Description of two genera and species of Late Eocene Anthropoidea from Egypt

(Catopithecus/Proteopithecus/Oligopithecus/primate evolution/earliest anthropoidea)

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ABSTRACT In 1987 and 1988 fossils of two previously unknown genera and species of Egyptian early Tertiary Anthropoidea were discovered in the Fayum Depression of Egypt. These are much older than all other Fayum, Oligocene primates and are believed to be Eocene in age. These genera, here named Catopithecus and Proteopithecus, come from a new Fayum site, L-41, and resemble Oligopithecus from the Jebel Qatrani Formation (lower sequence) at quarry E. They are here placed with the latter in a subfamily, Oligopithecinae, that is ranked in the Propriopithecidae. The level of L-41 is separated from Quarry E by at least one major unconformity and 47 m of section. Only a maxilla of Proteopithecus is known. Its molars and premolars resemble those of later Fayum Propriopithecus and Aegyptopithecus and do not resemble those of Apidium and Parapithecus, all of which come from the Jebel Qatrani Formation, upper sequence. The type specimen of Catopithecus confirms a lower dental formula of 2-1-2-3, as in Catarrhini. These species appear to be the oldest primates undoubtedly related to humans. Their dental anatomy points to a derivation of Anthropoidea from Eocene adapids.

The Jebel Qatrani Formation of the Fayum Province, Egypt, is the only region in the world that has yielded a diverse Oligocene primate fauna. This fauna, found between 1907 and 1988, comes from a sequence of quarries distributed through about 340 m of sediment and a time period of several million years. There are two main faunal zones in the Fayum that have been termed the lower and upper sequences (1). The vast majority of species totaling nearly a thousand specimens of Fayum primates have come from the upper sequence. A basin lying immediately above the upper sequence has been dated at 31 ± 1 million years (2). The basin lies on a major unconformity and below this there is a 100-m-thick portion of the Jebel Qatrani Formation between the basin and the uppermost level yielding primates; consequently the uppermost Fayum primates are perhaps more than 32 million years old. These include the well-known genera Propriopithecus, Aegyptopithecus, Apidium, and Parapithecus. Most of these fossils come from quarries I and M at about the 240-m level in the upper sequence. Primates from the lower sequence are much less well known, and only about 20 specimens including isolated teeth have been found. Previous to this paper they have only been reported from Quarry E, at about the 94-m level in the lower sequence (3-5).

Persistent searching in the upper Eocene Qasr el Sagha Formation that underlies the Jebel Qatrani Formation and in the lowest 94 m of the Jebel Qatrani Formation during a 27-year time period involving 19 field expeditions and countless man hours of collecting failed to find any primates below the level of Quarry E. In 1983 a new locality termed Locality-41 (L-41) was discovered in a green shale unit of the lower variegated beds at about the 47-m level of the Jebel Qatrani Formation. There is a major erosional unconformity above this shale that makes the actual stratigraphic separation of it from Quarry E impossible to calculate, but the fauna at L-41 is very different from the lowermost previously known primate fauna of the Fayum (Quarry E). All the mammals so far found in L-41 are more primitive than previously known species and all appear to differ from later Fayum forms at either the specific or generic level. For a variety of reasons, the fauna of L-41 may be of Eocene age. The question whether all of the Fayum beds or at least the lower sequence there is of Eocene age has been discussed from time to time, most recently by Rasmussen and Simons (6). Now that we know that the upper quarries of the Fayum are 4 or 5 million years older than was previously believed, an Eocene age for the lower part of the Formation seems highly probable. The assemblage and sedimentology at L-41 are unique. The site is unusual for the extremely high number and diversity of hyraxes found in it, for the remarkably high number of skulls, mandibles found with crania, associated mammalian post-cranial bones, and fish remains. The green clay matrix at L-41 is 12% sodium chloride. In sum, this quarry (L-41) is totally unlike any other in the Fayum, almost all of which are in sands and gravels.

In November of 1987, after hundreds of fossils had been discovered in Quarry L-41, the first primates were found there. These include five dental specimens (one isolated upper tooth, one maxilla with four teeth, and mandibles with, respectively, one, three, and five teeth). An additional two specimens were found in 1988. Most of these specimens appear to be referable to a single species, here given the name Catopithecus brownii. This species seems to have closest affinities with Oligopithecus savagei (3, 5). An isolated partial upper dentition of another genus and species, here given the name Proteopithecus sylviae, is also related to Oligopithecus. The evident Eocene age and much lower stratigraphic occurrence of C. brownii and P. sylviae make them the oldest known undoubted anthropoid primates yet found anywhere, with the possible exception of some isolated teeth believed to be of Eocene age from Algeria and Oman (7, 8). Two fossils from the Burmese Eocene have been called the oldest Anthropoidea. Nevertheless, these Burmese animals, Pondauga and Amphipithecus, are probably no older and could be younger than the L-41 site. Although species of these two genera have prior claims as earliest anthropoideans (9-11), the case for their inclusion in Anthropoidea rests on considerably less morphological evidence than can be put forward for Catopithecus.

SYSTEMATICS

Order Primates Linnaeus, 1758; Suborder Anthropoidea Mivart, 1864; Superfamily Hominoidea Gray, 1825; Family Propriopithecidae Straus, 1961; Subfamily Oligopithecinae, New Subfamily. Oligopithecines (Oligopithecus, Catopithecus) have low molar cusps that have more strongly developed
crests and higher trigonids and show paraconids present on M₃ (sometimes also M₂) relative to propliopithecines (Propliopithecus, Aegyptopithecus) that have lower trigonids and more bulbous molar cusps. The lower dentition of Proteopithecus is at present unknown. Upper premolars and molars of Oligopithecus, Catopithecus, and Proteopithecus have less bulbous cusps and sharper crests than do comparable teeth of propliopithecines. Molar hypocones are much smaller relatively and P¹ has only a slightly developed lingual cusp. Presently known Oligopithecines are all smaller than the known Propliopithecine species.

Catopithecus, New Genus

Generic Diagnosis. Catopithecus differs from Oligopithecus in having lower molars decreasing in size posteriorly so that M₁ > M₂ > M₃; Catopithecus differs from all Fayum anthropoids in having upper molars decreasing in size posteriorly so that M₁ > M₂ > M₃. Upper molars have a small mesostyle nodule as in Dolichocebus and Maharagha that is lacking in Oligopithecus and all other Fayum primates. Catopithecus differs from members of Parapithecidae but resembles Oligopithecus and other Propliopithecidae in having only two lower premolars and in showing anterior honing facets on the front blade of P₃ and P₄. Catopithecus has an M₁ lacking para- and metaconules that are found in parapithecids and has a strong hypcone on the distolingual cingulum as in propliopithecids. Catopithecus differs from Oligopithecus in a larger upper molar hypcone, in the presence of a slight paraconid on M₂, in possessing a P₄ with smaller metaconids in Oligopithecus and more poorly developed talonid basin, in having a P₃ that is less elongate mesiodistally and smaller relative to P₄. As in other propliopithecids, P₃ is distinctly higher than P₄. The mandible is relatively shallow, unlike the unusually deep mandible of Oligopithecus and similarly deep mandibles of other propliopithecids.

Type species. C. browni, new species.

Distribution. Fayum, Egypt, Quarry L-41.

Etymology. From Greek "cato," below, plus Greek "pithkos," one who plays tricks—thus an ape.

C. browni, New Species

Holotype. CGM 41885, right mandible with complete corpus and much of ascending ramus and coronoid process; P₃-₄ and M₃-₄ are intact; alveoli are present for I₁-₂ and canine.

Hypodigm. Type and DPC 7339, 7340, 7341, 8701, 8772.

Species diagnosis. Same as generic diagnosis.

Etymology. Named for Sylvia Cornero, Argentine anthropologist who found the type specimen.

Proteopithecus, New Genus

Generic diagnosis. Proteopithecus differs from Oligopithecus and Catopithecus in having a better developed hypcone on M₂. Second and third upper molars also differ from Catopithecus and probably Oligopithecus in being mesiodistally shorter and therefore relatively broader. Relative to the P³ of Catopithecus, the P³ of Proteopithecus is comparatively smaller with a less well-developed inner cusp. The upper molar series of Proteopithecus is 15% smaller in linear dimensions than the upper molars of Catopithecus. In turn, the lower P₃-M₃ of Catopithecus is 20% shorter than these same teeth are in Oligopithecus. Because of the large hypcone and greater transverse breadth, the M₂ of Proteopithecus more closely resembles the M₂ of the propliopithecines than do the upper molars of Catopithecus or, insofar as is known, Oligopithecus (a single M₁).

Type species. P. sylviae.

Distribution. Fayum, Egypt, Quarry L-41.

Etymology. From Greek "proteos," first, foremost, plus Greek "pithkos," one who plays tricks—thus an ape.

P. sylviae, New Species

Holotype. CGM 41886, left maxillary fragment with M₁-₃ and associated P₃; lingual third of M₁ broken away.

Hypodigm. Type specimen only.

Species diagnosis. Same as generic diagnosis.

Etymology. Named for Sylvia Cornero, Argentine anthropologist who found the type specimen.

DESCRIPTION AND COMPARISONS

Mandible. The mandible of Proteopithecus is not known. The mandible of Catopithecus (CGM 41885) (Fig. 1) represents a small-sized primate with an estimated jaw length of 3.5 cm from the anterior edge of the symphysis to the posterior surface of the condyle, giving a jaw size comparable to that of the golden lion tamarin (Leontopithecus rosalia). Under the molars the jaw of Catopithecus is shallow so that depth below M₁ is about the same as the length of M₁-₂. In Oligopithecus, the length of M₁-₂ is only 75% of jaw depth beneath M₁. Propliopithecus, Aegyptopithecus, and Oligopithecus, like many Miocene Anthropoidea, have unusually deep mandibles compared to the height of their cheek teeth. In parapithecids the jaw is also shallow. The coronoid process of Catopithecus is high and rises upward from the line of the cheek teeth at an angle of 60°. In five mandibles of Apidium phiomense this angle averages 65°, whereas in a late Eocene primate from west Texas, Mahgarita, this angle is 55°. The coronoid process of Catopithecus rises to a height of 2.1 cm above the base of the horizontal ramus or approximately three times the depth of the corpus. There is some damage to the posterior margin of the jaw so that the body of the articular process and part of the posterior rim below it are broken away. Nevertheless, following posteriorly from the mandibular body, the ventral edge of the angular process turns downward, suggesting that there was a well-developed angular process somewhat similar to that seen in the parapithecids. Measuring from front to back at the preserved base of the articular process, it is clear that the ascending branch of the mandible was not as deep comparatively as in Aegyptopithecus. In Catopithecus the ascending branch of the jaw is short anteroposteriorly, 1 cm, which is almost the same as M₁-₃ length. In the best preserved Parapithecus grangeri
mandible (DPC 5527) M1-3 length is 85% of the anteroposterior length of the ascending branch and in Aegyptopithecus zeuxis (YPM 21032) M1-3 length is 87.5% of length of the ascending ramus.

Symphysis. The type (right) mandible of C. browni has broken or separated almost exactly at the midline but this does not settle the question whether the symphysis was unfused or not because there are a number of parapithecid jaws and other propliopithecid jaws that are broken on or about the midline. We know from various specimens of Aegyptopithecus, Propliopithecus, Apidium, and Parapithecus that this region fuses in members of both families at an early individual age. The outline of the symphysis of Catopithecus is very much like that of propliopithecinines and resembles parapithecids as well, with both inferior and superior transverse tori separated by a genioglossal pit. The surface of the symphysis is filled with numerous pits and grooves that run over it in an irregular pattern. A similar pattern of grooves and pits can be seen on the symphysisal surface of a broken jaw of Aegyptopithecus zeuxis (DUPC 5391) that is from a species known to have symphysisal fusion.

Above the symphysis are two incisor sockets followed by a large canine alveolus. As is usually the case in Anthropoidea, the lateral incisors, judging from the sockets, are larger than the central incisors. The canine socket is longer mesiodistally than buccolingually and the alveolus is about the same size as the area of P3 roots. Judging from this size of the alveolus the canine crown was not large, so that perhaps this individual (CGM 41885) was a female.

Lower Dentition. No lower teeth of Proteopithecus are known. The P3 of Catopithecus, as in Oligopithecus, Propliopithecus, and Aegyptopithecus, has an anterior honing blade for the back of the upper canine. It is not rounded or bulbous as in parapithecid and does not have a metaconid. This tooth resembles that of other propliopithecinines in having a moderate lingual cingulum present, whereas buccally a cingulum is lacking. Proportionately P1 of Catopithecus is just as high as in Oligopithecus but the tooth is much shorter mesiodistally than in the former specimen (Fig. 2).

The P1 of Catopithecus is the lower tooth that differs most from its counterpart in Oligopithecus. The metaconid, located distolingually to the protoconid, is comparatively much smaller than in Oligopithecus. A talonid basin is present but not well developed. The P1 heel of Catopithecus is comparitively smaller than in Oligopithecus and, unlike it and other propliopithecinines, lacks any crest or cusps bordering the posterior edge of the talonid. The trigonid of P4 is shorter than in Oligopithecus with a relatively shorter preprotocristid and shows a trigonid open lingually, whereas in Oligopithecus the basin is closed lingually by crests from paraconid and metaconid. P4 differs from that of Aegyptopithecus, which has metaconid and protoconid subequal and high, whereas in Catopithecus the metacristid is low and much smaller. The M1 of Catopithecus is generally similar to that of Oligopithecus. The trigonid is relatively high compared to this structure in the propliopithecinines. Unlike propliopithecinines, but resembling Oligopithecus, a distinct paraconid is present. On the posterior edge of the broad, open talonid basin there is a hypoconulid “twinned” or paired with the entoconid. M1 is long, somewhat narrowed, and with a heel that is wider than that of M2.

The M2 generally resembles M1 except that the tooth is relatively shorter, and the hypoconulid is much larger and more distinct and of the specimens (DUPC 7341) bears a small but distinct paraconid on M2 of Oligopithecus or on M2 of the upper sequence propliopithecinines. Compared to M1, the M2 of Catopithecus is perceptionally smaller than that of Oligopithecus.

In contrast to M1-2, the M3 of Catopithecus is small as in Parapithecus and Propliopithecus and unlike the enlarged M3 of Aegyptopithecus and Apidium. As in the other molars the trigonid is high with a strong protoconid and metaconid but the paraconid is not present. The talonid is low and broad, and none of the molars shows a lateral cingulum.

Upper Dentition of Proteopithecus. The type (CGM 41886) left maxilla of P. sylviae (Fig. 3) preserves P1 (P2 missing), labial two-thirds of M1, and complete M2-3. The base of the zygomatic arch is also preserved, rising above the M2 and M3. The P1 is triangular in occlusal outline and is completely encircled by a basal cingulum. The crown shows a single large, nearly central cusp and a very small lingual cusp. In occlusal outline and general arrangement of structure this tooth is very similar to that seen in Mahgarita except that in the latter the buccomesial corner is more extended and the mesial cusp is smaller. P3 in Parapithecus grangeri and Aegyptopithecus zeuxis is also encircled by a basal cingulum, but in these younger taxa the tooth is much broader buccolingually and narrower mesiodistally. Also in these species the inner cusp has a cingulum across its lingual slope and the heel shows a small hypoconid.

The M1 of Proteopithecus is incomplete. As in Mahgarita and Eupolemur the M2 of Proteopithecus is entirely surrounded by a basal cingulum. On the buccal side rising from
the cingulum and between the paracone and metacone is a small cusp termed the "mesostyle nodule" by Fleagle and Bown (12). This small cusp is also present on upper molars of Dolichocebus and Mahgarita. This could be the remnant of either a mesostyle or a neomorph. There are no paraconule or metaconule cusps on this tooth, but a crest running mesiolingually from the paracone joins the crest between the basal cingulum and the apex of the protocone. At the point of joining there is a slight flexure but no cusp. A crest also runs between protocone and metacone but there are no cuspules. The trigon basin is fairly deep and is surrounded by cusps on all margins. On the posterolingual cingulum of the protocone a moderately large hypocone is situated. The tooth is relatively longer buccolingually than in either Catopithecus, Propliopithecus, or Aegyptopithecus. Both the anterior and posterior margins are compressed inward at the middle of the crown.

The ectoloph of M2 in Proteopithecus is only 80% as long mesiodistally as that on M1, and the paracone flares out further buccally than the metacone does, the opposite being true in M1. The trigon basin is open anteriorly because no crest runs down from the paracone to join the basal cingulum. A ridge running lingually from the protocone joins the basal cingulum with a small swelling or nodule just above the cingulum. This might be considered a pericone if additional finds should show the feature to be consistently present. The hypocone of M2 is much larger than that of M1 and bears a large distolingual bulge. In general, this tooth looks like a simplification of a propliopithecine tooth, differing mainly in having less bulbous or inflated cusps and being comparatively shorter mesiodistally. The proportion seen in Proteopithecus of having short, broad molars could reflect a significant phylectic trend since propliopithecines have upper molars that are longer from front to back and in Miocene hominoids the teeth are longer still. In some recent apes, even greater molar lengths are found.

The M3 of Proteopithecus is much smaller than the anterior molars and has a reduced metacone and no hypocone. Lingually the basal cingulum runs up toward the waist of the tooth and ends. Crests surround the trigon basin but link it anteriorly with the basal cingulum since there is no crest running down from the paracone to reach the cingulum. Simons et al. (13) described a lorisid upper M3 from a much higher Fayum level (Quarry I). The M3 of Proteopithecus bears no significant resemblance to that lorisid tooth. Propliopithecines often show upper third molars that are reduced in size relative to M1 and M2 but never to the extent seen here.

Upper Dentition of Catopithecus. In the field season of 1988 a flattened skull of C. browni (DPC 8772) was discovered. This find will be described in detail elsewhere. This specimen preserves P3-4 on both sides, with the lingual part of left M1 broken away (Fig. 4). The right canine alveolus is also preserved indicating an upper dental formula of ?2-1-2-3. This partial upper dental series matches closely the size of mandibular teeth in the type specimen of C. browni and the upper and lower series interlock perfectly, thus confirming allocation of the cranium to C. browni. The upper molars of Catopithecus probably resemble those of Oligopithecus more closely than they do those of Proteopithecus, at least the hypocones on M1-2 appear to be less well developed in these two genera compared to Proteopithecus.

The P3 of Catopithecus has a more anteriorly extended anterolateral corner and a slightly larger internal cusp relative to size of the molars. The P3 of Catopithecus is larger than that of Proteopithecus. Moreover, the upper teeth are overall about 15% larger in comparable measurements. Proteopithecus and Catopithecus have upper molar series that decrease in size posteriorly, but the anteroposterior length of the M1-3 series of Proteopithecus decreases more rapidly than in Catopithecus. Species of all three genera show well-developed cingula on all upper teeth.
DISCUSSION

*Caridactylus* and *P. sylviae* are probably the oldest African anthropoideans and therefore are the oldest known primate with well-established claims as relatives of, or ancestors to, the New and Old World higher primates, including humans. The closest resemblances of *Catopithecus* are to *Oligopithecus* but it is clearly more primitive and shows some archaic features, including the presence of a distinct paraconid on the second lower molar in at least some specimens and of a simple lower P4 with poorly developed talonid and indistinct metaconid. Presence of a mesostyle nodule on the upper molars appears to be a generalized or archaic feature, and possibly the pericone of M2 also constitutes a retention from earlier ancestors. Combined with these features, *Catopithecus* shares various anthropoidean characteristics already demonstrated for *Oligopithecus*. These resemblances include loss of first and second premolars, development of the anterior edge of P3 as a honing or sectorial blade, reduction of paraconids, and molar hypoconulids twinned with entoconids as in *Propithecus macaques*. In addition, the upper second molar is morphologically reminiscent of the upper molars of *propithecids*, with its very large hypocone and lack of paraconules and metaconules, its possession of an extensive basal cingulum in the upper teeth, and its lack of accessory cusuples typical of *parapithecids*. Comparisons with other Fayum primates, both anthropoid and prosimian, fail to disclose relationships for the L-41 primates other than those to *Oligopithecus* and the *propithecines* genera, *Aegyptopithecus* and *Propithecus*. None of the teeth of *Catopithecus* resembles those of *Afranius* or those of *parapithecids*. The upper dentition of *Propithecus* shows no significant resemblance to that of the *parapithecids*. In fact, *parapithecids* teeth are comparatively specialized and derived, showing little relationship as well to those of any Eocene primates. The lack of resemblance to the primitive lorisid M3 from Quarry I has been noted. Anaptomorphine premolars from Quarry E are also quite different from those of *Catopithecus*.

When comparisons with other Eocene primates are made, *Oligopithecus*, *Protropithecus*, and *Catopithecus* all show dental affinities with certain adapids, such as *Europolemur*, *Periconodon*, *Protopithecus*, *Huertzeria*, and *Mahgarita*. The incisor proportions are indicated by alveoli in *Catopithecus* and show that as in all other or later anthropoids (except for *Parapithecus*) the central incisor pair is smaller than the lateral pair. In omomyids, the central lower incisors are invariably the largest and often the only pair of incisors. Investigating other possible dental resemblances between *Oligopithecus* and *Catopithecus* on one side, and an array of omomyids on the other, has failed to uncover any significant resemblances in dental morphology. For instance, omomyids commonly have paraconules and metaconules not seen in the two *oligopithecines*; they also differ in having small canines, paraconids on all molars, and a nannopithecoid-fold on the upper molars and in lacking both hypoconulids and shearing premolar blades. The well-demonstrated relationships between certain Eocene adapids and *Oligopithecus*, *Propithecus*, and *Catopithecus*, on the one hand, and between them and the Fayum propliopithecids on the other, suggest a non-omomyid derivation for all higher primates.

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