

Anthropoid humeri from the late Eocene of Egypt

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A number of recent studies have, by necessity, placed a great deal of emphasis on the dental evidence for Paleogene anthropoid interrelationships, but cladistic analyses of these data have led to the erection of phylogenetic hypotheses that appear to be at odds with biogeographic and stratigraphic considerations. Additional morphological data from the cranium and postcranium of certain poorly understood Paleogene primates are clearly needed to help test whether such hypotheses are tenable. Here we describe humeri attributable to *Proteopithecus sylviae* and *Catopithecus browni*, two anthropoids from late Eocene sediments of the Fayum Depression in Egypt. Qualitative and morphometric analyses of these elements indicate that humeri of the oligopithecine *Catopithecus* are more similar to early Oligocene propliopithecines than they are to any other Paleogene anthropoid taxon, and that *Proteopithecus* exhibits humeral similarities to parapithecids that may be symplesiomorphies of extant (or “crown”) Anthropoidea. The humeral morphology of *Catopithecus* is consistent with certain narrowly distributed dental apomorphies—such as the loss of the upper and lower second premolar and the development of a honing blade for the upper canine on the lower third premolar—which suggest that oligopithecines constitute the sister group of a clade containing propliopithecines and Miocene–Recent catarrhines and are not most closely related to *Proteopithecus* as has recently been proposed.

Fossil primates from the late Eocene and early Oligocene sediments of the Fayum Depression, Egypt, continue to play a central role in debates surrounding the origin and early evolution of anthropoids and the two major extant anthropoid clades, Catarrhini and Platyrrhini. The interrelationships of early anthropoids have long been controversial, but recent phylogenetic analyses of living and extinct primates (1, 2) and discoveries of possible basal anthropoids in Asia (3–6) have led to even more diverse views of how various Fayum anthropoids fit into the broader temporal and biogeographic pattern of Paleogene anthropoid evolution. Recent papers have called into question the basal catarrhine status of the oligopithecines *Catopithecus* and *Oligopithecus* (1, 2, 7, 8), considered *Proteopithecus* to be a possible oligopithecine (2), suggested that propliopithecines are more closely related to a group of purported southeast Asian anthropoids than to any other Fayum primates (9, 10) and hypothesized that the early Oligocene Fayum primate *Afrotarsius* may be closely related to the otherwise Asian middle Eocene family Eosimiidae (2). Conclusions such as these are, however, in many cases fundamentally at odds with phylogenetic scenarios presented by other authors (11, 12), and there often appears to be very little agreement on some of the most critical issues bearing on our understanding of early anthropoid evolution.

Most current debates concerning the interrelationships of living and extinct anthropoids have been based almost entirely on dental morphology. Given the impasse that has arisen from such discussions (13), however, it is likely that cranial and postcranial morphology will now begin to play an increasingly important role in helping to resolve the lower-level systematics of Eocene anthropoids. Unfortunately, very little is known about the postcranial anatomy of anthropoids before the early Oligocene. Tarsals attributed to the purported basal anthropoid *Eosimias* have been described recently (14), but no postcranial

material is available for southeast Asian primates such as *Amphipithecus*, *Pondaungia*, *Siamopithecus*, and *Bahinia*, all of which have been claimed to be basal anthropoids on the basis of recently recovered dental remains (5, 6, 9, 10). In contrast, the postcranial anatomy of early Oligocene Fayum anthropoids is now fairly well documented (15–25), but with the exception of five isolated specimens described by Gebo *et al.* (26) and associated hindlimb remains of *Proteopithecus sylviae* recently described by Simons and Seiffert (27), very little is known about the postcranial morphology of the diverse anthropoid taxa preserved at the African late Eocene quarry L-41. Here we report on humeral material reliably referred to two anthropoids from quarry L-41, *Proteopithecus sylviae* and *Catopithecus browni*.

P. sylviae

Complete humeri attributable to *P. sylviae* have been recovered during each of the last 2 years (1998 and 1999) of excavation at quarry L-41. These specimens are best assigned to *P. sylviae* on the basis of size, relative abundance of anthropoid taxa at quarry L-41, and the probable association of one of the two specimens, DPC 20191, with a complete mandible of *P. sylviae* (D. DeBlieux, personal communication). *C. browni* and *P. sylviae* do not appear to overlap in size range and are by far the most abundant primates at L-41, with other anthropoid taxa such as *Arsinoea*, *Serapia*, and an as yet unnamed diminutive parapithecid species being exceedingly rare.

DPC 20191 (Figs. 1*D* and 2*B*) is a right humerus that preserves all morphological details of the distal articulation and midshaft, but the head is badly crushed. DPC 18256 (Fig. 1*C*) is complete and almost perfectly preserved aside from minor damage to the humeral head, a break on the ventral aspect of the distal shaft lateral to the entepicondylar foramen, and damage to the medial aspect of the trochlea. In many morphological details these humeri are most similar to DPC 1311, a specimen from quarry M (early Oligocene) referred to the parapithecid *Qatrania fleaglei* (22), than they are to the humeri of other Fayum primates.

DPC 18256 is 40.3 mm long. The shaft is moderately robust, with a very well-developed deltopectoral crest extending down about 40% the length of the bone. As in parapithecids, the insertions for *m. deltoideus* and *m. pectoralis major* are well defined and the shaft has a distinct sigmoidal curvature when viewed from the lateral or medial side. The supinator crest is also well defined but does not extend as far onto the dorsal side of the shaft as does the same crest in parapithecids. The brachialis flange is poorly developed when compared with that of most parapithecids and propliopithecines but is only slightly smaller than that of *Q. fleaglei*. The bicapital groove of *P. sylviae* is also more similar to that of *Q. fleaglei* than that of *Apidium phiomense*

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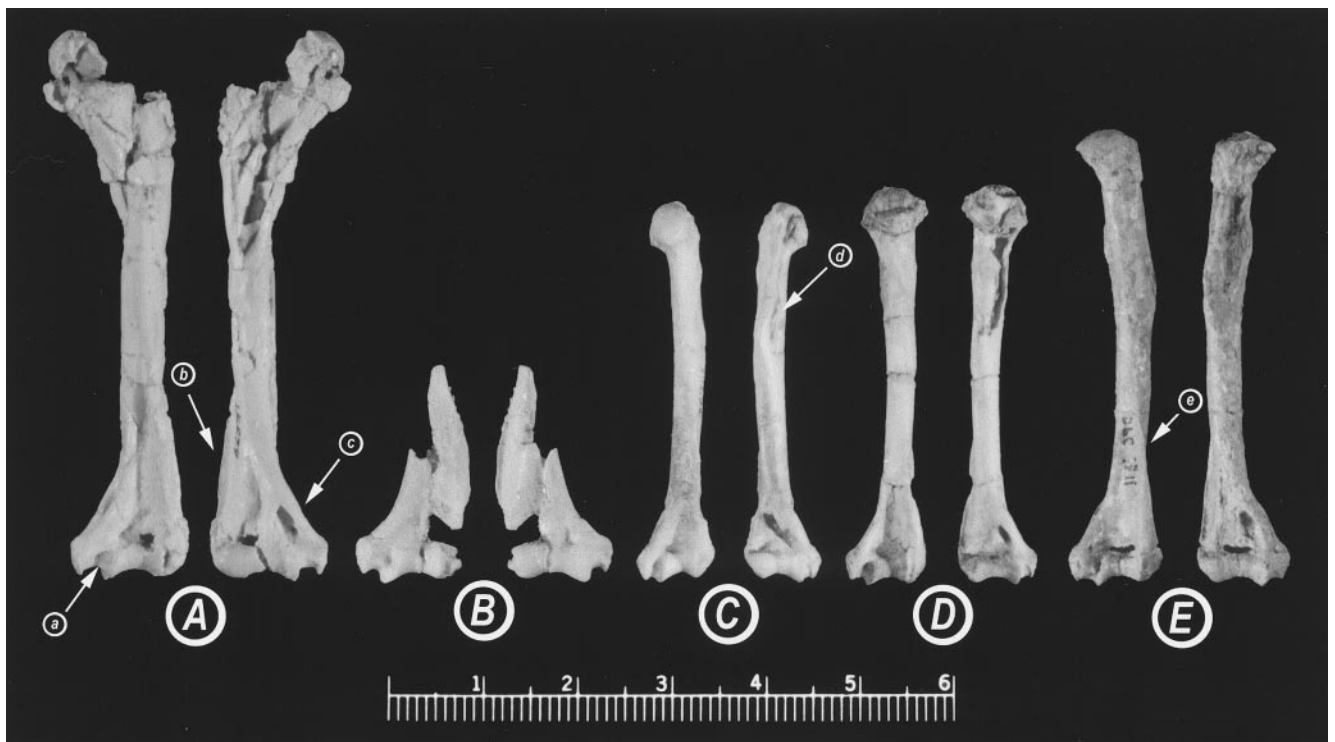


Fig. 1. Dorsal and ventral views of late Eocene anthropoid humeri from the Fayum Depression, Egypt, compared with the early Oligocene form *Q. fleaglei* (DPC 1311). (A) *C. browni* (DPC 12274). (B) *C. browni* (DPC 15522, reversed). (C) *P. sylviae* (DPC 18256). (D) *P. sylviae* (DPC 20191). (E) *Q. fleaglei* (DPC 1311). Scale is in centimeters. Lowercase letters denote dorsoepitrochlear fossa (a), brachialis flange (b), entepicondylar foramen (c), deltopectoral crest (d), and supinator crest (e).

and propliopithecines in being relatively narrow and more deeply incised.

The humeral head is oval and oriented almost directly dorsally, with a slight medial cant. The head is somewhat more oval than that of *Q. fleaglei* and propliopithecines, and there is no flattening of the most proximal articular surface nor any proximal elevation of the greater tuberosity above the articular surface as occurs in more terrestrial quadrupedal anthropoids. These features are most consistent with arboreal quadrupedal locomotion.

The morphology of the distal humerus is more similar to that of parapithecids such as *Q. fleaglei* than that of propliopithecines. As in parapithecids, the entepicondylar foramen (for passage of

the median nerve and brachial artery) is somewhat centrally placed relative to the humeroulnar articulation, and the strut defining the medial wall of the foramen is confluent with the medial edge of the trochlea. This pattern differs from that of propliopithecines, which have a more medially positioned entepicondylar foramen with the medial edge of the trochlea being either confluent with or more lateral to the lateral wall of the foramen. The distal articular surface is relatively narrow when compared with that of known parapithecids and propliopithecines. The capitulum is fairly broad mediolaterally and is essentially confluent with the relatively narrow trochlear surface, with no clear development of a zona conoidea or an intercondylar groove. The medial aspect of the trochlea is oriented distally as in parapithecids and propliopithecines and is flared both ventrally and dorsally. The dorsal trochlear surface also exhibits a fairly well-developed lateral lip within the olecranon fossa. Functionally, these trochlear features appear to resist adducting torques at the humeroulnar joint during pronation and maximize stabilization during the weight-bearing phase of quadrupedal locomotion (17, 25, 28, 29), particularly when the elbow is habitually flexed as in most arboreal primates (30–32). As in parapithecids and propliopithecines, the coronoid fossa is relatively shallow and the radial fossa is very deep, although neither of the two humeri is perforated in this region, and there is no development of a bony strut separating the two fossae. These features suggest that the locomotor repertoire of *P. sylviae* was characterized by habitual elbow flexion. The capitular tail is poorly developed and is a bit shorter than that of *Apidium* and some propliopithecines. As in other Fayum anthropoids, the medial epicondyle is dorsally directed at an angle of about 20° as is typical of many arboreal quadrupedal primates, and is not markedly elongate as in clinging primates such as callitrichines. As occurs in omomyiforms (33), in most platyrrhines, occasionally in cercopithecids (34), and in all known Fayum anthropoids,



Fig. 2. Distal views of humeri referred to *C. browni* (DPC 15522) (A) and *P. sylviae* (DPC 20191) (B). Note that there is a crack medial to the capitulum on DPC 15522 and that the lateral aspect of the capitulum is damaged. (Scale \approx 2.5 mm.)

there is a well-developed dorsoepitrochlear fossa (from which the ulnar collateral ligament arises) on the dorsal aspect of the distal humerus just medial to the trochlear surface.

When compared with DPC 18256, femoral material attributable to *P. sylviae* provides an estimated humerofemoral index of 73. Among primates, this index is more similar to that of cheirogaleids (35) than that of the small cebines (humerofemoral indices of ≈ 80 –85) that otherwise appear to be the most appropriate extant analogues for early anthropoid locomotion. This humerofemoral index is considerably higher than the index of approximately 62 estimated for *Apidium phiomense* [based on the mean measurements of humeral and femoral length reported in Fleagle and Simons (22)] as well as the indices of 64.6 and 59 that have been reported for the omomyiforms *Shoshonius* (36) and *Microchoerus* (37), respectively; these indices are, in turn, much higher than the humerofemoral indices of 45–50 seen in small extant vertical clingers and leapers such as *Tarsius*. As in cheirogaleids and many small platyrrhines, *P. sylviae* also has a relatively high crural index (27). In combination with a round femoral head, a short tibiofibular syndesmosis, and a proximally situated insertion for *m. semitendinosus* and *m. gracilis*, these limb proportions are most consistent with a pattern of arboreal quadrupedal locomotion that included a considerable amount of rapid running and pronograde leaping.

C. browni

Three distal humeri attributable to the oligopithecine *C. browni* have been recovered from quarry L-41. Two humeral specimens—DPC 8204, a fragment preserving most of the lateral half of the distal humerus including the capitulum, and DPC 7328, a distal humerus preserving most of the distal articular surface, the medial epicondyle, and the entepicondylar foramen—were tentatively referred to *C. browni* by Gebo *et al.* (26). The recovery of two additional distal humeri, DPC 12274 and DPC 15522 (the latter of which was directly associated with dental remains and a proximal ulna of *C. browni*), has since called into question Gebo *et al.*'s allocation of DPC 8204. Unlike all other humeri of *C. browni*, DPC 8204 has a very long and well-defined capitular tail whose mediolateral length relative to capitular width falls outside the range of all known living and extinct anthropoids. A long capitular tail appears to be a primitive trait within Primates (26), and the long capitular tail of a specimen mistakenly referred to *C. browni* initially presented the impression that *Catopithecus* might have had a more primitive postcranium than other living or extinct anthropoids. At the time of Gebo *et al.*'s study, it was not yet known that nonanthropoid primates were present at L-41, but it is now clear that three adapiforms (*Wadilemur*, *Anchomomys*, and *Aframomius*) are present (38, 39) and that the enigmatic *Plesiopithecus teras* is not an anthropoid (40) as was thought at the time of Gebo *et al.*'s study (41, 42). Although it is possible that DPC 8204 belongs to an L-41 anthropoid, this scenario now seems highly unlikely given the capitular morphology of *Proteopithecus*, *Catopithecus*, and all extant anthropoids, and we prefer to tentatively assign this specimen to *P. teras*, the only nonanthropoid primate falling within the approximate size range of *C. browni*.

DPC 12274 (Fig. 1A) is nearly complete but there is a fracture through the trochlea, the lateral epicondyle is damaged, and the proximal end is badly crushed. DPC 15522 (Figs. 1B and 2A) preserves the distal half of the humerus and fragments of the lateral half of the shaft. Morphological features of the shaft are difficult to discern because of damage, but it appears that the deltopectoral crest was considerably reduced when compared with that of *P. sylviae*. It is clear that there was a moderately developed brachialis flange comparable to that of *Apidium* but less developed than that of some propliopithecines.

Interestingly, DPC 15522 completely lacks an entepicondylar foramen. This foramen has been lost or is exceedingly rare in all

extant catarrhines and is absent or variably absent in certain platyrrhines (43). This foramen is present in DPC 12274, a specimen that is of the same size as DPC 15522 and otherwise very similar morphologically and is very small in DPC 7328; this condition is thus likely to be a case of intraspecific variation unique to *C. browni*. The entepicondylar foramen is present in all known propliopithecines, and, as in *Aegyptopithecus* and *Propliopithecus*, the entepicondylar foramen of DPC 12274 is medially placed, with the lateral wall of the foramen being confluent with the medial edge of the trochlea. The brachialis flange is not as well developed as is the same structure in many propliopithecines and most closely approximates the condition seen in parapithecids.

As has already been noted by Gebo *et al.* (26), the trochlea of *C. browni* is quite wide relative to capitular width, and in this respect is more similar to propliopithecines than parapithecids and *Proteopithecus*. The capitular tail is poorly developed, even less so than in most propliopithecines. The medial aspect of the trochlea is oriented distally and exhibits dorsal and ventral flaring as in other Fayum anthropoids, and there is a fairly well-developed lateral lip of the trochlea within the olecranon fossa. This lip is not quite so well developed in DPC 12274, but this appears to be due to postmortem damage. The coronoid fossa is relatively shallow but the radial fossa is deep, and a septal aperture is present in DPC 12274. This aperture may be due in part or in whole to breakage, but it is evident that the bony septum separating the radial and olecranon fossae is very thin regardless. As in other Fayum anthropoids, there is a well-developed dorsoepitrochlear fossa. Gebo *et al.* (26) noted that the medial epicondyle of *C. browni* is more medially directed when compared with other Fayum anthropoids, but this difference is slight (Fig. 2).

Because of extreme distortion of the proximal humerus in DPC 12274, it is impossible to provide an accurate estimate of humeral length, but, when compared with *P. sylviae* (Fig. 1)—a taxon that is approximately 80% the size of *Catopithecus* based on dental dimensions—it is evident that the humerus of *Catopithecus* must have been relatively long. An intermembral index estimate must await recovery of more complete material, but, on the basis of *Catopithecus*' humeral remains, we infer that the relative limb proportions of *Catopithecus* may have been more similar to slow-climbing primates such as lorisids, atelines, and Oligocene and early Miocene catarrhines than to many small-bodied platyrrhines, parapithecids, or *Proteopithecus*. In combination, these features are all consistent with a pattern of arboreal quadrupedal locomotion that may have been more similar to Upper Sequence propliopithecines than to any other Fayum anthropoid. This conclusion is consistent with Gebo *et al.*'s (26) analysis of humeral and femoral remains, which led them to suggest that *Catopithecus* might have moved more deliberately than the smaller sympatric arboreal quadrupeds preserved at L-41, possibly with a greater emphasis on climbing and less of a dependence on leaping.

Morphometric Analysis

Ten measurements were taken on the distal humeral articular surface of specimens belonging to members of the seven Fayum anthropoid species for which complete distal humeral specimens are available (see Table 1): (i) maximum proximodistal (PD) height of the medial aspect of the trochlea (PDHMEDT), (ii) minimum PD height at midtrochlea (PDHMIDT), (iii) maximum PD height of the capitulum (PDHC), (iv) maximum dorsoventral (DV) depth of the medial aspect of the trochlea (DVDMEDT), (v) minimum DV depth at midtrochlea (DVD-MIDT), (vi) maximum DV depth of lateral trochlea (DVDLT), (vii) maximum width of the ventral articular surface (MWVA), (viii) maximum width of the dorsal articular surface along its median axis (MWDA), (ix) maximum PD height of the dorso-

Table 1. Species means (in millimeters) for the 10 measurements employed in the distal humeral morphometric analysis

Measurement	<i>Aegyptopithecus zeuxis</i> (n = 2)	<i>A. phiomense</i> (n = 3)	<i>C. browni</i> (n = 2)	<i>P. grangeri</i> (n = 3)	<i>Propliopithecus chirobates</i> (n = 2)	<i>P. sylviae</i> (n = 2)	<i>Q. fleaglei</i> (n = 1)
PDHMET	10.97	5.07	4.29	5.95	8.39	3.39	3.88
PDHMIDT	6.90	2.87	2.88	3.22	5.84	2.10	2.36
PDHC	9.19	3.75	3.81	4.39	7.45	2.88	3.07
DVDMEDT	10.05	4.33	4.04	5.19	8.01	3.15	3.71
DVDMIDT	7.81	2.92	2.88	3.52	5.98	2.18	1.89
DVDLT	12.27	4.95	4.34	5.35	9.28	3.41	3.92
MWVA	22.29	8.56	9.15	10.18	17.46	6.12	6.52
MWDA	12.12	5.23	5.05	6.22	8.93	3.69	4.14
PDHLOF	11.08	4.75	4.01	5.48	7.84	3.50	3.61
MCW	8.97	3.97	3.45	4.64	6.34	2.74	3.29

lateral articular surface from the most distal point on the capitulum to the most proximal aspect of articular surface within the olecranon fossa (PDHLOF), and (x) maximum capitular width (MCW). In a few cases, measurements were estimated. These 10 measurements were divided by the geometric mean of all measurements for each individual, creating a set of 10 shape ratios [see Jungers *et al.* (44) for discussion and examples of the utility of this particular technique for size correction]. Pairwise Euclidean distances between all individuals were calculated in NTSYS-PC 1.80 (45), and a matrix of pairwise distances was then analyzed using the UPGMA clustering routine in NTSYS (Fig. 3). From the limited evidence available it is clear that, despite considerable differences in size, *C. browni* shows a greater phenetic resemblance to the propiipithecines *Aegyptopithecus* and *P. chirobates* than to other Fayum anthropoids. *Proteopithecus* falls within the parapiithecid assemblage and exhibits the greatest similarity to *Parapiithecus grangeri*.

Discussion

The humeral similarities that *Proteopithecus* and *Catopithecus* share with parapiithecids and propiipithecines, respectively, present a number of possible phylogenetic scenarios. If the features that *Proteopithecus* and parapiithecids share—such as a well-developed deltopectoral crest, relatively narrow trochlea,

and more centrally positioned entepicondylar foramen—are derived with respect to the morphology seen in *Catopithecus*, *Aegyptopithecus*, and *Propiipithecus*, then these features would provide limited support for a *Proteopithecus*–parapiithecid clade. Alternatively, if the morphology of *Catopithecus* and the propiipithecines is derived and the *Proteopithecus*–parapiithecid features are anthropoid symplesiomorphies, the morphology of the humerus would provide additional support for the placement of oligopithecines as the sister taxon of propiipithecines and all Miocene–Recent catarrhines, as already has been suggested by numerous authors (11, 21, 34, 42, 46). It is, of course, also possible that some or all of these similarities represent instances of convergence.

A *Proteopithecus*–parapiithecid clade has never been seriously considered on the basis of craniodental evidence, but *Proteopithecus* and *Apidium* do share at least one other postcranial feature—a “walled-off” intertrochanteric fossa (26, 27)—that is arguably derived [although a similar condition is also found in some omomyiforms (47)]. Gebo *et al.* (26) also noted that a partial innominate tentatively referred to *Proteopithecus* shows morphological similarities to that of *Apidium*. It is clear that *Proteopithecus* does not exhibit any of the hallmark postcranial specializations of parapiithecids, such as third trochanter loss and an extensive tibiofibular syndesmosis (27), and there are no compelling dental apomorphies that *Proteopithecus* and parapiithecids share to the exclusion of other living and extinct anthropoids. With regard to the morphology of the humerus, Fleagle and Kay (21) have suggested that there are no structural details of the *Apidium* humerus that would be inconsistent with the predicted ancestral platyrrhine morphotype. Given the otherwise considerable differences in the dentition and postcranium of *Proteopithecus* and parapiithecids, it seems preferable at this point to consider their shared humeral features to be anthropoid symplesiomorphies, but the polarity of features such as the relative position of the entepicondylar foramen are admittedly ambiguous given the paucity of postcranial material known for early anthropoids. If the postcranial features that *Proteopithecus* and parapiithecids share are derived and *Proteopithecus* proves to be a sister taxon of Parapiithecidae, it would suggest that postcranial, and not dental, adaptations might have driven the initial diversification of parapiithecids. In the absence of more compelling evidence for the possible parapiithecid affinities of *Proteopithecus*, however, we prefer to maintain that *Proteopithecus* probably belongs somewhere near the base of the radiation of extant anthropoids and is suitably generalized to have been a stem member of various anthropoid lineages.

Despite the recovery of abundant craniodental remains of *Catopithecus* (11, 48), the phylogenetic position of oligopithecines also continues to be a matter of debate. Simons and colleagues (11, 49), Fleagle and Kay (21), Harrison (34), and

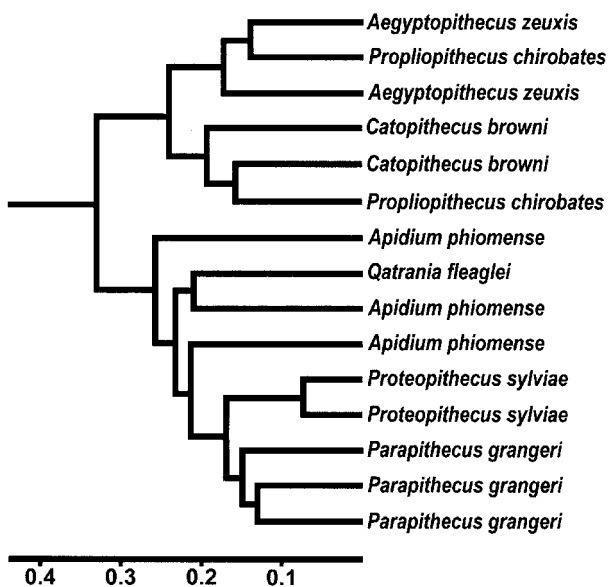


Fig. 3. Results of UPGMA analysis of average pairwise Euclidean distances based on size-adjusted variables defining the shape of the distal humeral articulation. Units represent linkage distance.

Gheerbrant *et al.* (46) have all argued that the loss of the upper and lower second premolar and the development of a canine honing blade on the lower third premolar justify a basal catarrhine status for oligopithecines, but recent phylogenetic analyses of living and extinct primates undertaken by Kay *et al.* (1) and Ross *et al.* (2) led these authors to suggest that oligopithecines are not basal catarrhines but rather the sister taxon of a clade containing parapithecids and all extant anthropoids. Ross *et al.* (2) have also recently suggested that *Proteopithecus* may be an oligopithecine (= “oligopithecoid” in their terminology) (2). The disparate humeral morphology of *Catopithecus* and *Proteopithecus* runs counter to this conclusion, however, as does the morphology of the proximal femur (26, 50).

Gebo *et al.* (26) have already noted that *Catopithecus* appears to have had a nontranslatory or slightly translatory humeroulnar joint, a feature that Rose (29) suggested may be one of the only postcranial synapomorphies supporting the monophyly of a clade containing propliopithecines and Miocene-Recent catarrhines. Gebo *et al.* (26) also noted, however, that *Apidium* appears to have had an only slightly translatory humeroulnar joint, and it now appears that *Proteopithecus* may have had an only slightly translatory configuration as well. The uncertain phylogenetic position of parapithecids and *Proteopithecus* leaves the polarity and phylogenetic significance of this feature unclear. If the distal humeral configuration of *Proteopithecus* and parapithecids is primitive within Anthropoidea, however, the relatively wide trochlea and more medially positioned entepicondylar foramen of *C. browni* would provide additional support for the monophyly of a clade containing oligopithecines, propliopithecines, and Miocene-Recent catarrhines to the exclusion of other living and extinct anthropoids regardless. The presence of other possible synapomorphies that *Catopithecus* shares with later catarrhines, such as a reduced deltopectoral crest and a relatively high intermembral index, seems probable based on available evidence, but this determination necessarily awaits the recovery of more complete material.

On the basis of our expanded knowledge of the anatomy of late Eocene anthropoids from the Fayum, there do not appear to be any postcranial features of *Catopithecus* or *Proteopithecus* that could be interpreted as being more primitive than the primitive morphotype of parapithecids, platyrrhines, and Oligocene-Recent catarrhines, and there are no postcranial fea-

tures excluding *Catopithecus* from being a stem catarrhine. Indeed, of the 14 humeral characters in Ross *et al.*'s (2) matrix that can be scored for *Catopithecus*, it now appears that only one, “entepicondylar foramen,” should be scored differently than *Aegyptopithecus* in being “variable” as opposed to being “present.” Similarly, Ankel-Simons *et al.*'s (50) recent description of the femur of *Aegyptopithecus* has indicated that this taxon exhibits a complex of features that is morphologically intermediate between the condition seen in *Catopithecus* and certain early Miocene catarrhines and that there are no major differentiae in the proximal femoral morphology of *Catopithecus* and *Aegyptopithecus* aside from the size of the third trochanter (which is slightly more prominent in *Catopithecus*). The third trochanter continues to be a controversial character in anthropoid systematics, and there remains considerable disagreement over whether certain taxa exhibit this feature (43, 51), but it is clear that a distinct third trochanter is present in certain extant platyrrhines such as *Aotus* as well as the extinct form *Homunculus* (50). Given the unequivocal presence of this feature in undoubted catarrhines and platyrrhines, the third trochanter is almost certainly a symplesiomorphy of extant anthropoids that has been lost or reduced independently in a number of different living and extinct anthropoid clades and cannot be convincingly interpreted as a condition more primitive than that seen at the common node of crown Anthropoidea.

On the primary basis of the loss of the upper and lower second premolar, the development of a honing blade for the upper canine on the lower third premolar, and a propliopithecine-like morphology of the humerus and femur, we rank oligopithecines as the sister taxon of a clade containing propliopithecines and Miocene-Recent catarrhines.

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