Reports

Ape Limb Bone from the Oligocene of Egypt

Abstract. *An ulna attributed to* Aegyptopithecus zeuxis *provides the first evidence for interpreting the locomotor behavior of the earliest apes. The fossil indicates that* Aegyptopithecus *was an arboreal quadruped and that the primitive hominoid locomotor pattern was most nearly analogous, among living primates, to that of* Alouatta, *the howler monkey.*

The earliest known fossil hominoids are from the Fayum region of Egypt. Although a considerable amount of dental and cranial material from these early apes has been described (*1*), their postcranial anatomy has remained virtually unknown. A nearly complete right ulna, YPM 23940, in the Fayum collections of the Peabody Museum, Yale University, has recently been identified as a limb bone of a fossil hominoid. We have made exhaustive comparisons of this ulna with those of nonprimate mammals, both terrestrial and arboreal, including such forms as *Procyon* and the African Oligocene creodonts, and in our opinion (agreed to by many other scientists who have reviewed this report) the ulna is that of a primate. The fossil is almost certainly attributable to *Aegyptopithecus zeuxis* Simons 1965 (*1*), a skull of which was found near it at the same quarry and level (*2, 3*).

The ulna was collected during the 1966–1967 Yale field season by Grant E. Meyer, associate in research at Yale, from Quarry M in the upper fossil wood zone of the Jebel el Qatrani Formation. This formation has been dated as older than 25 million years (*1*). Principal measurements of YPM 23940 are included in Table 1.

In order to investigate the functional significance of its morphology, we compared the fossil with ulnae from a selected group of nonhuman primates representing a wide range of locomotor types (Table 2). In this table *Varecia* has been included as an example of a relatively large prosimian with generalized, quadrupedal locomotor behavior (*4*). Two ceboid arm-swinging monkeys, *Ateles* and the more quadrupedal howler monkey, *Alouatta* (*5*), were chosen for comparison. The Old World monkeys tabulated were the terrestrial cercopithecine genus *Papio*, the more arboreal cercopithecine *Macaca fascicularis*, and the consistently arboreal *Presbytis cristatus*. YPM 23940 has been compared with two extant hominoids, *Pan troglodytes*, a knuckle-walker (*6*), and *Hylobates lar*, a brachiator, and a Miocene ape, *Pliopithecus vindobonensis* from Europe (*7*).

The measurements given in Tables 1 and 2 were taken on each specimen to provide a basis for comparing the major features of the different ulnae. Maximum ulna length indicates the relative sizes of the animals considered. Other measurements have been converted into indices to compare proportions.

The fossil ulna is nearly complete. The distal part of the shaft, including the styloid process, is missing, and parts of the posterior surface of the olecranon and shaft have been removed by wind erosion in situ. Although the shaft was broken in several places after fossilization, all the breaks align, and there is no indication of distortion (Fig. 1).

The length of the preserved portion of the ulna is 129.9 mm. The beginning of the pronator crest at the distal break indicates that only the most distal part of the shaft is missing. Comparison with ulnae of extant and fossil primates suggests that the maximum length was almost certainly between 140 and 160 mm. An estimate of 150 mm has been used in this study. This is approximately the size of ulnae of *Alouatta* or *Presbytis cristatus*.

The fossil ulna is quite robust. It has a robustness index, the ratio of the circumference at midpoint to the maximum length, greater than that of most extant primates listed in Table 2. Only *Pan* and *Varecia* show comparably high values of this index.

The olecranon process is, for a primate, long relative to the shaft (Fig. 2). Although the posterior surface of the process is extensively eroded, the entire length is preserved. The olecranon extends 19.0 mm proximally from the midpoint of the troch-

Table 1. Measurements of *Aegyptopithecus zeuxis* (referred) ulna, YPM 23940.

Parameter	Measurement (mm)
Maximum length of ulna (estimated)	150.0
Circumference of shaft at ulna midpoint	27.0
Length of olecranon (from midpoint of trochlear notch)	19.0
Length of trochlear notch (minimum length)	10.0
Breadth of trochlear notch at midpoint	9.0
Height of coronoid process above floor of trochlear notch	5.4

Table 2. Comparison of YPM 23940 with ulnae from a selected group of nonhuman primates. All measurements were made by J.G.F. on specimens in the Yale Peabody Museum; the Museum of Comparative Zoology, Harvard University; and the Naturhistorisches Museum, Vienna. Maximum ulna length and midpoint circumference were measured to the nearest 0.1 mm using dial calipers calibrated to 0.05 mm.

Ulna	*N*	Maximum ulna length (mm)	Circumference at midpoint (× 100)/ maximum ulna length	Olecranon length (× 100)/ maximum ulna length	Trochlear notch breadth (× 100)/ trochlear notch length	Coronoid process height (× 100)/ trochlear notch length
YPM 23940	1	150*	18.0	12.6	90.0	54.0
Pliopithecus	1	199.0	13.1	7.5	68.0	43.0
Pan	6	294.3	17.2	7.4	83.8	79.2
Hylobates	12	265.6	8.8	3.2	80.0	64.1
Papio	6	228.0	14.5	8.5	60.6	72.7
Macaca	12	131.8	13.9	9.3	63.5	65.5
Presbytis	12	144.8	14.3	8.9	66.4	62.5
Alouatta	4	161.0	14.8	12.0	61.0	55.8
Ateles	4	212.2	10.9	6.5	73.2	60.4
Varecia	3	109.3	20.1	13.6	65.9	64.8

*Estimate.

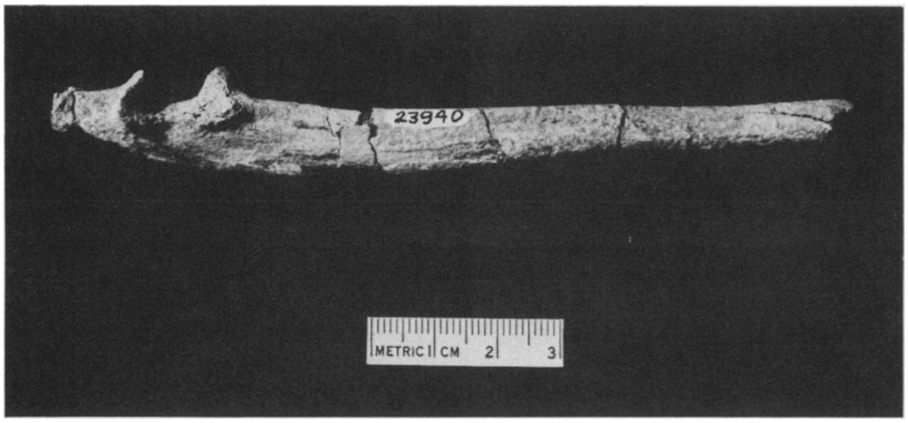

Fig. 1. Lateral view of the ulna of *Aegyptopithecus zeuxis*, YPM 23940. [Photograph by A. H. Coleman]

lear notch. This measurement approximates the distance from the joint axis to the insertion of the forearm extensors and has been used in calculating an index of relative olecranon length, the ratio of olecranon length to maximum ulna length. Of the extant primates, *Alouatta* and *Varecia* show comparable olecranons. Proximal lengthening of the olecranon increases the leverage of the forelimb extensors most effectively when the elbow is partly flexed and is characteristic of such arboreal quadrupeds as these. Among terrestrial quadrupedal primates, the olecranon tends to be deep anteroposteriorly in order to increase the leverage of the extensors when the elbow is in a more extended position (*8*). The shape of the olecranon in the fossil suggests that *Aegyptopithecus* was an arboreal quadruped which moved with its elbows partially flexed.

The trochlear notch of YPM 23940 is relatively broad. Along the sagittal midline the articular surface is raised to a slight crest running proximodistally, which is less distinct but similar to the sharp crest in extant hominoid ulnae. The articular surface on either side of the crest is gently convex. These features indicate that the articulating surface of the humerus possessed a relatively deep trochlea with distinct lateral and medial borders. It has been suggested that the deep humero-ulnar articulation characteristic of extant hominoids and incipiently developed in this fossil is an adaptation for maintaining elbow stability during climbing and forelimb suspension (*9*).

The coronoid process in the fossil ulna is relatively low. A relatively low coronoid is often found among arboreal quadrupedal primates. By contrast, terrestrial quadrupedal primates have relatively high, distally buttressed coronoids that help to brace the forelimb in an extended position (*8*).

The radial notch in the *Aegyptopithecus* ulna is small and separated from the trochlear notch as in extant and fossil hominoids, the larger ceboids, and some prosimians. This contrasts with the condition seen in Old World monkeys and many terrestrial mammals, in which the radial notch is excavated into the coronoid half of the trochlear notch. The former of the two conditions indicates a well-separated ulna and radius possibly related to increased mobility for supination and pronation of the forearm.

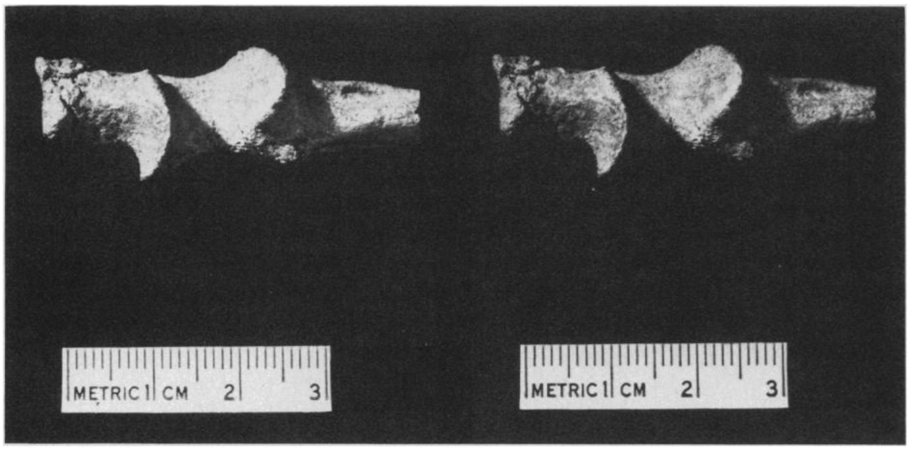

Fig. 2. Stereophotograph showing the anterior view of the trochlear notch and olecranon process of the ulna in YPM 23940. [Photograph by A. H. Coleman]

The laterally compressed shaft of the fossil ulna resembles ulnar shaft construction in *Pliopithecus* and *Alouatta*. The surface of the shaft is smooth, as in *Alouatta* and *Pan*, and lacks the sharp interosseus ridge seen in most Old World monkeys. The posterior surface of the shaft is flattened distally and shows the proximal flaring of a prominent pronator crest, as seen in the ulnae of the arboreal climbing forms such as *Alouatta* and many other New World monkeys.

The *Aegyptopithecus* ulna possesses a mosaic of features unlike the combination found in any one recent primate. Nevertheless, by evaluating the functional implications of the different morphological features, it is possible to make some general statement about the probable locomotor habits of this early ape. Its overall robustness and relatively long olecranon distinguish the fossil from ulnae of similar length in extant primates. In terms of hominoid evolution, these features almost certainly represent a primitive condition. For *Aegyptopithecus*, they suggest a comparatively heavy-bodied animal probably possessing relatively shorter forelimbs than in most extant hominoids. The shape of the olecranon, morphology of the shaft, and low coronoid process indicate that the animal was an arboreal quadruped. The breadth of the trochlear notch, presence of an incipient midline crest, and separation of the trochlear and radial notches are similar to the conditions seen in other hominoids and may be related to elbow stability and enhanced forearm rotation as adaptations to climbing and possible forelimb suspension. In overall morphology, the fossil ulna most closely resembles that of the extant howler monkey, *Alouatta*. Reports of the locomotor behavior of this New World primate indicate that howlers are primarily arboreal quadrupedal climbers (*5*). On the basis of presently available evidence, one fossil ulna, *Aegyptopithecus* is best viewed as a robust, arboreal climber with locomotor abilities comparable to those of the howler (with the reservation that there is no reason to believe that *Aegyptopithecus* possessed a prehensile tail).

As the oldest known limb bone of a hominoid primate, this ulna is of certain importance for reconstructing the history of locomotor behavior in higher primates. Anatomical and behavioral similarities between the larger New World monkeys and Old World hominoids (both living and fossil) have been noted previously by numerous workers (*10*). Nevertheless, the taxonomic homogeneity of the Old World higher primates has been interpreted by many students as evidence that the earliest hominoids resembled living cercopithecoids in their postcranial anatomy and locomotor behavior. Similarities between this *Aegyptopithecus* ulna and that of the extant New World howler monkey, together with the absence of any particular similarity to ulnae of Miocene to Recent cercopithecoids, argue against such an interpretation. Rather, the evidence presented here suggests that early locomotor behavior of hominoids somewhat resembled that of extant New World monkeys. Such a similarity need not imply a particularly close phyletic relationship between these two groups.

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References and Notes

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2. Although the ulna was not found in direct association with dental remains of *A. zeuxis*, assignment to that species appears highly probable for the following reasons. (i) On the basis of detailed morphological and metrical comparison (*3*) with mammalian ulnae from several orders, the fossil shows definite primate characteristics and is unlike the ulnae of rodents or carnivores. (ii) Among the known mammalian fauna from the Fayum [E. L. Simons and A. E. Wood, *Peabody Mus. Nat. Hist. Yale Univ. Bull. 28* (1968)] *Aegyptopithecus* is the most likely taxon to which this ulna could be assigned on the basis of the size of skull and dentition. There are no Fayum rodents or carnivores of a size correspondent to this ulna and all other Fayum primate species are disproportionately smaller. (iii) Limb bone fossils are much less common than teeth and jaws in the Fayum deposits and are known for only a few common animals. In consequence, it is improbable that this bone belongs to an animal not known from teeth or jaws (*3*). (iv) The bone is structurally that of an arboreal animal, but no group of arboreal nonprimates in this size range is known from any site throughout the whole Tertiary of Africa. (v) YPM 23940 resembles ulnae of Miocene apes and looks much like a robust version of the ulna of *Pliopithecus* from Czechoslovakia, which is, otherwise, the oldest well-preserved hominoid ulna.
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11. We thank C. Mack of the Museum of Comparative Zoology, Harvard University, for permission to study specimens under his care. We are also grateful to Friderun Ankel-Simons, B. Patterson, F. A. Jenkins, Jr., D. R. Pilbeam, P. D. Gingerich, and I. M. Tattersall for their comments and suggestions regarding this report. Part of the research reported here was made possible through NSF grant GA 723 and Smithsonian Foreign Currency Grant 1841, both to E.L.S.

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Horizontal Cells in Cat Retina with Independent Dendritic Systems

Abstract. *Cat horizontal cells are retinal neurons with two functionally distinct parts; the cell body receives signals predominantly from cones, while the terminal arborization receives predominantly from rods. The long thin process connecting these parts neither generates impulses nor allows significant passive electrotonic conduction between them.*

One class of horizontal cells in the mammalian retina has an extraordinary appearance (*1, 2*). A cell body with a radiating system of dendrites gives off a single, long, thin axon-like process that ends in an enormous terminal arborization (Fig. 1b) whose size far exceeds that of the dendritic field of the cell body (Fig. 1a). The terminals of this distant axonal arborization go only to rod spherules, while the dendrites at the cell body go only to cone pedicles (*2*). This pattern suggests that the cell is receiving signals from cones and conducting them to rods.

We have succeeded in recording from within the cell body and separately from within the terminal arborization of this type of horizontal cell in cat retina and have injected the structures in question with Procion Yellow (*3*). The results indicate that both ends of this cell receive signals from photoreceptors but that the long axon-like process plays no significant role in conducting these signals from one end of the cell body to the other.

Some horizontal cells injected with Procion bear a remarkable morphological similarity to axon-bearing, Golgi-impregnated cells (compare Fig. 2a with Fig. 1a). These horizontal cells have discrete round perikarya from which arise five main dendrites. The latter divide dichotomously, producing many overlapping wavy branches that in well-stained preparations can be seen to bear small clusters of terminals that are known to contact cone pedicles (*2*). The nuclei of these cells appear much brighter than the rest of the cell body and are thus readily discernible in preparations injected with Procion. Although the axon has not stained in our horizontal cells injected with Procion, we can distinguish the axon-bearing cell type by these morphological criteria and can thus be confident in attributing particular physiological responses to the correct structure.

The terminal arborizations of horizontal cells are quite different in appearance from cell bodies (compare Figs. 2b and 1b with Figs. 2a and 1a). The main axonal branches are, at their thickest, only about 5 μm in diameter, and we were surprised to be able to record from such small structures. A meshwork of ultrafine processes and bright dots can be seen in the Procion-injected terminal arborization of Fig. 2b, which is also particularly characteristic of Golgi-impregnated material and represents the fine branches and thousands of terminals that go to rod spherules (*2*). Nuclei have not been seen in these units.

Both cell bodies (*4*) and terminal arborizations respond to light of all wavelengths by hyperpolarizing shifts in membrane potential (S-potentials). The physiology of the terminal arborization is most reliably distinguished from the physiology of its cell body by the procedure shown in Fig. 1c. Responses were obtained to 658-nm (red) and 400-nm (blue) flashes which were adjusted to bleach equal amounts of rod pigment (*5*). The responses of the terminal arborization to these stimuli match at threshold and at low intensities, but those from the cell body do not match at any intensity. The fact that the low intensity responses of the terminal arborization have identical waveforms to these matched stimuli implies that the axon terminal is driven purely by rods at these intensities. The cell body, on the other hand, has a small rod input (*4*), but this is so insensitive that even at threshold the 658-nm light stimulates the cone input more strongly than the rod input (see Fig. 1d). Thus these traces are never superimposable.

At higher intensities the waveforms of the responses produced by the terminal arborization to rod-matched stimuli no longer match (Fig. 1c) because of a small cone input into this structure. Therefore, both terminal arborizations and cell bodies of these horizontal cells receive inputs from both rods and cones, but the proportion of these two inputs is quite different (*6*). In terminal arborizations about 80 ± 2 percent of the peak response was contributed by rods (three well-stained units), and the remainder by cones; in cell bodies, regardless of morphological characteristics, about 58 ± 14 percent of the peak response came from cones (five well-stained units), and the remainder from rods (means ± standard deviations).