 A, 3 C) or M_2 in juveniles (Osborn, 1908, fig. 4). Because of the very fragile nature of the bone in these fossils, the extensive ascending ramus shown by Osborn has disintegrated completely. The most complete specimen (fig. 3 C), and examples of *Metaphiomys* (fig. 7), suggest that Osborn's drawing of the ascending ramus may have been in error in showing such a high coronoid process. In all available phiomyid jaws, the coronoid and condyle are only slightly above the level of the occlusal surface of the cheek teeth.

As discussed below in connection with the individual species, the lower molars of *Phiomys* form a complete sequence from five-crested specimens of *Ph. andrewsi* through four-crested ones of the same species, to the nearly three-crested ones of *Ph. paraphiomyoides* and of *Ph. lavocati.* Since the first and last of these species are contemporaneous animals, it is possible to assume either that evolution is proceeding from five-crested to four-crested to three-crested, or the reverse sequence, or from four-crested in both directions. If the immediate ancestral source of the phiomyids were unquestionably identifiable, this problem could be solved. But since the source is still uncertain, the direction of evolution must also remain unknown. However, the probabilities seem strongest that the ancestor was a protogomorph, most likely a paramyid (p. 82). If this is correct, the four-crested teeth would be the most primitive, and evolution would be in both directions, toward simplification or complication.

The lower premolars, preserved only in *Ph. andrewsi,* can be recognized by the fact that the talonid is not molariform. In this respect, these teeth are completely different, not only from those of theridomyids (Stehlin and Schaub, 1951, figs. 317–320), but also from those of the Pseudosciuridae (Stehlin and Schaub, 1951, figs. 311, 313–315), where the hypoconid and entoconid are connected not only through the posterolophid but also directly, by way of a hypolophid. The pattern of P_4 in *Phiomys* (fig. 1 B, D), however, is very similar to that seen in many of the paramyids (see, for example, Wood, 1962a, figs. 9 B, 10 F, 25 B and 29 F). It does not seem reasonable to believe that this tooth has been derived from a more advanced type, even though it is clearly on its way toward being suppressed. However, the fact that it is being suppressed and that it has retained a primitive pattern may well be related. It should be pointed out that paramyids and some sciuravids are the only known Eocene rodents with this type of P_4, and that the sciurids, which are widely separated from *Phiomys* by being both sciuromorphous and sciurognathous, are the only other known forms with such a pattern that even approach the correct geologic age to provide ancestors for *Phiomys.*

Upper molars referred to this genus are very rare. The one certainly identifiable specimen of *Ph. andrewsi* that shows any pattern (fig. 2 D) has six transverse crests, which clearly must represent a secondary increase. Two upper molars from Quarry G (fig. 3 D), referred to *Ph. paraphiomyoides,* have a more normal five-crested pattern. This is probably also the pattern of the very badly worn teeth of *Ph. andrewsi* (fig. 2 C). The upper cheek teeth figured by Schlosser (1911, pl. 13, figs. 10 and 10a), and refigured by Stehlin and Schaub (1951, fig. 36) and by Schaub (1958, fig. 58, upper half), are too large to be referred to *Ph. andrewsi.* They agree very closely both in size and in pattern with the upper teeth referred below to *Metaphiomys schaubi* and are here referred to that form.

The incisors, both upper and lower, are narrow with a fairly heavy enamel cap. The pulp cavity is long and slender.

Discussion. As suggested above, this genus could be derived from Eocene paramyids, though the gap is large. Since there do not seem to be any other very logical candidates, the most probable supposition is that the immediate ancestors of *Phiomys* were Old World paramyids. Analogy with the origin of the South American rodents would suggest that they reached Africa, as paramyids, in the early part of late Eocene time, and rapidly differentiated, in the absence of all gnawing competitors, into the Phiomyidae. Members of the Paramyidae are known from the Eocene of Europe, but on the basis of their tooth structure, only the lower Eocene forms would seem to be possible phiomyid ancestors. The family is unknown from the Eocene of Asia or Africa, but in view of the rarity of known Eocene rodents in Asia and their absence in Africa, this proves nothing as to whether they were in those areas at that time.

The distribution of specimens of this genus among the various quarries seems to indicate that an appreciable amount of evolution was taking place during the deposition of these sediments (Section 1, p. 21).

The lowest levels (Quarries A and B) contain only one species of *Phiomys*—*Ph. andrewsi*—although there are isolated incisors referred to both *Metaphiomys* and *Gaudeamus.* In Quarry E, *Ph. andrewsi* is very abundant, and *Ph. lavocati* is well represented as a smaller and more advanced species. It presumably had differentiated somewhere else and migrated into the area represented by the collections. By the time the level of Quarry G is reached, *Metaphiomys* has become the dominant rodent, and material referable to *Ph. andrewsi* is relatively rare, as if it had been forced out of this area, or into a different type of ecology, perhaps by competition from the progressively dominant *Metaphiomys schaubi.* A number of specimens from Quarry G approach the dental pattern characteristic of *Ph. lavocati,* but are much larger than the material of that species, being at or close to the lower limit of size of *Ph. andrewsi* (compare Tables 1–6). These are interpreted as being representatives of the *Ph. andrewsi–Ph. lavocati* transition, which had survived after the establishment of the descendant species, and which had been able to reinvade the area after the removal of the competition from *Ph. andrewsi.* They are differentiated enough to be considered a separate species, *Ph. paraphiomyoides.* In the highest levels, from Quarry I, four additional specimens of this sort have been found, separable from both *Ph. andrewsi* and *Ph. paraphiomyoides,* and discussed below as *Ph.* aff. *paraphiomyoides.*

The largest measurements of the specimens of M_{1-2} referred to *Ph. lavocati* are more than three standard deviations smaller than the corresponding means of *Ph. andrewsi,* and some of the measurements deviate by over four SD's. In the incisors, however, the specimens of *Ph. lavocati,* except for the measurements at the tip of the incisor of the juvenile, are within the observed range for *Ph. andrewsi,* so that *Ph. lavocati* can be differentiated on tooth pattern, molar measurements, and relative size of the incisors and cheek teeth. Most of the measurements of the early population of *Ph. paraphiomyoides* are smaller than the observed range of *Ph. andrewsi,* but only in the case of the width of the hypolophid of M_1 do any differ by over three SD's from the mean of *Ph. andrewsi.* So this species must be considered to be less differentiated from *Ph. andrewsi* than is *Ph. lavocati.*

Phiomys andrewsi Osborn
Figures 1 and 2

OTHER ILLUSTRATIONS. Osborn, 1908, figs. 3–4; Schaub, 1958, fig. 58 (lower half only); Stehlin and Schaub, 1951, fig. 324.

Phiomys andrewsi Osborn, 1908, p. 269.

The maxilla figured in the upper half of Schaub, 1958, fig. 58; Schlosser, 1911, pl. 13, figs. 10 and 10a; and Stehlin and Schaub, 1951, fig. 36, is referred below to *Metaphiomys schaubi.* The lower jaw figured by Schlosser, 1911, pl. 13, figs. 7 and 7a and by Stehlin and Schaub, 1951, fig. 445, is referred below to *Gaudeamus aegyptius.*

HOLOTYPE. AMNH 13275, right jaw with P_4–M_3 and incisor, M_{2-3} being damaged.

HYPODIGM. Holotype; AMNH 8224, 13271, 13272, and 13274, lower jaws, and 13277, isolated incisors and lower molar; YPM 18021, 18025, 18027, 18039, 18043, 18049, 18054, 18058, 18060, 18062, 18064, 18066, 18071, 18076, 21286 and 21287, lower jaws with or without teeth; 18090, 18091, 18195, 18207 and 18214, isolated lower incisors; 18051, maxilla with very badly worn M^{1-2}; 18035, isolated M^2; and 18198, 18199, 18208 and 18215, isolated upper incisors.

DISTRIBUTION. American Museum Quarries A and B, Yale Quarry E in silicified wood zone; YPM 18088 and 21287 are from Yale Quarry G; Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. Medium-sized species, variable both in size and in tooth pattern; lower molars generally four-crested, with posterior arm of protoconid and mesolophid represented by a single crest; anterior cingulum of molars weak; P_4 basically two-crested, with anterior cingulum and short, low mesolophid, and with entoconid connected to posterior cingulum; dP_4 usually five-crested, with long mesolophid, but sometimes mesolophid is absent; dP_4 retained for an unusually long time; lower incisor frequently with thickening of enamel along median side; upper cheek teeth at least sometimes with complex pattern; tooth measurements as given in Tables 1–2.

DESCRIPTION. The measurements (Tables 1–2) and figures (figs. 1 and 2) of the teeth of the specimens referred to this species indicate a highly variable population, if it really represents one species. Initially, it was thought that two species were represented by these specimens, but there is intergradation in most measurements between the type, which is one of the two smallest jaws in the population, and the larger specimens. It is possible that the type and YPM 18054 are the only specimens referable to Osborn's species, but, since they were found in the same quarries with larger specimens, since there is size intergradation, and since the tooth pattern, as discussed below, is highly variable with no consistency, it seems more conservative to leave them all together, at least until enough additional specimens are found to demonstrate that they must be divided, especially in view of Hooper's study showing how much tooth variation is present in single species of recent rodents (Hooper, 1957), and unpublished studies of variation in fossil rodent teeth from a single ant hill (Rice, mss.).

The lower jaw (fig. 1 A, and Osborn, 1908, fig. 4) is fairly slender. Due to the extremely fragile nature of the bone, the posterior portions of jaws disintegrate very easily, and no trace remains of the ascending ramus figured by Osborn for AMNH 13271. None of the other specimens of this species are complete in this area, but it seems probable, on the basis of material referred to other phiomyids, that Osborn's figure is in error in this region. The masseteric fossa is very pronounced, ending beneath the anterior end of M_1, where there is a faint depression isolated from the rest of the fossa. Another distinct portion of the fossa lies near its dorsal surface, indicating a marked incipient subdivision of the masseter. Ventrally, the masseteric fossa is separated from the ramus by a strong ridge, that curves ventrolaterally into the angular process, which thus arises lateral to the plane of the incisor in a typical hystricognathous manner. The long, gently slop-

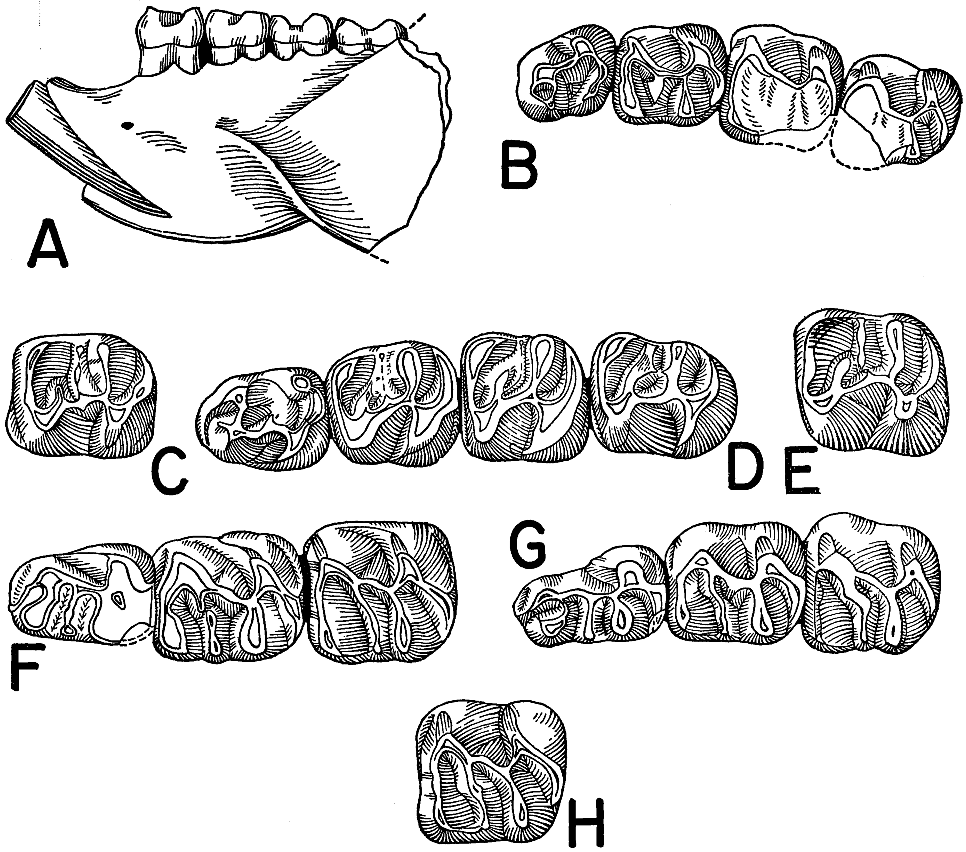


FIGURE 1. Jaw and teeth of *Phiomys andrewsi*. Jaw × 5, teeth × 10.
A. Lateral view of left lower jaw, YPM 18071. B. Right P_4–M_3, AMNH 13275, holotype. C. Left M_1, YPM 18060. D. Left P_4–M_3, YPM 18071. E. Left M_2, AMNH 13274. F. Right dP_4–M_2, YPM 18064. G. Right dP_4–M_2, AMNH 13271. H. Right M_2, YPM 18076.

ing coronoid process shown by Osborn (1908, fig. 4) would be very distinctive, if, as seems unlikely, the figure is correct. In Osborn's figure, the coronoid process passes the alveolar border at the rear of M_2, whereas in YPM 18071 (fig. 1 A) it passes it at the rear of M_3. This, however, is because the former specimen is a juvenile and the latter is an adult, and in each one, the coronoid arises by the rear of the tooth row. There is a single small mental foramen high on the mandible, just in front of the anterior root of P_4. In adult specimens, there is a corrugated area behind M_3, median to the coronoid and above the alveolus of the incisor that is absent in juveniles.

The lower premolar is present on the holotype (fig. 1 B), and on YPM 18071 (fig. 1 D). The protoconid and metaconid are close together, as in paramyids, and the metaconid is considerably higher than the protoconid. In the holotype, these cusps are united at the front of the tooth by anterior ridges, as well as at their rear to form a metalophid. In the second specimen, only the second of these ridges is present, the anterior arm of the metaconid extending along the

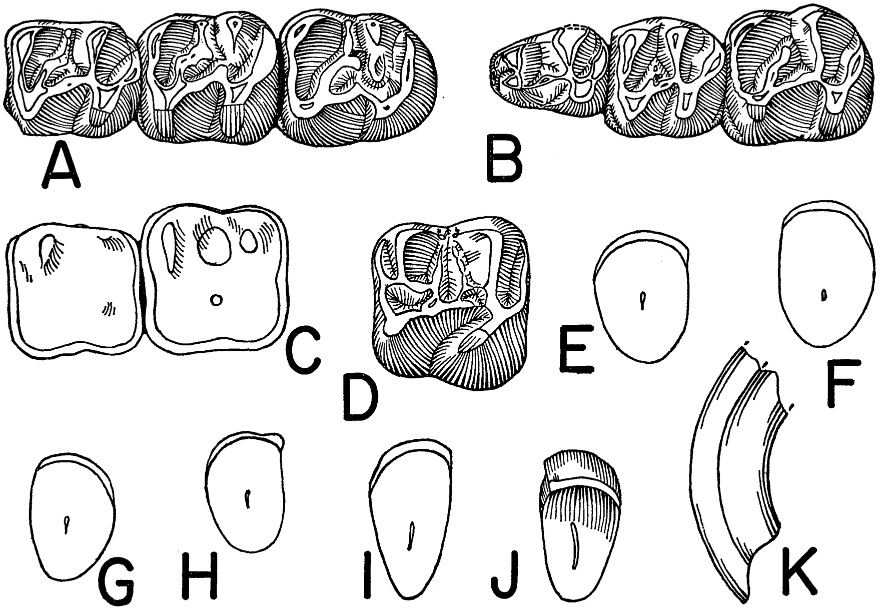


FIGURE 2. Teeth of *Phiomys andrewsi*, × 10.
A. Left M_{1-3}, YPM 18021. B. Left dP_4–M_2, YPM 18043. C. Left M^{1-2}, YPM 18051. D. Right M^3, YPM 18035, anterior end to the right. E. Cross section of left I_1, AMNH 13724. F. Occlusal surface of right I_1, YPM 18064. G. Occlusal surface of right I_1, AMNH 13271. H. Cross section of left I_1, YPM 18071. I. Cross section of right I^1, YPM 18199. J. Occlusal surface of left I^1, YPM 18199. K. Lateral view of same specimen, YPM 18199.

margin of the tooth as an anterior cingulum. The ectolophid is long and slender, with a slight swelling marking the position of the mesoconid. In the holotype, there is a small, low swelling in the talonid basin, indicating the mesolophid. This is absent in YPM 18071, where there is a short crest from the mesoconid. The entoconid unites with the hypoconid through the posterior cingulum, which has enlarged to form a well-developed hypoconulid. The entoconid is rounded. This tooth is quite different in pattern from the molars.

All the lower molars agree in their basic pattern (fig. 1 B–H, 2 A, B). There is a crest along the anterior margin of the tooth, connecting the metaconid with the anterior arm of the protoconid. There is a small anterior cingulum on the buccal side of the tooth, which extends a variable distance across the anterior face of the tooth as a very faint ridge. At least in part, its length is an age characteristic, interdental wear resulting in its progressive elimination. The ectolophid is strong, connecting with a buccal crest from the entoconid and the anterior arm of the hypoconid, except in YPM 18021 (fig. 2 A), where the hypolophid is interrupted. The hypoconid extends into the posterior cingulum, which expands to form a hypoconulid of rather variable size. The tip of the posterior cingulum unites with the base of the entoconid. The hypoconid is generally extended forward along the buccal margin of the tooth in a long, slender arm, frequently worn (fig. 1 D). There is likely to be a small posterobuccal cingulum, though it may be exceedingly faint.

The most variable area in the molars is that involving the posterior arm of the protoconid, the mesoconid, and the mesolophid. A structural series can be made. At one extreme is M_1 of YPM 18060 (fig. 1 C), where the mesoconid is well-developed, extending both buccad and linguad from the ectolophid; and the mesolophid is long, reaching the lingual margin of the tooth, and partly subdivided into two cuspules, at least in the relatively unworn tooth. A unique feature of this specimen is that the posterior arm of the protoconid is directed toward the metaconid, rather than toward the mesolophid. In M_1 of YPM 18027, the mesolophid starts toward the metaconid and then bends mesiad as a very low crest, reaching the lingual margin of the tooth. It cuts off the very short posterior arm of the protoconid. A slightly different stage is shown by M_1 of AMNH 13274 and YPM 18071, where the posterior arm of the protoconid is long, and there is a distinct mesoconid which is continued to the lingual margin of the crown as a very low mesolophid (fig. 1 D). In M_1 of YPM 21286, the mesolophid connects with both the posterior arm of the protoconid and the mesoconid, surrounding a small basin. M_2 of AMNH 13274 is similar to M_1 of the same specimen, except that the mesolophid is nearly as high as the other crests, and ends equidistantly from the posterior arm of the protoconid and the mesoconid (fig. 1 E). There is essentially no difference between this tooth and M_1 of YPM 18066. In M_2 of YPM 18071 (fig. 1 D), the mesoconid seems to be absent, and the long, low mesolophid joins the side of the posterior arm of the protoconid. M_1 of the holotype (fig. 1 B) represents about the same stage, except that the mesolophid is shorter, and there may be a mesoconid here. In M_1 of YPM 18064 (fig. 1 F), the mesolophid consists of two cusps, isolated and slightly offset from the posterior arm of the protoconid. There is a slight swelling of the ectolophid showing where the mesoconid once was. A slightly different pattern is present in M_1 of AMNH 13271 (fig. 1 G) where, although there is a well-developed mesoconid, the mesolophid is firmly joined to the posterior arm of the protoconid and reaches the lingual margin of the tooth where it expands slightly as a mesostylid. In M_2 of this same specimen and of YPM 18027, the mesoconid is absent, though after extreme wear there would be a dam connecting the ectolophid with the mesolophid (fig. 1 G). However, in M_2 of YPM 21286, there is a clearly marked mesoconid, widely separated from the mesolophid which is attached to the protoconid. The mesolophids of M_{1-3} of YPM 18021 are similar to this, being attached to the tip of the posterior arm of the protoconid (fig. 2 A). On M_1 there is a posterior wiggle of the mesolophid and the lingual third of this crest is low, even though it is unworn. On M_2 and M_3 there is a strong posterior process of the mesolophid, not present on M_1, reaching nearly to the hypolophid. This process is a forerunner of the one that is found in *Metaphiomys,* where it has been called the protospur. This protospur is larger than in any other specimen of *Ph. andrewsi,* but it only represents the extreme of variability in this manner. It is not clear whether or not there are mesoconids on M_{2-3}. At first glance there appears to be one in the figure (fig. 2 A), but it seems more probable, at least on M_2, that the supposed mesoconid is really the curve of the ectolophid toward the entoconid, marking the beginning of the hypolophid, a crest that is interrupted in this specimen both on M_2 and on M_3. In M_2 of YPM 18064, M_3 of YPM 18071 (fig. 1 D, F), and M_{1-2} of YPM

18025, the situation is similar, except that there is no suggestion of a mesoconid and the hypolophids are not interrupted. In M_3 of YPM 18071, a protospur from the mesolophid nearly meets a forward crestlet near the buccal side of the entoconid (fig. 1 D). M_2 of YPM 18076 (fig. 1 H) is similar to that of YPM 18064, except that the metaconid connects to the lingual tip of the mesolophid. In all three molars of the holotype (fig. 1 B) and in M_2 of YPM 18043 (fig. 2 B), the mesolophid is fairly short, extending about two-thirds of the way to the lingual margin of the tooth, and with no mesoconid. Finally, M_1 of YPM 18043 (fig. 2 B) has a very short posterior arm of the protoconid, an indistinct mesoconid, and a short, faint mesolophid connecting with both. Among other specimens, M_2 of YPM 18054 agrees with the M_1 of YPM 18043 in having a short posterior arm of the protoconid, which is directed toward the metaconid as in figure 1 C. There is, however, no mesolophid in this specimen. A similar situation is present in YPM 18062 where there seems to be no mesolophid, mesoconid, or posterior arm of the protoconid, although this specimen is difficult to interpret as it is badly worn.

Upper cheek teeth of this species are represented only by YPM 18051, consisting of very badly worn LM^{1-2}, and YPM 18035, an unworn RM^2. The former specimen shows nothing except that the teeth apparently were five-crested, that there was little interdental wear, and that the enamel does not extend as far rootward on the buccal side as on the other three sides (fig. 2 C). The unworn M^2 is most unusual in that there are six transverse crests, including two between the protoloph and metaloph (fig. 2 D). The metaloph connects with the middle of the posterior cingulum and the metaconule is extended forward to meet the mesoloph, so that a deep and isolated basin is formed. A subsidiary crest arises from the mure in front of the mesocone, paralleling the mesoloph but at a slightly lower elevation. This crest seems to be homologous to what looks like an incipient crest in some specimens of *Metaphiomys schaubi* (fig. 11 A, D). There is a connection between this crest and the protoconule, surrounding a second deep basin. Although it is impossible to be sure, it seems probable that the worn specimen only had the normal five crests. Which was the usual pattern for this species cannot, of course, be determined from two specimens.

The lower milk tooth is present on a very considerable number of specimens, including YPM 18062 and 21287 where the first molar is more worn than in any other specimens available, yet the milk tooth is still present. This looks as though this species was in the process of retaining the deciduous tooth and suppressing its permanent successor, but that the permanent tooth still erupts in some individuals. Possible selective advantages of retention of dP_4^4 are discussed below (p. 83). There is considerable variation in the pattern of dP_4. What may be considered the standard pattern is present in AMNH 13271 (fig. 1 G). The metaconid and protoconid unite at their posterior ends and a crest runs anteromesiad from the protoconid, turning abruptly laterad as a cingulum along the anterior end of the tooth. In YPM 21286, the cingulum extends mesiad as well, there being a distinct anteroconid. The mesolophid of AMNH 13271 is long and well-developed, reaching the lingual margin of the crown. The pattern of the hypoconid, entoconid and hypoconulid is like that of the molars. This tooth of YPM 18064 (fig. 1 F) is very similar, but is somewhat wider in the anterior portion. The milk teeth of YPM 18027 and 21286 differ only in that the mesolophid is very low. The deciduous teeth of YPM 18043 (fig. 2 B) and 21287, and AMNH 13272 are much shorter, with the anterior arm of the metaconid curving to the buccal margin of the tooth, and no reversed anterior cingulum or crest from the protoconid. These teeth also have no mesolophid and a small mesoconid. A separation of this population into two species on the basis of the deciduous molars would not agree with any separation on the basis of the molars, although the mesolophids may be shorter on the molars of these specimens with small deciduous teeth (fig. 2 B).

The lower incisor is a stocky tooth, with thick enamel. There is some variation in proportions (fig. 2 E–H), but they are not very striking. The pulp cavity is small near the anterior end of the tooth. A number of specimens (for example, fig. 2 E, H) show a peculiar knob of enamel at the median margin. Isolated incisors included in AMNH 13277 show that this is an age characteristic, present at the growing end of some teeth, but absent at the gnawing surface. The median knob reaches the wear surface on adult specimens. There is considerable variation in the size of the incisor in juveniles, the anteroposterior diameter of YPM 18066 increasing from 1.17 to 1.36 mm and its transverse diameter from 0.88 to 1.00 mm in a longitudinal distance of 1.5 mm. This age factor is responsible for the great variability in the lower incisors, as indicated by the observed range and the coefficient of variation (Table 1).

A series of upper incisors are referred to this species on the basis of their cross-sectional outline and size. They agree with the lower incisors in their narrow, rounded anterior faces, in the relatively thick enamel, and in the narrow, slit-like pulp cavity which usually reaches the wear surface (fig. 2 I–J). Since none of these teeth is directly associated with cheek tooth specimens of this species, it is possible, though not likely, that their reference here is incorrect. An interesting feature is the concentration of the wear in the dentine just behind the enamel cap, so that a pronounced pocket is formed with wear (fig. 2 K). Another feature visible on these teeth is an interdental wear surface on the enamel of the median margin of the tooth, which has apparently not been previously commented on among rodents. On some specimens, including one of YPM 18199 (fig. 2 J), there is a faint groove along the median edge of the enamel, which disappears toward the base of the tooth, as in the lower incisors.

An attempt has been made to use the ratio of the two diameters of the incisor as a taxonomic character, to eliminate the effects of change of size with age. This is clearly much less variable than either of the direct measurements, having a V of only 4.35 ± .33 (Table 1), and could well turn out to be a taxonomically significant measurement.

Several observed measurements of this form seem to be of taxonomic significance (Table 1). M_1 is larger than P_4 and wider than dP_4. M_2 is wider but no longer than M_1. In M_1, the width across the hypolophid is always greater than that across the metalophid; in M_2, there is no predominance of either measurement being the larger (metalophid greater in 7; hypolophid greater in 5; two measurements equal in 1). M_3 is longer than M_2; the metalophid width of this tooth is equal to that of M_2, but the hypolophid width is much less. Where V was computed for the molars, it was large but within the expectable range. It was beyond what is expectable for a unified population in the incisors (Tables 1, 7), presumably due to age variations in incisor diameter (Wood, 1962a, p. 7), but the incisor ratio has a value indicative of a unified population for both upper and lower incisors.

DISCUSSION. These specimens can be interpreted as representing either a single, highly variable population of one species or several species. If the latter point of view were adopted, the holotype and YPM 18054 could be considered to be a small species with short mesolophids or long posterior arms of the protoconid and no mesoconids. On the other hand, they could be considered to represent two species, since the tooth (M_2) of YPM 18054 is essentially three-crested, whereas that of the holotype is four-crested. It is probable that YPM 18054 is best interpreted as an extreme variant of *Ph. andrewsi* in the direction of *Ph. paraphiomyoides,* and that it could be referred to that species, although it would presumably have been part of the *Ph. andrewsi* breeding population. The larger specimens are mostly four-crested, though they vary as to the position of the crest, and it could be considered that most of them were a different species from the first two discussed. YPM 18043 would differ from this species in its approach to the three-crested pattern of the smaller YPM 18054. YPM 18021 would represent another species, in which the hypolophid was breaking up. In addition, there is the small species described below as *Ph. lavocati,* which is on the boundary between *Phiomys* and *Paraphiomys.* The single area of Quarry E would thus be supplying about five closely related species, which seems unreasonable. But, if there are not five species, the only valid separation in Quarry E is between the main part of the collection and the small *Ph. lavocati.* The amount of variability in this population, if it is indeed a single species, is high, but Hooper's work on *Peromyscus* (1957) and incomplete investigations on the North American Oligocene *Eumys* (Rice, mss.) show that there may be much more intraspecific variation in tooth patterns than has generally been admitted.

Phiomys paraphiomyoides n. sp.

Figure 3

HOLOTYPE. CM 26904, lower jaw fragment with LdP_4–M_3 and the incisor, from Quarry G.

HYPODIGM. Holotype and YPM 18227 and 21288–90, lower jaws, all from Quarry G, and YPM 18233, upper teeth, from 1 yard above Quarry G.

DISTRIBUTION. Known only from Quarry G, middle levels; Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. Jaw slender; cheek teeth significantly smaller than in genotype, but incisors nearly as large; mesolophid or posterior arm of the protoconid present but small; mesoconid not distinguishable; hypoconulid rather distinct; anterior cingula strong; metaloph connects with both posteroloph and mesoloph; diametric ratio of lower incisors about .64; tooth measurements as given in Tables 2 and 3.

DESCRIPTION. The lower jaw (fig. 3 C and G) is more slender than that of *Ph. andrewsi* (fig. 1 A) or of *Metaphiomys* (fig. 8 E–F). The coronoid process slopes backward and is low and broad, separated by a narrow notch from the condyle. Perhaps some of these differences from the genotype are due to the fact that the jaw of YPM 21288 (fig. 3 C) is that of a young individual, in which M_3 has not yet erupted. A strut supporting the condyle extends backwards from the base of the incisor, but is not quite straight, as it is in *Metaphiomys*. The mandibular foramen lies above the posterior part of this strut, below the notch between the coronoid and condyloid processes.

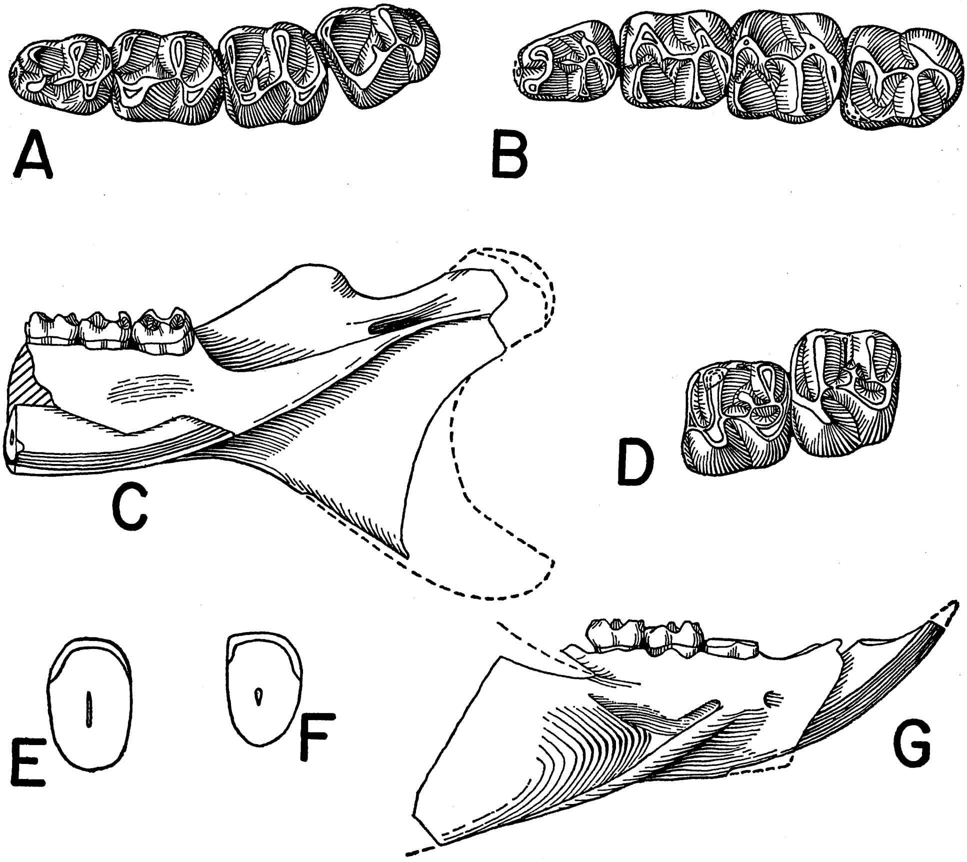


FIGURE 3. Jaws and teeth of *Phiomys paraphiomyoides*. Jaws × 5, teeth × 10. A. Left dP_4–M_3, CM 26904, holotype. B. Right dP_4–M_3, YPM 21289. C. Medial view of lower jaw, YPM 21288. D. Left M^{1-2}, YPM 18233. E. Cross section of left I_1, CM 26904, holotype. F. Cross section of right I_1 below P_4, YPM 21288. G. Lateral view of lower jaw, YPM 21290.

This species is characterized by the great reduction of both the posterior arm of the protoconid and of the mesolophid. The anterior cingula are strong, as in *Ph. andrewsi*. M_1 of the holotype is essentially three-crested, with a slight swelling where the posterior arm of the protoconid should be (fig. 3 A). In other specimens (YPM 18227, 21288 and 21290) there is a faint posterior arm. In the fifth specimen, there is a distinct mesolophid, and the nubbin of the posterior arm of the protoconid is directed toward the metalophid. This latter crest is sharply angulate at its middle, with a distinct break between the protoconid and metaconid (fig. 3 B). In some specimens, the buccal end of the metaconid is displaced posteriorly, and in YPM 21289 it comes close to the posterior arm of the protoconid, suggesting the situation in *Ph. lavocati.*

There is no trace of a mesoconid on M_2, but there is a clearly marked, but short, posterior arm of the protoconid, which drops off rapidly in height in three specimens (fig. 3 A) to be continued as a very low swell. In YPM 21289 (fig. 3 B) there is a ridge from the metalophid, similar to that on M_1, which almost meets the posterior arm of the protoconid.

On the last molar there is a crest from the ectolophid, which varies slightly in position (fig. 3 A–B), but which is more probably the posterior arm of the protoconid than the mesolophid.

None of the specimens shows replacement of the premolar. The pattern of this tooth is like that of the short dP_4 of *Ph. andrewsi.* It is difficult to decide whether this tooth averages more or less wear than M_1, but it seems probable that it is a retained dP_4, which erupted at about the same time as M_1.

One specimen including LM^{1-2} (fig. 3 D), YPM 18233, is referred here. The most striking feature of these teeth is the connection from the mesoloph to the metaloph to the posterior cingulum, agreeing with the upper molar referred to *Ph. andrewsi* (fig. 2 D). The mesoloph is weak on M^1, whereas on M^2 it looks more like the doubled ridge of *Ph. andrewsi.* It is quite distinct from anything seen in *Metaphiomys.*

The lower incisor (fig. 3 E–F) is intermediate in structure between those of *Ph. andrewsi* and of *Ph. lavocati,* described below. It is widest at or just behind the extreme lateral tip of the enamel cap. The incisor ratio ranges from .63 to .66, overlapping the low range of the ratio in *Ph. andrewsi,* and above the limits in all but very young specimens of *Ph. lavocati.*

The isolated incisors, YPM 18088, from Quarry G were originally identified as *Ph. andrewsi,* because they are basically similar to those of that species from the lower levels. After the discovery of the several jaws from Quarry G that are here described as *Ph. paraphiomyoides,* a plot was made of the incisor sizes of all the *Phiomys* material from Quarry G, and it was found that they fall into two distinct populations with distinct incisor ratios and regression lines. The narrower set of incisors are now referred to *Ph. paraphiomyoides,* even though they overlap the size and incisor ratios of specimens of *Ph. andrewsi* from the lower levels. The measurements are given in Tables 3 and 5.

A comparison was made of the means of the measurements of M_{1-2} of *Ph. paraphiomyoides* with those of *Ph. andrewsi* (Tables 1 and 3), in order to determine the likelihood that the two samples could have been taken from populations with identical means. This was done using Student's t test (Simpson, Roe and Lewontin, 1960, p. 176). It was found that the probability that the population means were the same was less than .01 for the length of M_1, less than .005 for the length of M_2, and less than .001 for the four width measurements. Similar comparisons of the incisor diameters gave P values about .1 for differences in anteroposterior diameter of the incisors; between .02 and .05 for the transverse diameter; but less than .001 for the incisor ratios. This substantiates the validity of the size criteria included in the diagnosis.

Phiomys paraphiomyoides is structurally intermediate between *Ph. andrewsi* and *Ph. lavocati* in size, incisor shape, incisor ratios, and length of the posterior arm of the protoconid. It is closer to *Ph. andrewsi* in the first three characters and to *Ph. lavocati* in the last. It seems very probable that it represents a structural stage of *Phiomys* leading toward *Paraphiomys.* However, since all the material of this species is from Quarry G whereas that of the equally *Paraphiomys*-like *Ph. lavocati* is from the earlier beds of Quarry E, and since a fully differentiated species of *Paraphiomys* is present in Quarry I, *Ph. paraphiomyoides* could only represent a late survival of the transitional stock.

Phiomys aff. *paraphiomyoides*

Figure 4

Description. Four lower jaws, YPM 21292–94 and 21366, from the upper level (Quarry I) are tentatively identified as *Ph.* aff. *paraphiomyoides.* In molar pattern they are indistinguishable from *Ph. paraphiomyoides* (compare figs. 3 A and 4 A), but they are of considerably larger size (compare Tables 2 and 3).

The jaws are slender, as in *Ph. paraphiomyoides* (compare figs. 3 C and G with 4 B), but differ from all other specimens referred to *Phiomys* in the extremely high position of the mental foramen on the jaw. The foramen is just below and in front of the anterior root of P_4 (fig. 4 B).

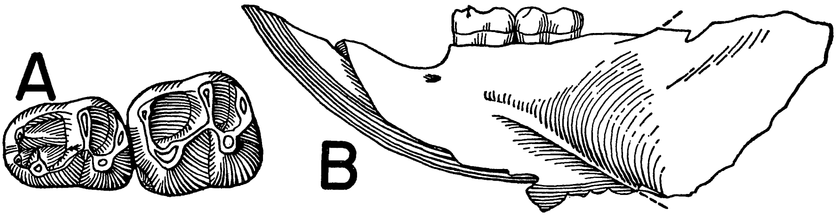


FIGURE 4. Jaws and teeth of *Phiomys* aff. *paraphiomyoides,* YPM 21294. A. left dP_4–M_1, × 10. B. Lateral view of lower jaw, × 5.

The pattern of dP_4 is slightly more progressive in the material from Quarry I. In one of the two specimens (YPM 21293) the anteroconid is connected to the anterior arm of the protoconid, and in the other (YPM 21294, fig. 4 A) the anteroconid has united with both the protoconid and metaconid and forms the principal connection between these two cusps, with the metalophid greatly reduced.

In the molars the pattern seems to be identical with that in the type of *Ph. paraphiomyoides* (fig. 3 A) with no posterior arm of the protoconid on M_1 and a very slight one on M_2. The enamel seems to be proportionately thicker than in the specimens from Quarry G.

The measurements of the incisors of these specimens differ slightly from those of *Ph. paraphiomyoides* (Table 3), but the incisor ratios are quite instructive in that for two specimens the ratio is larger than for any specimen from Quarry G and for the third it is smaller, suggesting that a larger sample from Quarry I might be indistinguishable in this respect from the material from Quarry G.

The measurements of the cheek teeth, however, seem to point to a distinction between the two populations (Table 3). Results from the use of Student's t test show that the probability of the two collections belonging to the same population is less than .01 for all measurements. The probability approximates .001 for the length of dP_4 and is less than .001 for the metalophid width of dP_4, M_1 and M_2 (the only teeth available), for the hypolophid width of M_1, and for the length of M_2.

On the other hand, the specimens from Quarry I are within the observed range of the population of *Ph. andrewsi* in all measurements except the metalophid width of dP_4, which is wider in the Quarry I specimens. The tooth pattern, however, is more progressive than that of *Ph. andrewsi* in the essentially complete loss of the posterior arm of the protoconid and of the mesoconid and mesolophid (compare fig. 4 A with fig. 1).

The specimens of *Ph.* aff. *paraphiomyoides* from Quarry I, then, are a group of animals significantly larger in cheek tooth dimensions than those of *Ph. paraphiomyoides* from Quarry G, and appreciably different in cheek tooth pattern from those of *Ph. andrewsi.* Presumably the Quarry I specimens represent a descendant population either of *Ph. paraphiomyoides* that has increased significantly in size without undergoing any other important changes observable in the present material, or of *Ph. andrewsi* that has paralled the early *Ph. paraphiomyoides* in pattern simplification with no change in size. There is little to choose between these alternatives. The former is adopted simply to make a choice. Whether the Quarry I population deserves separation at an infraspecific level, and if so, from which species, can best be left undecided until considerably larger collections are available.

Phiomys lavocati n. sp.*

Figure 5 A–E

HOLOTYPE. CM 26903, right lower jaw with M_{1-3} and the incisor, from Quarry E, collected by D. E. Russell.

HYPODIGM. Holotype; YPM 18011, left lower jaw with dP_4–M_1 and incisor; YPM 18057, left lower jaw with dP_4–M_2 and incisor; YPM 18085, 18203 and 18196 (in part), isolated lower incisors; and YPM 18197, 18209 and 18213, isolated upper incisors.

DISTRIBUTION. Quarry E, silicified wood zone, Jebel el Qatrani Formation, early Fayum Oligocene of Egypt.

DIAGNOSIS. Cheek teeth much smaller than in genotype; no trace of mesolophid or mesoconid in any molars; posterior arm of the protoconid varying from very short to almost nonexistent; hypoconulid of M_{1-2} very distinct and set off from hypoconid by a prominent valley; small crestlet from near base of metaconid tends to extend to or toward protoconid, cutting off a pseudo-trigonid basin; anterior cingula weak or nonexistent; protoconid and metaconids of dP_4 connected at their posterior ends, and not through the anterior cingulum; diametric ratio of lower incisor usually about 0.55; measurements as given in Table 4.

DESCRIPTION. One of the striking features of this species is the very small size of the cheek teeth, as compared with those of *Ph. andrewsi* and *Ph. paraphiomyoides.* However, the incisors and apparently the jaws are very similar in size

---

* This species is named for Dr. René Lavocat, in recognition of his extensive work on fossil rodents, particularly those from Africa.

to those of these two species. Unfortunately all three jaws of the present species are badly broken and corroded, so that little more can be told than that they are hystricognath and similar to those of other phiomyids.

No specimens include P_4.

The molars are functionally three-crested. Superficially this is very different from the four-crested teeth of many specimens of *Ph. andrewsi.* However, as indicated above, at least some specimens of the latter have essentially lost the mesolophid (YPM 18043, M_1, fig. 2 B), and there is a complete transition within the species from four- (or, even, four-and-a-half-) crested teeth to three-crested ones. *Ph. paraphiomyoides* has almost and *Ph.* aff. *paraphiomyoides* has fully reached the three-crested pattern demonstrated by *Ph. lavocati.* This series of species of *Phiomys,* as here interpreted, is in the midst of a rapid transition in cheek tooth pattern that leads to *Paraphiomys* in which the teeth are entirely three-crested. The generic separation is drawn, at the present time, to place all of these forms in *Phiomys* because the teeth are low-crowned and still clearly show their constituent cusps in contrast to the conditions in *Paraphiomys* (compare figs. 3, 4 and 5).

In M_1 of the holotype and of YPM 18011 and in M_1 and M_2 of YPM 18057 (fig. 5 A, C, D), there is a small accessory crest extending from the metalophid near the base of the metaconid, backward or backward and linguad, cutting off a valley after wear between the metaconid and protoconid, and resembling the trigonid basin of paramyids. It seems clear, however, from the conditions described in *Ph. paraphiomyoides* that this is a neomorph developing in this species. Its absence in *Paraphiomys occidentalis* from Beni Mellal suggests that it had no future development.

The posterior arm of the protoconid varies from being a short crest con-

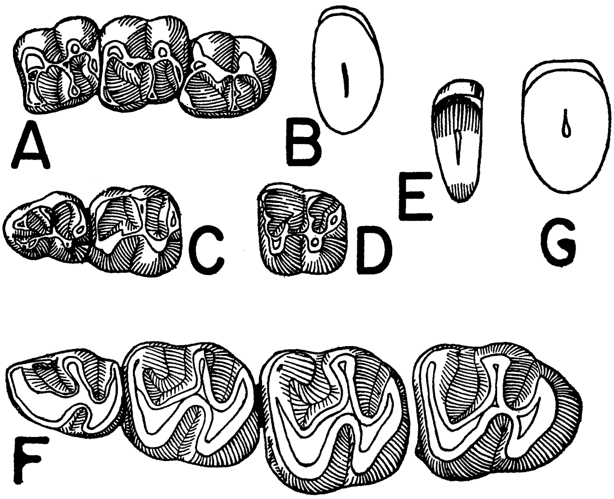


FIGURE 5. Teeth of *Phiomys lavocati* and *Paraphiomys simonsi.*
A–E. *Phiomys lavocati,* × 10. A. Right M_{1-3}, CM 26903, holotype. B. Occlusal surface of right I_1, CM 26903, holotype. C. Left dP_4–M_1, YMP 18011. D. Left M_2, YPM 18057. E. Occlusal surface of isolated right I^1, YPM 18197. F–G. *Paraphiomys simonsi,* CM 26908, holotype, × 5. F. Left dP_4–M_3. G. Occlusal surface of left I_1.

tinued a little way across the talonid basin in M_2 of YPM 18057 (fig. 5 D) to being a mere nubbin on the mesolophid (CM 26903, M_{2-3}; YPM 18011, M_1; YPM 18057, M_1) and finally to a slight irregularity in the outline of the protoconid (M_1, CM 26903, fig. 5 A).

Anterior cingula are essentially absent, as is true of *Paraphiomys*. The only tooth that shows any trace of such a structure is M_1 of YPM 18011. Here the anterolingual corner of the tooth is expanded slightly in a manner similar to that in some specimens of *Ph. andrewsi* where this results in the formation of a distinct cingulum.

The hypolophid shows some irregularities. In M_1 of the holotype there is a faint swelling near its middle. In M_3 of the same specimen and in M_2 of YPM 18057 (fig. 5 D), there is a distinct enlargement extending back toward the posterior cingulum. The hypoconulid is large and bulbous in all specimens except M_3 of the holotype where it forms a smooth curve, as in other species of *Phiomys*. If the hypoconulid is large, it is set off from the hypoconid by a prominent valley behind the posterolophid.

Deciduous teeth are present in both of the referred jaws, dP_4 of YPM 18057 being considerably worn and that of YPM 18011 preserving the pattern (fig. 5 C). This tooth resembles the shorter type of dP_4 in *Ph. andrewsi* (fig. 2 B) which, being associated with the molars with the weaker mesolophids, may represent that end of the *Ph. andrewsi* population closest to *Ph. lavocati*. The anterior cingulum is less well-developed than in *Ph. andrewsi*, being primarily a forward continuation of the protoconid and showing no connection with the metaconid, and it does not block the valley as in *Ph. paraphiomyoides*. The basin between the protoconid and metaconid is large, as the metalophid curves backwards at its middle. There is no mesoconid. The entoconid is far forward and the posterolophid curves forward into it, isolating a distinct basin. The hypoconulid is very large. This tooth is structurally much closer to that of *Ph. andrewsi* than to that of *Paraphiomys pigotti* where the anterior cingulum extends from the protoconid around to the front of the metaconid. There does not seem to be a connection of the two cusps at their posterior ends. This tooth of *P. pigotti* has already become molariform, whereas in *Ph. lavocati* it has not made this change.

The incisor enamel is similar to that of *Ph. paraphiomyoides,* no specimens showing the medial knob seen in *Ph. andrewsi*. The anterior face may be slightly flatter than in *Ph. andrewsi* (fig. 5 B) and the widest part of the tooth is posterad of the enamel cap. The anteroposterior diameters of the incisors are similar to those of the other species of *Phiomys* but there is a much smaller transverse diameter, so that the incisor ratio is about .55 rather than .65. The only exception is the very young YPM 18011, in which the ratio is about .75, the greater relative width being presumably an age character. On the basis of this general difference in incisor shape, several isolated incisors are referred to this species. A number of isolated, small, *Phiomys*-type incisors from Quarry E, with a ratio in the vicinity of .65, are considered most probably to be referable to juveniles of *Ph. andrewsi*.

Some upper incisors are referred to this species on the basis of size and pattern, as was the case with those referred to *Ph. andrewsi* and *Ph. para-*

phiomyoides. They are proportionately narrower than those of *Ph. andrewsi,* having incisor ratios in the range of .40–.45 rather than .50–.55 (fig. 5 E).

DISCUSSION. This species could almost equally well be referred either to *Phiomys* or to *Paraphiomys* and has been transferred back and forth from one genus to the other during this study. It differs from *Paraphiomys* in the structure of the deciduous premolar, in prominence of cusps, and in size, but agrees in molar pattern. The presence of a small species of *Paraphiomys* in the Miocene of Kenya (Lavocat, 1962, p. 290) shows that size would not rule it out from that genus. Assigning this species to *Paraphiomys* would stress its relationships with the Miocene forms rather than with its contemporaries. Presumably, there was a closer genetic relationship between *Ph. andrewsi, Ph. paraphiomyoides* and *Ph. lavocati* than between the last and *P. pigotti, P. occidentalis,* or the undescribed form from Kenya, but *Ph. lavocati* seems to represent the beginners of the *Paraphiomys* line. However, the presence of the typical *Paraphiomys* species, *P. simonsi,* in the higher levels of the Fayum emphasizes the differences between the genera, and has led to the final decision to place *Ph. lavocati* in *Phiomys.*

GENUS *Paraphiomys* Andrews 1914

GENOTYPE. *Paraphiomys pigotti* Andrews, 1914.

REFERRED SPECIES. *P. occidentalis* Lavocat, 1961; and ***P. simonsi,*** n. sp. At least one undescribed species is listed by Lavocat (1962, p. 290).

DISTRIBUTION. Oligocene and Miocene of Africa.

EMENDED DIAGNOSIS. Phiomyid with cheek teeth higher crowned than in *Phiomys;* both mesolophid and posterior arm of protoconid weak or nonexistent in lower teeth; crests rather than cusps dominating the tooth pattern; dP_4^4 proportionately smaller than in *Phiomys.*

DESCRIPTION. *Paraphiomys* was characterized by Andrews (1914, p. 178) as being very similar to *Phiomys* except that the posterior arm of the protoconid was weak or nonexistent. In this he was followed by Lavocat (1961, p. 45). As indicated above in the emended diagnosis, this is one of the basic diagnostic criteria of this genus, separating it from all material of *Metaphiomys* and from most of the material of *Phiomys. Paraphiomys* agrees with *Metaphiomys* in being distinctly higher crowned than *Phiomys* and in having the teeth formed of crests on which the cusps can be distinguished, rather than of cusps united by crests. This last difference is hard to define, but shows up easily both in the specimens and the figures (compare the *Paraphiomys*-like *Ph. lavocati* of fig. 5 A, C and D with *P. simonsi* of fig. 5 F). In addition the premolar (surely dP_4^4 and not P_4^4) is much smaller proportionately than in *Phiomys* or *Metaphiomys.*

As Lavocat notes, Schaub (1958, p. 705) stressed the increased width of the posterior half of the molars and the structural complexity of the premolar of *Paraphiomys* as compared with *Phiomys.* This greater complexity is presumably due to the fact that the anterior cheek tooth in *Paraphiomys pigotti* is dP_4 rather than P_4. This is indicated both by comparison of its pattern with that of P_4 and dP_4 of *Phiomys andrewsi* and by the fact that it is considerably more worn than is M_1 (Andrews, 1914, pl. 28, fig. 7).

The premolar of *Ph. andrewsi* figured by Osborn (1908, fig. 3 A and fig. 1 B, above), on which Schaub based his understanding of the premolars of *Phiomys,* is P_4. The great width of the posterior half of the molars is much more striking in Andrews' figure of the genotype of *Paraphiomys* than in Lavocat's illustrations (1961, fig. 6 B, pl. 4, fig. 4) of *P. occidentalis* and is probably at most a specific characteristic. Measuring from Andrews' illustration (1914, pl. 28, fig. 7), the ratio of metalophid to hypolophid widths (M/H) is .828 on M_1 and .895 on M_2; measuring from Stehlin and Schaub's figure (1951, fig. 325) the values are .812 and .895 respectively. Lavocat's two stereoscopic photographs of M_2 of *P. occidentalis* (Lavocat, 1961, pl. 4, fig. 4) give ratios of .923 and .894, respectively, whereas his text figure (1961, fig. 6 B) gives a ratio of .97. In *P. simonsi,* the ratios are .975 for M_1 and 1.04 for M_2, similar to those in *Phiomys.* In *Ph. lavocati* the ratio for M_1 averages .924, a lower figure than for either of the other species of *Phiomys,* but that for M_2 averages 1.065. Thus there would seem to be some tendency toward increasing the width of the hypolophid of M_1 in *Paraphiomys,* but it does not seem to be as significant a feature as Schaub thought.

Paraphiomys simonsi n. sp.*

Figure 5 F–G

HOLOTYPE. CM 26908, a badly damaged left lower jaw with dP_4–M_3 and the incisor.

HYPODIGM. Holotype only.

DISTRIBUTION. Yale Quarry I, upper levels; Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. No trace of mesolophid or mesoconid, and a very faint suggestion of the posterior arm of the protoconid on M_2 only; wear surface from metaconid extending into talonid basin; dP_4 is much the smallest of the four cheek teeth, and is considerably smaller than in *P. pigotti;* molars about the size of those in the two described Miocene species, but none significantly wider than long; incisor similar in cross section to that of *Ph. lavocati;* mental foramen very high on jaw, almost as high as the alveolar border; tooth measurements as given in Table 4.

DESCRIPTION. This species is the largest rodent so far recovered from the Jebel el Qatrani Formation, being approximately the size of a muskrat or a prairie dog. There is no possibility of confusing it with any other species from the Jebel el Qatrani Formation.

The lower molars have the simplified, three-lophed pattern characteristic of the genus, resulting from the complete suppression of the posterior arm of the protoconid and of the mesoconid and mesolophid (fig. 5 F). There is a strong connection between the protoconid and the metaconid along the anterior margin of the teeth. A small basal cingulum lies along the anterior side of the protoconid, rising into a small cuspule which is, however, much below the level of the occlusal surface of the molars. This cuspule could easily give rise to the much more prominent, conical, cingular tubercle, that Lavocat (1961, p. 46 and fig. 6 B) figures and describes in *P. occidentalis* and which he states also occurs in *P. pigotti.* The metaconids are continued backward by broad swellings,

---

* This species is named for Dr. Elwyn Simons, who turned the Fayum rodents over to me for study.

filling much of the lingual part of the talonid basins. The nearly square M_2 is the widest tooth; M_3 is the longest (Table 4).

The premolar can be recognized as a deciduous tooth by the fact that it is much more worn than is M_1. It also has a very low crown and thinner enamel than do the other teeth. It is the smallest of the cheek teeth. The posterior half of the tooth is similar to that of the molars or to the corresponding part of dP_4 of *Ph. lavocati.* The anterior half, which is badly worn (fig. 5 F), obviously had an anterior metaconid, extended backward along the lingual margin of the tooth, and a large protoconid. It is impossible to tell whether the protoconid and metaconid were separated by a deep valley, as in dP_4 of *Ph. lavocati,* or whether an anteroconid was present. Andrews' figure of *P. pigotti* (1914, pl. 28, fig. 7) suggests that there was no anteroconid in that species.

The lower incisor (fig. 5 G) is basically similar to that of *Phiomys* except for its larger size.

The lower jaw is badly broken, and little of significance can be seen in most of the bone. However, the mental foramen is preserved. It is very high on the side of the mandible, almost up to the alveolar border of the diastema, and is distinctly in front of the anterior root of P_4. This is identical to the situation in the material from Quarry I identified as *Ph.* aff. *paraphiomyoides* (fig. 4 B). The symphysis in *P. simonsi* is rugose and it seems probable that there was little free motion between the mandibles.

DISCUSSION. It is, perhaps, somewhat difficult to separate this species from the genotype, *P. pigotti,* from Kenya (Andrews, 1914, p. 178), or from *P. occidentalis* from Morocco (Lavocat, 1961, p. 45). On the basis of the published descriptions, these two seem very similar. Lavocat distinguishes *P. occidentalis* from *P. pigotti* solely by stating "Molaires inférieures comme *Paraphiomys pigotti,* mais mésolophide vestigial" (1961, p. 45) and "la plus grande réduction du mésolophide montre qu'elle est plus évoluée" (1961, p. 46). A comparison of Lavocat's figures of the isolated lower molar of *P. occidentalis,* which he considers probably to have been M_2 (1961, fig. 6 B and pl. 4, fig. 4), with his redrawing of M_2 of *P. pigotti* (1961, fig. 6 C) or with Andrews' original figure (1914, pl. 28, fig. 7) suggests that the posterior arms of the protoconid (NOT the mesolophids—see below) are very short and essentially vestigial in both forms. This difference in length of the crests probably is not due to wear but is entirely expectable as an individual variant, especially if individual variation in Miocene phiomyids were anywhere near as great as in the Oligocene ones. Lavocat states (1961, p. 46) that the small anteroexternal cingular cusp is present in *P. occidentalis* as in *P. pigotti.* Therefore, all one can say at present is that these two species do not seem readily separable on the basis of M_2, the only comparable part known. *Paraphiomys simonsi* is clearly more advanced than either of the Miocene forms in the reduction of the posterior arm of the protoconid. Andrews' figure (1914, pl. 28, fig. 7) suggests that the protoconid and metaconid of dP_4 were not separated by a basin and that there was no anteroconid, both of which could also have been true in *P. simonsi.* However, this species is separable from *P. pigotti* on the basis of measurements, dP_4 being much smaller in the Fayum species and all three of the anterior cheek teeth being much narrower.

Lavocat's identification of the small crest in *P. occidentalis* as the mesolophid (1961, p. 45) was entirely reasonable at the time he wrote, both on the basis of what was visible in his specimens and what is known of rodent tooth evolution in general. However, the sequence of tooth patterns in the Fayum rodents described in the present paper shows clearly that the mesolophid was rapidly lost among these forms and that the second crest from the front of the lower molars, which was also in process of reduction in this group and which is the crest that is vestigial in *P. pigotti* and *P. occidentalis,* was the posterior arm of the protoconid.

GENUS *Metaphiomys* Osborn 1908

GENOTYPE. *Metaphiomys beadnelli* Osborn, 1908.

REFERRED SPECIES. ***Metaphiomys schaubi*** n. sp.

DISTRIBUTION. Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. Larger than *Phiomys;* infraorbital fenestra large; large palatine fossa containing the anterior palatine foramina; palatine extends forward to anterior end of tooth row; coronoid process of lower jaw extends slightly above occlusal level of cheek teeth; dental formula: P_1^2, M_3^3; dP_4 and (presumably) dP^4 persistent apparently throughout life; cheek teeth basically lophate, with cusps relatively poorly indicated; no suggestion of a mesolophid, and essentially none of a mesoconid, both being functionally replaced by the prominent posterior arm of the protoconid; usually a posteriorly directed spur (protospur) from posterior arm of protoconid; posterior arm of protoconid progressively unites with metaconid, and lingual tip of posterolophid tends to unite with entoconid, both surrounding deep basins; well-developed mesoloph on upper molars; lower incisor with flat anterior face; upper incisor with rounded anterior face.

DESCRIPTION. This genus is much closer to *Phiomys* than was indicated by Osborn's description (1908, p. 270) and *M. schaubi* almost fills the gap between the two genotypes. Indeed, in the initial stages of this study, *M. schaubi* was considered to be an advanced species of *Phiomys,* and the separation between the two genera as here defined is not great.

The skull is represented in *M. schaubi* by a number of fragments of the maxillary including the cheek teeth, and one premaxilla including the incisor. The last has been identified by the shape of the incisor. From these fragments the skull would seem to have been very similar to those of the modern *Petromus* and *Thryonomys* and the description is based on a comparison with those forms, especially the former. It is obviously also very similar to the skulls of *Paraphiomys* from East Africa discussed by Lavocat (1962, p. 290–291).

The premaxilla is flat, laterally, except for a slight elevation over the incisor (fig. 6 C). In this it differs from the living genera where there is a deep depression on the lateral surface of the premaxilla, within the curve of the incisor, for the origin of the pars anticus profundus of the masseter. This muscle must have had a much smaller anterior extension in *Metaphiomys* than in *Petromus* or *Thryonomys,* which is not surprising in view of their relative ages. Ventrally, the anterior palatine fenestrae are large and not sunk into a palatal depression as much as in *Petromus* or *Thryonomys,* although there is a shallow depression

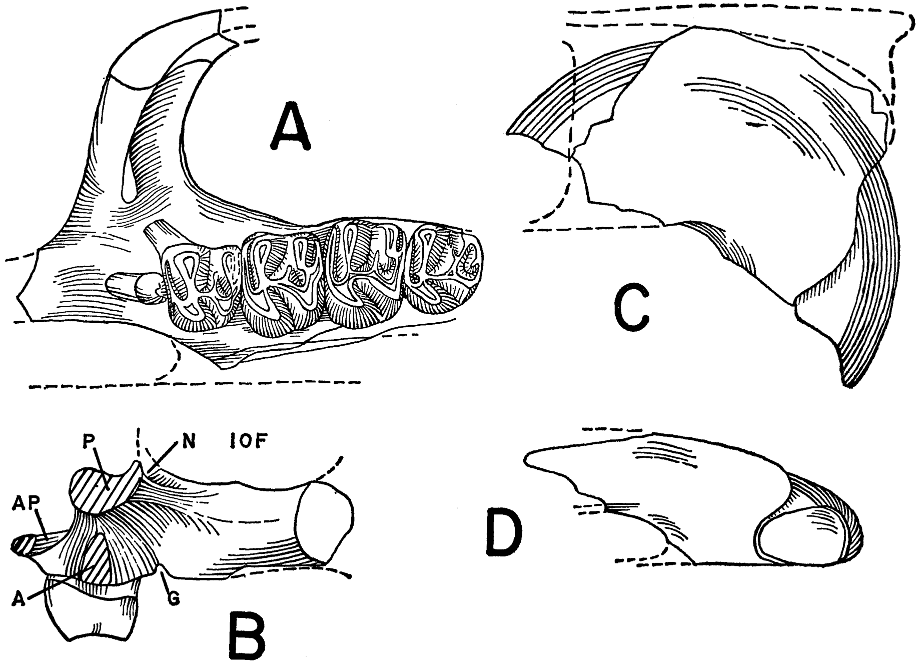


FIGURE 6. Skull fragments of *Metaphiomys schaubi,* × 5.
A. Ventral view of left maxilla, composite restoration. YPM 21309 shaded, outlined areas based on YPM 18228 and 21320. B. Anterior view of maxilla, YPM 21309.
Abbreviations: A–alveolus for ?dP^3; AP–fossa containing anterior palatine fenestra; G–groove, perhaps for platysma; IOF–infraorbital fenestra; N–groove for infraorbital nerve and blood vessels; P–broken end of palate. C-D. Premaxillary, YPM 21303. C. Lateral view. D. Ventral view.

lateral to the fenestra (fig. 6 D), within which the fenestrae lie, which suggests the initial stages of the *Petromus* type of modification. The palatine fenestra is more rounded anteriorly than in the recent genera. No suggestion of an interpremaxillary foramen is present in any of the genera, although there is a paired foramen at the anterior end of the anterior palatine fenestra in *Petromus* and *Thryonomys* not seen in *Metaphiomys.* Posteriorly, there is a broad depression extending as far back as the anterior end of dP^4 (fig. 6 A), which seems to be identical to the deep fossa that contains the anterior palatine fenestrae in *Petromus* and *Thryonomys.* There is a shallow depression in front of P^3 for the origin of the zygomaticus muscle, as in *Petromus.* The palatine extends far forward, apparently reaching to or nearly to the palatal fossa, at about the level of the anterior end of the tooth row. This is a most unusual length for the palatine but this situation is also found in *Petromus* and *Thryonomys.* The infraorbital fenestra is large and rounded (fig. 6 B), and is very similar to the corresponding portions of those of *Petromus* and *Thryonomys.* As in the recent genera, there is a distinct groove (fig. 6 B, N) between the main body of the fenestra and its median wall for the infraorbital nerve and blood vessels, separated from the muscle by a ridge of bone. In *Petromus* this ridge serves for the attachment of a strip of connective tissue that runs up to the ventral surface of the lacrimal and it seems probable that the same condition existed in *Meta-*

phiomys. Between the masseteric tubercle and the anteroexternal root of dP^4 there is a groove (fig. 6 A, B, G) which is not as well developed in *Petromus* but is about as prominent in *Thryonomys* as in *Metaphiomys*. This may have carried the anterodorsal branch of the platysma.

The jaw is badly damaged in most of the available specimens, but it is fairly complete in one specimen of *M. schaubi* (YPM 18222, fig. 7 A, B). It seems almost identical, except for size, with those of *Phiomys* and *Paraphiomys* and it is also very similar to that of *Petromus* which has been used in the restoration of the posterior portion. There is a well-developed pit at the upper end of the masseteric fossa for the pars anticus profundus of the masseter, which is, however, much weaker than in *Petromus* or *Thryonomys*. The main masseteric fossa is deep. The mental foramen lies beneath the anterior root of dP_4 as in all Fayum genera. The eversion of the angle would seem to have been the same as in *Phiomys*. From the available space, it would seem that the coronoid process must have been low (fig. 7 A, B), though it was probably somewhat higher than in *Petromus* or *Phiomys*, and perhaps lower than in *Thryonomys*. The condyle was slightly above the grinding surface of the cheek teeth instead of being at the same level as is true of *Petromus*. On the median side the base of the incisor is immediately beneath M_3, again resembling the situation in

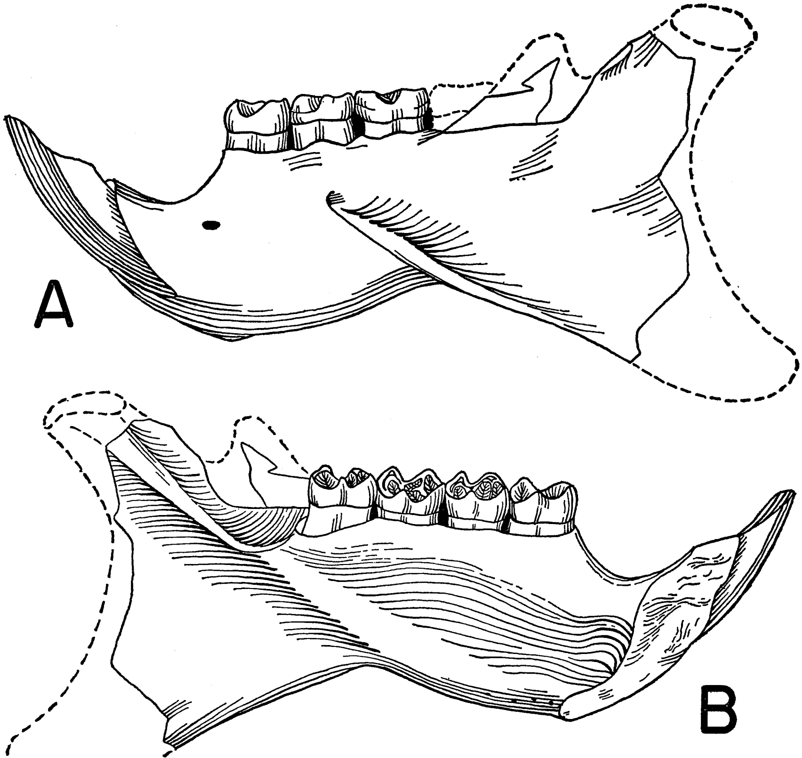


FIGURE 7. Lower jaw of *Metaphiomys schaubi*, YPM 18222, with coronoid process and teeth restored from YPM 18001, × 3. A. Lateral view. B. Medial view.

Petromus, and is continued backward by a heavy strut (fig. 7 B) which extends to the condyle, exactly as in *Petromus.* This strut is apparently considerably heavier than in *Ph. paraphiomyoides* (fig. 3 C), unless the postdental portions of the jaw were much longer in *Metaphiomys* than the restoration would indicate. The angle at which the strut rises suggests that this was not the case. The pit for the genioglossal muscle is less developed than in *Petromus* and is much weaker than in *Thryonomys,* but the long posterior tail of the symphysis is similar to that of the recent genera. The absence of strong rugosities on the symphysis suggests that there was a well-developed transversus mandibulae muscle as in *Petromus.* The mandibular foramen is not preserved in any specimen of *Metaphiomys.* Therefore, it must have been higher on the coronoid process than in *Petromus,* where it lies at the bottom of the fossa immediately behind and below M_3. In this *Metaphiomys* was apparently identical with *Phiomys paraphiomyoides* (fig. 3 C) and with *Thryonomys.*

Upper teeth are known only for *M. schaubi,* but these are represented by eleven specimens. There were two upper premolars and three molars. No direct evidence is available, but analogy with the lower teeth suggests that the premolars are deciduous, although, as I pointed out (1962a, p. 68), there is considerable uncertainty as to whether there were both dP^3 and P^3 in the paramyids (and hence, presumably, in later members of the order). If only one of these teeth occurs, there is complete uncertainty as to whether it is dP^3 or P^3.

The upper molars are basically five-crested, although there is very considerable variation in the length of the mesoloph which may or may not reach the buccal margin of the crown; sometimes it joins the metaconule. The metaloph is incomplete, the metaconule connecting with the posterior cingulum rather than with the hypocone. M^3 does not have a hypocone, though an angulation of the posterior cingulum seems to mark where it is about to develop. In this respect this genus is much more primitive than either *Thryonomys* or *Petromus.* The enamel of dP^4 is thinner than that on the molars and the crests are not quite so nearly parallel, both traits characteristic of rodent deciduous teeth. Otherwise it is very molariform. In front of it is a small, conical tooth, dP^3 or P^3. As in primitive paramyids, it has a very simple pattern.

The lower teeth are slightly more lophate than are those of *Phiomys* but show very little increased complexity. The variability of the mesoconid area seen in *Phiomys* is absent and there is a rather uniform pattern as indicated in the diagnosis. Osborn's figure (1908, fig. 5) is not clear in many of the details, especially of M_2, and does not distinguish between areas that are broken away and areas that show the pattern. This is why these illustrations were misinterpreted and erroneously redrawn for the figure in Stehlin and Schaub's monograph (1951, fig. 327).

The lower molars show a pronounced ridge running from the protoconid to or toward the metaconid. In the earlier *M. schaubi,* it arises from the posterior end of the protoconid; in *M. beadnelli,* from farther forward. On the basis of the sequence described in *Phiomys* this ridge is interpreted as the posterior arm of the protoconid that has functionally replaced the mesolophid and which has then shifted farther forward. There is usually (but not always) a posterior crest from the middle of the posterior arm of the protoconid, termed the protospur, extending backward toward the middle of the hypolophid. The cusps show merely as slight enlargements of the crests, not clearly indicated until after wear.

The lower premolar is unknown. All specimens show the retained dP_4, as demonstrated by its being universally more worn than is M_1. The pattern of this tooth is rather variable, but in general it is more complex than is P_4 of *Phiomys* and usually less complex than dP_4 of that genus. The main upper premolar also seems to be a retained deciduous tooth. It seems probable either that P_4^4 have been suppressed in this genus or that they erupt very late in life. The former is much more probable, since even YPM 21296, a specimen of *M. schaubi* with highly worn molars, still retains dP_4. This tooth, like that of *Phiomys,* has a molariform posterior portion, whereas the anterior end consists of the closely associated protoconid and metaconid connected with the posterior portion by a long ectolophid.

The lower incisor has a broad, nearly flat anterior face, with the enamel extending very short distances onto the lateral and median surfaces. As a result of the greater width, the incisor ratios are higher than in *Phiomys* (cf. Tables 1 and 9). There is no trace of the median knob seen in *Phiomys.* This would have been much more efficient as a gnawing tool than the incisor of *Phiomys* which was probably used more as a cutting tool.

No upper incisors are associated with cheek teeth of this genus. Among the large number of isolated incisors, however, there are a number of the correct size and proportions to belong to this genus. One, YPM 21303, is in a damaged premaxilla (fig. 6 C–D).

DISCUSSION. *Metaphiomys* clearly was derived from *Phiomys.* To make the transition, all that is needed is a slight increase in hypsodonty; a slight increase in the strength of the lophs and a concomitant reduction in the importance of the cusps; and the fixation of a lower molar pattern with a prominent posterior arm of the protoconid. In the other direction, the tooth pattern of *Metaphiomys* does not seem to be very similar to that of *Thryonomys* (Wood, 1962b, fig. 2 A–B). However, there are suggestions, in the forward displacement of the posterior arm of the protoconid in *M. beadnelli* (fig. 8 C) of the condition accurately illustrated by Stromer (1926, pl. 41, figs. 25 C, 32 C) in *Pomonomys* and *Diamantomys,* although the protospur is more widely separated from the base of the entoconid than in Stromer's forms. *Diamantomys* is more primitive than *Pomonomys,* the latter having high-crowned teeth with the valleys along the buccal margins of the teeth (between protoconid and anterior cingulum and between protoconid and hypoconid) filled with cement. There is some cement along the lingual margin of the crown, but it does not extend into the lingual valleys. There is no cement on the teeth of *Diamantomys. Pomonomys* or *Diamantomys,* in turn, could have led to the tooth pattern seen in *Petromus* (Wood, 1926b, fig. 1 E–F).

Stromer (1926, p. 137–138) placed *Diamantomys* and *Pomonomys* and an isolated upper molar that he identified as *"Cfr. Phiomys Andrewsi* Schlosser (non Osborn)" together in the "Theridomyidae?". Stromer's description and illustrations of the isolated molar (lost during World War II) indicate that it is neither *Phiomys* nor at all close to what Schlosser called *Phiomys andrewsi,* discussed below on p. 73 as *Gaudeamus aegyptius.* Stromer's reference of these forms to the "Theridomyidae?" was in accord with the then-current ideas of the relationships of the Phiomyidae. However, Stromer did not think his forms were related to those from Egypt, saying of *Diamantomys,* "Mit *Phiomys* Osborn, *Metaphiomys* Osborn . . . scheint mir weder in der Kiefer- noch in der Zahnform eine Ähnlichkeit zu bestehen (1926, p. 138)." Schaub (1958, p. 786) erected a new family, Diamantomyidae, for *Diamantomys* and *Pomonomys,* stating that the lower molars have a "structure difficile à interpréter, sans rapports avec les autres plans structuraux des Simplicidentés." This pattern, however, is interpretable in terms of what we now know to have been happening in *Metaphiomys*; and the loss of the valley between the metaconid and the posterior arm of the protoconid in the Miocene genera would lead to the conditions found in *Petromus.* I (1955, p. 172) placed *Diamantomys* in the Phiomyidae. Lavocat (1962, p. 291) agrees with this and has also placed *Pomonomys* in this family where it surely belongs.

Metaphiomys beadnelli Osborn
Figure 8

OTHER ILLUSTRATIONS. Osborn, 1908, fig. 5; and Stehlin and Schaub, 1951, fig. 327.

Metaphiomys beadnelli Osborn, 1908, p. 270.

HOLOTYPE. AMNH 13273, a left lower jaw with M_{1-2} and the incisor.

HYPODIGM. Holotype and YPM 18226, a crushed left jaw with dP_4–M_3 and the incisor.

DISTRIBUTION. Uppermost level, Jebel de Qatrani Formation, Fayum early Oligocene of Egypt.

DIAGNOSIS. Lower molars with long posterior arm of protoconid and long posterolophid uniting with metaconid and hypoconid, respectively, after slight or very slight wear, surrounding closed basins; posterior arm of protoconid arises far forward from middle of protoconid or from metalophid; protospur strong and sometimes compound; anterior cingulum strong; essentially no crests extending backward from middle of hypolophid; hypoconulid rather distinct largely due to its backward growth; incisor proportionately wide; tooth measurements as given in Table 8.

DESCRIPTION. Both molars of the holotype are badly broken (fig. 8 A). Although the teeth are quite accurately shown by Osborn (1908, fig. 5), especially in his enlarged drawing of M_1, his figures do not clearly indicate the areas of breakage nor do they distinguish between enamel ridges and broken edges of the enamel. As a result, his figure of M_2 looks as though there were a bifurcation of the lingual end of the hypolophid; as though there were two ridges running buccally and posteriorly, respectively, from the hypoconid; and as though the posterior arm of the protoconid did not unite with the metaconid. All of these appearances, which are incorrect, are accurately reproduced by Stehlin and Schaub (1951, fig. 327), and are commented on by Stehlin (op. cit., p. 218) as striking peculiarities of this form, as indeed they would be if they existed.

In both specimens, the protoconid of the molars is connected with the metaconid both by way of the metalophid and through the posterior arm of the protoconid. In YPM 18226 the tip of the posterior arm does not extend as

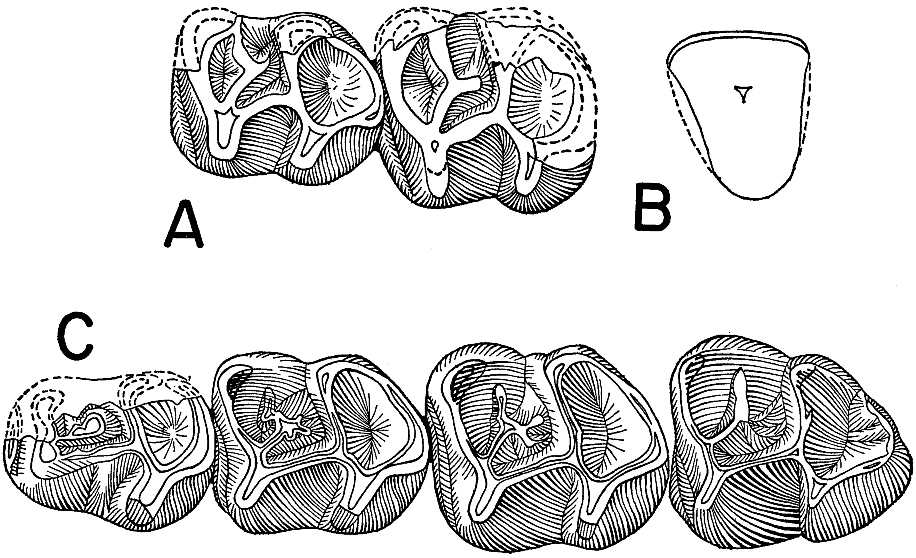


FIGURE 8. Teeth of *Metaphiomys beadnelli,* × 10.
A–B. Holotype, AMNH 13273. A. Left M_{1-2}. B. Occlusal surface of left I_1. C. Left dP_4–M_3, YPM 18226.

high on the metaconid as in the type (fig. 8 A, C), which may be due to differences in wear. The posterior arm of the protoconid has moved its buccal end farther forward than in *Phiomys* or *M. schaubi* and it attaches to the middle of the protoconid (fig. 8 A) or even to the metalophid (fig. 8 C). As a result of this displacement, the crest formed by this arm is curved with a strong protospur arising at the posterior point of the curve. The protospur is single in the holotype but compound on the referred specimen (fig. 8 C). There is slightly less closure of the anterior basin in M_3 than in the other teeth. This anterior basin is homologous to that in *Diamantomys* (Schaub, 1958, fig. 220), an animal whose teeth differ surprisingly little in pattern from what one would expect in equally worn teeth of *M. beadnelli.* The hypoconulid extends backward so that the posterior basin, surrounded by the hypolophid and posterolophid, is nearly circular. The buccal valley between the hypoconid and the hypoconulid is prominent but, as in *M. schaubi,* it seems to have been less prominent on M_2 than on M_1 and still less on M_3. The hypoconulid is not united with the entoconid on M_3, which may in part be due to its lack of wear (fig. 8 C). There is no trace on either tooth of the holotype of the crest from the hypolophid into the posterior basin, frequently seen in *M. schaubi* (figs. 9 A, E, F, and 10 E), although there are faint irregularities of the enamel here on M_{2-3} of the referred specimen. The anterior cingulum is large and prominent, well below the level of the rest of the crown, as in *Diamantomys.* It is about half as long on M_3 as on the other molars and limited to the buccal half of the tooth, whereas in *Diamantomys* (Schaub, 1958, fig. 220) it is of about equal length on all teeth.

The premolar is present on YPM 18226 but is badly broken (fig. 8 C). The hypoconulid is strong but seems to have been farther from the entoconid than in the anterior molars. A faint swelling of the ectolophid is present, showing the position of the mesoconid, and there were two rounded cusps at the anterior end of the tooth, as in the shorter type of dP_4 of *Ph. andrewsi* (fig. 2 B). There was a strong anterior cingulum. A ridge extends backward from the protoconid, just mesiad of the ectolophid, almost reaching the hypolophid, as in the holotype of *M. schaubi.*

The lower incisor of the holotype has been eroded on each side so that it appears more pinched near the wear surface than it does farther back. It has been restored in figure 8 B. It shows the characteristic flat anterior face of the genus, which is more pronounced in this species than in the earlier and more primitive *M. schaubi.* The pulp cavity is very small at the wear surface, but is essentially triangular in shape. The incisor of the referred specimen is very similar.

The lower jaw is similar to that of *M. schaubi* and to that of *Phiomys.* Both specimens are so badly eroded that very little more can be told, except that the mental foramen, as shown by Osborn (1908, fig. 5), is slightly farther forward than in *Phiomys.* The jaw clearly was hystricognathous, but few details are visible. There were numerous nutritive foramina in the chin region. The masseteric fossa was similar to that described below for *M. schaubi.*

Metaphiomys schaubi n. sp.*
Figures 6, 7, 9, 10, 11, 12

OTHER ILLUSTRATIONS. Schaub, 1958, fig. 58, upper half; Schlosser, 1911, pl. 13, figs. 10 and 10a; and Stehlin and Schaub, 1951, fig. 36.

HOLOTYPE. CM 26910, left lower jaw with dP_4–M_3.

HYPODIGM. Holotype; YPM 18001-2, 18014, 18219–20, 18222–25, 18229–30, 21295–6, 21299, 21301–2, 21305–8, 21310–19 and 21321–30, lower jaws with cheek teeth; 18004 and 21297, lower jaws with incisor but no cheek teeth; 18192–3 and 21331–2, isolated upper and lower cheek teeth; 18020, 18204 and 18232, isolated lower cheek teeth; 18005, 18206, 18221, 18228, 18231, 21298, 21300, 21303–4, 21309 and 21321, upper jaw fragments with one or more teeth; 18088, 18199 and 18214 and AMNH 13277B, isolated lower incisors; and YPM 18201, 18210 and 18216, isolated upper incisors.

DISTRIBUTION. Yale Quarry G; YPM 18192–3, 18199, 18201 and 18216 are from Quarry E and AMNH 13277B from Quarry B. Lower Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. Posterior arm of protoconid and posterolophid of lower molars not united with metaconid and entoconid until after considerable wear; sometimes a crest extending backward from middle of hypolophid; usually a similar crest (protospur) from posterior arm of protoconid, occasionally reaching hypolophid; posterior arm of protoconid generally straight, arising from junction of protoconid and ectolophid; hypoconulid not extended far backward; dP_4 occasionally has what may be a mesolophid; mesoloph variable in length, sometimes reaching buccal margin of teeth and sometimes quite short; short mesolophs sometimes directed into metaloph; often a small ridge on posterior side

---

* This species is named for the late Dr. Samuel Schaub, in recognition of his outstanding work on fossil rodents.

of the protoloph paralleling mesoloph; sometimes a spur from protoconule toward anterior cingulum; posterior half of M^3 quite variable; tooth measurements as given in Tables 2, 7 and 9.

DESCRIPTION. As indicated in the generic discussion, the permanent premolar is unknown in this form.

The lower molars are essentially four-crested, with the anterior and posterior pairs of crests fairly closely united at the lingual margins, though the intervening basins would be open lingually much longer than in *M. beadnelli.* There is a great deal of dental variability, both in these characteristics and in others, and advanced characteristics in one tooth are not necessarily associated with similar conditions in other teeth of the same specimens.

In M_1 of the holotype and of YPM 21311, 21319, 21321 and 21326, the posterior arm of the protoconid comes close to the buccal base of the metaconid, and has a posterior spur, the protospur (fig. 9 A). A faint rugosity is present on the posterior side of the entoconid, but there is no crest at this place. The isolated RM_1 included in YPM 18204 is essentially similar, but there is a small crest from the metalophid extending toward the posterior arm of the protoconid (as is also true in YPM 18224); the protospur is closer to the ectolophid; the tip of the posterior arm of the protoconid grades into the lingual surface of the metaconid (which may be the result of wear); the hypoconulid is more angulate; and the irregularity of the hypolophid is slightly more pronounced (fig. 9 F). The isolated M_1 from Quarry E, YPM 18192, is essentially like the holotype, except that there is no suggestion of any irregularity on the rear of the hypolophid. The broken M_1 of YPM 18001 differs from the holotype only in that there is a faint swelling of the ectolophid, indicating a very small mesoconid. In this tooth of YPM 18014, the posterior arm of the protoconid curves around to join the metaconid, as in *M. beadnelli,* and there is a faint backward crest from the middle of the metalophid (fig. 9 B), as also true in YPM 18002, 18223 and 21322. The isolated tooth of YPM 18020 shows a few differences. The posterior arm of the protoconid has a short lingual continuation, while its main trend is backward through the protospur, as is also true of YPM 18230, 21302, 21306, 21308, 21310, 21312, 21325, 21329 and 21330. The posterolophid is almost united with the entoconid, and there is a prominent crest from the hypolophid toward the posterolophid. The hypoconulid is prominent (fig. 9 E), foreshadowing the condition in *M. beadnelli.* In YPM 18229 and 21316, the posterior arm of the protoconid meets the lingual crest from the rear of the metaconid, and there are several minor irregularities in the middle of the posterior arm (fig. 9 C). The tooth of YPM 21328 is essentially like this, but there is a forwardly directed crestlet from the posterior arm of the protoconid, about the same size and shape as the protospur (fig. 12 H). YPM 21295 and 21305 are more like *Ph. andrewsi* (and presumably are more primitive) than any of the other specimens in that the posterior arm of the protoconid is very short and there is no protospur (fig. 10 A). The posterior arm of the protoconid of YPM 21307 is similar, but slightly longer.

The second lower molar is somewhat more variable than the first, as well as being larger. Most of the variations involve crests from or toward the posterior arm of the protoconid, especially the protospur, although the anterior cingulum

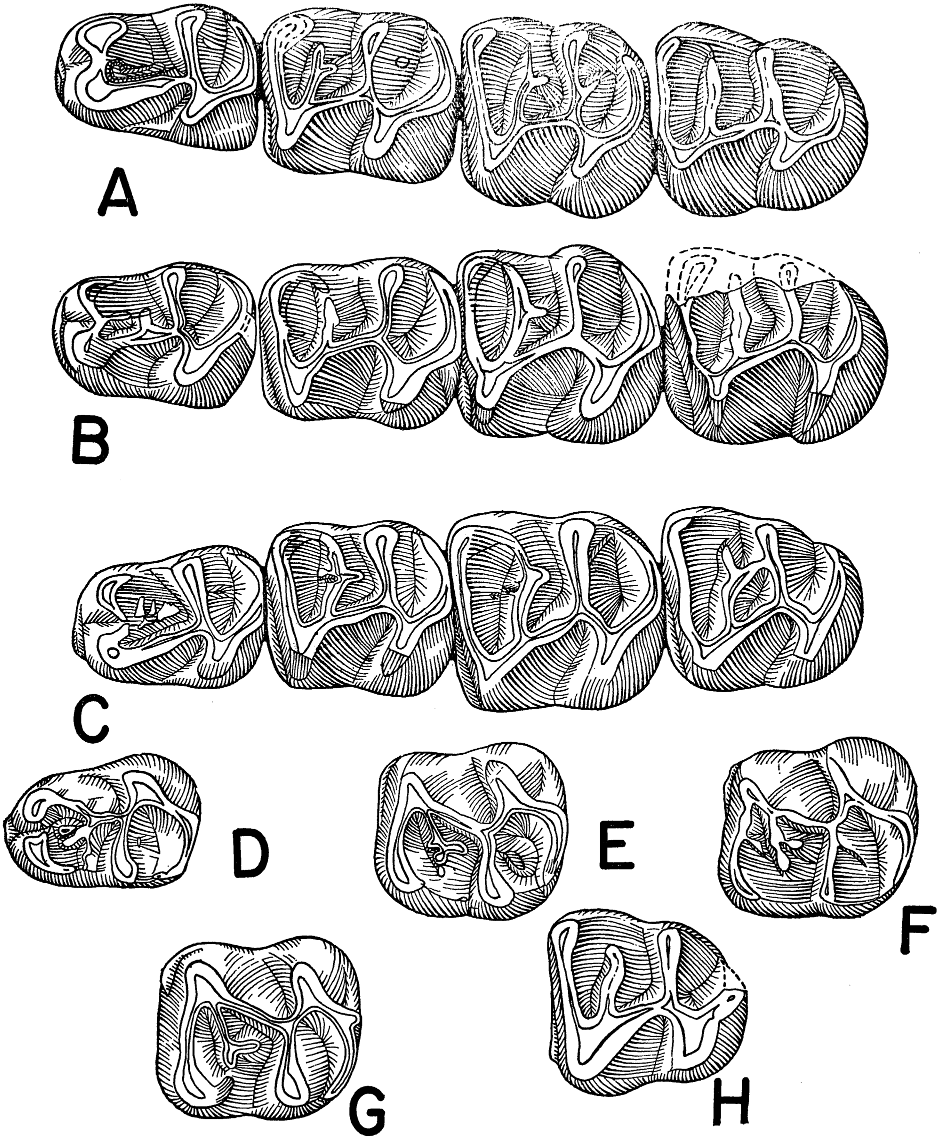


FIGURE 9. Lower teeth of *Metaphiomys schaubi*, × 10.
A. Left dP$_4$–M$_3$, CM 26908, holotype. B. Left dP$_4$–M$_3$, YPM 18014. C. Left dP$_4$–M$_3$, YPM 21316. D. Right dP$_4$, YPM 18204. E. Right M$_1$, YPM 18020. F. Right M$_1$, YPM 18204. G. Right M$_2$, YPM 18232. H. Left M$_3$, YPM 18204.

is also of quite diverse size. The most primitive specimen is YPM 21301 in which the posterior arm of the protoconid is essentially a straight crest (fig. 10 D) as in the most usual type of *Ph. andrewsi* (fig. 1 F). In YPM 21302 and 21306 this same pattern occurs, but there is also a laterally directed spur from the posterior end of the metaconid, which extends to or toward the tip of the posterior arm of the protoconid, as in M$_1$ of YPM 18014 (fig. 9 B). The most usual pattern of M$_2$ shows the lateral spur of the metaconid and a well-developed protospur

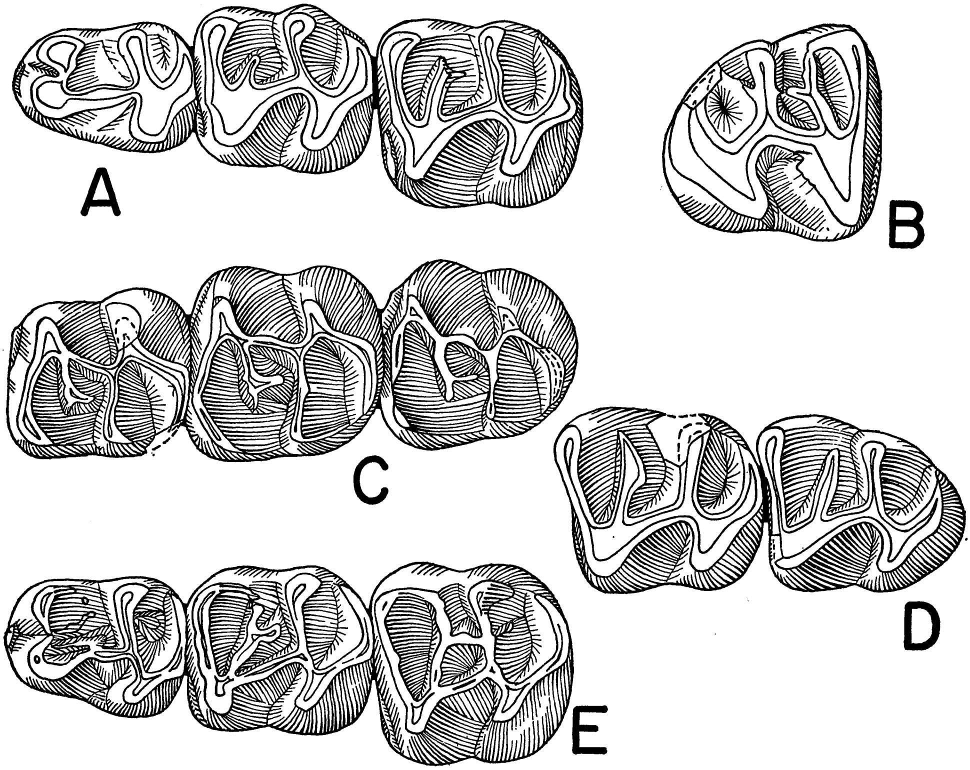


FIGURE 10. Lower teeth of *Metaphiomys schaubi*, × 10.
A. Left dP$_4$–M$_2$, YMP 21295. B. Right M$_3$, YPM 21331, anterior end to right. C. Right, M$_{1-3}$, YPM 18220. D. Left M$_{2-3}$, YPM 21301. E. Right M$_{1-3}$, YPM 21310.

(fig. 9 G). This is seen in YPM 18232 (which is unusual in the large size of the hypoconulid, foreshadowing the condition in *M. beadnelli*) and in YPM 18002, 18225, 18230, 21299, 21308, 21312, 21321 and 21329. A very similar pattern is seen in YPM 21311 where there is, in addition, a faint ridge on the anterior side of the hypolophid, extending toward the protospur. In a few specimens (YPM 18014 and 18229) the pattern is the same as in the common type except that the posterior arm of the protoconid reaches the lingual border of the tooth (fig. 9 B) rather than there being a spur from the metaconid. The isolated M$_2$ of YPM 21331 and M$_2$ of YPM 21330 are of the common type with the addition of a faint backwardly directed ridge from the middle of the metalophid. Another variant occurs in YPM 18222, where there is a crest from the hypolophid that runs just laterad of the protospur, very nearly closing the valley between the protospur and the ectolophid. In the holotype (fig. 9 A) and in YPM 18229 and 21319, the anterior half is of the usual pattern, but there is a posteriorly directed crest from the middle of the hypolophid, similar to the protospur. This latter crest is present, but very weak, in YPM 18223 and 21307. The tooth of YPM 18001 is generally similar to that of the holotype, but there are several minor ridges radiating from the posterior arm of the protoconid, and the posterior basin is partly dammed by a crest from the hypoconulid, as well as by the more usual one from the hypolophid. The pattern of this tooth of YPM 18004 and 21313 is similar to that of the holotype, but approaches that of *M. beadnelli,* since the posterior arm of the protoconid swings around to the rear of the metaconid. A somewhat different trend is suggested by YPM 18220 and 21325, where the posterior arm of the protoconid drops in height toward the metaconid, but the protospur is a high level crest almost reaching the hypolophid (fig. 10 C). Among the most specialized second molars is that of YPM 21328 which has an anterior crest from the posterior arm of the protoconid reaching the metalophid; a crest from the hypolophid reaching toward the large protospur; and a large backwardly directed ridge from the hypolophid (fig. 12 H). Perhaps the most specialized M_2 is seen in YPM 21310, where the posterior arm of the protoconid connects with the metaconid, and the protospur unites with the hypolophid behind which it is continued by a prominent crest extending half-way across the posterior basin (fig. 10 E).

The last lower molar is more triangular than are the other teeth, the posterior half ranging from somewhat (fig. 9 A, B) to considerably (figs. 9 C, 10 B, D) narrower than the anterior. Except in YPM 21325 and 21328 (fig. 12 H), there is never any crest extending from the hypolophid across the posterior basin and the posterolophid is generally short. In some specimens, such as YPM 18204 (fig. 9 H) and 21311, the posterior arm of the protoconid is shorter than usual. In the holotype and several other specimens (figs. 9 A, H, 10 D) there is no protospur. A very faint protospur occurs in YPM 21312. A small one is present in YPM 18192 from Quarry E and in YPM 18229, and one of medium size in YPM 18220 (fig. 10 C) and 21330. A large protospur, reaching to or nearly to the hypolophid, is present in YPM 18219, 21316 and 21331 (fig. 9 C, 10 B), and in 21331 there is a faint forwardly directed rugosity on the hypolophid, which would lead to the condition in 21316.

There are 20 specimens of upper cheek teeth of *M. schaubi* available, ranging from isolated teeth to maxillary fragments containing as many as four teeth, in addition to the maxilla figured by Schlosser (1911, pl. 13, figs. 10 and 10a) as *Ph. andrewsi,* which clearly belongs here, on the basis both of size and of tooth pattern. The largest upper tooth is M^2 (Table 2), and the crests of dP^4 are not quite as parallel as in the other teeth.

The upper teeth differ from those of *Phiomys* in being consistently pentalophate, whereas in the small number of available teeth of *Phiomys* the area of the mesoloph is quite variable. As in the lower teeth, the cusps have firmly united into crests which are the dominant part of the tooth. The conules are very indistinctly shown, the protoconule, especially, showing as a faint angulation of some teeth or as a slight swelling of the protoloph in some stages of wear (fig. 11). The mesoloph is variable in length. In some teeth (fig. 11 A, M^{1-2}) it is long, reaching to the buccal margin of the crown. In others (fig. 11 D, M^{1-2}) it is somewhat shorter, being just blocked from the margin of the tooth by the forward tip of the metacone. In other specimens (fig. 11 B, dP^4–M^2) the mesoloph is short and is directed toward the base of the metacone so that the valley behind the mesoloph is closed at its buccal tip. In some specimens of dP^4 (fig. 11 C), the mesoloph is directed toward the buccal margin of the tooth, but reaches only about a third of the way from the ectoloph. Generally there is an

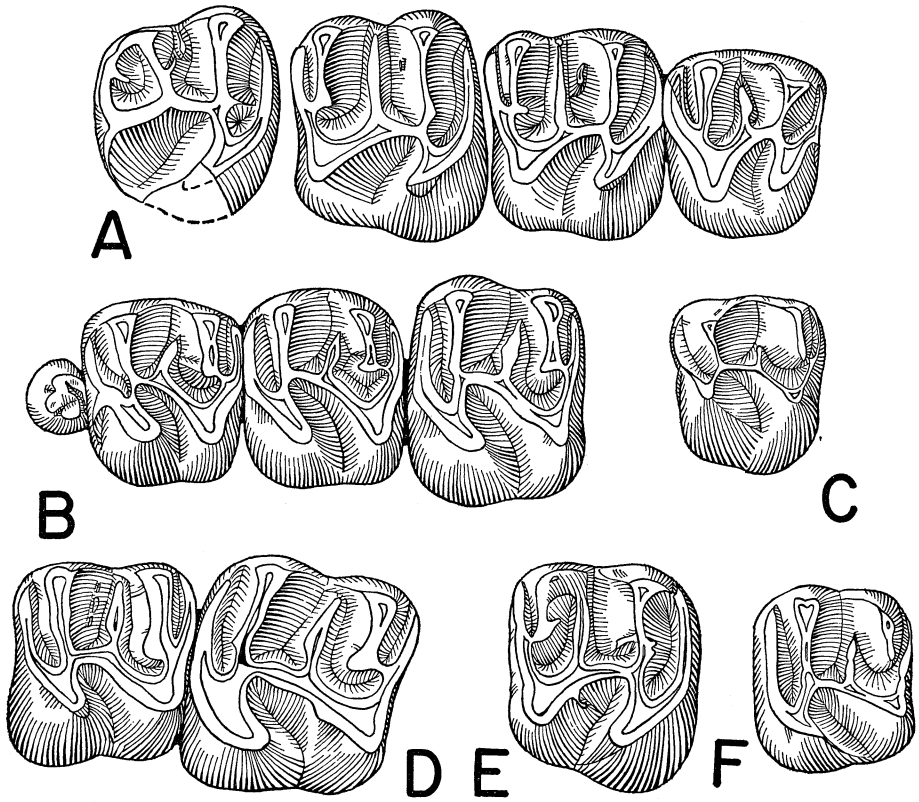


FIGURE 11. Upper cheek teeth of *Metaphiomys schaubi*, × 10.
A. Right dP^4–M^3, YPM 18228, anterior end to the right. B. Left dP^3–M^2, YPM 21320. C. Left dP^4, YPM 21331. D. Left M$^{1-2}$, YPM 18005. E. Right M^2, YPM 21331, anterior end to the right. F. Left M^1, YPM 21331.

enlargement of the middle of the mesoloph. The anterior cingulum extends lingually on dP^4 (fig. 11 A–C), but this does not occur on the molars. There often is a faint ridge, made up of one or more cuspules, on the posterior slope of the protoloph (fig. 11 A, D). The metaloph unites with the middle of the posterior cingulum on dP^4 to M^2, usually before wear, though exceptions occur (fig. 11 C, F). The metaconule usually extends forward as a prominent spur. A similar spur may (fig. 11 A, M^2) or may not (fig. 11 A, M^1) arise from the protoconule. On one specimen (fig. 11 E) there is a spur extending backward from the protoconule.

The anterior half of M^3 is similar to the corresponding parts of M$^{1-2}$. The protocone curves posteriorly along the median margin of the tooth. The mure forms a crest which is usually (fig. 12 A), but not always (fig. 12 B), a straight line to the posterior end of the tooth. From the middle of the mure, a crest extends buccad toward the posterobuccal part of the tooth where there is a distinct metacone. In two of the four specimens, this crest unites with the metacone in a manner that makes it look like a metaloph (figs. 11 A, 12 B), but in the other two it seems to be distinct and to represent a mesoloph (fig. 12 A).

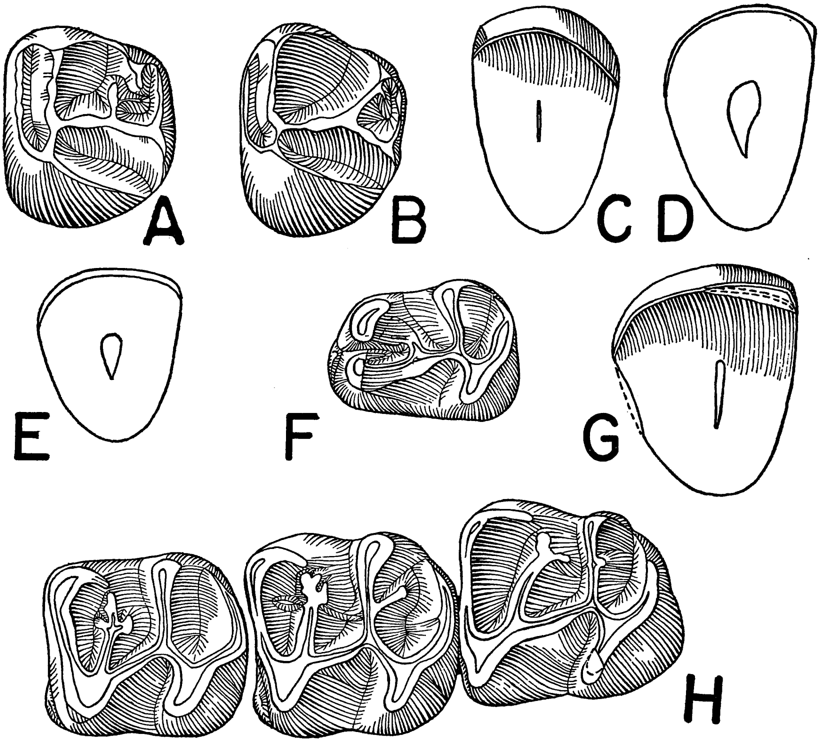


FIGURE 12. Incisors and upper and lower cheek teeth of *Metaphiomys schaubi,* and upper incisor of *Metaphiomys* sp., × 10.
A. Left M^3, YPM 21331. B. Left M^3, YPM 21331. C. Occlusal surface of left I^1, YPM 18210. D. Posterior end of same specimen as fig. 12 C. E. Cross section of left I_1, YPM 18088. F. Left dP_4, YPM 21323. G. Occlusal surface of right I^1, YPM 18212, *Metaphiomys* sp. H. Left M_{1-3}, YPM 21328, *M. schaubi.*

There is an elevated posterior cingulum running from the posterior end of the mure to the metacone and surrounding a basin. The point where the mure meets the posterior border of the crown may be extended lingually as an incipient hypocone.

The anterior tooth (P^3 or dP^3) is very small with indistinctly separable cusps on its crown. It is similar to the corresponding tooth in most paramyids (Wood, 1962a, figs. 10 D, E; 22 C; or 66 C) and seems to consist of two cusps with a posterior cingulum. The tooth extends only about half way down the anterior face of dP^4. The available data offer no evidence as to whether it is dP^3 or P^3. The frequent absence of this tooth in fossil paramyids (although the alveolus is always present) suggests that the tooth was much less well attached in the jaw than were the molars, which may indicate that it is a retained deciduous tooth. Schlosser (1911, p. 91) gives the dental formula of *Ph. andrewsi* as $\frac{1.0.1.3.}{1.0.1.3.}$. Neither in his text nor on his figure (pl. 13, fig. 10 a) is it suggested that any trace of the alveolus of this tooth was present, but it may have been overlooked because of its small size and because there is no P^3 in the Theridomyidae, to which group Schlosser was referring his material. On the other hand, the fact that he did not note an alveolus may indicate that this tooth is lost during the individual lifetime in *Metaphiomys* and that the alveolus becomes filled with bone. This filling may be in the process of occurring on YPM 21309, where the outline of the alveolus is barely distinguishable.

The lower deciduous tooth is present in the type and most of the other specimens of lower jaws, and there are six isolated specimens, making a total of over 30 representatives. All show essentially the same pattern, though there are individual differences. They agree in basic pattern with the shorter group in *Ph. andrewsi,* rather than with the usual condition in that species, since there is a mesolophid or mesoconid only in about a third of the specimens (fig. 9 B). In one specimen included in YPM 18204 (fig. 9 D), there are three crestlets in the talonid basin, converging on the mesoconid. The posterior one of these can be interpreted as a mesolophid, but it is very faint—probably fainter than indicated in the figure—and the two anteroposteriorly directed ridges are more prominent, suggesting the initial stages in the formation of the longitudinal ridge paralleling the ectolophid, which is present in most of the typical members of the species (figs. 9 A, C, 10 E). An unusual pattern is exhibited by YPM 21323 (fig. 12 F), in which there is a broad, low ridge running diagonally from the posterior slope of the metaconid to the apparent mesoconid. In a few specimens (YPM 18002, 18230, 21295, 21305 and 21315), there is no trace of either a mesolophid or a longitudinal ridge (fig. 10 A). The anterior cingulum is distinct but of variable size (figs. 9 A–D, 10 A, E) and is never connected to the protoconid as it is in *Ph. andrewsi* (fig. 1 F, G). In most specimens it extends only across the middle of the front of the tooth, but in about a third of the specimens (YPM 18014, 18225, 18230, 21305–7, 21311, 21317 and 21331–2) it reaches across most of the front of the tooth (fig. 9 B). The metaconid frequently extends backward as a crest along the lingual margin of the tooth (fig. 9 D). The valley between the protoconid and metaconid may be closed (fig. 9 A, B), widely open (fig. 9 D), or at an intermediate stage of development. In a few specimens there is a slight irregularity on the posterior side of the hypolophid, not large enough to be considered a cusp (fig. 9 A, D). This is large enough to be considered a faint ridge in a few specimens (YPM 21307, 21310 and 21318, fig. 10 E) and is a double ridge in one specimen. A small stylid occurs at the buccal border of the buccal valley of one specimen.

The lower incisor (fig. 12 E) is similar to that in *M. beadnelli,* but the anterior face is not quite so flat, the lateral margin of the tooth, especially, being more rounded. The pulp cavity is also rounder than is that of the genotype. At the wear surface, the pulp cavity forms a tiny circular opening. The incisor ratios (Table 9) are somewhat lower than in *M. beadnelli,* though still appreciably larger than in *Phiomys.*

A series of upper incisors are referred to this species on the basis of size. These are present both at Quarry E and Quarry G and are of appropriate size and shape to belong with the lower incisors of *M. schaubi.* They have a rounded anterior face and the enamel extends well onto the lateral face of the tooth (fig. 12 C, D). Away from the wear surface, the pulp cavity is slightly narrower and more elongate than in the lowers, but also is closed, or essentially closed, at the wear surface. As in *Ph. andrewsi,* the dentine is entirely worn away from behind the tip of the enamel which stands up as a strong crest.

DISCUSSION. The measurements given by Schlosser (1911, p. 91, upper teeth only) differ slightly from those in Tables 2 and 9. The length of P^4–M^3 he gives is 9.5 mm., essentially the same as for the only complete tooth row in the present collection. However, Schlosser's anteroposterior diameters of dP^4 and M^2 exceed the values for the largest specimens in the present collection by an appreciable amount. This difference is probably due to the difficulty of measuring diameters of individual teeth when included in complete series.

For the cheek teeth, there is a considerable gap between the observed range of the measurements for this species and for *Ph. andrewsi.* The mean of *M. schaubi* exceeds the maximum for *Ph. andrewsi* by over four SD in fourteen out of eighteen measurements, whereas the overlap is very much greater in the incisors. It was not considered necessary to calculate the probability that the means were different for the two in the cheek tooth measurements. For all the incisor measurements and ratios, the probability that the means of the two populations were not different was calculated to be considerably less than .001 (Simpson, Roe and Lewontin, 1960, p. 176).

Similar comparisons were made between *M. schaubi* and *M. beadnelli.* These gave p values between .01 and .2, indicating that the measurements available do not show any significant difference between these species. However, the referred specimen of *M. beadnelli* is larger than the largest known specimen of *M. schaubi* in length of tooth row; metalophid width of M_1; length of M_3; metalophid width of M_3; and transverse diameter of I_1. In several of the other measurements only one specimen of *M. schaubi* is as large as YPM 18226. The holotype of *M. beadnelli* is slightly smaller than the referred specimen. It seems probable, however, that additional specimens of *M. beadnelli* would permit its valid separation on size alone from *M. schaubi.*

An upper molar from the Miocene of Southwest Africa was identified as "Cfr. *Phiomys Andrewsi* Schlosser (non Osborn)" by Stromer (1926, p. 137 and pl. 42, fig. 24 a-b). He points out that it is improbable that the upper and lower jaws figured by Schlosser belonged to the same form, or that the lowers were referable to *Ph. andrewsi.* He states that his material is either identical with or very closely related to the form represented by Schlosser's upper jaw specimen, which is here referred to *M. schaubi.* However, there clearly were major differences between Stromer's specimen and *M. schaubi* in the shape of the tooth, the length of the mesoloph, and the connection between the hypocone and posterior cingulum, indicating that, while these are certainly related forms, they cannot be congeneric. Unfortunately, Stromer's specimen was destroyed during World War II.

Phiomys or *Metaphiomys* sp. indet.

Figure 13

A number of isolated cheek teeth seem to represent either an unknown species of one of these genera (more probably *Metaphiomys*), or are from individuals that were ideal intergrades between the two genera. Since they are all isolated teeth, it is clearly unjustified to erect a new taxon for them at present.

Isolated right lower molars from Quarry G (YPM 18205) and Quarry E (YPM 18194) are slightly above the upper limit of size of material referred to *Ph. andrewsi* (compare Tables 1 and 3), and slightly below the lower limits of *M. schaubi* (Tables 3 and 9). They could be considered simply as aberrant individuals of either form. On the other hand, the presence of a strong posterior arm of the protoconid directed toward the base of the metaconid and bearing a pronounced protospur (fig. 13 A) is diagnostic of *Metaphiomys*. However, the posterior arm of the protoconid reaches the metaconid at a very low level and there is a swelling of the ectolophid representing a mesoconid; both are primitive features. Analysis of these specimens, using the t test (Simpson, Roe and Lewontin, 1960, p. 182) shows that they cannot be separated either from *Ph. andrewsi* or from *M. schaubi*. The probabilities that the measurements are not distinct from those of *Ph. andrewsi* range from about .005 for the hypolophid width to about .08 for the length; compared with *M. schaubi* the p values range from something less than .01 to something over .01.

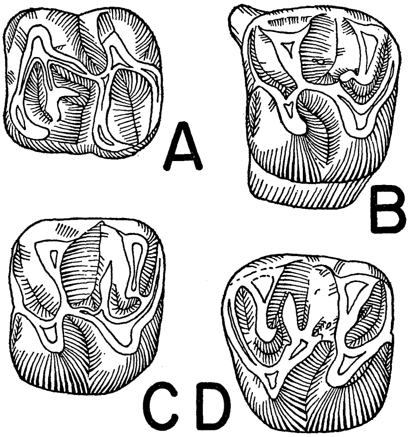


FIGURE 13. Isolated teeth of *Phiomys* or *Metaphiomys* sp. indet., × 10.
A. Right M_1, YPM 18205. B. Left dP^4, YPM 18089. C. Left M^1(?), YPM 18089. D. Right M^2(?), YPM 18089, anterior end to the right.

Three isolated upper cheek teeth from Quarry G (YPM 18089, fig. 13, B–D) are of the correct size to belong with these two lower molars, and are distinctly more primitive than are the upper molars of *M. schaubi*. The mesoloph is short (fig. 13 C), multiple (fig. 13 D), or absent (fig. 13 B). The first of these suggests *M. schaubi;* the second, *Ph. andrewsi;* and the third seems to be unique. The anterior cingulum extends to the lingual as well as to the buccal margin of the teeth, a character not found in any of the other teeth in the collections. Not enough specimens of upper teeth of *Ph. andrewsi* are known to permit size comparisons to be made. Five of the nine measurements fall within the observed range of *M. schaubi* (Table 2), although the four width measurements for M^1 and M^2 fall below it. For these four, the probability that they are not different from *M. schaubi* ranges from $p = .005$ to $p = .05$. These teeth, then, seem significantly more primitive than those of *M. schaubi* in pattern, but show no significant size difference.

A series of isolated lower incisors, of the *Phiomys* type, from Quarry G (YPM 18207) are tentatively referred to this form.

Three isolated upper incisors, YPM 18211 and 18217 from Quarry G and AMNH 13277D from Quarry B, are tentatively referred to this population. They were originally referred to *M. schaubi* on the basis of size, but were among the smallest so assigned and have incisor ratios of .53 to .58. The incisors referred to *Ph. andrewsi* range from .48 to .54, and those referred to *M. schaubi* range from .60 to .69. The enamel agrees in thickness with that of *Phiomys* rather than *Metaphiomys.*

If these teeth all belong to one species, they can probably best be interpreted as a population derived from *Ph. andrewsi,* that was evolving toward *Metaphiomys* in cheek tooth pattern, but which still retained the incisor shape and size of *Phiomys.* However, until jaws associating cheek teeth and incisors are found, it will not be possible to clarify this point. Considerably better material than is now available will be needed, moreover, to decide whether this material should be considered a new species, a subspecies of *Ph. andrewsi,* one of *M. schaubi,* or merely extremes of normal variation.

Cf. *Metaphiomys* sp. indet.

Two isolated upper incisors, YPM 18202 and 18212 from Quarries G and E respectively, are heavier than those referred to *M. schaubi,* having an incisor ratio of .80, whereas the range in *M. schaubi* is .60 to .69. These are similar to those of *M. schaubi,* except for their greater width (fig. 12 G), in which respect these specimens are so widely different that it does not seem possible that it is merely an age or individual variant.

GENUS ***Gaudeamus*** n. gen.*

GENOTYPE. ***Gaudeamus aegyptius*** n. sp.

DISTRIBUTION. Jebel el Qatrani Formation, Fayum Oligocene of Egypt.

DIAGNOSIS. Phiomyid very similar in cheek tooth pattern to *Thryonomys,* but crests not as well developed as in that form; upper and lower molars basically three-crested, the upper molar crests being the anteroloph-protocone, paracone-protoconule-hypocone and metacone-posteroloph-hypocone respectively and the lower molar crests being metaconid-anterolophid, entoconid-ectolophid-protoconid, and posterolophid-hypoconid respectively; P_4^4 similar to molars, but more cuspate; dP_4 five-crested, with a three-cusped mesolophid in front of which are two two-cusped crests; dP_4^4 replaced by P_4^4 fairly late in life; teeth of medium crown height; lower incisor with rounded anterior face, but heavier than in *Phiomys;* jaw hystricognathous; infraorbital foramen large.

DESCRIPTION. The fragment of the maxilla, including P^4–M^3, of YPM 18044 shows a number of interesting features. When seen from the front (fig. 14 B), part of the ventral and medial surfaces of the infraorbital foramen can be

---

* The native collectors whom Dr. Simons used were not as fluent in English as they were accurate in their taxonomic identifications. They recognized small fossils with teeth as jaws, and so when they found rodent jaws would announce the discovery as "Joy mouse." Dr. Mary Dawson hit upon the felicitous name *Gaudeamus* as an approximate translation of this vernacular identification, and I am grateful to her for permission to use the name.

identified, showing that this opening was of large size, being essentially hystricomorphous, although it does not seem to have been as large as in *Metaphiomys* (fig. 6 B). The ridge of bone that separates the masseter from the infraorbital foramen, *sensu stricto,* cannot be identified, but could have been present in the broken area. There is a depression on the maxillary just in front of P^4, which suggests the similar condition in *Thryonomys,* and may indicate a similar short diastema. The specimen is badly broken, but the palate certainly looks as though it were grooved, as in *Thryonomys.* The maxillary-palatine suture is not preserved.

The lower jaw (fig. 14 C, F) is even more strikingly hystricognathous than is that of *Phiomys* or *Metaphiomys.* The jaw is slender, dorsoventrally, with a short diastema, as in the other genera, but it is deeper through the diastema than they are. The mental foramen is very small and varies in its position on the jaw in front of P_4. In this respect this animal is more like *Thryonomys,* in which the mental foramen is exceedingly minute, than like *Phiomys.* The anterior end of the masseteric crest lies beneath the rear of P_4, being, if anything, slightly farther forward than in *Thryonomys.* The crest slopes posteroventrally and passes the ventral border of the ramus below the rear of M_2, as in *Metaphiomys.* The masseteric fossa is deeper than in either *Phiomys* or *Metaphiomys.* The anterior face of the coronoid process passes the alveolar border at the level of the middle of M_2 in the holotype (fig. 14 C). In YPM 18036, which belonged to an older individual, the anterior face passes the alveolar border opposite M_3, although the actual beginning of the coronoid is opposite M_2. This variation is probably an age character. There is a deep groove between the coronoid process and the alveoli (fig. 14 F).

The upper teeth of *Gaudeamus* are represented by YPM 18044, a fragment of the maxilla containing P^4–M^3 right, and YPM 18012, an isolated left upper molar, probably M^1.

As in *Thryonomys* (Wood, 1962b, fig. 2 B), the molars are three-crested, with an anterior crest and a posterior V. The anterior crest consists of the anteroloph and protocone. The anterior arm of the V involves the paracone, protoconule and hypocone. The posterior crest is the metacone, posteroloph (or metaloph?) and hypocone (figs. 14 A, 15 A). The protoconule appears as a distinct cuspule on the two specimens of M^1, but is not visible on M^2. There is a divide in the valley between the two anterior crests that marks the former position of the protocone-protoconule connection. The third molar differs in that it has a narrower posterior portion, with what is here interpreted as the metacone in a very posterior position, as in *Paramys* (Wood, 1962a, fig. 16 B). By analogy with M^3 of *M. schaubi* (figs. 11 A, 12 A–B), the posterior V would seem to be formed of the paracone, protoconule, mure, posterior cingulum, and metacone, though the differences are rather great.

The anterior tooth of the series is apparently P^4, in view of its high crown, simple pattern, and the fact that it is probably less worn than is M^1. This last point is somewhat uncertain because its wear is slightly different (fig. 14 A). The tooth is slightly higher crowned than are the molars, and the enamel is the same color, suggesting that this is the permanent tooth. The three crests are united lingually, there being little or no valley between the protocone and hypocone.

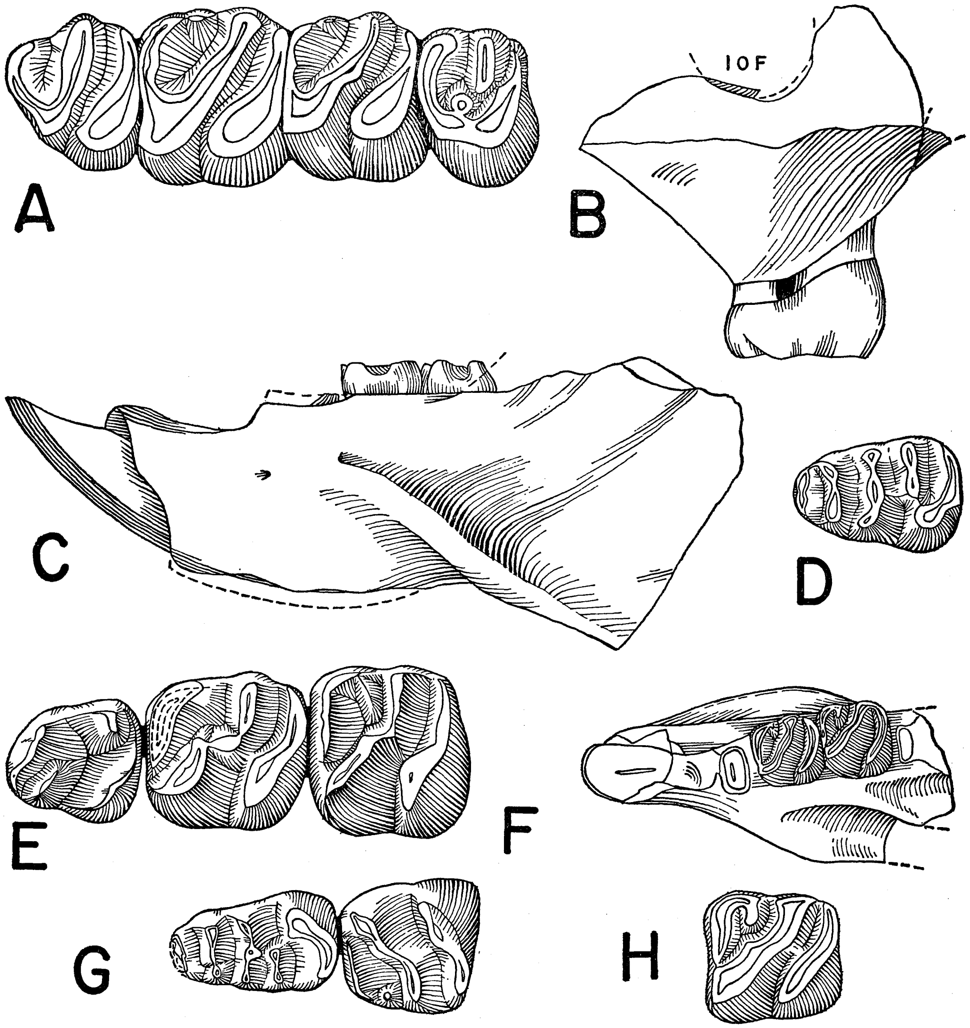


FIGURE 14. Bones and teeth of *Gaudeamus aegyptius.* Lower jaws × 5, rest × 10. A. Right P^4–M^3, anterior end to the right, YPM 18044. B. Anterior view of YPM 18044, showing presumed size of infraorbital foramen. C. Lateral view of lower jaw, CM 26920, holotype. D. Left dP_4, CM 26920, holotype. E. Left P_4–M_2, CM 26920, holotype. P_4 shown rotated into same plane as other teeth, and erupted. F. Superior view of left lower jaw, YPM 18036. G. Right dP_4–M_1, YPM 18022. H. Left M_2, AMNH 8225.

The protoconule is united with the metacone and separated from the paracone by a valley as deep as that between the paracone and the anterior cingulum.

The lower molars are similar in their basic pattern to those of *Phiomys,* but are much more lophate. The protoconid extends to the anterior margin of the tooth, and the metaconid ends linguad of it. In most unworn teeth (figs. 14 E, G, 15 B, C), the two are separated. However, in YPM 18024 and 18032 (fig. 15 E, G) there is no separation between the two. The metaconid may curve posteriorly and end in an arc, as in M_1 of the holotype (fig. 14 E) and of YPM 18024; there may be a buccal swelling of the end of the metaconid, as in M_2 of YPM 18024

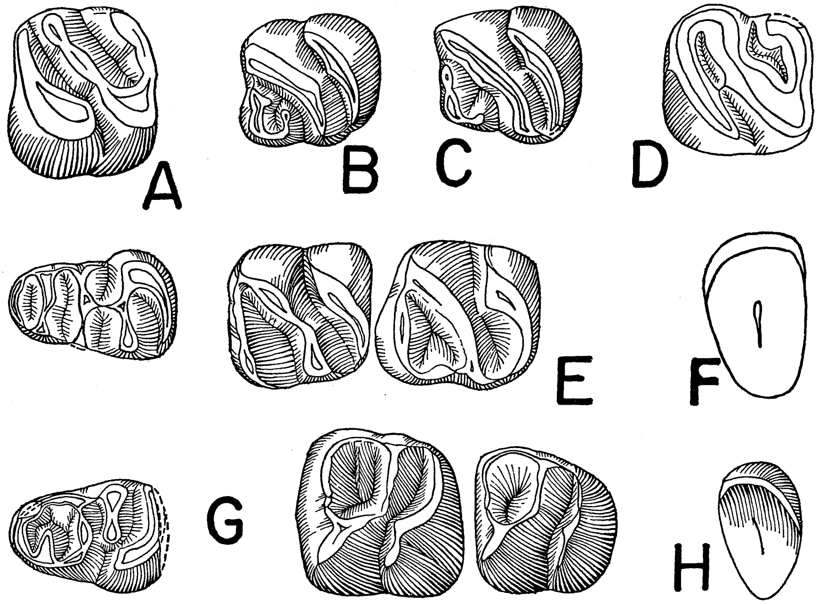


FIGURE 15. Teeth of *Gaudeamus aegyptius*, × 10.
A. Left M^1, YPM 18012. B. Right M_1(?), YPM 18047. C. Right M_2(?), YPM 18047. D. Right M_1, YPM 18012, anterior end to the right. E. Right dP_4–M_2, YPM 18024. F. Cross section of left I_1, below diastema, YPM 18032. G. Left dP_4, M_{2-3}, YPM 18032, teeth rotated so crowns are in same plane. H. Occlusal surface of right I_1, YPM 18024.

(fig. 15 E); there may be a strong transverse ridge at this point with no cusp (M_2 of the holotype and YPM 18032; figs. 14 E, 15 G); or there may be a distinct, rounded cusp as in YPM 18022, 18036 and 18047 and in AMNH 8225 (fig. 14 G). This accessory cusp or ridge is similar to what is seen in *Thryonomys* (Wood, 1962b, fig. 2 C). The entoconid is a diagonal crest that joins the lingual end of the protoconid, with which it forms a crest that is nearly straight on most specimens (figs. 14 G, 15 E). However, there is an angulation in the crest of some specimens, especially pronounced on the teeth of the holotype, where the situation suggests the presence of an ectolophid (fig. 14 E). The other specimens, especially YPM 18024 and 18047 (fig. 15 B, C, E), are much more like *Thryonomys* in this respect (Wood, 1962b, fig. 2 A). The hypoconid-posterolophid crest extends all across the tooth, as in *Thryonomys*. The hypoconid is usually a distinct cusp, even on unworn teeth, whereas in *Thryonomys* it does not become distinct until after wear. There is a shallow point in the posterior valley marking the former position of the ectolophid which would allow the hypoconid to unite with the buccal end of the entoconid after wear, as in *Thryonomys*. This union would take place closer to the time of union of the metaconid and protoconid than is the case in *Thryonomys* (fig. 15 D).

In most of the specimens, there is a pattern of three transverse ridges, the two anterior uniting to form a V, and the third separate until after appreciable wear. However, YPM 18032 shows the teeth with a complete lingual union of all three crests, even though they are unworn (fig. 15 G). These teeth are also higher crowned than are the other specimens in the collection. The differences of this specimen from the holotype suggest that it might be at least specifically distinct, especially since the deciduous premolar is rather different from any of the others in the collection. However, study of YPM 18024 (fig. 15 E) makes this interpretation seem to be incorrect. In this last specimen, M_2 is like that of YPM 18032 but M_1 is like that of the remaining members of the population, and the deciduous tooth is likewise of the normal style. Thus, it seems most reasonable to conclude that this was a variable species, advanced members having higher crowned teeth with the crests connected on the lingual margin. The first of these features would be a trend toward conditions in *Thryonomys,* whereas the latter would not. The more worn molars of YPM 18036 (fig. 14 F) are very like *Thryonomys.* A posterior hook is present on the metaconid on both M_1 and M_2 of this specimen. The posterolophid unites with the entoconid about the time the metaconid and protoconid do and much earlier than do the hypoconid and entoconid. M_1 of YPM 18022 (fig. 14 G) is appreciably lower-crowned and more like *Phiomys* than are the other specimens, though it is still clearly referable to *Gaudeamus.* Among other Fayum phiomyids the closest resemblances to *Gaudeamus* are found in *P. lavocati.*

The lower premolar (fig. 14 E) is present only in the holotype, where it is partially exposed intra-alveolarly after the removal of dP_4. It consists of four cusps, elongate in a diagonal direction. The anterior two, presumably metaconid and protoconid, would unite at or near the base of the crown, after wear. The hypoconid is continued into a posterolophid that reaches the median margin of the crown. The entoconid is more nearly circular than are the other cusps and has almost as close relationships with the metaconid as with the protoconid. This is not like anything seen in *Thryonomys,* since P_4^4 have been suppressed in that form. It is also quite distinct from P_4 of *Ph. andrewsi* (fig. 1 B, D) and looks as though it is aberrant.

Lower deciduous teeth are present in four specimens, including the holotype (figs. 14 D, G, 15 E, G). While there is much variation, no two of them being identical, that of YPM 18032 is the only one that is very different (fig. 15 G). In all, there are five crests, homologous with those of the five-crested teeth of *Ph. andrewsi* (fig. 1 F, G). There is a strong tendency for the entoconid crest to be isolated from the hypoconid until after considerable wear (fig. 14 D), though the two are united early in YPM 18024 (fig. 15 E). Where the crest is isolated, it has two cusps, the buccal one apparently lying on the ectolophid, but not being a mesoconid. The next crest forward is made up of three cusps, the central one (by analogy with *Phiomys*) being the mesoconid and the other two representing buccal and lingual derivatives of the mesolophid (fig. 14 G). The ectolophid does not continue forward to the trigonid, but there may be either a buccal (fig. 15 E) or a lingual (fig. 15 G) connection between the mesolophid and the trigonid. Typically, the trigonid consists of two cross crests, the posterior interpreted as the metaconid and protoconid, and the anterior as an anterolophid which may (fig. 14 D) or may not (fig. 15 E) be subdivided into two cusps. The anterolophid may connect with the metalophid at either end, or not at all. In YPM 18032 (fig. 15 G), the metalophid does not form a complete crest, the protoconid being a large cusp, and the metaconid being merely a swelling in a continuous marginal ridge formed by the anterolophid, metaconid, mesolophid and protoconid. The lingual end of the mesolophid also unites with the entoconid in this specimen.

Basically, the pattern of dP_4 is thus essentially like that of *Thryonomys* (Wood, 1962b, fig. 2 A), and the variability is also suggestive of that seen in the recent form (Wood, 1962b, p. 319).

The lower incisors are quite variable in size (Table 10), the variation being only partly correlated with age, since the two oldest specimens are YPM 18036 and AMNH 8225, the former having one of the largest incisors in the population, and the latter one of the smallest. However, there is a trend toward an increase of the incisor ratio with age, which may be more significant. The younger specimens have ratios ranging from .51 to .62, and the older ones from .71 to .73. The incisor is smaller and narrower than in *Metaphiomys,* with heavier enamel and a longer and more slender pulp cavity (fig. 15 F, H). It is flatter anteriorly than in *Phiomys,* and the median ridge is not present in any of the available material.

The upper incisors are not known.

DISCUSSION. Schlosser (1911, p. 90–92 and pl. 5, fig. 7) describes two lower jaws that he refers to *Ph. andrewsi.* One is a jaw with no cheek teeth, that cannot be identified from his description. The one that he figures, however, is clearly referable to *G. aegyptius,* both in tooth pattern and in size (Table 10).

Gaudeamus aegyptius n. sp.*

Figures 14–15

OTHER ILLUSTRATIONS. Schlosser, 1911, pl. 13, fig. 7a; Stehlin and Schaub, 1951, fig. 445.

Phiomys andrewsi Osborn, of Schlosser, 1911, in part.
Genus novum aus dem Fayum, Stehlin and Schaub, 1951, p. 266.

HOLOTYPE. CM 26920, left jaw with dP_4–M_2 and unerupted P_4.

HYPODIGM. Holotype; AMNH 8225, jaw with M_2; YPM 18022, 18024, 18032 and 18036, lower jaws; 18044, maxilla with dP^4–M^3; 18012 and 18047, isolated molars; 18218, isolated incisors; and right jaw with M_{1-2} in the Stuttgart collection, figured and described by Schlosser, 1911.

DISTRIBUTION. All Yale specimens are from Quarry E; AMNH 8225 from lower levels (Quarry A or B). Jebel el Qatrani Formation, Oligocene of Egypt.

DIAGNOSIS. As for the genus; tooth measurements as given in Tables 2 and 10.

GENUS ***Phiocricetomys*** n. gen.†

GENOTYPE. ***Phiocricetomys minutus*** n. sp.

DISTRIBUTION. Jebel el Qatrani Formation, Oligocene of Egypt.

DIAGNOSIS. Small rodent; well-developed hystricognath jaw with highly everted angle and with lower incisor very similar to that of other phiomyids; main masseteric fossa of mandible extending forward to beneath the rear of M_1 but continued forward by a narrow depression, presumably for the anterior portion of the masseter profundus, that reaches as far forward as anterior end of

---

* The specific name indicates the geographic origin of the fossils.

† The generic name is a combination of *Phiomys* and *Cricetus,* to suggest that this genus is a phiomyid with some parallelisms to the Cricetidae.

M_1; mental foramen below anterior end of masseteric fossa; cheek teeth reduced to M_{1-3}; no trace of mesoconid, mesolophid or posterior arm of protoconid; very prominent marginal cingula on which cusps are beginning to develop; cusps rounded, lophs of lesser prominence; hypoconulids prominent on M_{1-2}.

DESCRIPTION. The lower jaw is basically similar to that of other phiomyids. The angle arises from the side of the mandible, well laterad of the incisive alveolus, from which it is separated by a pronounced groove (fig. 16 B). The angular process extends about twice as far from the midline as the farthest point of the cheek teeth (fig. 16 A). The anterior end of the main body of the masseteric fossa is beneath the rear of M_1, but there is a narrow depression continuing the fossa forward, that reaches as far forward as the front of M_1. This section extends very high on the mandible and lies above the mental foramen, which is unusually low on the jaw for a phiomyid (fig. 16 C). The anterior section seems certainly to represent the insertion of the anterior end of the masseter profundus, and its distinctness from the rest of the fossa suggests that the anterior portion of this muscle may have been separable from the posterior portion. In the bottom of the masseteric fossa are two long, narrow grooves which probably mark the position of blood vessels. The relationship of the masseteric fossa and the mental foramen suggests that there was a shortening of the anterior part of the jaw associated with the reduction of the length of the tooth row, and that this resulted almost in a telescoping of the jaw, forcing the masseteric fossa above the mental foramen.

The coronoid process rises gently, passing the alveolar border well behind M_3 (fig. 16 C). Its general appearance suggests that it was similar in size and position to that in *Ph. paraphiomyoides* (fig. 3 C). The coronoid process is separated from the alveoli of the cheek teeth by a deep fossa, seen most clearly from above (fig. 16 A). There is some minor breakage of bone within this fossa, so that it is impossible to be certain whether or not there is a small foramen near the anterior end of the fossa, as there is in *Petromus* but not in *Thryonomys.*

There is a very pronounced chin process, lying beneath the middle of the diastema (fig. 16 B, C). On the median side the symphysis has an anterior smooth area above and in front of a rugose area consisting of a vertically elongate depression in the center of which is a vertical ridge (fig. 16 B). This would make a good joint surface to permit scissors movement of the mandibles, and presumably a strong transversus mandibulae muscle was present. Just behind this joint area is a very deep, oval pit for the genioglossus. Behind and ventral to the pit is a pronounced concavity which is probably the area of attachment of the transversus mandibulae (fig. 16 B).

The most striking feature of the dentition is the reduction of the cheek teeth to three. The specimen was clearly fully grown, the third tooth having the rounded posterior end that is characteristic of the posterior tooth in a tooth row. The widths of the teeth taper in both directions from the middle, again suggesting that a complete tooth row is present. In all other phiomyids M_2 is the widest of the lower cheek teeth, and its greatest diameter is usually at the anterior end. Since the anterior end of the middle tooth in *Phiocricetomys* is the widest part of the cheek teeth, this suggests that this tooth is M_2. The anterior tooth probably has basically the same pattern as does the middle tooth,

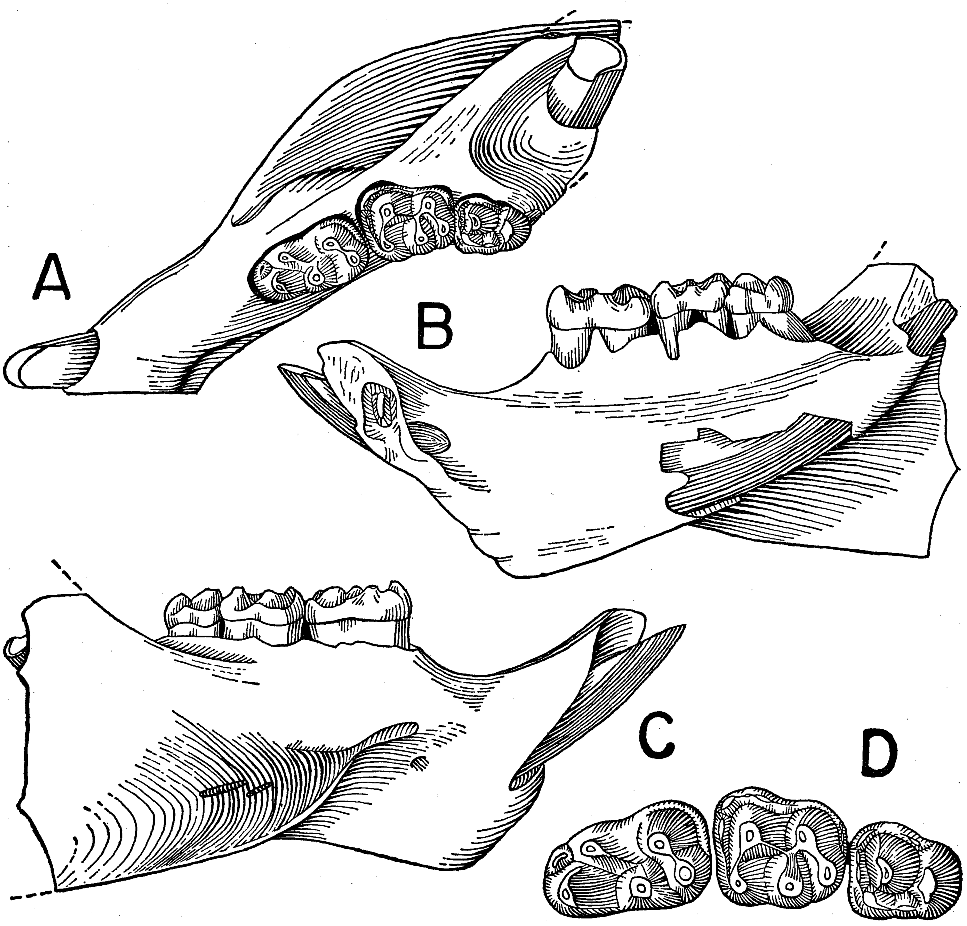


FIGURE 16. Jaw and teeth of *Phiocricetomys minutus*, CM 26925. Crown view of teeth × 15, others × 10.
A. Superior view of jaw. B. Medial view of jaw. C. Lateral view of jaw. D. Right M_{1-3}.

differing largely because of a secondary elongation, which presumably was associated with the reduction in the number of teeth. The general proportions of the anterior tooth are closest to those of some deciduous teeth of *Ph. andrewsi* (fig. 1 F, G), but the pattern is rather different. For all these reasons the three teeth are identified as being M_{1-3}.

In all the molars, the cusps are more prominent than in any other known phiomyids, being well rounded and connected by slender ridges. This roundness is probably primitive. There are very prominent anterior, buccal and posterior cingula on M_2 and the adjacent portions of M_1 and M_3, often developing accessory cuspules on their crests.

In M_1 (fig. 16 D) the metaconid is very far forward, being a crescentic cusp whose arms curve backward, along the lingual edge of the crown and toward the protoconid, respectively. A deep valley separates the protoconid from the buccal arm of the metaconid, and the two cusps would be connected only at a very late stage of wear. Lateral to the metaconid is a large cingular cusp which may be called the anteroconid. The protoconid is rounded and extends backward as a long, slender ridge that gradually loses elevation. This ridge is almost certainly the ectolophid and not the posterior arm of the protoconid. This latter crest would seem to be completely absent in *Phiocricetomys.* The entoconid, at the middle of the lingual side of the tooth, sends a low swelling, not a clearly indicated crest, toward the ectolophid. At about the middle of the tooth, the branches of the ectolophid from the protoconid and hypoconid and the buccal crest from the entoconid meet at a point only very slightly elevated above the intervening valleys. The hypoconid is connected by one of the better marked crests to a large, round hypoconulid, about as large as the hypoconid. Along the buccal and posterior margins of the hypoconid is a very prominent cingulum that shows only very faint incipient subdivision.

The anterior part of M_2 is the widest part of the tooth row. This width is accentuated by the presence of a very prominent cingulum laterad and anterad of the protoconid that becomes weaker posteriorly and unites with the front of the metaconid at its other end (fig. 16 D). As in other phiomyids, the metaconid is connected by a continuous crest with the anterior side of the protoconid. The metaconid is conical and has no posterior arm along the lingual margin of the tooth. The posterior half of the tooth is basically similar to what is seen in M_1, except that the entire ectolophid and the crest joining it from the entoconid are sufficiently elevated to be distinguishable. The posterior cingulum bears three small cuspules.

The pattern of M_3 (fig. 16 D) seems to be derivable from that of M_2. The metaconid is connected to the anterior cingulum and to the protoconid, as in M_2, but also has a posterior crest extending along the lingual margin. At about the middle of the lingual side, there is an enlargement of this crest which is probably a highly reduced entoconid. The anterior cingulum has three distinct cuspules along the front of the protoconid. There is a secondary anterior cingulum in front of the metaconid. The protoconid is a large, rounded cusp, the dominant feature of the tooth. It is concave forward, convex backward, and reaches back of the middle of the tooth. There is a deep valley separating it from the anterior cingulum and another between it and the entoconid and hypoconid. There is no trace of an ectolophid or of a buccal crest from the entoconid in this tooth. A cingulum cusp blocks the buccal valley between the protoconid and hypoconid. The posterior two-fifths of the tooth is formed of a large, transversely elongate cusp that represents a hypoconid with a highly reduced and barely distinguishable posterolophid component extending toward the lingual margin behind the entoconid.

The incisor unfortunately slid back into the alveolus after death and before fossilization so relatively little can be told about it. The enamel has approximately the same pattern and distribution as, for example, in *Phiomys* (fig. 2 E–H). The intra-alveolar portion of the tooth is partially twisted into a spiral, so that below M_2 a median view of the tooth shows not only the median enamel but at least half the anterior enamel (fig. 16 B).

DISCUSSION. *Phiocricetomys* seems indisputably to be a phiomyid. It equally seems to be a highly aberrant member of the family. There do not seem to be any described rodents to which it could be ancestral. It is equally difficult to visualize its ancestry. The general pattern of reduction and elimination of the posterior arm of the protoconid and of the mesoconid and mesolophid seems to be in accord with what is happening in the other members of the family. However, an ancestor of *Phiocricetomys* must have reduced not only the permanent premolar but also the deciduous one, in sharp contrast to what took place in the rest of the family. Once the premolars were eliminated, selection for the maintenance of a tooth row approximating the ancestral length would have resulted in the modification of M_1 to give the elongate tooth in *Phiocricetomys.* Such a sequence would probably indicate a divergence of this genus from the other phiomyids some time before Jebel el Qatrani time. The rounded nature and prominence of the cusps also suggests that this form was derived from a much more primitive phiomyid than any that are known. The hypoconulids are often well-developed in phiomyids (figs. 2 B, 8 C) but *Phiocricetomys* has greatly accentuated this trend. The ectolophid has been proportionately weakened, though in a different manner, in *Gaudeamus* (figs. 14–15). Finally, the prominent cingula represent a special feature of *Phiocricetomys.*

In spite of an overall superficial similarity in tooth pattern, there can be no doubt that *Phiocricetomys* has absolutely no genetic relationships with any muroids or dipodoids.

Phiocricetomys minutus n. sp.
Figure 16

Holotype. CM 26925, a left lower jaw with all three cheek teeth and the incisor.

Hypodigm. Holotype only.

Distribution. Quarry I, Jebel el Qatrani Formation, Oligocene, of Egypt.

Diagnosis. As for the genus; tooth measurements as given in Table 11.

3. DISCUSSION

Relationships of the Fayum Rodents

Phiomys, Paraphiomys and *Metaphiomys* are clearly closely related genera. In fact, as pointed out above, the boundaries between *Phiomys* and the other two are indistinct; *Phiomys lavocati* and *Ph. paraphiomyoides* could be referred to *Paraphiomys*; and *Metaphiomys schaubi* could also be referred to *Phiomys. Phiomys,* however, seems the most primitive of the three. These three genera represent the central stock of the Phiomyidae, and it is from them that most of the Miocene phiomyids have probably been derived. The ancestry of *Petromus* is presumably to be sought in this group of genera (fig. 17).

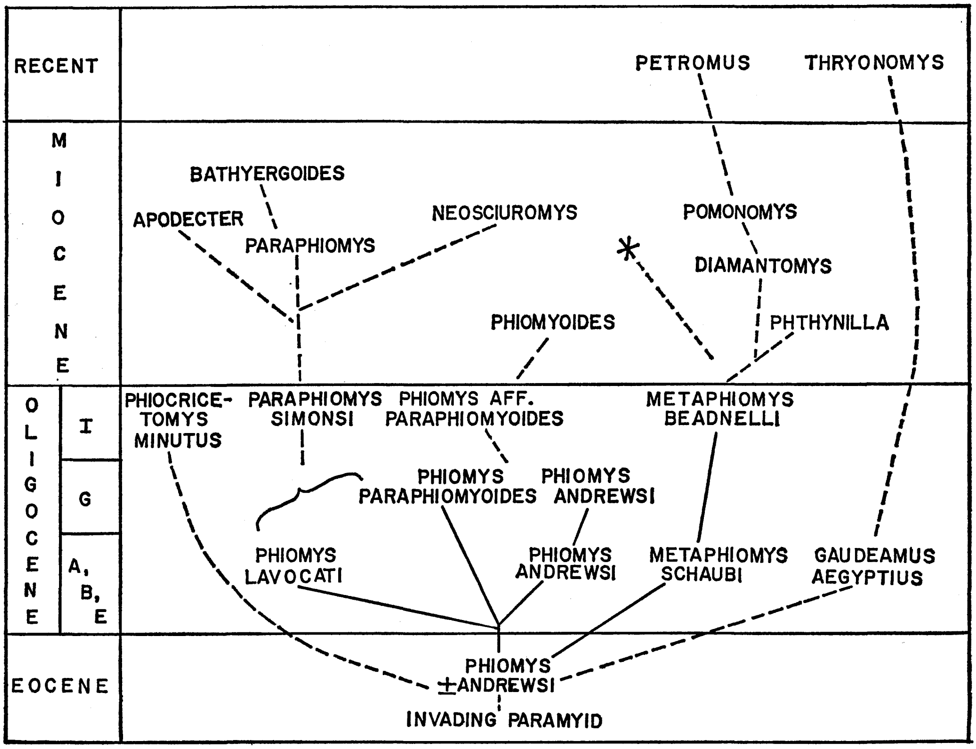


FIGURE 17. Possible relationships of Miocene and Recent genera of the Thryonomyoidea with the Oligocene forms. Placement within the Miocene is intended to indicate morphological rather than temporal relationships; within the Oligocene, both are intended. The form indicated by the * is the specimen Stromer called "Cfr. *Phiomys Andrewsi* Schlosser (non Osborn)" (Stromer, 1926, p. 137, pl. 42, fig. 24a, b). By error, *Metaphiomys schaubi* was omitted from the level of Quarry G.

Gaudeamus is widely separated from the other three. In fact, it is so distinct that it probably belongs in another subfamily, as indicated by Lavocat in manuscript notes of April, 1963. This course has not been followed here, not because it seems unreasonable, but because the classification of the Thryonomyoidea is in such a state of flux that it would be better to wait to establish subfamilies within the Phiomyidae until it is possible to tie together the history of the African rodents a little better than can be done at present. Certainly *Gaudeamus* is more specialized than the first three genera and presumably diverged from them before they separated from each other. However, it seems quite clear that *Gaudeamus* was descended from a *Phiomys*-like ancestor—presumably one living in the late Eocene (fig. 17).

Finally, *Phiocricetomys* is just as distinct as *Gaudeamus,* but in a completely different manner. In some respects this is the most specialized Jebel el Qatrani rodent; in others, one of the most primitive. It seems certain that it must have diverged from the other phiomyids about the same time that *Gaudeamus* did. There are no suggestions of special affinities between *Phiocricetomys* and any known later rodents (fig. 17).

The presence of all the slightly different variant populations of *Phiomys* that are described above as *Ph. paraphiomyoides, Ph.* aff. *paraphiomyoides* and *Ph. lavocati,* suggests the complexity of the evolutionary changes going on in the Oligocene phiomyids. The close similarity of all of these variants suggests that the phiomyids were still actively expanding into a wide variety of available ecologic niches, and that presumably the initial differentiation of the phiomyid population did not antedate Jebel el Qatrani time by very long, in spite of the greater diversification of *Gaudeamus* and *Phiocricetomys.* The forms from the upper levels are more advanced than those from the lower ones, but it seems improbable that there was any great time interval, as we seem to be dealing with tachytelic evolution.

Whereas all known Oligocene African rodents are phiomyids, Lavocat's studies (1961, 1962) emphasize that the Miocene of Southwest Africa includes bathyergids and pedetids as well as an ochotonid; the Miocene of Beni Mellal, Morocco includes members of the Sciuridae, Cricetidae, Phiomyidae, Pedetidae, Gliridae, Ctenodactylidae (or Tataromyidae), as well as a lagomorph (?Ochotonidae); and the Miocene of Kenya includes cricetids, pedetids, bathyergids and anomalurids, as well as a wide variety of phiomyids. That is, the known rodent fauna of the Oligocene was much more unified than that of the Miocene and clearly originated from a single stock. Certainly there were few or no connections between North Africa and Europe or, probably, Asia in the late Eocene or early Oligocene, as indicated by the striking endemism of the Fayum faunules. The uniformity of the Fayum rodents, derivable from a single, *Phiomys*-like ancestor, suggests that such a form had reached North Africa not long before Fayum times by island-hopping, but from an unknown source.

If one considers all the available data, it does not seem probable that this common ancestor had any close relationships with the Theridomyidae, in spite of Schaub's tentative placing of the phiomyids in such a position (Schaub, 1958, p. 705). Certainly, the lower molar pattern of *Phiomys* can be readily interpreted as being in transition from a five-crested tooth, like that of *Theri-*

domys, to a four-crested one, with similar changes continuing in the other phiomyid genera. The patterns of the upper molars are superficially even closer in the two families.

However, the presence of P^3 (or dP^3) in *Metaphiomys* represents a more primitive dental formula than is found in any theridomyid. I have found no reference to this tooth being present in the Pseudosciuridae, but Stehlin and Schaub (1951, fig. 22) figure a maxilla of *Adelomys siderolithicus* from the late Eocene of Mormont-Eclépens in which there appears to be an alveolus for a minute third premolar. A similar situation exists in Basel Naturhistoriches Museum G. C. 358, a maxillary fragment, also *A. siderolithicus*, from the late Eocene Gösgen Canal locality, Canton Solothurn, Switzerland, where a minute alveolus is present in front of dP^4. Another maxilla of the same species from the same locality, but with P^4 in place (Basel G. C. 824), shows no trace of an alveolus. This is also true of three late Eocene adult skulls of *Adelomys* (one from Gösgen Canal in the Museum of Olten; one from Montauban in Basel; and Basel Q. T. 756, "*Sciuroides* B", from Quercy). There is also no trace of an alveolus in front of P^4 in the skull, Basel Ek. 245, belonging to a primitive species of *Adelomys* from the middle Eocene of Egerkingen. It would seem probable, therefore, that *Adelomys* possessed both dP^3 and dP^4, but that the permanent dentition included only P^4. This situation in *Adelomys* suggests that the pseudosciurids might have been ancestral to the phiomyids, if the anterior tooth in *Metaphiomys* were dP^3, as seems probable.

However, all of the phiomyids are strictly hystricognathous, a condition not represented in any theridomyid (Lavocat, 1955, p. 634) or pseudosciurid. At the same time they have a hystricomorphous infraorbital foramen, similar to that in both the theridomyids and pseudosciurids. Both of these characters are advanced in the phiomyids and must have originated from a sciurognathous and protrogomorphous ancestral pattern, if I (1962a, p. 246) am correct in believing that the paramyids are the ancestral stock of the order. At the present time, the evidence is inadequate to trace the transitions from sciurognathous to hystricognathous jaws, or from protrogomorphous to hystricomorphous zygomasseteric structures, in any group. Clearly the two are associated in the Caviomorpha, Hystricidae, and Thryonomyoidea; clearly the Theridomyoidea, Pedetidae, Ctenodactylidae and Anomaluridae have the hystricomorphous condition but are sciurognathous. Only the Bathyergidae could be interpreted as being hystricognathous without being hystricomorphous. In the absence of known fossil series showing the origin of any of these structures, it is permissible either to believe that the hystricomorphous structure developed first and that some of the hystricomorphous forms later became hystricognathous; or to believe that whatever modifications of the masseter and pterygoid took place, they occurred simultaneously. The latter seems intrinsically more probable, however, to me, since this involves a single set of coordinated changes that took place in a relatively brief time as adaptations to a single series of selective pressures.

There is no suggestion of the retention of deciduous teeth in the theridomyids, although it is probable that this peculiarity was just beginning to develop in the Fayum phiomyids, and it may well not have characterized the original immigrants to North Africa.

There are strong similarities in the cheek tooth pattern between *Phiomys* and *Theridomys,* as pointed out by Schlosser (1911, p. 91–94), Viret (1955, p. 1551), and McKenna (1962, p. 26, footnote), as well as by Schaub (1958, p. 705). These are much more pronounced than the similarities to eomyids stressed by Osborn (1908, p. 269), and there is universal agreement at present that there is no connection between the eomyids and the phiomyids. A possibility that cannot be positively ruled out is that the phiomyids are derived not from theridomyids but from the Pseudosciuridae, a group presumably ancestral to the theridomyids. This still does not eliminate the problem of the structure of the angle, but it allows a longer time to bring about the change.

Aside from the two families of the Theridomyoidea, the only known group that might provide the ancestry of the phiomyids would be the Protrogomorpha. These could be Old World paramyids, Asiatic sciuravids, or they could be members of some as yet unknown Old World protrogomorph stock. There is ample room for the discovery of such forms. The dental patterns of the Paramyidae suggest that a variety of members of this family were incipiently developing crested teeth, although never with a mesoloph or mesolophid (Wood, 1962a). The family also includes incipiently hystricognathous forms (Wood, 1962a, p. 122) and at least one form with an enlarging infraorbital foramen (Wood, 1962a, p. 148). The pattern of the permanent lower premolars of the phiomyids is also suggestive of fairly strong paramyid affinities. In these teeth the metaconids are the highest cusps, as in paramyids, and the teeth are much less evolved in pattern than are the molars. In fact P_4 of *Phiomys* (fig. 1 B, D) is very similar to the corresponding tooth of various early Eocene species of paramyids (Wood, 1962a, *Paramys copei,* fig. 14 D; *P. excavatus,* fig. 18 0; *Reithroparamys debequensis,* fig. 45 D; *Microparamys lysitensis* (fig. 54 L). This similarity is in strong contrast to the fully molariform posterior halves of the permanent premolars figured by Stehlin and Schaub for *Adelomys, Pseudosciurus* and *Theridomys* (1951, figs. 314, 315 and 317). This would seem to make the pseudosciurid or theridomyid ancestry of *Phiomys* almost impossible and the immediate paramyid ancestry quite probable.

Phiomys, Paraphiomys and *Metaphiomys* are close to the Miocene phiomyids of Africa and could be directly ancestral to these (fig. 17). Some of the Miocene forms, as pointed out by Lavocat (1962, p. 290–291) are very close to the modern cane rat, *Thryonomys.* However, in many respects *Gaudeamus* is closer to the cane rat, and it seems probable that the modern genus has been derived from this more specialized branch (subfamily?) of the phiomyids and that the *Phiomys–Paraphiomys* line represents merely a primitive ancestral stock that has survived after the development of more specialized derivatives (fig. 17).

Lavocat (1962, p. 291) believes that unworn teeth of *Petromus* are of a phiomyid pattern and that that genus should likewise be derived from something very close to *Paraphiomys.* My earlier figures of unworn *Petromus* teeth (Wood, 1962b, fig. 1 C–F) look like something rather different from those of *Phiomys* in the present paper. However, the skull and jaw structure of *Metaphiomys* is very close to that of *Petromus.* As suggested above the tooth pattern of *Metaphiomys,* especially that of *M. beadnelli,* is an excellent starting point for evolution toward *Petromus,* with such Miocene forms as *Phthynilla, Dia-*

mantomys and *Pomonomys* being intermediate in cheek tooth structure (fig. 17).

If, as seems clear from the present study and from Lavocat's work, the Fayum rodents and their Miocene relatives (the Phiomyidae) and the Thryonomyidae and Petromuridae are closely related, they should certainly be grouped in a superfamily Thryonomyoidea. The details as to whether there should be one family, containing two or three subfamilies, two families (and if so, which), or three families, are matters that still are not clear, though the publication of Lavocat's investigations on the Kenya rodents may clarify the matter. This, basically, is the reason why *Gaudeamus* has not been placed in a distinct subfamily—it is different from *Phiomys,* but should it belong to the Gaudeamurinae or to the Thryonomyinae?

The Phiomyidae and their descendants have played a much more important role in the development of the African rodent fauna than has been realized until very recently (Lavocat, 1962, p. 289–291), and one that certainly is much more important than would be imagined from the living representatives of the group. Although it may ultimately prove advisable to erect a separate suborder for these rodents (Thaler, 1966, p. 11–12), there does not seem to be adequate justification for such action at present, in view of the fact that perhaps all these rodents should be placed in a single family (Thaler, 1966, p. 12). If this were done, the family should be called the Thryonomyidae, as this term has priority. For the present, I continue to place these rodents in the superfamily Thryonomyoidea, containing the Pleistocene to Recent families, Petromuridae and Thryonomyidae, and the Oligocene to Miocene family Phiomyidae. There is no longer any valid reason for associating these forms with the Hystricidae, as I did in 1959 (p. 172). This last family probably developed in southern Asia independently of the African thryonomyoids (Lavocat, 1962, p. 292–293).

It is still impossible to trace the detailed relationships of the Fayum rodents to the Miocene phiomyids, since the largest number of these are still being studied by Lavocat. But the Fayum population seems sufficiently varied to permit the source of the Miocene forms to be found within populations of this general type.

Evolutionary Significance of Retention of Deciduous Teeth

A number of different families of rodents have retained the deciduous premolar. This is clearly occurring in *Phiomys* and *Gaudeamus* and has presumably already occurred in *Metaphiomys* and perhaps in *Paraphiomys.* It has taken place in the Echimyidae and Capromyidae (Wood and Patterson, 1959, p. 301, 324), in *Thryonomys* and *Petromus* (Wood, 1962b). It has often been suggested that this has occurred, together with the loss of M_3^3, in the Cricetidae and Muridae (Friant, 1954, p. 234, and various authors there cited; Hooper, 1955). However, there does not seem to be any good evidence to support this point of view at present, especially if, as seems probable, Schaub (Stehlin and Schaub, 1951, p. 367) is correct that the middle Eocene sciuravid *Pauromys* is ancestral or close to ancestral to the Cricetidae, since *Pauromys* has a greatly reduced P_4.

The retention of dP_4^4 seems to be much more prevalent among rodents than in any other group of Eutherians (except, perhaps, the Proboscidea), and it might be profitable to inquire as to the selective basis for such a condition.

It seems to be a general condition among mammals that dP_4^4 are more molariform than their permanent replacements. This can readily be explained on the basis that these teeth carry on the molar function when the animal is small and the molars have not yet erupted, whether or not it also indicates that the permanent molars belong to the deciduous series. In most mammals, the tooth row consists of rather distinct incisors, canines, premolars and molars, each functioning in a different manner. In the rodents, however, the reduction of the dentition leaves an area of gnawing and an area of chewing. This latter area functions as a unit, rather than being divided into premolar and molar portions. It would seem reasonable, under such conditions, that there would be a strong selective pressure to make the premolar area more molariform. This could be brought about in two ways—either by increasing the molariformity of P_4^4 (and this has taken place in many rodents, including castorids, mylagaulids, eomyids, theridomyids, and erethizontids, to name a few selected at random), or by increasing the height of crown of the already molariform dP_4^4 and retaining these teeth for a longer period of time, until eventually P_4^4 are suppressed. This is what was occurring in the early Oligocene phiomyids.

If such increasing molarization of the premolars were to take place simultaneously with increasing hypsodonty of the molars, it might be just as likely that hypsodonty would affect the deciduous premolar as that it would be restricted to the permanent one. In the former case, the increased hypsodonty of dP_4^4 would lead quickly to the suppression of the permanent premolars.

It is entirely possibly that P_4^4 are much more likely to be suppressed if they have lagged in the race to become molariform, as is certainly the case in both *Phiomys* and *Gaudeamus* (figs. 1 B, 14 E). However, it is equally possible that the causation is reversed, and that the longer persistence of dP_4^4 has resulted in the premolars being left behind in the amount of molarization. Much more detailed information is needed to decide between these two interpretations.

In those forms where both P_4^4 and dP_4^4 have been suppressed, there could well be a selective advantage in increasing the length of the tooth row, which could result in the development of complexities at the anterior end of M_1^1, as in *Phiocricetomys* or in the cricetids. This seems much more probable than the suppression of M_3^3 and the modification of M_2^2 to look like M_3^3, since the last teeth of such early cricetids as *Eumys* have the distinct appearance of M_3^3, especially in the absence of a hypocone in the upper tooth. This is borne out, as indicated above, by the similarities of *Pauromys,* with a greatly reduced P_4, to the cricetids.

Such a secondary elongation of the tooth row could also be associated with an increase in the length of the individual teeth, permitting the development of such neomorphs as the mesoloph and mesolophid as a result of such an elongation (Wood, 1962a, p. 248).

COMPARISON OF AFRICAN AND SOUTH AMERICAN RODENT RADIATIONS

There are very interesting parallels between the evolution of the African and South American rodents during the Tertiary. Among other things, if the interpretations given above are correct, these include the development of end stages so similar that the African *Thryonomys* and *Petromus* have often been referred to South American subfamilies.

In both cases the earliest known rodents occur in the early Oligocene. In both cases the animals are fully hystricomorphous and hystricognathous. In both the incisor enamel is already multiserial. In neither case is there any known ancestral stock in the rest of the world from which they could be derived except with rather marked changes. In both cases fairly primitive paramyids have been suggested as the source. The rodents of the Deseado (Wood and Patterson, 1959) are clearly a closely related group and must have been derived from a single ancestral stock not long before the Deseadan. The same is true of the Fayum rodents. The Deseadan rodents are separated into numerous families, not because of their diversity, but because their relationships have been established to the highly diversified later caviomorph families. The Fayum rodents have been left in one family because there are more gaps between them and later forms and because their descendants apparently did not become quite so diversified. In both continents the initial rodent invasion resulted in an adaptive radiation that introduced rodents to a large variety of ecologic niches. The great variety of phiomyids present in the African Miocene (Lavocat, 1962, p. 290) suggests the corresponding variety of caviomorphs in the Santa Cruz. However, there was one important difference. The caviomorphs were able to evolve, without interference, in South America until the late Pliocene or early Pleistocene invasion of cricetids, sciurids and, to a lesser extent, heteromyids. The resulting competition has not yet greatly reduced the variety of caviomorphs. The phiomyids, however, were only just getting started on their Miocene adaptive radiation when they had to meet the competition of invaders. These included sciurids, cricetids, glirids and ctenodactylids ("tataromyids") in Beni Mellal (Lavocat, 1961) and cricetids in Kenya (Lavocat, 1962, p. 290). In addition, both these areas and Southwest Africa have pedetids; Kenya and Southwest Africa have bathyergids; and there are anomalurids in Kenya (Lavocat, 1962, p. 290). The origin of these last three families is at present unknown. In view of their complete absence from the Fayum, it is perhaps simpler to assume that they invaded Africa dry-shod in the Miocene along with the sciurids, cricetids, glirids and ctenodactylids, and that there was only a single island-hopping invasion of the continent by the phiomyids. Other rodent types presumably invaded Africa even later.

This outside competition would appear to have been too much for the phiomyids, and they and their descendants dwindled rapidly from their dominance in the Miocene to their minor place in the fauna today, where the only phiomyid descendants are *Thryonomys* and *Petromus*.

TABLES

Standard statistical measurements for the teeth are included in the tables. These include the number of available specimens (N); the observed range (OR); the mean (M); the standard deviation (σ); and the coefficient of variation (V). Means are calculated when N = 2 or more; the other parameters only when N = at least 10. Standard errors for M, σ and V are also given when N = 10 or more.

All measurements were made with dial calipers, with a scale graduated to 0.01 mm., and statistical values were also calculated to the nearest 0.01 mm.

The measurements of the holotypes are included, not because these specimens are any more significant than any others, statistically, but because they are the individuals most likely to be cited by other workers.

The incisor ratios are transverse/anteroposterior.

TABLE 1 MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Phiomys andrewsi*

	N	OR	M	σ	V	Holotype AMNH 13275 R
P_4- M_3 alveolar	3		7.32			
P_4- M_3 tooth length	2		6.46			5.80
P_4 anteroposterior	2		1.51			1.27
width, metalophid	2		1.02			0.97
width, hypolophid	2		1.25			1.18
M_1 anteroposterior	15	1.40 - 1.94	1.70 ± .04	.16 ± .03	9.41 ± 1.72	1.45
width, metalophid	15	1.26 - 1.70	1.50 ± .03	.12 ± .02	8.00 ± 1.46	1.26
width, hypolophid	15	1.31 - 1.71	1.57 ± .03	.11 ± .02	7.01 ± 1.28	1.31
M_2 anteroposterior	14	1.48 - 1.93	1.77 + .04	.16 ± .03	9.04 ± 1.71	1.48
width, metalophid	14	1.43 - 1.88	1.73 ± .04	.14 ± .03	8.09 ± 1.53	1.55
width, hypolophid	13	1.33 - 1.88	1.73 ± .04	.15 ± .03	8.67 ± 1.70	

TABLE 1 MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF Phiomys andrewsi(cont.)

		N	OR	M	σ	V	Holotype AMNH 13275 R
M_3	anteroposterior	3		1.81			1.53
	width, metalophid	2		1.72			
	width, hypolophid	3		1.51			1.29
dP_4	anteroposterior	9	1.41 - 2.05	1.72			
	width, metalophid	7	0.86 - 0.97	0.94			
	width, hypolophid	8	1.09 - 1.32	1.20			
I_1	anteroposterior	86	1.18 - 2.10	1.67 ± .02	.20 ± .02	11.98 ± .91	1.50
	transverse	86	0.83 - 1.43	1.14 ± .01	.13 ± .01	11.40 ± .87	0.98
	ratio	86	0.62 - 0.76	0.69 ± .003	.03 ± .002	4.35 ± .33	0.65

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF UPPER CHEEK TEETH OF PHIOMYIDS

				Metaphiomys schaubi		
		N	OR	M	σ	V
dP^4 - M^3		1	9.6			
dP^3	anteroposterior	2	0.63 - 0.78	0.71		
	transverse	2	0.93 - 0.95	0.94		
dP^4	anteroposterior	11	2.02 - 2.18	2.11 ± .02	.05 ± .01	2.37 ± 0.51
	width, protoloph	11	2.12 - 2.43	2.26 ± .04	.12 ± .03	5.31 ± 1.13
	width, metaloph	11	2.16 - 2.53	2.33 ± .04	.12 ± .03	5.15 ± 1.10
M^1	anteroposterior	14	1.92 - 2.33	2.15 ± .03	.10 ± .02	4.65 ± .88
	width, protoloph	14	2.33 - 2.76	2.56 ± .03	.12 ± .02	4.69 ± .89
	width, metaloph	14	2.29 - 2.60	2.48 ± .03	.10 ± .02	4.03 ± .76
M^2	anteroposterior	12	1.97 - 2.72	2.36 ± .05	.19 ± .04	8.05 ± 1.64
	width, protoloph	12	2.63 - 3.14	2.89 ± .05	.16 ± .03	5.54 ± 1.13
	width, metaloph	12	2.38 - 2.90	2.64 ± .04	.15 ± .03	5.66 ± 1.16
M^3	anteroposterior	5	2.15 - 2.37	2.27		
	width, protoloph	5	2.60 - 2.97	2.80		
	width, metaloph	4	1.90 - 2.45	2.23		

TABLE 2 (cont.)
MEASUREMENTS (IN MILLIMETERS) OF UPPER CHEEK TEETH OF PHIOMYIDS

		Phiomys andrewsi		Phiomys paraphiomyoides	Metaphiomys or Phiomys sp. indet.		Gaudeamus aegyptius	
		YPM 18051 L	YPM 18035 R	YPM 18233 L	YPM 18089 (unassoc.) R	L	YPM 18044 R	YPM 18012 L
P^4-M^3							6.88	
dP^4	an					2.10		
	w, p					2.24		
	w, m					2.26		
P^4	an						1.47	
	w, p						2.11	
	w, m						2.00	
M^1	an	1.75		1.37		2.02	1.71	1.85
	w, p	1.76		1.43		2.24	2.21	2.20
	w, m	1.69		1.40		2.27	2.16	2.22
M^2	an	1.85	2.08	1.40	2.25		1.91	
	w, p	1.98	2.25	1.70	2.30		2.37	
	w, m	1.87	2.03	1.50	2.30		2.31	
M^3	an						1.73	
	w, p						1.92	
	w, m						1.80	

an=anteroposterior
w=width
p=protoloph
m=metaloph

TABLE 3
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF
Phiomys paraphiomyoides

		Holotype CM 26904	YPM 18227	YPM 21288	YPM 21289	YPM 21290	M
dP$_4$-M$_3$ al		5.65			5.87		5.76
dP$_4$	an	1.35		1.38	1.32		1.35
	w, m	0.78		0.78	0.80		0.79
	w, h	1.01		0.96	1.04		1.00
M$_1$	an	1.44	1.58	1.25	1.46	1.52	1.45
	w, m	1.17	1.22	1.18	1.23	1.37	1.23
	w, h	1.19	1.29	1.24	1.28	1.42	1.28
M$_2$	an	1.37	1.46	1.52	1.43	1.48	1.45
	w, m	1.33	1.36	1.33	1.42	1.48	1.38
	w, h	1.33	1.50	1.29	1.45	1.49	1.41
M$_3$	an	1.43			1.56		1.50
	w, m	1.33			1.35		1.34
	w, h	1.10			1.26		1.18
I$_1$	an	1.70	1.48	1.50	1.63	1.59	1.58
	t	1.09	0.98	0.98	1.03	1.09	1.03
	r	0.63	0.66	0.65	0.63	0.68	0.65

al=alveolar
an=anteroposterior
w=width
m=metalophid
h=hypolophid
t=transverse
r=ratio

TABLE 3 (cont.)
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF
P. aff. paraphiomyoides

		YPM 21292	YPM 21293	YPM 21294	YPM 21366	M
dP_4	an		1.63	1.65		1.64
	w, m		1.09	1.10		1.10
	w, h		1.22	1.20		1.21
M_1	an	1.81	1.70	1.64	1.84	1.75
	w, m	1.52	1.47	1.52	1.49	1.50
	w, h	1.60	1.52	1.51	1.54	1.54
M_2	an	1.72	1.81		1.80	1.78
	w, m	1.68	1.77		1.70	1.72
	w, h	1.71	1.67		1.61	1.66
I_1	an		1.50	1.49	1.80	1.60
	t		1.08	1.11	1.10	1.10
	r		0.72	0.75	0.61	0.69

TABLE 4

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF Phiomys lavocati

		Holotype CM 26903	YPM 18011	YPM 18057	M
dP_4-M_3 al		4.50			
dP_4	an		1.12	1.32	1.22
	w, m		0.72	0.73	0.73
	w, h		0.91	0.87	0.89
M_1	an	1.08	1.15	1.20	1.14
	w, m	1.06	1.09	1.05	1.07
	w, h	1.10	1.17	1.20	1.16
M_2	an	1.15		1.12	1.14
	w, m	1.23		1.18	1.20
	w, h	1.16		1.10	1.13
M_3	an	1.10			
	w, m	1.19			
	w, h	1.03			
I_1	an	1.68	*0.90/1.25	1.72	
	t	0.91	*0.58/0.92	0.98	
	r	0.54	*0.64/0.74	0.57	

*Measurements taken at points 6.5 mm. apart, the smaller being anterior

al=alveolar
an=anteroposterior
w=width
m=metalophid
h=hypolophid
t=transverse
r=ratio

TABLE 4 (cont.)
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF Phiomys OR Metaphiomys sp. indet. AND Paraphiomys simonsi

		Phiomys or Metaphiomys sp. indet.		Paraphiomys simonsi
		YPM 18205	YPM 18194	Holotype CM 26908
dP_4-M_3 al				15.1
dP_4	an			3.11
	w, m			1.90
	w, h			2.23
M_1	an	2.05	2.10	3.39
	w, m	1.91	1.85	3.10
	w, h	2.00	1.97	3.18
M_2	an			3.80
	w, m			3.81
	w, h			3.66
M_3	an			4.25
	w, m			3.60
	w, h			3.43
I_1	an			3.47
	t			2.30
	r			0.66

TABLE 5 MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF LOWER INCISORS OF *Phiomys paraphiomyoides*

	N	OR	M	σ	V
Anteroposterior	13	1.47 - 1.66	1.57 ±.02	.07 ±.014	4.46 ±.87
Transverse	13	0.96 - 1.06	1.01 ±.008	.03 ±.006	2.97 ±.58
Ratio	13	0.61 - 0.69	0.64 ±.006	.02 ±.004	3.13 ±.61

TABLE 6 MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF LOWER INCISORS OF *Phiomys lavocati*

	N	OR	M	σ	V	Holotype CM 26903 R
Anteroposterior	12	0.90 - 1.72	1.28 ±.07	.24 ±.05	18.75 ±3.83	1.68
Transverse	12	0.58 - 0.98	0.73 ±.04	.13 ±.03	17.81 ±3.64	0.91
Ratio	12	0.50 - 0.74	0.58 ±.02	.07 ±.01	12.07 ±2.46	0.54

TABLE 7
MEASUREMENTS (IN MILLIMETERS) AND RATIOS OF UPPER INCISORS OF PHIOMYIDS

	N	OR	M	σ	V
Phiomys andrewsi					
anteroposterior	21	1.43 - 2.30	2.04 ± .05	.21 ± .03	10.29 ± 1.59
transverse	21	0.72 - 1.30	1.09 ± .03	.14 ± .02	12.84 ± 1.98
ratio	21	0.48 - 0.63	0.53 ± .009	.04 ± .006	7.55 ± 1.16
Phiomys lavocati					
anteroposterior	4	1.45 - 1.57	1.51		
transverse	4	0.58 - 0.65	0.63		
ratio	4	0.37 - 0.45	0.42		
Metaphiomys schaubi					
anteroposterior	8	2.31 - 2.98	2.57		
transverse	8	1.48 - 1.95	1.68		
ratio	8	0.60 - 0.69	0.66		
Phiomys or *Metaphiomys* sp. indet.					
anteroposterior	3	2.28 - 2.73	2.43		
transverse	3	1.26 - 1.44	1.34		
ratio	3	0.53 - 0.58	0.55		
Metaphiomys sp. indet.					
anteroposterior	2	2.95 - 3.02	2.99		
transverse	2	2.35 - 2.43	2.39		
ratio	2	0.80	0.80		

TABLE 8

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Metaphiomys beadnelli*

		Holotype AMNH 13273 L	YPM 18226 L
$dP_4 - M_3$			12.0
dP_4	anteroposterior		2.78
	width, hypolophid		ca. 2.1
M_1	anteroposterior	2.80	2.80
	width, metalophid	2.13	2.37
	width, hypolophid	2.27	2.34
M_2	anteroposterior	ca. 2.75	3.15
	width, metalophid	ca. 2.6	2.75
	width, hypolophid	ca. 2.5	2.69
M_3	anteroposterior		3.08
	width, metalophid		2.82
	width, hypolophid		2.47
I_1	anteroposterior	2.21	2.54
	transverse	1.91	2.13
	ratio	0.87	0.84

TABLE 9
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Metaphiomys schaubi*

		N	OR	M	σ	V	Holotype CM 26910 L
dP_4-M_3		9	9.67 - 10.90	10.32			10.60
dP_4	an	35	2.14 - 2.80	2.49 ± .03	.15 ± .02	6.02 ± 0.71	2.67
	w, m	34	1.36 - 1.65	1.49 ± .02	.09 ± .01	6.04 ± 0.73	1.53
	w, h	36	1.63 - 1.96	1.80 ± .02	.09 ± .01	5.00 ± 0.59	1.91
M_1	an	37	2.21 - 2.80	2.44 ± .02	.12 ± .01	4.92 ± 0.57	2.58
	w, m	36	1.96 - 2.32	2.11 ± .02	.09 ± .01	4.27 ± 0.50	2.16
	w, h	36	2.03 - 2.42	2.20 ± .02	.09 ± .01	4.09 ± 0.48	2.21
M_2	an	32	2.27 - 3.18	2.58 ± .03	.19 ± .02	7.36 ± 0.92	2.45
	w, m	32	2.27 - 2.90	2.52 ± .03	.16 ± .02	6.35 ± 0.79	2.51
	w, h	31	2.25 - 2.77	2.48 ± .03	.16 ± .02	6.45 ± 0.82	2.54
M_3	an	17	2.38 - 2.90	2.64 ± .04	.15 ± .03	5.68 ± 0.97	2.65
	w, m	16	2.29 - 2.80	2.49 ± .04	.14 ± .02	5.62 ± 0.99	2.56
	w, h	16	2.00 - 2.50	2.22 ± .04	.14 ± .02	6.31 ± 1.12	2.21
I_1	an	40	1.63 - 2.67	2.25 ± .03	.22 ± .02	9.78 ± 1.09	
	t	40	1.31 - 2.12	1.79 ± .03	.18 ± .02	10.06 ± 1.12	
	r	40	0.71 - 0.88	0.80 ± .006	.04 ± .004	5.00 ± 0.56	

an=anteroposterior; w=width; m=metalophid; h=hypolophid; t=transverse; r=ratio.

TABLE 10
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Gaudeamus aegyptius*

		CM 26920 Holotype L		YPM 18012 R	YPM 18022 R	YPM 18024 R	YPM 18032 L	YPM 18036 L
P_4	anteroposterior	1.75*	2.20^d		ca. 2.20^d	2.18^d	1.97^d	
	width, metalophid	1.3*	1.14		0.96	1.09	1.05	
	width, hypolophid	1.6*	1.49		1.32	1.46	1.48	
M_1	anteroposterior	2.10		1.95	1.70	1.87		1.75
	width, metalophid	1.95		1.82	1.60	1.87		1.76
	width, hypolophid	2.02		1.98	1.80	1.82		1.82
M_2	anteroposterior	2.05				2.15	2.17	1.79
	width, metalophid	2.21				1.87	2.21	1.84
	width, hypolophid	2.28				1.88	2.10	1.93
M_3	anteroposterior						1.85*	
	width, metalophid						1.95*	
	width, hypolophid						1.70*	
I_1	anteroposterior	1.74				1.80	2.20	2.07
	transverse	0.88				1.11	1.32	1.51
	ratio	0.51				0.62	0.60	0.73

* unerupted tooth; greatest visible diameter.
d= deciduous

TABLE 10 (cont.)
MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Gaudeamus aegyptius*

		YPM 18047 R	AMNH 8225 L	YPM 18218				N	M	after Schlosser, 1911, p. 91 R
$P_4 - M_3$										8.5
P_4	an							4^d	2.14	
	w, m							4^d	1.06	
	w, h							4^d	1.44	
M_1	an	1.75						6	1.85	2.
	w, m	1.67						6	1.78	
	w, h	1.76						6	1.87	2.
M_2	an	1.84	1.72					6	1.95	2.3
	w, m	1.61	1.70					6	1.91	
	w, h	1.80	1.63					6	1.94	2.3
I_1	an		1.43	2.32	2.16	2.19	2.48	9	2.04	
	t		1.02	1.60	1.47	1.27	1.60	9	1.31	
	r		0.71	0.69	0.68	0.58	0.65	9	0.64	

an=anteroposterior; w=width; m=metalophid; h=hypolophid; t=transverse; r=ratio; d=deciduous

TABLE 11

MEASUREMENTS (IN MILLIMETERS) OF LOWER TEETH OF *Phiocricetomys minutus*, CM 26925

M_1	anteroposterior	1.50	M_3	anteroposterior	0.98
	width, metalophid	0.75		width, metalophid	0.83
	width, hypolophid	0.90		width, hypolophid	0.69
M_2	anteroposterior	1.22	M_{1-3}	anteroposterior	3.56
	width, metalophid	1.03	I_1	transverse	0.50
	width, hypolophid	0.93			

LITERATURE CITED

Andrews, C. W., 1901a. Preliminary note on some recently discovered extinct vertebrates from Egypt. Part I: Geol. Mag., IV, v. 8, p. 400–409.

———1901b. Preliminary note on some recently discovered extinct vertebrates from Egypt. Part II: Geol. Mag., IV, v. 8, p. 436–444.

———1901c. Preliminary note on some recently discovered extinct vertebrates from Egypt [abs.]: Nature, v. 64, p. 582.

———1901d. (Bradytherium amended to Barytherium): Geol. Mag., IV, v. 8, p. 528.

———1901e. A new name for an ungulate: Nature, v. 64, p. 577.

———1902. Preliminary note on some recently discovered extinct vertebrates from Egypt. Part III: Geol. Mag., IV, v. 9, p. 291–295.

———1903. Notes on an expedition to the Fayûm, Egypt, with descriptions of some new mammals: Geol. Mag., IV, v. 10, p. 337–343.

———1904. Further notes on the mammals of the Eocene of Egypt: Geol. Mag., V, v. 1, p. 157–162.

———1905. Notes on the species of *Palaeomastodon:* Geol. Mag., V, v. 2, p. 562–563.

———1906. A descriptive catalogue of the Tertiary Vertebrata of the Fayûm, Egypt. Based on the collection of the Egyptian government in the Geological Museum, Cairo, and on the collection in the British Museum (Natural History). London: Brit. Mus. [Nat. Hist.], London, 324 p.

———1914. On the Lower Miocene vertebrates from British East Africa, collected by Dr. Felix Oswald: Geol. Soc. London Quart. Jour., no. 70, p. 163–186.

Andrews, C. W. and Beadnell, H. J. L., 1902. A preliminary note on some new mammals from the Upper Eocene of Egypt: Egypt Survey Dept., Pub. Works Min., Cairo, p. 1–9.

Beadnell, H. J. L., 1902. A preliminary note on *Arsinoitherium zitteli* Beadnell from the upper Eocene strata of Egypt: Egypt. Survey Dept., Pub. Works Min., Cairo, 4 p.

———1905. The topography and geology of the Fayûm province of Egypt: Egypt Survey Dept., Pub. Works Min., Cairo, 101 p.

Blankenhorn, M., 1900. Neues zur Geologie und Paläontolgie Aegyptens: Abdruck a.d. Zeitschr. d. Deutsch. geolog. Gesellschaft, v. LII, p. 21–47.

Dames, W., 1883. Ueber eine Tertiäre Wirbelthierfauna von der westlichen Insel der Birket-el-Qurun, im Fajum (Aegypten): Sitz.-Ber. Akad. Wiss., Berlin, 1883, p. 129–153.

———1894. Ueber Zeuglodonten aus Aegypten und die Beziehungen der Archaeoceten zu den übrigen Cetaceen: Geol. Paläont. Abh., ser. 2, v. 1, no. 5, 36 p.

Dart, R. A., 1923. The brain of the Zeuglodontidae (Cetacea): Zool. Soc. London Proc., 1923, p. 615–648.

Friant, M., 1954. Sur les rongeurs fossiles de Lagoa Santa, Minas Geraes, Brésil: Dansk Naturh. Foren. Vidensk. Medd., v. 116, p. 233–250.

Hooper, E. T., 1955. Extra teeth in the pygmy mouse, *Baiomys musculus:* Jour. Mammal., v. 36, p. 298–299.

———1957. Dental patterns in mice of the genus *Peromyscus:* Univ. Mich., Mus. Zool., Misc. Pub. no. 99, 59 p.

Hopwood, A. T., 1929. New and little-known mammals from the Miocene of Africa: Amer. Mus. Novitates, no. 344, 9 p.

Hürzeler, Johannes, 1956. *Oreopithecus,* un point de repère pour l'historie de l'humanité à l'ère tertiaire: Colloq. Internat. Cent. Nation. Recherch. Sci., v. 60, p. 115–121.

Kellogg, R., 1928. The history of whales—their adaptation to life in the water: Quart. Rev. Biol., no. 3, p. 29–76.

Lankester, E. Ray, 1903. A new extinct monster: Sphere, p. 238.

Lavocat, R., 1955. Sur les relations systématiques entre les Theridomyidés et divers rongeurs fossiles d'Afrique: Acad. Sci. (Paris) Comptes Rendus, v. 240, p. 634–635.

———1961. Le gisement de vertébrés miocènes de Beni Mellal: Serv. Geol. Maroc, Notes et Mémoires, no. 155, p. 1–144.

———1962. Réflexions sur l'origine et la structure du groupe des rongeurs: Problèmes Actuels de Paléontologie, Colloques Internat., Centre Nat. Recherche Sci., no. 104, p. 287–299.

Matsumoto, H., 1921. *Megalohyrax* Andrews and *Titanohyrax* g.n.—A revision of the genera of hyracoids from the Fayûm, Egypt: Zool. Soc. London Proc., 1921, p. 839–850.

———1922. Revision of *Palaeomastodon* and *Moeritherium:* Amer. Mus. Novitates, no. 51, 6 p.

———1923. A contribution to the knowledge of *Moeritherium:* Amer. Mus. Nat. Hist. Bull., no. 48, p. 97–140.

———1924. A revision of *Palaeomastodon,* dividing it into two genera, and with descriptions of two new species: Amer. Mus. Nat. Hist. Bull., no. 50, p. 1–58.

———1926. Contribution to the knowledge of fossil Hyracoidea of the Fayûm, Egypt, with description of several new species: Amer. Mus. Nat. Hist. Bull., no. 56, p. 253–350.

McKenna, M. C., 1962. *Eupetaurus* and the living petauristine sciurids: Amer. Mus. Novitates, no. 2104, 38 p.

Moustafa, Youssef Shawki, 1954. Additional information on the skull of *Prozeuglodon isis* and the morphological history of the Archaeoceti: Proc. Egyptian Acad. Sci., v. IX, 1953.

Osborn, H. F., 1907. Hunting the ancestral elephant in the Fayûm Desert: Century Mag., v. 74, p. 815–835.

———1908. New fossil mammals from the Fayûm Oligocene, Egypt: Amer. Mus. Nat. Hist. Bull., no. 24, p. 265–272.

———1909. New carnivorous mammals from the Fayûm Oligocene, Egypt: Amer. Mus. Nat. Hist. Bull., no. 26, p. 415–424.

———1936. Proboscidea. A monograph of the discovery, evolution, migration and extinction of the mastodonts and elephants of the world. I. Moeritherioidea, Deinotheroidea, Mastodontoidea: Amer. Mus. Nat. Hist., N.Y., 802 p.

Petronievics, B., 1923. Remarks on the skulls of *Moeritherium* and *Palaeomastodon:* Ann. Mag. Nat. Hist., v. 9, no. 12, p. 55–61.

Piveteau, J., 1957. Traité de Paléontologie; Tome VII, Primates: Masson et Cie, Paris, 675 p.

Pontier, G., 1907. Sur une espèce nouvelle de *Palaeomastodon (P. barroisi):* Ann. Soc. Geol. Nord., no. 36, p. 150–154.

Rice, E. R., (mss.) Early Oligocene cricetid rodents from Nebraska: Unpublished Master's thesis, Amherst College.

Said, R., 1962. The geology of Egypt: Amer. Elsevier Pub. Co. New York, 377 p.

Schaub, S., 1958. Simplicidentata, *in* Traité de Paléontologie: Jean Piveteau Ed., Masson et Cie., Paris, v. 6, pt. 2, p. 659–818.

Schlosser, M., 1910. Über einige fossile Saugetiere aus dem Oligocän von Ägypten: Zool. Anz., no. 35, p. 500–508.

———1911. Beiträge zur Kenntnis der Oligozänen Landsäugetiere aus dem Fayûm (Ägypten): Beitr. z. Paläont. u. Geol. Österreich-Ungarns u.d. Orients, v. 24, p. 51–167.

Schmidt, M., 1913. Ueber Paarhufer der fluviomarinen Schichten des Fajum: Geol. Paläont. Abh., v. 15, p. 153–264.

Schweinfurth, Georg, 1886. Reise in das Depressionsgebiet im Umkreise des Fajūm im Januar 1886: Zeitschr. Ges. Erdkunde Berlin, v. XXI, p. 96–149.

Simons, E. L., 1959. An anthropoid frontal bone from the Fayum Oligocene of Egypt; the oldest skull fragment of a higher primate: Amer. Mus. Novitates, no. 1976, 16 p.

———1960. *Apidium* and *Oreopithecus:* Nature, v. 186, p. 824–826.

———1961. An anthropoid mandible from the Oligocene Fayum beds of Egypt: Amer. Mus. Novitates, no. 2051, 5 p.

———1962. Two new primate species from the African Oligocene: Yale Univ., Peabody Mus., Postilla, no. 64, 12 p.

———1963. A new phylogeny of Oligocene catarrhines, *in* M. S. Walton (ed.) Kline Geology Laboratory: Yale Univ. Press, New Haven.

———1965. New fossil apes from Egypt and the initial differentiation of Hominoidea: Nature, v. 205, p. 135–139.

Simpson, G. G., A. Roe and R. C. Lewontin, 1960. Quantitative Zoology: Harcourt, Brace and Co., New York.

Stehlin, H. G. and S. Schaub, 1951. Die Trigonodontie der simplicidentaten Nager: Schweizerischen Paläont., Abh. 67, p. 1–385.

Stromer, E., 1903. Zeuglodon—Reste aus dem oberen Mitteleocän des Fajûm: Beitr. Paläont. Geol. Öst.-Ung., no. 15, p. 59–100.

———1926. Reste Land- und Süsswasser-bewohnender Wirbeltiere aus den Diamantenfeldern

Deutsch-Südwestafrikas, *in* E. Kaiser, Die Diamantenwüste Südwestafrikas: Dietrich Reimer, Berlin, v. 2, p. 107–153.

Thaler, L., 1966. Les rongeurs fossiles du Bas-Languedoc dans leurs rapports avec l'histoire des faunes et la stratigraphie du Tertiaire d'Europe: Mus. Nat. d'Hist. Natur. Mém. n.s., Ser. C., v. 17, p. 1–295.

Viret, J., 1955. Rodentia fossiles. La denture des rongeurs actuels et fossiles, *in* Traité de Zoologie. Anatomie, Systématique, Biologie: P.-P. Grassé Ed., Masson et Cie., Paris, v. 17, pt. 2, p. 1526–1564.

Wilson, J. A., 1966. A new primate from the earliest Oligocene, West Texas, preliminary report: Folia Primat., no. 4, p. 227–248.

Wood, A. E., 1955. A revised classification of the rodents: Jour. Mammal., v. 36, p. 165–187.

———1958. Are there rodent suborders?: Systematic Zool., v. 7, p. 169–173. [1959]

———1962a. The early Tertiary rodents of the Family Paramyidae: Amer. Philos. Soc. Trans., n.s., v. 52, p. 1–261.

———1962b. The juvenile tooth patterns of certain African rodents: Jour. Mammal., v. 43, p. 310–322.

Wood, A. E. and B. Patterson, 1959. The rodents of the Deseadan Oligocene of Patagonia and the beginnings of South American rodent evolution: Mus. Comp. Zool. Bull., v. 120, p. 281–428.