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A FOSSIL COLOBUS SKULL FROM THE SUDAN (PRIMATES, CERCOPITHECIDAE)

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ABSTRACT

A fossil monkey skull recovered from the "Old Alluvium" of presumed Pleistocene age near Wad Medani in the Central Sudan is described. This find represents a variant of *Colobus polykomos abyssinicus*, a living species whose habitat is restricted to forest canopy. Since this skull is not abraded and is unlikely to have been water-transported more than a few kilometers to its site of burial, it provides evidence that continuous forest cover once reached northwest across the Sudan to the vicinity of Wad Medani.

No. 111

INTRODUCTION

A fossil cercopithecoid monkey skull assignable to the subfamily Colobinae and apparently representing a variety of the living subspecies *Colobus polykomos abyssinicus* (Oken) was discovered in Nile alluvial deposits of the Sudan in the vicinity of Wad Medani, Blue Nile, in 1938. This find was made by Mr. W. P. Archdale, at that time with the Sudan Geological Survey. In February 1940, the skull was sent by Gerald Andrew, Government Geologist of the Sudan, to Professor Otto Zdansky, then Chairman of the Geology Department, Cairo University. Although this cranium, thickly encrusted with matrix, was partly cleaned by Dr. Zdansky, it was left undescribed by him. Later he gave the specimen to Y. S. Moustafa, who took over Dr. Zdansky's duties in Vertebrate Paleontology at Cairo University in 1950. The skull was recently (1963) presented by Dr. Moustafa to the Peabody Museum at Yale University.

GEOLOGICAL AGE

The age of this fossil within the Pleistocene is not known but the deep burial in the Old Alluvium of the Gezira Plain, the permineralization of the bone and the surrounding dense concretion all attest to an age prior to the Recent. Some minor morphological differences from a considerable series of Colobus polykomos and C. badius at the American Museum of Natural History, New York, exist and although not warranting taxonomic distinction at present these do suggest considerable antiquity for the skull. Even if it is of early Pleistocene age there is no a priori reason why this skull should differ in any conveniently definable set of morphological features from living Black Colobus. For example, in the case of another primate genus, Simpson (1965) has recently reported that specimens of fossil galagos from Bed I, Olduvai Gorge, Tanzania, are extremely similar to the two living subspecies, Galago senegalensis moholi and G. s. braccatus, of that region although they are about 1.75 million years older. He remarked (p. 15):

"I do not mean to suggest that the fossils belong to the living subspecies of the same region, or even that such sub-

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A FOSSIL Colobus SKULL FROM THE SUDAN

species are definable and valid as now recognized..... The fact that the fossils cannot be definitely distinguished from living *Galago senegalensis* does not amount to absolute determination that they are of that species. Larger series, especially with upper dentitions and skulls, might well demonstrate a distinction, but the parts now known in the Olduvai Bed I form do suffice to indicate that it is in any event very closely related to the living lesser Galago of the same general region."

The question of absolute age of this skull of *Colobus* is consequently of some interest. At least one method of geochemical dating may apply in this case and this is currently being investigated further at Yale. If this skull contains measurable uranium and if the bulk of this uranium entered the skull shortly after burial so that the time of mineralization of the bone was short compared with subsequent time then a possibility exists that this skull could be dated by the Thorium 230/Uranium 238 method. This method has already been utilized for fossil bones as reported by V. V. Cherdyntsev (1965: Engl. transl).

ECOLOGICAL SIGNIFICANCE

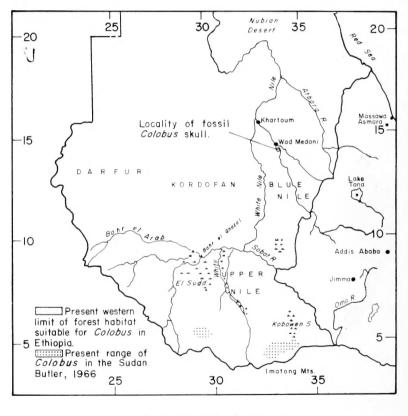
The skull exhibits no abrasion or other evidence of significant fluviatile transportation so it must be assumed that the occurrence of this fossil in the Old Alluvium near Wad Medani appears to establish the fact that within only a few kilometers of that city, dense forest conditions once existed. *Colobus* monkeys are entirely confined to canopy forest habitat and do not normally travel on the ground even for short distances. As Schenkel and Schenkel-Hulliger (1966) have recently reported, their observation of *Colobus polykomos* in Kenya indicates that even in partly cutover forest these monkeys when seen on or near the ground preferentially leap or walk on fallen branches. Thus range extension for these primates can be accomplished only by travel through virtually continuous forest canopy.

This specimen is therefore of particular zoogeographic interest, for it was found about 400 km. west of the present possible range in Ethiopia of members of this genus (see Figure 1). Within the Sudan itself one has to look 1,050 km. to the south in the

3

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Imatong mountains to find present-day *Colobus*. The prior existence of *Colobus polykomos abyssinicus* in the vicinity of Wad Medani thus strongly suggests a much wetter climate in the Central Sudan formerly and implies that there once existed continuous forest cover, perhaps running several hundred kilometers westward from the highland forests now existing in the Lake Tana region of Abyssinia at the headwaters of the Blue Nile.



0 100 200 300 400 500 600 760 500 KILOMETRES

COLOBINE FOSSILS

Most fossil monkeys so far recovered from Pliocene-Pleistocene localities in Africa (species of *Simopithecus, Cercopithecoides, Gorgopithecus,* among others) have been ranked with the cercopithecine division of Old World monkeys. However, some early colobines may also exist among known African materials. Considering the different ecologic requirements of members of these two subfamilies, the taxonomic allocation of certain fossil species requires serious attention. DeVore and Washburn (1963) stated that Cercopithecoides williamsi from the Pleistocene of South Africa is a colobine monkey. Stromer (1913) figured a partial maxillary dentition from the Egyptian Pliocene (Wadi Natrun) which he regarded as a semnopithecine, now colobine, monkey. As the dentition is much worn, little that is diagnostic remains and the subfamilial allocation is consequently uncertain. Libypithecus markgrafi, which Stromer described from this same site, is based on a good skull which has generally been taken to represent a primitive baboon. Piveteau (1957), however, included his discussion of the Natrun skull of L. markgrafi among his section on colobine monkeys. More recently, Verheyen (1962) has devised an index, interorbital width x 100/length from glabella to prosthion, in which almost all cercopithecine and colobine monkeys differ. In this index Libypithecus falls in the same general zone as species of Papio and Macaca and well away from those of Mesopithecus and Cercopithecoides. MacInnes (1943:148, pl. 24) discussed fossils of a cercopithecine species, which he regarded as belonging to *Mesopithecus*, from Miocene deposits on Rusinga and Kiboko Islands, Kiverondo Gulf, Lake Victoria, Kenya. The type species of genus Mesopithecus comes from the European early Pliocene. Pikirmi faunas of Greece and Turkey has also been generally treated as belonging to the colobine (= semnopithecine) group (Gaudry, 1862; Piveteau, 1957). Such an assignment was strongly questioned by Patterson (1954) but a careful investigation of the subfamilial assignment of *Mesopithecus* from the Pontian of southern Europe has yet to be undertaken. Since MacInnes (1943) published on this African early Miocene monkey, however, additional material has been found that has been under study by Von Koenigswald at Utrecht. He has recently pointed out (personal communication, 1966) that this undescribed material from Kenya is not Mesopithecus but represents a new genus and species - the oldest undoubted monkey. His analysis of this species, when published, may help to clarify the place and time of differentiation of the two cercopithecoid subfamilies.

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LOCALITY AND LITHOLOGIC ASSOCIATION

The Sudanese fossil monkey skull was found weathering out of a bluff of alluvial deposits on the east bank of the Blue Nile 15 km SSE of Wad Medani, latitude 14° 18 1/2' N, longitude 33° 37' E, approximately 1.5 km upstream from Abu Suheli Gubba (an existing landmark on the west bank). It was discovered lying in a position which indicated derivation from a dark clay horizon. These clays, locally called "Old Alluvium," are often heavily impregnated with fresh-water limestone (kankar) nodules or beds, as are the sands and gravelly sands underlying the clays. On discovery, the skull reported here was also covered with a kankar concretion. These dark clays compose the "cotton-soil" of the Gezira Plain, the so-called "aeolian clays" of early authors, and are very thick (12-20 meters). In this region the river flows in a valley probably 30 meters deep below the Gezira Plain, with about four or five meters of cracked soil and aeolian clay overlying the Old Alluvium from which the skull was derived. In some areas, the Old Alluvium is cut into Pliocene sediments but its temporal position in the Pleistocene is at present unknown.

Systematics

Order Primates, Linneus, 1758 Suborder Anthropoidea Mivart, 1864 Family Cercopithecidae Gray, 1821 Subfamily Colobinae Elliot, 1913 Genus Colobus Illiger, 1811 Colobus polykomos abyssinicus (Oken) 1816 Figures 2, 3

Verheyen (1962) in the most recent revision of the genus *Colobus* distinguished three species of Black Colobus: *C. poly-komos, C. abyssinicus,* and *C. satanas.* Schwartz (1929) regarded these three varieties as members of one species, a view continued by Fiedler (1956) and a usage followed herein.

This skull resembles female skulls of the black *Colobus* subspecies group, particularly *Colobus polykomos abyssinicus*, much more closely than those of the Red *Colobus*, *C. badius*. However, it is noticeably different from *C. p. abyssinicus* in several details,

No. 111

some of which suggest a certain degree of primitiveness compared to the present-day East African varieties. These features of difference from typical members of modern *Colobus polykomos* subspecies include a slightly smaller cranial vault, well-defined frontal bosses, more quadrate orbits, palate bowed out more widely, development of a deep groove on the posterior face of upper canines, and a heavy ridge running posteroventrally on the lateral external walls of the orbits. Inasmuch as the variation of such cranial structures in *Colobus* is broad and only this single specimen of unknown age is available from the Wad Medani region, it does not seem advisable to name a new subspecies in this case.

In fact, naming subspecies among Tertiary (or earlier) mammals is generally inadvisable. This is because any "subspecific" metrical or morphological differences noted between two or more type specimens might equally well have been specific. Since it is impossible to test interfertility in fossils representing populations which might be either species or subspecies, these two taxonomic levels cannot be clearly distinguished in fossil samples. Subspecific names of fossil vertebrates often become mere "handles" for one or more individual specimens which seem different, and are thus applied in a different manner from common usage of subspecies by most neontologists. In addition, there is disagreement as to whether subspecies can truly be defined even among living organisms.

MORPHOLOGICAL DESCRIPTION

GENERAL MORPHOLOGY. The fossil skull (YPM 19063) is remarkably well preserved. It is uncrushed and nearly complete, with only the tympanic bullae, zygomatic arches, incisors, and left canine missing. The left orbital wall shows slight damage posterolaterally, and the distal portions of the nasal bones are partly broken off. The upper incisors and the left canine were lost before fossilization. The specimen seems to have suffered little deformation except for a slight displacement internally of part of the occipital beneath the upper margin of this bone.

Judging from the relative cranial proportions, this skull (YPM 19063) probably belonged to a young adult. The third upper molar is almost at the level of the other molars, which would

indicate the animal was not fully mature. Other evidences of (individual) age are that the frontoparietal suture is not entirely closed and the interparietal is open. Across the frontals, the distance between the two supratemporal ridges (temporal crests) is about 25 mm. In many full adults of black *Colobus* species these crests run closer to the midline.

The size of the canine and gracile skull morphology suggest that the individual represented is female. The base of the canine is not particularly large in cross-sectional area and its root is comparatively short. In addition, the rostral face of the maxilla lacks the canineroot buttress which normally accompanies the relatively larger canine root of male *Colobus*. Although the tip of the right canine is chipped off, projection of the lateral planes of the basal portion of this tooth suggests that it did not extend much beyond the general level of the upper tooth row. If the specimen under consideration were male, the canine would have to be much larger and longer than it is.

SKULL ROOF. This skull shows a remarkably short face. As in present day Colobus polykomos the nasal bones are also comparatively short. Although broken distally, the curvature of the dorsal surface of the nasals indicates these bones were turned slightly upward at their ventral extremity. The interfrontal suture is closed, but in its position a shallow groove running anteroposteriorly separates two slightly elevated frontal bosses. These two bosses reflect the modeling of the frontal lobes of the brain somewhat more clearly than is usually the case in existing members of Colobus. This lower vaulting of the frontal may also indicate a slightly smaller volume for the frontal lobes than is typical of present-day Colobus skulls of comparable size. The superorbital ridges are fairly well marked, and posterior to them is a distinct transverse depression. In modern species of Colobus the frontal portion of the braincase is generally more expanded anteriorly. In this character, the Abu Suheli skull seems perceptibly more primitive.

Slightly anterior to the point of juncture of the frontal and the interparietal suture, the skull vault is depressed below the general dorsal arc of the braincase. The maximum diameter of the skull in the parietal region is 55.7 mm, as compared with the



FIGURE 2 — YPM 19063 A. Facial view, \times approx. 1.25. B. Right lateral view, \times 1.

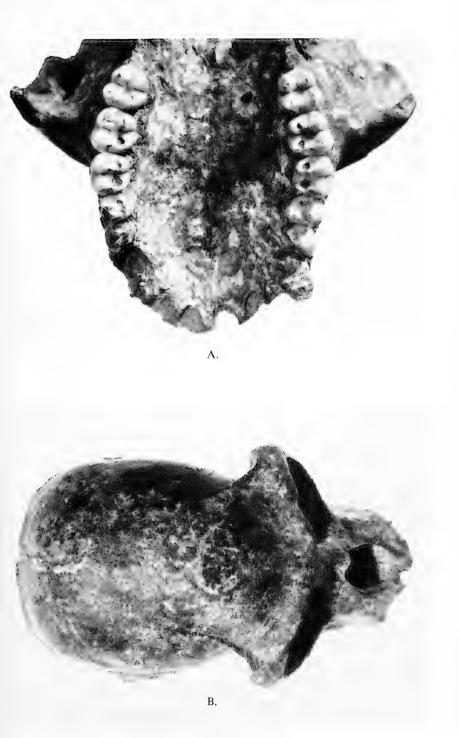


FIGURE 3 — YPM 19063 A. Palate, \times 1.7. B. Dorsal view, \times 1.

width across the postorbital bar, 44.3 mm. The constriction behind the orbits is more pronounced than in most living *Colobus poly-komos abyssinicus*.

A medial suborbital wing of the jugal (malar) contacts the lacrimal, thus excluding the maxillary facial surface from the orbital rim. As is typical of Cercopithecidae, the lacrimal foramen is located well within the orbit. On each side there appears to be but a single infraorbital foramen. There is no evidence of the occurrence of a supraorbital foramen on either side of the skull. Just below the median extremities of the supraorbital rims there are indications of the presence of a pair of venous foramina located on either side of the interorbital septum. The orbits are nearly circular in outline, with greatest transverse diameter in each approximately 23.8 mm, and greatest vertical diameter, 22.8 mm.

A somewhat unusual structural feature is a crest which runs ventrally for about 10 mm on the temporal face of the postorbital plate, arising at the point of junction of sutural contact between the external angular process of the frontal with the jugal (malar). This crest fades smoothly into the surface of the postorbital plate, forming a shallow fossa anterior to it. At this point, as a consequence of the presence of this subsidiary crest, the dorsoexternal corner of the orbit is comparatively massive. As is typical of Colobinae, the parietal in this skull joins an upward extension of the alisphenoid at the pterion, thus forming a sphenoparietal suture. Among cercopithecine monkeys these two cranial elements are commonly separated by a forward extension of the squamosal which makes sutural contact with the frontal.

PALATE. The hard palate extends beyond the posterior end of the tooth row. The posterior choanae are comparatively narrow transversely, and, as in most Anthropoidea, open a short distance posterior to a transverse line across the posterior faces of the third molars. The palatal surface is flat and lies nearly 10 mm above the lingual bases of the teeth. Since the skull shows no signs of having been laterally compressed, the position of the U-shaped dental arcade may be safely assumed to be undisturbed. The outward bowing of the cheek teeth and the relatively small teeth are resemblances to *Colobus polykomos polykomos* rather than to *Colobus polykomos abyssinicus*. Since in most other features, YPM 19063 is more like *C. p. abyssinicus*, this suggests, perhaps, that the population represented by this specimen was more generalized than either of these two present-day subspecies.

OCCIPUT. The supraoccipital ridge (lambdoidal crest) is rather weakly developed; it does not project markedly at the inion which is slightly displaced to the right of the midline, thus offsetting the supraoccipital suture from the latter. The supraoccipital surface seems to have been fractured along a curved line which runs parallel to the supraoccipital ridge. It also appears that the fractured occipital surface ventral to the fracture had slipped under the fixed dorsal remainder of the bone, thus decreasing the exposed area of the occiput above the foramen magnum. This fracturing is most probably related to the factor that caused the loss of the tympanic bullae.

DENTITION. The dental arcade exhibits the U-shaped outline characteristic of Old World monkeys. The four upper incisors are missing; however, the situation of their alveoli indicates they were procumbent, and the lateral incisors were separated basally at least by a slight diastema from the canines. There is no diastema, however, between the canine and the upper third premolar.

The cross-section of the canine at its base is roughly oval, with a relatively broad front curvature. There is a distinct ridge which runs along the lingual surface of the canine, tapering posteriorly.

The third and fourth upper premolars, P^a and P^4 , are bicuspid and although the protocone of P^a is somewhat damaged, this tooth appears to be slightly narrower transversely than P^4 . At the posterior end of P^4 there is a posterior fovea, bounded by a distinct posterior crescentic ridge connecting the apices of the protocone and ectocone. The apices of the two cones of P^4 indicate greater wear than those of P^a .

The first upper molar, M^1 , is a simple quadritubercular tooth, with the two lingual cusps — protocone and hypocone — considerably worn compared with the labial cusps — metacone and paracone. There is no distinct cingular development on either side of M^1 or the other cheek teeth. Foveae are present on the anterior face of the paracone and the posterior face of the metacone. Pronounced transverse ridges connect the tips of 1) the protocone and paracone and 2) the metacone and hypocone. These ridges are not interrupted by wear.

The second upper molar, M^2 , is the largest of the three molars. It conforms closely to the basic pattern displayed by M^1 , except that the crest which connects metacone and hypocone is less clearly expressed.

The third upper molar, M^3 , is the second largest molar; it generally resembles M^2 except for a slight shortening of its anteroposterior diameter. The labial groove between paracone and metacone is more deeply incised in this tooth than in either M^1 or M^2 . The crest that connects metacone and hypocone in M^1 and M^2 is broken in M^3 between the two cusps. In this respect, the arrangement of cusps on M^3 deviates from the bilophodont pattern of the other two molars.

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