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## Crania of *Apidium*: Primitive Anthropeoidean (Primates, Parapithecidae) from the Egyptian Oligocene

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### ABSTRACT

Cranial remains of parapithecoid primates found in Oligocene deposits of the Fayum badlands southwest of Cairo, Egypt, are assigned to two species of the genus *Apidium*. A new partial skull confirms reference of an earlier described frontal bone to the genus and species *Apidium phiomense*. Together these two finds demonstrate that several

anthropeoidean cranial characteristics had been developed in the African parapithecoids by Oligocene times, 34 million years ago. Parapithecoida may be a sister group to Catarrhini. One partial cranium discussed here belongs to a new species described below.

### INTRODUCTION

In 1959, I published on a primate frontal with anthropeoidean characteristics that had been collected in the Fayum badlands in 1908 by Richard Markgraf and sent to the American Museum of Natural History (AMNH), New York, in early 1909 (figs. 1, 2). The exact location site of this fossil frontal, numbered AMNH 14456, is not indicated on the field label. The attached matrix appeared to be identical with that on other small fossils re-

covered by Markgraf in 1908 in an area 1 or 2 km to the northwest of the quarries named A and B and worked in 1906 and 1907 by an AMNH expedition. This would presumably put it in or near quarries I, P, or J. Because there were no other fragments associated with this nearly complete frontal, it seems that it must have been deposited in river sands as a separate bone.

Although this specimen was early identi-

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fied as a "primate," it was not announced scientifically other than in a passing reference by Gregory (1922). His sole observation was that the frontal closely resembles the corresponding bone in some of the smaller Old World monkeys. When I first noticed the frontal in 1956, its importance seemed clear. It gave the first clue that postorbital closure, a fundamental characteristic of higher primates, had been achieved by Oligocene times. Prior to this frontal's description (Simons, 1959), there was no evidence, other than through relationships suggested by dental features, that any Oligocene primate had reached the anthropoidean grade of organization.

Reference of this isolated frontal to a particular Fayum primate species was not possible because it is about the size expected for the type species of two different genera: *Apidium* and *Parapithecus*, Simons (1959). Since then, a series of expeditions to the Fayum badlands originating first from Yale (between 1961 and 1968) and then from Duke (from 1977 to date) has resulted in the discovery of hundreds of mandibles, maxillae, and postcranials of small primates, the commonest of which is *Apidium phiomense*, Osborn (1908). The type specimen of *A. phiomense*, a mandible with a fourth premolar and three molars was, like the frontal, also found by Markgraf but somewhat earlier. The original field label of this type said: "NW of Quarry [A] . . . new genus ?primate, Feb. 17, 1907, collr. R. Markgraf."

*Apidium phiomense* occurs (principally) in the upper sequence of the Fayum deposits at quarries I and M, and quarry I lies in a NW direction from quarry A. Over the years, several other isolated small primate frontals resembling that described in 1959 have been discovered in quarry I. The first of these was reported, Simons (1967), as probably being referable to *A. phiomense*. Simons subsequently (1971) described another frontal fragment found associated with separate teeth of *A. phiomense*. This find appeared to indicate, with some certainty, that the AMNH frontal and other small frontals subsequently recovered at quarry I belonged to *A. phiomense*. Even so, a temporal fragment found at the same spot with the upper teeth and the piece of frontal bone from the region of the interorbital septum, subsequently proved not

to be primate. The specimens of the then apparent association were described by Gingerich (1973). Much later Cartmill et al. (1981) reviewed additional material that included four isolated primate petrosals from quarry I. These are YPM 25972, YPM 25973, YPM 25974, and YPM 23968. The first of these is about 25% larger than the remaining three, which Cartmill et al. (1981) considered to belong to *Apidium phiomense*. In reviewing the anatomy of the petrosal in the three specimens of *Apidium*, the latter authors noted that Gingerich (1973) was correct in concluding that the carotid canal lacks a stapedia branch, resembles Anthropoidea in this regard, and differs from early tarsioids as well as most other prosimians, although they remarked that (p. 9): "certain grooves running from the carotid canal across the promontory's ventral surface may have contained caroticotympanic arteries . . . one of which may represent a vestige of the stapedia stem." The detailed discussion of Cartmill et al. (1981) emphasizes that the anatomy of several isolated petrosals is anthropoid-like and does not reveal any particular resemblance to the tarsiero-momyid group. They also show that the association of *Apidium* material cataloged under the number YPM 23968 contained a squamosal that must belong to a nonprimate, that had erroneously been labeled as part of *Apidium*. Because of this squamosal not being primate, the conclusion of Gingerich (1973) that *Apidium* had an ectotympanic that was "free and intrabullar" now lacks proof. If the isolated petrosals indeed are of *Apidium* then the ectotympanic is a simple annulus like that of ceboids and of *Aegyptopithecus*, fused to the squamosal at both ends.

Although *Apidium phiomense* is the commonest small mammal in the upper sequence of the Jebel Qatrani Formation, *Parapithecus fraasi*, another similarly sized primate species described from the Fayum early in this century by Schlosser (1911), has continued to be known only from the type specimen. Meanwhile, Simons (1974) proposed a second species of the genus, *Parapithecus grangeri*, and this species occurs with *A. phiomense* at quarries I and M. Although their molar structure is quite different, certain similarities in the dentition, such as, among an-

thropoideans, a unique central cusp on the upper premolars, show that *Apidium* and *Parapithecus* belong in the same family. In comparable parts, *Parapithecus grangeri* is about 20% larger than *A. phiomense* and, consequently, would have a frontal distinctly larger than that described in 1959 (AMNH 14456).

No specimen of *Parapithecus fraasi* has ever been found in the upper sequence localities of the Fayum and therefore the type surely came from a different, presumably lower, part of the section. Because it is both larger than would be expected for *P. fraasi* and apparently younger, the frontal described in 1959 could not belong to the type species of *Parapithecus*. The only other common larger primates at the quarry I-M level are *Parapithecus grangeri*, *Aegyptopithecus zeuxis*, and *Propliopithecus chirobates*, all of which have frontals larger than that of AMNH 14456. At quarry M there is an additional small parapithecoid—known from a single mandible—*Qatrania fleaglei*, but this animal is too small to relate to this frontal. Eliminating all these other species that differed in size and/or level of occurrence strengthens, but does not prove, the conclusion that AMNH 14456 belongs to *A. phiomense*.

In 1989, after 27 years of collecting at quarry I, a partial cranium of *Apidium phiomense*, DUCP 9867, with five attached upper molars was discovered (figs. 1, 2). This specimen has the frontal largely intact and it definitely establishes that the frontal discovered by Markgraf, AMNH 14456, indeed belongs to *Apidium phiomense* (see fig. 1). Regrettably, DUCP 9867 does not preserve the petrosal on either side and, consequently, the earlier found petrosals of *Apidium* must still be referred only provisionally.

In 1984 at quarry V, about 78 m below the I/M level, Dr. Thomas Bown of the U.S. Geological Survey, Denver, quarried out an associated frontal, partial face, and upper dentition of a new small species of *Apidium* (DPC 5264). During the 1980s, cranial parts of *Parapithecus grangeri* were also being found. At quarry I, in 1986, an associated left maxilla and frontal of *Parapithecus grangeri* (DPC 6641) were collected. Earlier at I in 1978, we had also recovered another pertinent specimen (DPC 1098), which consists

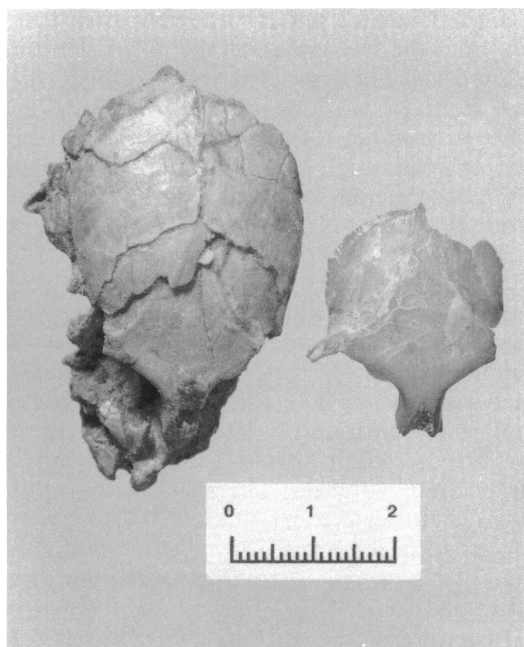


Fig. 1. Cranial remains of *Apidium phiomense*, dorsal view. Left, Duke specimen, DPC 9867; right, American Museum specimen, AMNH 14456.

of attached partial parietals that on grounds of size are assignable to *P. grangeri*. These new specimens are described below.

#### ACKNOWLEDGMENTS

I thank Friderun Ankel-Simons and Thomas M. Bown for helpful criticism during preparation of the manuscript together with H. H. Covert and P. D. Gingerich for reviewer's comments. This research was supported by several NSF grants in Anthropology, the most recent of which are BNS-85-46024, BNS-88-09776, and BNS-91-08445. Abbreviations: YPM = Yale Peabody Museum; AMNH = American Museum of Natural History; CGM = Cairo Geological Museum; DUCP = Duke University Primate Center. Photographic illustrations have been prepared by R. L. Uesry, Duke Audiovisual Services, and by the author. This is Duke Primate Center Publication No. 550.

#### DESCRIPTION

The partial cranium, DPC 9867, is slightly larger than that of the common marmoset,

*Callithrix jacchus*, and is somewhat more than  $1\frac{1}{2}$  times the size typical of the mouse lemur, *Microcebus murinus*. Anteroposteriorly, the new frontal is no longer than it usually is in the owl monkey, *Aotus trivirgatus*, but the parietals are much less broad than in the latter. Consequently, the brain volume of *Apidium phiomense* is considerably smaller than that of *A. trivirgatus*. In the palate of DPC 9867 upper teeth are preserved that confirm the assignment of this skull to *Apidium phiomense*. The teeth that remain in this skull include the left  $M^{1-3}$  and the somewhat damaged right  $M^{1-2}$ . The absolute size of these molars is considerably larger than in *Aotus* or *Saimiri*, extant primates that clearly have larger brain volumes. The molar size in this fossil is closer to those of *Callicebus torquatus*. As with *Aotus* and *Saimiri*, the brain volume of *Callicebus* is much greater than that estimated for *Apidium phiomense*.

In its present condition, DPC 9867 is 5.3 cm long from the inion to the anteriormost remaining part of the rostrum. The complete cranium would not have projected farther posteriorly and, because the face is somewhat distorted and flattened dorsoventrally, the rostrum also was probably not much longer in life, with a total anteroposterior length estimated to be from 5.5 to 5.8 cm. Relying particularly on AMNH 14556, which is more complete in the orbital region, an estimate of 2.75 cm for the maximum breadth across the orbits is plausible. It is clear from these determinations that *Apidium phiomense* had a brain volume that was only about 60 to 75% the volume of that in a modern platyrrhine such as *Callicebus torquatus* with teeth of similar size. This partial cranium shows, as does the frontal, AMNH 14556, that the dorsal margin of the orbit is relatively flat with the rather angular dorsomesial corner of each orbital opening adjacent to the interorbital septum and is structured in outline somewhat like the squared-off orbits of modern *Callicebus*. DPC 9867 is important as well in confirming that parapithecids had full postorbital closure, a fact also indicated by the postorbital plate of the frontal, AMNH 1456, although this was first reported when the latter's familial affinities were not known. Even though part of the zygomatic rim of the right orbit is broken away, much of the interior of

the eye socket is preserved. The bones have been crushed together in such a way that the exact size and position of the orbitotemporal opening cannot be determined. However, on the orbital floor, side, and back, portions of the maxillary, zygomatic, and frontal plates can be seen enclosing the eye socket. The medial wall of the orbit, with a large lacrymal foramen, is the least distorted part of the orbit. On the dorsal surface of the skull, the temporal crests, or lines, run backward from the external angular processes and converge in the midline at the fronto-parietal suture. Back of this, the interparietal suture can be followed posteriorly to the inion. The original frontal, AMNH 14556, exhibits a ledge of bone, particularly on the left side, that would have extended back under the parietal. In this region of the skull in platyrrhines, there is a frontal/alisphenoid contact, whereas in catarrhines the parietal has a sutural contact here with the jugal. Fleagle and Kay (1988) suggested that this posterior ledge, or extension of the frontal, may have achieved such a platyrrhine-like sutural contact with the alisphenoid. In DPC 9867, the right parietal is shifted forward onto the zygomatic area in such a way as to leave this possibility equivocal. The same situation obtains for AMNH 14556; consequently at present this issue cannot be resolved.

Examination of the basicranium of DPC 9867 (fig. 2) indicates that the posterior margin of the hard palate probably extended somewhat backward beyond a transverse line across the posterior sides of the third molars and graded off into the pterygoid wings. The basicranium is considerably damaged, but on the right side the glenoid fossa and the part of the squamosal at the back of the zygomatic arch are still preserved. Unfortunately, there is almost no detail left in what fragments remain of the right auditory region. This cranium (in overall view) is rather elongate compared to its breadth and, in this regard, is reminiscent of crania of *Saimiri* and *Callithrix*, in contrast to skull shape in most other living monkeys. This difference may only arise because all Miocene-Recent anthropoideans have distinctly larger brains, compared to size of teeth and overall body size.

From quarry I in the Fayum upper sequence there is a partial right maxilla and

face, DPC 6641, of *Parapithecus grangeri*, a somewhat larger relative of *Apidium*. As stated above, this specimen was directly associated with a frontal of comparable size. As mentioned from quarry I, there is also a pair of parietals that appear to belong to *Parapithecus grangeri*. Although not from the same individual as the frontal DPC 6641, these parietals, DPC 1098, articulate well with it. The internal surface of the braincase in the skull DPC 9867 is almost featureless. However, these latter two specimens show enough of the modeling of the dorsal surface of the brain to indicate some resemblance to that in *Aegyptopithecus zeuxis*. Placing the parietals together with a relatively complete mandible of *Parapithecus grangeri* makes it possible to prepare a composite reconstruction of the skull of this strangely adapted parapithecoid, which had a greatly foreshortened face (fig. 3). The original frontal of *A. phiomense* (AMNH 14556) can now be combined (similarly) with a right maxilla (CGM 26929) and mandible (YPM 21018) in order to partially reconstruct the splanchnocranium of *Apidium phiomense* (fig. 3). From these reconstructions it is clear that in both contemporaneous species from quarries I, M, and J there existed foreshortened faces, rather rectangular orbital openings, and dorsally converging temporal lines. The left maxilla of DPC 6641, *P. grangeri*, has a conjoined zygomatic bone, which contains a noticeably large zygomatic foramen. The large size of this foramen is a primitive platyrrhine or prosimianlike feature and this foramen in *P. grangeri* is comparatively much larger than in various Fayum specimens of *Aegyptopithecus* (family Propliopithecidae). The parietals here assigned to *Parapithecus grangeri*, DPC 1098, are too small to be from the two propliopithecids, *Aegyptopithecus zeuxis* and *Propliopithecus chirobates*, that are its contemporaries at quarries I and M. Hence it seems reasonable to associate them with *P. grangeri*. As arranged in figure 3, parietal architecture suggests a relatively long, low cranial vault similar to that preserved in *Apidium phiomense* (DPC 9867, cf. figs. 1, 3). The parietals of *P. grangeri* (DPC 1098) are solidly fused along the midline but are both broken off irregularly at their lateral, ventral margins. Situated anteriorly is the suture for

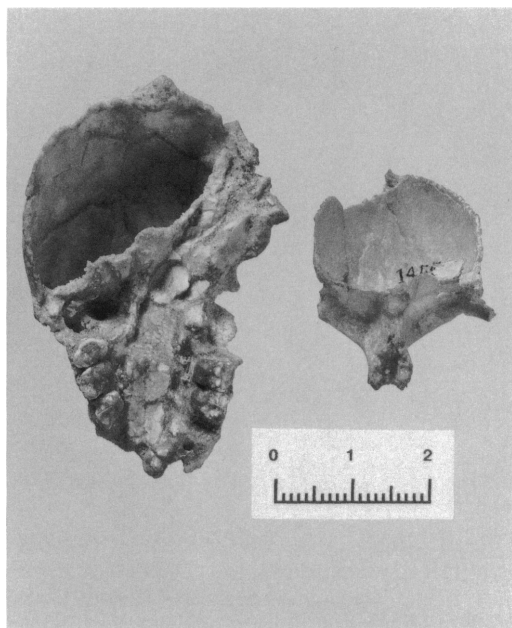


Fig. 2. Ventral view of partial skull of *Apidium phiomense*. Left, DPC 9867; right, frontal of same species, AMNH 14556.

contact with the frontal and, on its internal surface a faint imprint of the dorsal surface of the brain is preserved.

Under the orbital opening of another *Parapithecus grangeri*, DPC 6641, there is a distinct infraorbital foramen. The lachrymal bone and lachrymal foramen are both situated inside the orbit, a feature characteristic of higher primates. In this specimen the zygomatic arch rises relatively far forward, just above a line between first and second molars. The ascending external face of the maxilla is deep and rises medially to the point of contact with the nasals. There is no distinct canine fossa. Viewed from below, the palate extends medially from the root sockets of the upper P<sup>2-3</sup> to a well-developed midline suture. As far as presentation of the specimen allows, this shows that anteriorly the upper tooth rows converge markedly and are separated by a reduced transverse space, other evidence of a very foreshortened face. On the associated frontal fragment, the metopic suture is fully fused but the temporal lines have not yet quite joined where they pass off the frontal

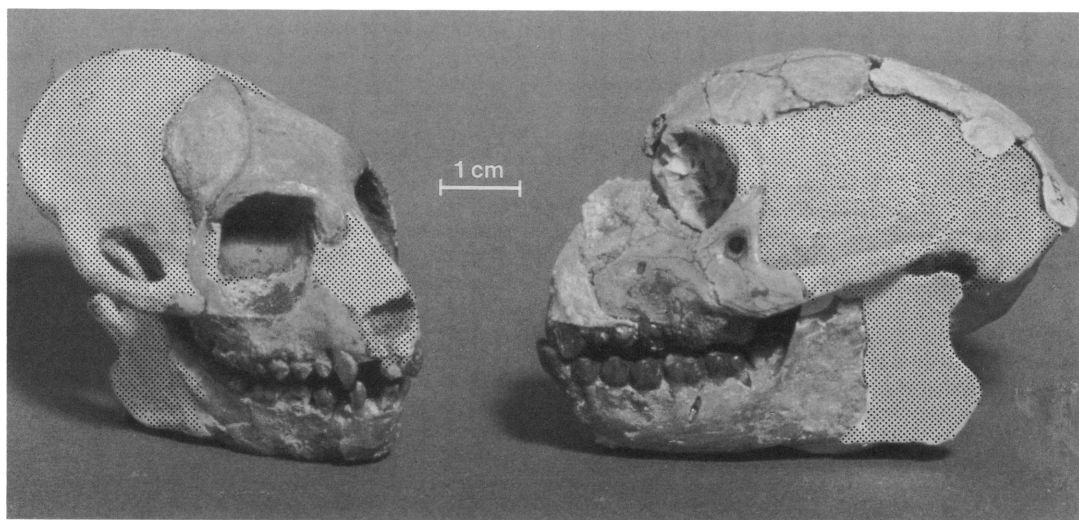


Fig. 3. **Left**, three-quarter view of *Apidium phiomense*. Composite reconstruction of skull: frontal, AMNH 14556; right maxilla, CGM 26929; mandible, YPM 21018; canine and upper incisors isolated finds. **Right**, lateral view of skull of *Parapithecus grangeri*. Composite reconstruction of skull: left anterior maxilla with canine, P<sup>3-4</sup>, DPC 2385; posterior maxilla and frontal, DPC 6641; parietals, DPC 1098; and mandible, DPC 2807.

posteriorly. *Parapithecus grangeri* has a strange adaptation, not seen in *Apidium*, in that all lower incisors have been lost, and the lower canines are the anteriormost pair of teeth. The canines are closely appressed with wear facets on their contacting mesial faces, proving unequivocally that the lower incisors are gone. This adaptation is unique among primates (see Simons, 1986), and it is not certain whether or not upper incisors existed in *P. grangeri*, as no premaxillae are known. However, occluding the upper and lower dentitions indicates that there was rather restricted space for upper incisors between the large, blunt upper canines, a condition also suggested by the very narrow anterior palate. Because of lower incisor loss (and, at the very least, incisor reduction above) the front of the face in *Parapithecus grangeri* is foreshortened, blunt and, seen from the sides, has an almost parrotlike, rounded aspect in profile. This conformation is quite unlike the condition seen in the related species *Apidium phiomense* where incisor development is like that typical of all other Anthropeidea.

*Apidium* also shows another basal anthropeoid character: the central lower incisor pair is smaller than the lateral. As in YPM

21018, figure 3, these larger lateral incisors have almost always fallen out. This is because the lateral incisors have straight, conical roots which do not hold the teeth in their sockets. Isolated teeth of *Apidium phiomense* are so common at quarry I that many upper incisors of this species have been identified. These teeth demonstrate that, as is typical of anthropoideans, the lateral incisor pair is distinctly smaller than the central. All these features combine to produce a rostrum in *A. phiomense* that is less abbreviated than in *P. grangeri*, and one that therefore looks similar to the snout of a typical marmoset.

Finally, figures 4 and 5 show the partial splanchnocranium of *Apidium* from quarry V (DPC 5264). This find belongs to a new species of *Apidium* described below. This discovery provides little additional anatomical knowledge of the cranium of *Apidium*. It does show that the posterior margins of the two nasal bones form an M like sutural outline, a condition that closely resembles the structure of this region in some specimens of *Aegyptopithecus zeuxis*. DPC 5264 also confirms the central fusion of the metopic suture originally reported by Simons (1959) for AMNH 14556.

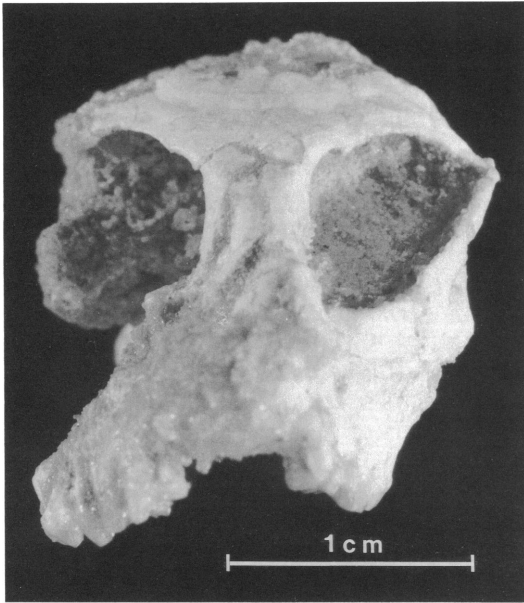


Fig. 4. Frontal view of *Apidium bowni*; preserving partial maxillae, nasals, and frontal bone, DPC 5264.

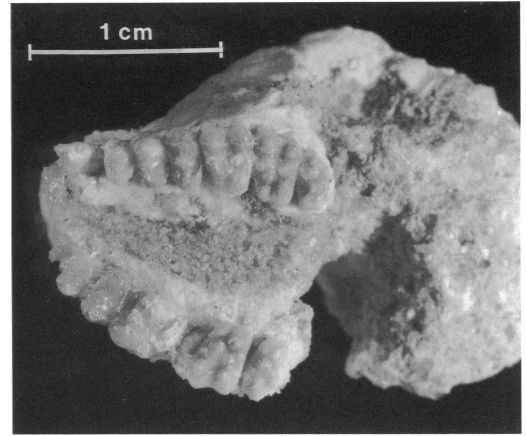


Fig. 5. View showing partial palate with upper dentition of *Apidium bowni*, DPC 5264. Specimen preserves: left canine C, M<sup>3</sup>, right P<sup>2-4</sup>, and M<sup>2-3</sup>.

## SYSTEMATICS

ORDER PRIMATES LINNAEUS, 1758

SUBORDER ANTHROPOIDEA MIVART, 1864

SUPERFAMILY PARAPITHECOIDEA, KÄLIN, 1961

FAMILY PARAPITHECIDAE, SCHLOSSER, 1911

Genus *Apidium* Osborn, 1908

**REVISED GENERIC DIAGNOSIS:** *Apidium* differs from other parapithecids in having premolars and molars that are more cuspidate than in other genera in the family—*Serapia*, *Qatrania*, and *Parapithecus*. Cheek teeth with inflated cusps; large hypocone, displacing the protocone somewhat labially toward the paracone and metacone; labial cingulum cuspidate. Lower molars typically increasing in size posteriorly or with the M<sub>2</sub> and M<sub>3</sub> subequal. Unworn lower molars with distinct centroconid in middle of the central basin. Hypoconulid of M<sub>3</sub> is normally flanked by many small cusps. *Parapithecus* differs from all other parapithecids in lacking cuspidation on tooth crowns and in having molars subequal in size, particularly M<sub>2-3</sub>. Differs from *Qatrania* in lacking large trigonid

open lingually without a premetacristid and where buccal cingulum and cetroconid are invariably lacking. Differs from *Serapia* which has P<sub>2</sub> that is larger than P<sub>3-4</sub> in having P<sub>2-4</sub> series that increases in size posteriorly.

### *Apidium bowni*, new species

Figure 4

**TYPE SPECIMEN:** CGM 42199 (DPC 8921), a right mandibular corpus with root sockets of I<sub>1-2</sub>, C<sub>1</sub>, and P<sub>2</sub>, and P<sub>3</sub>–M<sub>3</sub> complete.

**HYPODIGM:** Type and DPC 2958, 3884, 5406, 5411, and 6282; mandibular fragments with teeth; DPC 6295, right maxilla with C–M<sup>3</sup> and DPC 5264 splanchnocranium with upper dentition lacking incisors, right canine, and right M<sup>1</sup>. For comparative measurements see Appendix 1.

**LOCALITY:** Fossil vertebrate quarry V, at the 165 m level, Jebel Qatrani Formation (lower Oligocene), Fayum Province, Egypt. Considerably older than the basalt overlying this formation  $31 \pm 1$  Ma [Fleagle et al., 1986]. Recent dates for the basalt overlying the Jebel Qatrani Formation reported in Kappelman et al., 1992, that are younger than  $31 \pm 1$  are not based on samples from the lowest Jebel Qatrani basalt (contra Kappelman et al., 1992: 653) and hence do not invalidate it.

**DIAGNOSIS:** *Apidium bowni* resembles *Apidium phiomense* and *A. moustafai* and differs from species of *Parapithecus* and *Qatrania* in having distinct, well-developed centroconids on the lower molars. Differs from *Qatrania* in having relatively larger  $M^2$  and  $M^3$  compared to  $M^1$ . Differs from *A. phiomense* and more nearly resembles *A. moustafai* in that  $M^2$  is similar in length to  $M^3$ , rather than  $M^3$  being distinctly longer than  $M^2$  as is typical of *A. phiomense*. Differs from the other two species of *Apidium* in its much smaller size, being a third to a quarter smaller than average *A. moustafai* from quarry G, as well as from several specimens of *Apidium* (cf. *A. moustafai*) also found at quarry V.

**ETYMOLOGY:** Named for Thomas M. Bown who found one of the specimens, in recognition of his significant additions to our knowledge of the geology, paleontology, paleoecology, and biostratigraphy of the Fayum.

**DESCRIPTION:** The type specimen, CGM 26919 (= DPC 8921), a right mandible, is the most complete known lower dentition and is comparable with the types of all other

known parapithecoid species, all of which are mandibles. The upper dentition of DPC 5264 is more dentally complete and its choice as a type was considered but rejected because distinctions between upper dentitions have never been drawn for parapithecoids and, in fact, upper dentitions are either not known, or incompletely known in five of the eight parapithecoid species, namely in *Parapithecus fraasi*, *Qatrania wingi*, *Qatrania fleaglei*, *Serapia eocaena*, and *Apidium moustafi*.

The type specimen shows detailed anatomy of the five posterior teeth as well as the root sockets of the right side. The right mandible seems to have separated, in this case, at or about the midline suture. Numerous other finds of *Apidium* show that the mandibular suture is fused even in subadult individuals. CGM 26919 shows clearly the comparatively large size of  $M_{2-3}$  relative to  $M_1$  that typifies this species. The molar centroconids, although distinctly discernible, are not as clearly defined as in DPC 3884, DPC 5406, DPC 5411, and DPC 6282, probably because the type has suffered some abrasion to the teeth, and may also be of a somewhat older individual with more advanced tooth wear.

## DISCUSSION AND CONCLUSIONS

The parapithecoids discussed here are a group of anthropoideans that in Africa had reached the "monkey" grade of organization with postorbital closure and metopic and symphyseal fusion. The arrangement of bones at the back of the jugal may be closer to that of Platyrrhini than of Catarrhini. No speci-

mens of *Apidium* or any other parapithecoid yet known definitely establish the construction and placement of the ectotympanic. Simons and Kay (1988) and Fleagle and Kay (1988) have discussed in detail the status of knowledge of the relationships of parapithecoids to other primates.

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APPENDIX 1  
Comparison of Representative *Apidium phiomense*, and *A. moustafai* with *A. bowni*

			Measurements (mm)			
			Length	Breadth	Trigonid	Talonid
DPC						
<i>A. moustafai</i>	10705	C	3.22			
		P <sub>2</sub>	2.85	2.18		
		P <sub>3</sub>	3.03	2.15		
		P <sub>4</sub>	2.79	2.51		
		M <sub>1</sub>	3.39		2.83	2.97
		M <sub>2</sub>	3.42		3.12	3.10
		M <sub>3</sub>	3.4e			3.00
<i>A. moustafai</i>	8707	P <sub>3</sub>	2.4	1.78		
		P <sub>4</sub>	2.86	2.09		
		M <sub>2</sub>	3.68		2.71	2.66
		M <sub>3</sub>	3.61		2.52	2.07
<i>A. moustafai</i>	3830	P <sub>4</sub>	2.69		2.40e <sup>a</sup>	
		M <sub>1</sub>	3.18		2.50e	2.50e
		M <sub>2</sub>	3.57		2.80	2.83
		M <sub>3</sub>	4.10		2.90	2.69
<i>A. moustafai</i>	5670	P <sub>4</sub>	2.44	2.37		
		M <sub>1</sub>	—		2.54	—
		M <sub>2</sub>	3.78		2.97	3.08
<i>A. bowni</i>	3884	P <sub>4</sub>	2.07	1.78		
		M <sub>1</sub>	2.82		2.18	2.36
		M <sub>2</sub>	2.87		2.47	2.34
		M <sub>3</sub>	2.87		2.28	1.75
<i>A. bowni</i>	5406	M <sub>2</sub>	3.07		2.33	2.12
		M <sub>3</sub>	2.96		2.12	1.95
<i>A. bowni</i>	2958	C	2.00	1.80		
		P <sub>2</sub>	1.75e	1.35		

APPENDIX 1—(Continued)

		Measurements (mm)			
		Length	Breadth	Trigonid	Talonid
<i>A. bowni</i>	5411	P <sub>3</sub>	1.50e	1.55e	
		P <sub>4</sub>	2.10e	1.70e	
		M <sub>2</sub>	2.97	2.30e	2.26
		M <sub>3</sub>	2.70	2.25	1.85
<i>A. bowni</i>	8921	P <sub>3</sub>	1.95	1.62	
		P <sub>4</sub>	2.20	1.94	
		M <sub>1</sub>	2.68	2.10	2.24
		M <sub>2</sub>	2.82	2.46	2.43
		M <sub>3</sub>	3.02	2.36	2.1
<i>A. bowni</i>	6282	P <sub>3</sub>	2.2	1.45	
		P <sub>4</sub>	2.12	1.73	
		M <sub>1</sub>	2.81	1.85	2.20
		M <sub>2</sub>	3.12	2.65	2.50
		CGM			
<i>A. bowni</i>	26919 <sup>b</sup>	P <sub>3</sub>	1.97	1.58	
		P <sub>4</sub>	2.07	1.92	
		M <sub>1</sub>	2.66	2.12	2.23
		M <sub>2</sub>	2.69	2.44	2.35
		M <sub>3</sub>	3.03	2.35	1.85
<i>A. phiomense</i>	20905	YPM			
		P <sub>3</sub>	2.64	2.06	
		P <sub>4</sub>	2.65	2.20	
		M <sub>1</sub>	3.51	2.60	2.64
		M <sub>2</sub>	3.45	3.0	2.85
<i>A. phiomense</i>	20914	M <sub>3</sub>	3.45	2.89	2.54
		P <sub>3</sub>	2.48	2.0	
		M <sub>1</sub>	3.26	2.52	2.42
		M <sub>2</sub>	3.25	2.71	2.46
		M <sub>3</sub>	3.13	2.52	2.11
<i>A. phiomense</i>	20911	P <sub>2</sub>	2.32	2.48	
		P <sub>3</sub>	2.58	2.32	
		P <sub>4</sub>	2.81	2.52	
		M <sub>1</sub>	3.52	2.8	2.75
		M <sub>2</sub>	3.54	3.09	3.15
<i>A. phiomense</i>	20920	P <sub>3</sub>	2.59	2.05	
		P <sub>4</sub>	2.74	2.37	
		M <sub>1</sub>	3.73	2.85	2.89
		M <sub>2</sub>	3.8	3.24	3.0
		M <sub>3</sub>	3.75	3.03	2.51
	20911	P <sub>2</sub>	2.32	2.48	
		P <sub>3</sub>	2.58	2.32	
		P <sub>4</sub>	2.81	2.52	
		M <sub>1</sub>	3.52	2.8	2.75
		M <sub>2</sub>	3.54	3.09	3.15

<sup>a</sup> e = estimate.  
<sup>b</sup> Type was DPC 8921.



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