

The Stuttgart collection of Oligocene primates from the Fayum Province of Egypt

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With 4 figures and 3 tables in the text

Abstract: In 1907, R. MARKGRAF made a small collection of Oligocene fossil primates from Egypt for the Staatliches Museum für Naturkunde in Stuttgart. Circumstances of discovery suggest that this collection came from the same stratigraphic horizon (the Upper Fossil Wood zone) and possibly the same locality as a similar collection made earlier that year by MARKGRAF for the American Museum of Natural History in New York. Three new genera and species were described by SCHLOSSER, based on the Stuttgart collection. *Parapithecus fraasi* SCHLOSSER is a junior synonym of *Apidium phiomense* OSBORN. "*Parapithecus*" *grangeri* SIMONS is placed in the new genus *Simonsius*. *Propliopithecus haeckeli* SCHLOSSER and *Moeripithecus markgrafi* SCHLOSSER have previously been recognized as synonyms. In addition, *Aegyptopithecus zeuxis* SIMONS is known from the Upper Fossil Wood zone.

Zusammenfassung: Eine von R. MARKGRAF 1907 dem Stuttgarter Naturienkabinett übergebene Sammlung oligozäner Primaten aus Ägypten stammt vermutlich aus dem gleichen stratigraphischen Horizont ("Upper Fossil Wood zone") und vielleicht auch von derselben Lokalität wie eine von ihm schon vorher an das American Museum of Natural History in New York gegebene Sammlung. Letztere wurde von OSBORN (1908) beschrieben, das Stuttgarter Material von SCHLOSSER (1910, 1911). *Parapithecus fraasi* SCHLOSSER ist ein jüngeres Synonym von *Apidium phiomense* OSBORN. *Propliopithecus haeckeli* SCHLOSSER und *Moeripithecus markgrafi* SCHLOSSER wurden schon früher als Synonyme erkannt. Für *Parapithecus grangeri* SIMONS (1974) wird die neue Gattung *Simonsius* aufgestellt. Auch sie stammt aus der "Upper Fossil Wood zone" (Obergrenze der »fluviatil-marinen« Serie des Fayums). Zwei sichere Vertreter der Hominoidea aus dieser Fundschicht sind *Propliopithecus haeckeli* SCHLOSSER und *Aegyptopithecus zeuxis* SIMONS.

Introduction

Primate fossils from Oligocene strata of the Fayum Province of Egypt are the earliest good record we have of higher primates and they are thus of fundamental importance to our understanding of the origin of Anthrooidea. The first primate from the Fayum was described by OSBORN (1908) and named *Apidium phiomense* (Fig. 1). Two years later SCHLOSSER (1910, 1911) named and described three additional genera and species *Parapithecus fraasi*, *Propliopithecus haeckeli*, and *Moeripithecus markgrafi*. These four genera and species were based on a total of four specimens, all collected by Richard MARKGRAF. They have been beautifully illustrated by KÄLIN (1961). Two additional primate specimens, one a frontal and the other an edentulous mandible were collected by early expeditions but not described until relatively recently (SIMONS 1959, 1961).

This was the extent of our knowledge of early Anthrooidea until E. L. SIMONS of Yale University organized a series of new expeditions to the Fayum during the 1960's. Many additional primate specimens were discovered, which were subsequently described

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in a series of publications by SIMONS (1962, 1965, 1967a, 1967b, 1968, 1969a, 1969b, 1970, 1971a, 1971b, 1972, 1974a, 1974b). Much has been written about these finds by others as well, including CACHEL (1975), CONROY (1976a, b), CONROY, SCHWARTZ & SIMONS (1975), DELSON (1975), DELSON & ANDREWS (1975), FLEAGLE, SIMONS & CONROY (1975), GINGERICH (1973), KAY (1977), KAY & HIEMÄE (1974), PREUSCHOFF (1974), and RADINSKY (1973).

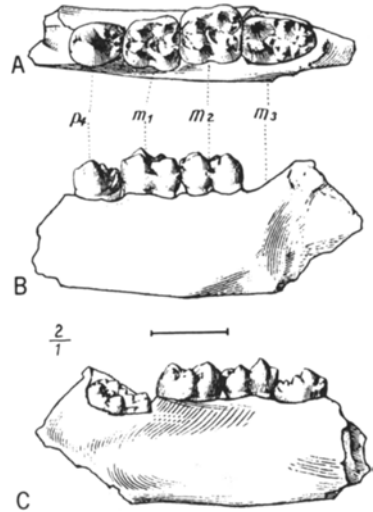


Fig. 1. Type specimen of *Apidium phiomense*, left mandible collected by R. MARKGRAF in 1907 from the Upper Fossil Wood zone, Fayum Province, Egypt. Specimen is in American Museum of Natural History, New York (no. 13370). Illustrated twice natural size in occlusal (A), lateral (B), and medial (C) views. Scale bar is 5 mm. Note erupting P₄ and M₃. Figure from OSBORN (1908).

Most of these publications have been concerned with the anatomy, behavior, and environment of Fayum primates, but SIMONS (1962, 1965, 1974) also added several new taxa to the Fayum primate fauna, including *Oligopithecus savagei*, *Apidium moustafai*, *Aegyptopithecus zeuxis*, *Aeolopithecus chirobates*, and *Parapithecus grangeri*. The stratigraphic distribution of Fayum primates, as understood here, is given in Tab. 1. I was recently able to study all of the type specimens of primate species in New Haven, Ludwigsburg, and Cairo, and made detailed comparisons using very sharp epoxy resin casts. These comparisons indicate that the type specimen of *Apidium phiomense* (Fig. 1) and the holotype of *Parapithecus fraasi* (Fig. 2) are probably conspecific, and hence the names are almost certainly synonyms. The implications of this are discussed below.

Tab 1. Stratigraphic distribution of type specimens of Fayum primate species. See text and SIMONS (1968) for discussion.

Stratigraphic Interval	Species			
Upper Fossil Wood zone	<i>Apidium phiomense</i> (<i>Parapithecus fraasi</i>)	<i>Simonsius grangeri</i>	<i>Propliopithecus haeckeli</i> (<i>Moeripithecus markgrafi</i>) (<i>Aeolopithecus chirobates</i>)	<i>Aegyptopithecus zeuxis</i>
Quarry G level	<i>Apidium moustafai</i>		<i>Propliopithecus</i> sp.	
Lower Fossil Wood zone			<i>Oligopithecus savagei</i>	

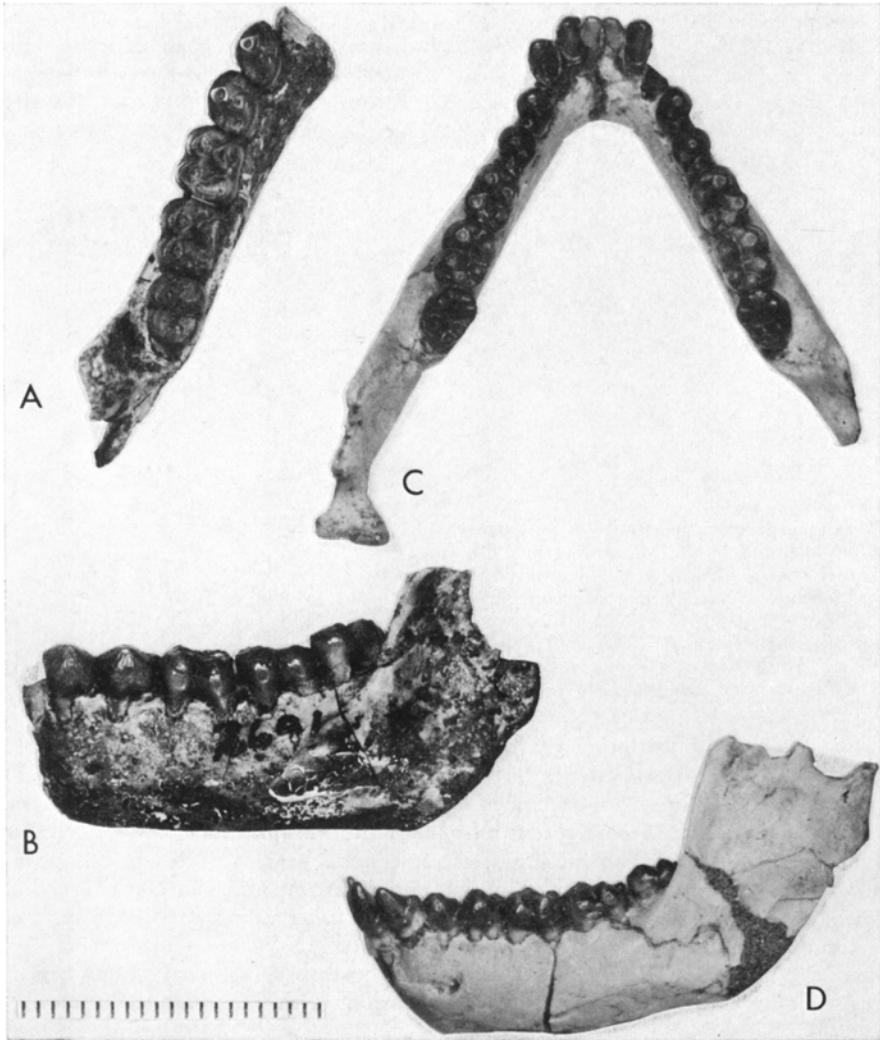


Fig. 2. Two species of Parapithecidae from the Upper Fossil Wood zone, Fayum Province, Egypt. A and B Type specimen of *Simonsius grangeri* (SIMONS 1974), left mandible in occlusal and lateral view. Specimen is in Cairo Geological Museum (no. 26912). C and D Specimen of *Apidium phiomense* (holotype of *Parapithecus fraasi*), left and right mandibles collected by R. MARKGRAF in 1907 (see text) in occlusal and lateral view. Specimen is in Staatliches Museum für Naturkunde Stuttgart (Ludwigsburg). Figures twice natural size, scale in mm.

Type specimens of *Apidium phiomense* and *Parapithecus fraasi*

The type specimens of *Apidium phiomense*, first described by OSBORN (1908), and *Parapithecus fraasi*, described by SCHLOSSER (1910), are illustrated and compared in Fig. 3. Both have been considered closely related (e. g. SIMONS 1962), but it is only very recently that high quality casting techniques have become available permitting one

to make very accurate epoxy casts, and thus make detailed comparisons of specimens housed in distant museums. On comparing an epoxy resin cast of the type specimen of *Apidium phiomense* with that of *Parapithecus fraasi*, it appeared that the two were much more closely related than previously thought, both possibly being derived from the same population, and almost certainly representing the same species. The near identity in most comparable tooth measurements is shown in Tab. 2.

Tab. 2. Measurements of the teeth in the type specimen of *Apidium phiomense* and *Parapithecus fraasi*. Measurements in mm.

	<i>Apidium phiomense</i> Type (American Museum 13370)		<i>Parapithecus fraasi</i> Type (Stuttgart Museum)	
	Length	Width	Length	Width
I ₁	—	—	—	—
I ₂	—	—	1.5	1.7
C	—	—	2.8	1.8
P ₂	—	—	2.7	2.3
P ₃	—	—	2.7	2.5
P ₄	3.2	2.8	3.0	2.8
M ₁	3.7	3.5	4.0	3.5
M ₂	3.9	3.7	4.2	3.9
M ₃	5.1	3.4	4.2	3.3

There are three obvious differences between comparable parts of the two specimens (Fig. 3): (1) the third molar of *Apidium phiomense* is relatively much larger than that of *Parapithecus fraasi*, (2) the type of *A. phiomense* has a well-developed centroconid on the molars and *P. fraasi* lacks it, and (3) the teeth of the type of *A. phiomense* are unworn (in fact it represents an immature individual, Fig. 1) whereas the teeth of the type of *P. fraasi* are moderately worn. Each of these differences is commonly found when individuals of a variable population are compared.

Comparison of the two type specimens in Fig. 3 and Tab. 2 shows that M₃ in *A. phiomense* is relatively much longer than that in *P. fraasi*, having a length/width ratio of 1.50 compared with 1.27 in *P. fraasi*. In two specimens of *Apidium moustafai* from Quarry G this ratio is 1.20 and 1.38, respectively (SIMONS 1962), so the type specimen of *A. phiomense* appears to have an abnormally long M₃ compared to other specimens of *Apidium*. In fact, the difference between the ratio for the *A. phiomense* type and that for the *P. fraasi* type, 1.50 less 1.27, or .23, is well within the range of variation seen in single species of fossil primates that have been studied quantitatively. In species of *Plesiadapis*, *Nannodectes*, or *Pronothodectes*, for example, there is a range of variation in this ratio of about .29 to .33 (based on data summarized in GINGERICH 1976). Thus the range from 1.20 in YPM 18018 (SIMONS 1962) to 1.50 in AM 13370 (Tab. 2) is about the range to be expected in *Apidium*, and the type specimen of *Parapithecus fraasi* falls well within this range.

The type specimen of *Apidium phiomense* differs from the type of *Parapithecus fraasi* in having much better developed centroconids on the molars, but this too is a variable feature in *Apidium*. The type specimen of *Apidium moustafai*, for example, lacks a centroconid entirely (SIMONS 1962). The final difference, degree of occlusal wear, makes the dentitions appear more different than they would otherwise, but it is of no systematic significance. Hence, morphologically, the type specimen of *Parapithecus fraasi* lies well within the range of variation to be expected in a sample of *Apidium phiomense*.

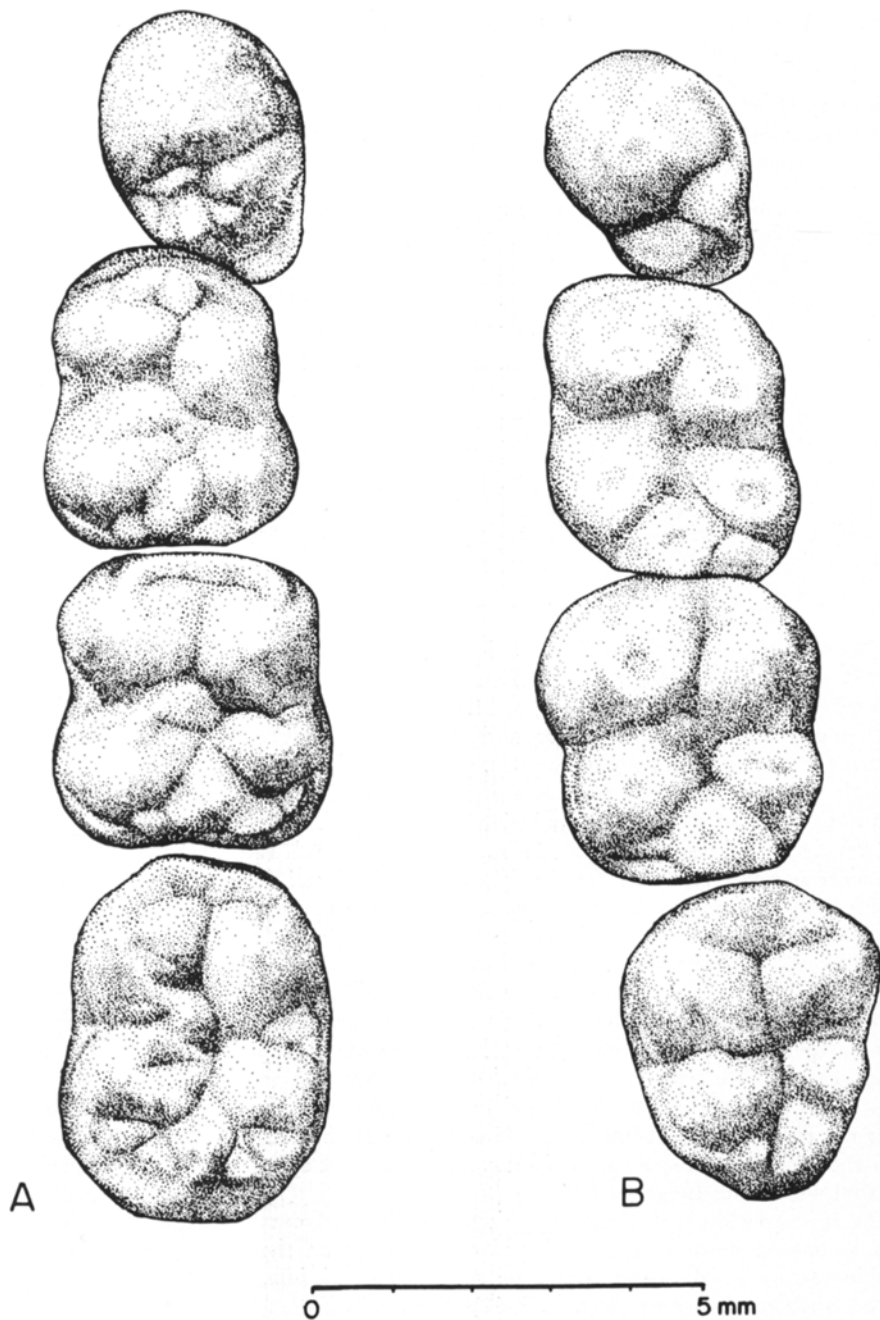


Fig. 3. Comparison of type specimen of *Apidium phiomense* (A) with comparable part of left mandible of holotype of *Parapithecus fraasi* (B). Ms of *Apidium* type drawn as if fully erupted. See Figs. 1 and 2, and text for discussion.

Early collection of Fayum primates

Considering how similar the type specimens of *Apidium phiomense* and *Parapithecus fraasi* are morphologically, the question arose as to whether they might not be specimens of the same species. It would be extremely unlikely that two specimens so similar in morphology represented different species if they came from the same stratigraphic horizon, and thus I attempted to reconstruct the history of discovery of each type specimen.

It has long been known that the type specimen of *Apidium phiomense* was collected by Richard MARKGRAF, a German-Bedouin resident of Egypt, on the upper level of the Fluvio-Marine beds of the Fayum (OSBORN 1908), or in SIMONS' terminology the Upper Fossil Wood zone (Tab. 1). Examining the archives of the American Museum of Natural History in New York, I was able to determine from letters sent by WALTER GRANGER and others that the *Apidium* holotype was one of a series of 23 specimens (most were the anthraconthere "*Ancodon*") collected by MARKGRAF northwest of Quarry A. MARKGRAF presented the specimens to GRANGER on February 17, 1907, at which time he was invited to join the American Museum's expedition working in the Fayum. MARKGRAF joined the American Museum expedition, but retained his own camels and men and continued to work independently, prospecting for new localities while GRANGER and his men worked in quarries A and B in the Lower Fossil Wood zone.

GRANGER wrote to OSBORN, in a letter dated March 25, 1907: "MARKGRAF has retained his full outfit, camels and men. He said he could not disband, on account of his agreement with them. For the work which he has been doing it has been better for him to keep his camels. He thinks now that he must leave about April 1st. Says he must get back to Cairo to attend to some business and that he may return later on in the month to look for some small things (hyraces, etc.) for Dr. FRAAS. So by another week he will probably be gone. I thought he had best continue prospecting where he is for a few days longer and then spend the remainder of his stay here searching for another 'pocket' in the upper horizon, where he obtained the small jaws before, while you were out here."

Thus MARKGRAF was clearly aware of the importance of small specimens, and he intended to collect more for FRAAS of Stuttgart in April, 1907, within only two months or so after finding the *Apidium phiomense* type.

Unfortunately, all accession records for the Stuttgart Fayum collection, and correspondence between FRAAS and MARKGRAF were destroyed in the last war. However, it is clear that MARKGRAF did return to the Fayum to collect for FRAAS as he intended, since a note published shortly afterward describes the Fayum primates in the Stuttgart collection as "von Herrn MARKGRAF 1907 gesammelten Material" (FRAAS 1911). This is the only record I have been able to locate of the time of collection of the type specimens of *Parapithecus fraasi*, *Propliopithecus haeckeli*, and *Moeripithecus markgrafi*, and it indicates almost certainly that they were collected in the spring of 1907. The desert area where the fossils were found is uninhabitable during most of the rest of the year.

Considering the rarity of small mammals in early Fayum collections, the importance attached to these by GRANGER, and the fact that MARKGRAF personally collected all four of the original primate type specimens himself, probably within the space of only two or three months early in 1907, it seems very likely that all came from the same geological horizon, the Upper Fossil Wood zone. This, plus the morphological similarity of the type specimens of *Apidium phiomense* and *Parapithecus fraasi* is very strong circumstantial evidence that the two species are synonymous.

Taxonomic implications

Synonymy of *Parapithecus fraasi* SCHLOSSER 1910 with *Apidium phiomense* OSBORN 1908 reduces the number of valid species of Fayum primates to six or seven, at least four of which come from the Upper Fossil Wood zone (Tab. 1).

The species "*Parapithecus*" *grangeri* is certainly distinct at the specific level from contemporary *Apidium phiomense* and, as outlined below, it is sufficiently distinctive to warrant separate generic status. Since the type species of *Parapithecus* is synonymous with *Apidium phiomense*, the name *Parapithecus* is no longer available and I here propose a new genus for "*Parapithecus*" *grangeri*.

Simonsius, new genus

Parapithecus (in part), SIMONS 1969b: 323; 1972: 191; 1974b: 3.

Genotype: *Parapithecus grangeri* SIMONS 1974.

Diagnosis: The one known species of *Simonsius* resembles species of *Apidium* in retaining three premolars and in the general pattern of cusps on the molars, but differs from species of *Apidium* in being larger, in having premolar metaconids medial to the protoconid rather than posteromedial, and in having higher-crowned cheek teeth (for comparison, crown height divided by length of M_1 for the relatively little worn type specimens of *Apidium moustafai*, *A. phiomense*, and "*P.*" *fraasi* are .68, .66, and .65, respectively, and the same measurement on the heavily worn type of *Simonsius grangeri* is .65 — unworn specimens would have a value of about .75 to .80 in *Simonsius grangeri*). *Simonsius* differs from the remaining Fayum genera in retaining three premolars and in its premolar morphology and molar crown pattern.

Etymology: Named for Professor E. L. SIMONS, who collected the type, in recognition of his very important contributions to our knowledge of Fayum primates and the origin of higher primates.

Discussion: Little need be added to the extensive discussion of the type species of *Simonsius*, "*Parapithecus*" *grangeri*, since SIMONS has already discussed it extensively (most recently in 1974b). It should, however, be noted that *Simonsius* is the Fayum genus most closely resembling early Cercopithecoidea, not *Apidium* (= *Parapithecus*). KAY (1977) has reaffirmed SIMONS' conclusion that cercopithecoids were derived from a *Simonsius*-related stock. However, DELSON (1975) disagrees and suggests that cercopithecoids evolved from a genus that more closely resembled *Propliopithecus*. Both arguments seem to have merit, but at the same time it must be recognized that there is a gap in the fossil record of perhaps 10 million years between *Simonsius grangeri* in the Upper Fossil Wood zone of the Fayum and earliest known cercopithecoids such as *Prohylobates* from the ?early Miocene of Wadi Moghara, another Egyptain locality. Thus either hypothesis must necessarily be tentative.

Propliopithecus and *Aegyptopithecus*

One additional implication of this new evidence regarding the first fossil primates discovered in the Fayum needs to be mentioned. Given that the type specimen of *Parapithecus fraasi* was found in the Upper Fossil Wood zone, it seems equally likely, under the circumstances, that the type specimens of *Propliopithecus haeckeli* and *Moeripithecus markgrafi* were also found in the Upper Fossil Wood zone. To date a

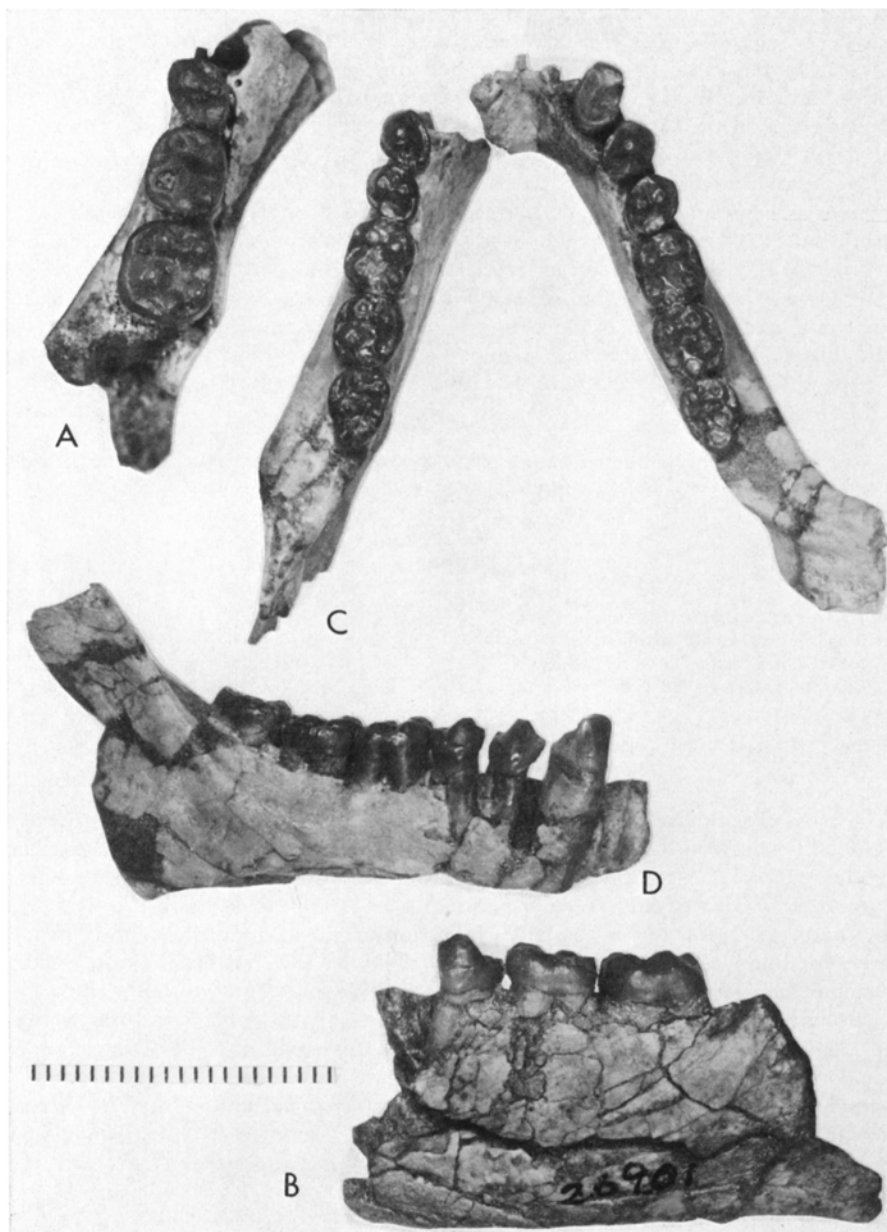


Fig. 4. Two species of Hominoidea from the Upper Fossil Wood zone, Fayum Province, Egypt. A and B Type specimen of *Aegyptopithecus zeuxis* SIMONS 1965, left mandible in occlusal and lateral view. Specimen is in Cairo Geological Museum (no. 26901). C and D Type specimen of *Propliopithecus haeckeli* SCHLOSSER 1910, left and right mandibles in occlusal and lateral view. Specimen is in Staatliches Museum für Naturkunde Stuttgart (Ludwigsburg). Figures twice natural size, scale in mm.

total of four species of early hominoid primates, each in a separate genus, have been described from the Upper Fossil Wood zone. Fortunately, the size of the first lower molar can be measured in each of these, and the measurements are listed in Tab. 3. Measurements of M_1 are used because this tooth is one of the most highly correlated with body size in primates ($r = .94$), and because it is one of the least variable of the cheek teeth. Using an approach outlined previously (GINGERICH 1974), logarithms of the length multiplied by width have been calculated to facilitate comparison of the hominoid type specimens from the Upper Fossil Wood zone. The distribution of tooth measurements in Tab. 3 shows that there are clearly two sizes of hominoids represented. *Propliopithecus haeckeli*, *Moeripithecus markgrafi*, and *Aeolopithecus chirobates* all cluster between a log M_1 value of 1.30 to 1.36, whereas *Aegyptopithecus zeuxis* is a distinct outlier at 1.50. No living primate species shows this kind of bimodality in M_1 measurements, and the differences cannot be due to any kind of sexual dimorphism. The type specimens of *Propliopithecus haeckeli* and *Aegyptopithecus zeuxis* are compared in Fig. 4.

Tab. 3. Comparison of tooth size in the type specimens of four Fayum hominoids from the Upper Fossil Wood zone. Measurements in mm.

	M_1		Log (L × W) of M_1
	Length	Width	
<i>Propliopithecus haeckeli</i> SCHLOSSER 1910	4.9	4.7	1.36
<i>Moeripithecus markgrafi</i> SCHLOSSER 1910	4.6	4.7	1.33
<i>Aeolopithecus chirobates</i> SIMONS 1965	4.7	4.2*	1.30
<i>Aegyptopithecus zeuxis</i> SIMONS 1965	6.0	5.3	1.50

* Minimum estimate using correlation of width with length for M_1 in *Aegyptopithecus*.

The most economical interpretation is that two hominoid species are represented in the Upper Fossil Wood zone, one the small *Propliopithecus haeckeli* and the other the large *Aegyptopithecus zeuxis*. The major difference between the type specimens of *Propliopithecus haeckeli* and *Aeolopithecus chirobates* appears to be in the relative size of the canine teeth, but this is possibly a reflection of sexual dimorphism and not specific difference. Almost all enamel is missing in the *Aeolopithecus* type, so its tooth morphology cannot be compared with that of *Propliopithecus* and *Moeripithecus*. The type and only specimen of *Moeripithecus markgrafi* has more inflated molars and less well-developed cingulids than *Propliopithecus haeckeli*, but this could only be a reflection of individual variation. Future discoveries may indicate that more than one species is represented, but at present it appears that *Propliopithecus haeckeli*, *Moeripithecus markgrafi*, and possibly *Aeolopithecus chirobates* are all sampled from a single species. *Aegyptopithecus zeuxis*, on the other hand, is distinctive and clearly represents a separate evolutionary lineage.

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