An Anthropoid Frontal Bone from the Fayum Oligocene of Egypt: the Oldest Skull Fragment of a Higher Primate

By Elwyn L. Simons¹

INTRODUCTION

Recent preparation and study of an almost complete frontal bone of a primate from the Fayum deposits of Egypt in the collections of the American Museum of Natural History indicate that it is a member of the Order Primates and of the Suborder Anthropoidea. Hence the specimen, which is of early Oligocene age, is the oldest known fragment of an anthropoid skull. The bone is complete enough to show that the orbital cavity was entirely closed behind, a character that, among all living and fossil Primates, occurs only in the Anthropoidea and that apparently does not exist in other mammals.

In addition to postorbital closure, the Fayum primate has a vertically deepened fore brain and a foreshortened muzzle, all advanced characters for the order not previously known to have existed in the Oligocene epoch. These features, however, confirm structures which one would theoretically expect to see in such an ancient anthropoid.

ACKNOWLEDGMENTS

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regarding provenance of the specimen and of Mr. Chester Tarka for making the photographs included here is gratefully acknowledged. Miss C. M. Court of the Department of Human Anatomy at Oxford University drew figures 2 and 4.

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ABBREVIATIONS OF INSTITUTIONS CITED

A.M.N.H., the American Museum of Natural History
B.M.N.H., British Museum (Natural History)
M.C.Z., Museum of Comparative Zoology at Harvard College
P.U.O.C., Princeton University (Osteological Collection)

HORIZON AND LOCALITY

Fluvio-marine formation, early Oligocene, Fayum, Egypt.

DISCUSSION

The Fayum primate frontal bone was collected by Richard Markgraf northwest of the quarries worked (1906–1907) by the American Museum of Natural History field parties. It was found by him in 1908 and sent to the American Museum early in 1909. Markgraf, a professional collector living in Cairo during the early part of the present century, worked with the American Museum expeditions of 1906 and 1907 and also recovered part of the primate and other vertebrate fossils at the Stuttgart Museum described by Schmidt (1913), Schlosser (1911), and others. His skill in locating the smaller mammalian fossils is noted in contemporary reports. The quarries developed by the American Museum near the locality of this fossil are to the north of Birket-el-Qurun, a brackish lake, about 50 miles southwest of Cairo.

The Egyptian fluvio-marine formation is considered to be of early Oligocene age (Osborn, 1936). The primate frontal apparently came from the upper part of the formation. Osborn (1908) lists the following fauna from these upper beds:

Arsinoitherium sp. indet.
Metaphiomys beadnelli
Apidium phiomensis (sic)
Apterodon macrognathus
Ancodon (?) minus
?Geniohyus
Megalohyrax eocaenus
The frontal bone, A.M.N.H. No. 14556, was in a loosely consolidated quartz arenite, identical in appearance with that adhering to several other small fossils recovered by Markgraff in 1908 in the area to the west and north of the American Museum quarries. Field records do not indicate how far to the northwest of the quarries the bone was found, but its recovery from the fluvio-marine formation was not questioned, and the quartz associated with this specimen is typical of the formation. Matrix recovered with the frontal bone consists of about 95 per cent quartz grains (mostly rounded and polished), a few iron-stained granules, and with virtually no cementing material. Such a delicate bone, which shows few signs of abrasion, could not have been transported very far before burial. Dissociation from the rest of the skull may have taken place before the specimen was deposited, as no other fragments that could possibly belong with it were collected. The specimen was early identified as "?primate," but because several loose fragments pertaining to the orbital plates of the frontal were not attached until recently, its anthropoid status could not then have been maintained with any certainty. A reference, evidently to this specimen, was made by Gregory (1922, p. 289) who remarked that it "resembles closely the corresponding part of some of the smaller Cercopithecinae."1

DESCRIPTION
SIZE OF THE SPECIMEN

Comparison of this small primate with the Old World anthropoids is rather difficult, because other fossil and recent cercopithecoid, pongid, and hominid skulls are larger. The frontal bone, A.M.N.H. No. 14556, is a little bigger than that of the Common Marmoset, Callithrix [Hapale] jacchus, and in most features indicates a similar degree of advance over the Eocene lemuroids and tarsioids. An apparently primitive feature is the midline convergence of the temporal ridges, as in Notharctus, Hemiacodon, and Necrolemur. Nevertheless, these ridges are not nearly so distinct as in the latter Primates, and the frontal expansion above the orbits is somewhat greater, being broader (with reference to the size of the skull) than in the ceboids. A more closely comparable size, and (with less certainty) a similar degree of evolutionary advance, have led to the principal comparisons

1 For further references on the fauna and sedimentology of the Fayum early Oligocene of Egypt, see Schmidt (1913, p. 110), Matsumoto (1926, p. 110), and Osborn (1936, p. 761).
of the Fayum anthropoid frontal that are made here with ceboïd skulls. Such comparisons should not be taken as an indication of a close phyletic relationship between the Fayum specimen and the South American monkeys. To date, there is no basis for assuming that any ceboïds ever occurred in the Old World.¹

Present knowledge of the rise of the Anthropoidea begins with specimens from the early Oligocene beds of the Fayum, Egypt, thought to be about 35 million years old. Parts of four lower jaws with teeth from these deposits have heretofore been referred to the Order Primates. The least well known of these is Moeripithecus markgrafi Schlosser, based on a type with only the lower m1–2 and a part of the horizontal ramus preserved. Its taxonomic position is uncertain. A second form, Propliopithecus haeckeli Schlosser, of about the same size (that of a small gibbon) is known from a specimen which retains the c–m3 of both sides, much of the horizontal ramus, and parts of the coronoid processes. This primate jaw (which is much too large to belong with the frontal described here) is widely accepted as belonging to a true pongid. Nevertheless it is a very generalized form. The p3 and p4 do not exhibit the heterodont condition seen in pongids, nor is the p3 larger than the p4, as is elsewhere the case in this family. A third primate, Apidium phiomiense Osborn, is known from a lower left jaw fragment containing p4–m3. The last and most completely known of the Fayum Primates is Parapithecus fraasi Schlosser. This specimen consists of both sides of the mandible, preserved largely intact, with all the lower teeth except for the third antemolar tooth of the right side. These latter two mandibles indicate a body size comparable to that of the Golden Marmoset, Leontocebus [Leontopithecus]. As there has been prolonged disagreement about the taxonomic positions of Apidium and Parapithecus, they are discussed in more detail in the following pages. Present evidence regarding the foregoing forms does not suggest that the Anthropoidea (as currently defined) existed as a distinct taxon much before the late Eocene.

Apparently the Fayum primate frontal is about the size to be ex-

¹ Ceboïd relationships for Amphipithecus from the Eocene of Burma have been suggested. Such a relationship is most implausible and is based apparently on the sole observation that this primate has three lower premolars. A higher premolar count for the ancestors of the Old World Anthropoidea must be assumed, in any event, and at least two European Eocene Primates, Caenopithecus and Protoadapis, have long been known to possess three premolars below. Consequently, there is no need to imagine that there were Old World ceboïds because of the dental formula of Amphipithecus.
pected for *Parapithecus* (or, equally, *Apidium*) as is suggested by the measurements in table 1. *Apidium* is not included in the table because the length of the mandible cannot be determined.

### TABLE 1

**Comparative Measurements (in Millimeters) of Two Ceboids and Two Fayum Primates**

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td><strong>Maximum length</strong>&lt;br&gt;from alveolar border beneath incisors to back of condyle</td>
<td>35.5</td>
<td>29.0</td>
<td>36.0</td>
<td>—</td>
</tr>
<tr>
<td><strong>Depth of jaw</strong>&lt;br&gt;beneath m2</td>
<td>7.0</td>
<td>6.0</td>
<td>7.4</td>
<td>—</td>
</tr>
<tr>
<td><strong>Maximum width</strong>&lt;br&gt;of frontal across supraorbital border</td>
<td>26.5</td>
<td>24.0</td>
<td>—</td>
<td>27.6</td>
</tr>
<tr>
<td><strong>Greatest postorbital width of frontal</strong></td>
<td>23.0</td>
<td>23.0</td>
<td>—</td>
<td>22.3</td>
</tr>
<tr>
<td><strong>Least width of rostrum between orbits</strong></td>
<td>6.2</td>
<td>5.4</td>
<td>—</td>
<td>5.9</td>
</tr>
</tbody>
</table>

### Rostrum

**Figures 1, 2**

On the dorsal surface of the preserved portion of the rostrum can be seen the nasofrontal sutures which come to a point 2 mm. short of the medial extremities of the supra-orbital ridges. Consequently, the nasals had no posterior expansions as in some lemuroids. In a vertical plane between these sutures is the anterior edge of the nasal spine of the frontal. The maxillofrontal suture, ending dorsally in an S-shaped curve, is present on the left anterior extremity of the rostrum. This position of the maxillofrontal juncture demonstrates that there was no contact between the lacrimal and the nasal, which is sometimes the case in living lemurs and ceboids. As can be seen in
Fig. 1. Frontal bone of A.M.N.H. No. 14556. A. Dorsal view. B. Right lateral view. For key, see figure 2. Approximately ×2.75.
Fig. 2. Key to figure 1. Abbreviations: Eap, external angular process; Ec, anterior and posterior ethmoidal canals; F-ps, area of frontoparietal suture; M-fs, maxillofrontal suture; N-fs, nasofrontal suture; S-om, supra-orbital margin; Tc, temporal crest; Vf, venous foramen; Z-fs, zygomaticofrontal suture.
table 1, the interorbital width, when compared to the maximum breadth of the frontals (in the region of the supra-orbital margins) is smaller relatively than in some ceboids. This fact, together with the general appearance of the remaining portion of the rostrum, suggests a much foreshortened face, comparable to that of Callithrix or Tarsius.

**Orbit**

The parts of the orbital cavities preserved indicate an orbit that is larger than in ceboids of the same approximate size. The degree of forward direction of the orbits is a little less than in Leontocebus, judging from the angle between the midline of the skull and the main axis of the supra-orbital margin (see table 2). Along the center this margin is rather straight, but near the rostrum and the end of the external angular process there are rather sharp downward bends—a condition not unlike that seen in some skulls of Notharctus and Smilodectes, and, to a lesser extent, in the marmoset skull. Clearly, the parts preserved here do not indicate a smoothly rounded orbit such as that of Nycticebus and Tarsius. Nor is the orbit large enough relative to the rest of the frontal to give any suggestion of nocturnal habits in the Fayum anthropoid. On the anteromedial wall of the orbit under the median end of the supra-orbital margin is a large foramen. This connects with the sagittal venous sinus.1 Two small openings on the medial orbital wall of the right side (the left is not preserved in this area) are presumably the anterior and posterior ethmoidal canals (see fig. 2B). In the vertical dimension the orbital plate is quite deep, and at its ventral margin (a broken surface) no indication remains of the optic foramen. A part of the back wall of the orbit near the ventral margin projects, on the right side, almost to the midline of the skull and thus indicates that the interorbital septum was quite thin—a condition that distinguishes this form from all the known Eocene primate crania, with the possible exception of those of Necrolemur, Pseudoloris, and Tetonius. On the lateral wall of the orbital aperture of A.M.N.H. No. 14556 is a deep groove run-

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1 It appears that in man and the anthropoid apes the sagittal venous sinus at its anterior end receives a small vein from the nasal cavity through a median aperture (the “foramen caecum”). In the lower Primates, and in mammals generally, the beginning of the sinus is formed by bilateral tributaries which connect with intraorbital veins through openings perforating the dorsomedial wall of the orbital opening.
ning vertically and turning medially at its dorsal end. This condition is not to be observed so clearly developed in other Primates, living or fossil, but there is a suggestion of a similar trough in some marmosets.

Perhaps the most interesting feature to be observed on this specimen is the very rugose sutural area running along the edge of the lateral extremity of the orbital cavity from the most ventral part preserved up to, and across, the external angular process of the frontal. This suture can be interpreted only as a zygomaticofrontal contact. It indicates that the orbital cavity was completely enclosed laterally by an orbital plate of the zygoma.

**Dorsal Surface of the Frontal**

**Figures 1, 2**

The temporal crests of the frontal run backward on each side from the region of the external angular processes and converge to the midline at the frontoparietal suture. Between these crests and the dorsal margins of the orbit is a slightly depressed central area. There is no evidence of a central suture of the frontal, but a postmortem crack slightly to the left of the midline runs posteriorly from the apex of the nasofrontal sutures. This is not to be mistaken for an interfrontal suture. About 4 mm. medial to the right tip of the external angular process and just behind the temporal crest is a small foramen. There are also numerous small foramina scattered in the area of the anterodorsal part of the frontal.

A reasonably accurate index of the forward direction of the orbits in fossil Primates can be calculated by measuring the angle between the midline of the skull and a line drawn along the supra-orbital margin. The greater the angle the more anteriorly directed is the orbital aperture. For fossil Primates this index is particularly useful for two principal reasons. First, the facial region, including the orbital apertures, is often much crushed or missing; this is less often the case with the anterodorsal part of the frontal which includes the supra-orbital margins. Second, in the known Eocene and Oligocene Primates the supra-orbital border is usually disposed in a straight line, facilitating measurement of this angle, and unlike the semicircular margin of the orbit above seen in most modern anthropoids and in Prosimii such as *Nycticebus* and *Tarsius*. In table 2 this angle is listed for several living and fossil Primates, including the Fayum primate frontal.

Along the right posterior margin of the frontal can be seen a broad sutural area for the articulation with the parietal. This area is about
FIG. 3. A. Endocranial cast of anterior part of brain of A.M.N.H. No. 14556, dorsal view. B. Endocranial cast of anterior part of brain of Callithrix. For key, see figure 4. Approximately $\times 3$. 
A

Fig. 4. Key to figure 3. Abbreviations: Isc, internal sinus canal; ob, olfactory bulb; Of, olfactory fasciculus.
as broad transversely as in specimens of Callithrix jacchus observed. At the posterior tip of the bone is a short central spine. The postero-dorsal surface of the frontal is broadly expanded, with no suggestion of a ventral recurving of its edges. One can assume, therefore, that the posterior part of the brain case was large.

**BRAIN**

Figures 3, 4

The vertical expansion of the frontal lobes can be indicated for the Fayum primate by measuring the angle between the floor of the brain immediately behind the fossae for the olfactory bulbs and the internal surface of the frontal above the fore brain. In A.M.N.H.

<table>
<thead>
<tr>
<th>TABLE 2</th>
<th>ANGLE BETWEEN AXIS OF SUPRA-ORBITAL MARGIN AND MIDLINE OF SKULL IN SOME LIVING AND FOSSIL PRIMATES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nicrolemur, B.M.N.H. Nos. M-4490, M-3747</td>
<td>43°</td>
</tr>
<tr>
<td>Notharctus, A.M.N.H. No. 11466</td>
<td>48°</td>
</tr>
<tr>
<td>Adapis, B.M.N.H. No. M-4669</td>
<td>49°</td>
</tr>
<tr>
<td>Lemur, P.U.O.C. No. 22</td>
<td>51°</td>
</tr>
<tr>
<td>Fayum frontal, A.M.N.H. No. 14556</td>
<td>55°</td>
</tr>
<tr>
<td>Leontocebus, P.U.O.C. No. 198</td>
<td>61°</td>
</tr>
<tr>
<td>Callithrix, P.U.O.C. No. 487</td>
<td>68°</td>
</tr>
<tr>
<td>Macaca, P.U.O.C. No. 195</td>
<td>80°</td>
</tr>
</tbody>
</table>

No. 14556 the angle here is about 60 degrees, but in Callithrix it is usually around 40 degrees. Part of this difference is the result of the much greater expansion of the orbital fossae posteriorly in the South American form. When the orbital plate is held at the same angle from the horizontal, as it typically is in ceboids and cercopithecoids, a much higher skull vault is indicated than is common in the latter groups. In place of the juga cerebralia of the anteromedial floor of the frontal fossa, seen in man and in other anthropoids, A.M.N.H. No. 14556 has only a gently rounded and raised area. Further, instead of a median ridge along the attachment of the falx cerebri there is only a shallow groove in this position, ending near the rostral margin of the posterior opening into the olfactory fossa.

1 Ateles may be exceptional in this regard; the frontal in some individuals of this ceboid is considerably vaulted. Elsewhere among the Primates this degree of frontal vaulting occurs primarily in pongids and hominids.
Above this opening are the two foramina for the internal sinus canals. Relative to the volume of the frontal lobes the olfactory bulbs are greatly reduced, in sharp contrast to such Eocene Primates as *Adapis* (see Le Gros Clark, 1945, p. 1) and *Necrolemur* (see Hürzeler, 1948, p. 33). Unlike the condition in *Tarsius* (in which there is only a single fasciculus on each side), the olfactory nerve bundles passing in through the cribiform plate are multiple. An endocast of the Fayum frontal bone shows that in this position there are at least three paired nerve bundles. Frontal convolutions are not evident but if present they would presumably have been concealed by the dura mater, as in *Callithrix* (see figs. 3 and 4). In the endocast of the Fayum primate a few blood vessels can be traced near the frontoparietal suture. Moreover, a recurving of the right lateral and ventral extremity of the cast presumably indicates the Sylvian fissure, a distinctively primate character.

**Post-cranial Skeleton**

A right calcaneum, A.M.N.H. No. 14607, from the fluvio-marine beds (upper level) has also been located. This bone seems more like that of a primate than the bones of members of the other mammalian orders present in the Fayum beds. It is about the size of that of *Leontocebus* and agrees well in structure with calcanea of *Notharctus* and *Adapis*.

**Conclusions**

A taxonomic reference of this specimen cannot be made at present, but the size of the frontal from the Egyptian early Oligocene is about that estimated for *Apidium* or *Parapithecus*, insofar as this can be judged. Clearly, this skull fragment indicates that there were anthropoids smaller than *Propliopithecus* in Egypt during the time the Fayum beds were being deposited, hence reinforcing the primate status of those two smaller forms from these beds, *Apidium* and *Parapithecus*, the reference of which to this order has recently been questioned by Piveteau (1957) and Hürzeler (1958). Even the taxonomic position of *Propliopithecus* is rendered less equivocal by this specimen, for, although its pongid status has seldom if ever been challenged, there was formerly no actual evidence that any definitively anthropoid cranial characters had been attained in the early Oligocene.

An examination of the type of *Apidium phiomiense*, A.M.N.H. No. 13370, at the American Museum has recently been made and there does not seem to be a good case for its having affinities with *Phe-
nacodus as suggested by Hürzeler (1958, p. 32). Phenacodus has a sub-molariform lower fourth premolar, an unbroken crista obliqua on the lower molars, and lacks the separate cusp between protoconid and entoconid of m2, which is particularly distinct in both Apidium and Oreopithecus. The only other Primates which have any suggestion of this cusp, and in them its existence is doubtful, are Pliopithecus, Dryopithecus, and Gigantopithecus.

In spite of the great time separation between Apidium and Oreopithecus, there are many interesting similarities between these genera in cusp patterns of the lower teeth which the writer will treat at greater length elsewhere, but a few points are relevant here. The almost complete correspondence between the molar cusps of these two forms was pointed out by Gregory long ago (1922, pp. 286–288). Both exhibit a central molar cusp between the protoconid and entoconid which can be called a mesoconid or centroconid—a most unusual feature among Primates. Further, they agree in the striking increase in lower molar size from front to back and in showing a fairly pronounced constriction between the trigonid and talonid of m1 and m2. Almost every cuspule on the large and complex m3 of Apidium can be homologized with a similar structure in Oreopithecus third lower molars. As Gregory observed, there is also a slight suggestion of an incipiently bilophodont p4 in Apidium. Moreover, although the teeth anterior to p4 are missing, one can see that the antero-internal extremity of the horizontal ramus begins to turn medially towards the symphyseal area at about the anterior margin of p4, thus strongly suggesting that this animal had a reduced number of premolars.

Apidium was recovered from the upper levels of the fluvio-marine formation, and this also appears to be the stratum from which the frontal bone here described was collected. Hence, some probability for an assignment of the frontal to Apidium exists, particularly when taken together with the size of the mandibular fragment of the latter. Insofar as size is relevant, this is also true for Parapithecus, which, however, may be a little large, the depth of the mandible under m2 being 7.4 mm. For Apidium the corresponding measurement is 7.2 mm., and in both genera the anteroposterior length of lower m1–3 is 13.4 mm. However, the Parapithecus dentition appears somewhat less anthropoid than that of Apidium and is, almost certainly, from slightly earlier deposits than the skull fragment.

Until the current study of Parapithecus fraasi being undertaken by Dr. J. Kälin of Fribourg, Switzerland, is published, it is not advisable to comment extensively on the taxonomic position of this
species. However, even if it does have a lower dental formula of 1.1.3.3., as originally suggested by Schlosser (1911) and recently by Piveteau (1957, p. 167), this in itself does not indicate that the form is not a primate, for such a formula would be consonant with that expected for an Oligocene primate of tarsioid affinities. It is unlikely that any final judgment as to whether the second or third tooth in the dental series of Parapithecus is the true canine can be reached at present. The second incisor and canine of Callithrix, for example, are subequal in size and have the same basic conformation. Consequently, it is largely by extrapolation from the upper dentition and the dentitions of other ceboids that they can be identified with certainty in this New World primate. In the current state of knowledge such extrapolations cannot be made for Parapithecus, but there are two undoubted Primates from Eocene deposits in Europe, Caenopithecus and (with less certainty) Protoadapis, that have a lower dental formula of 1.1.3.3. There is little in the cusp patterns and jaw structure of Parapithecus to suggest that it is not a primate. Typical condylarths never have such a reduced number of antemolar teeth, and, as mentioned above, the resemblance of some of the Condylartha (such as Phenacodus and Hyopsodus) to Primates is marginal at best. Nothing is resolved by a reference of Parapithecus to this group of protungulates. It can now be concluded, however, that Parapithecus is not very close to the hominid stem, as has sometimes been maintained. Actually, Parapithecus shows some similarities to the Eocene tarsioids and a few possible features of resemblance to anthropoids. Perhaps it is mainly because this species occurs in the Oligocene “dark ages” of primate history that it is difficult to find exact analogies in other forms for its dental patterns.

The convergence of the tooth rows to a point anteriorly in Parapithecus has frequently been mentioned as a similarity to Tarsius. This sort of lower tooth arrangement is unusual among Primates, but it is also to be seen in Callithrix. As the latter two genera also have very much foreshortened muzzles there may be a correlation between a short rostrum and sharply converging tooth rows. If this is so, the narrow rostrum between the orbits of the Fayum primate frontal would also agree well with the mandibular conformation of Parapithecus.

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SCHMIDT, M.

STEHLIN, H. G.