ated with this anomaly. We observed it at the beginning and end of our experiment, and the historical data suggest that the circulation features with which it may be associated persist for a few months. Its longevity may have been increased by the extreme conditions that we observed. For example, one can posit a metastable condition in which oxygen deficiency near the surface tends to maintain itself by restricting the living space of herbivores and other higher organisms. This stress would permit a higher fraction of organic material to sink from the photic zone before being consumed and would favor a shift toward the sinking of individual cells vis-à-vis rapidly sinking fecal pellets. More slowly sinking particles might favor enhanced bacterial metabolism within the shallow nitrite maximum.

On the basis of a primary production rate of 0.5 g of carbon per square meter per day, only ~10% of the primary production off Peru and Chile is required to drive a denitrification rate of 20×10^{12} g/year (*2*), so that only a modest redistribution of the carbon produced by our estimated average primary production rate of 2 g m^{-2} day^{-1} would be required to cause the observed changes.

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Paleoenvironment of the Earliest Hominoids: New Evidence from the Oligocene Avifauna of Egypt

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Analysis of fossil birds from the Oligocene Jebel Qatrani Formation in the Fayum depression of Egypt, site of the oldest known hominoid primates, allows precise paleoenvironmental reconstruction of the climatic and biotic conditions that influenced some of the earliest stages of hominoid evolution. Unlike the fossil mammals of the Fayum, which belong largely to extinct groups, most of the birds are referable to living families, with some being close to modern genera. The avifauna consists mainly of aquatic species, with such forms as jacanas (Jacanidae) and shoebilled storks (Balaenicipitidae) indicating expanses of freshwater with dense floating vegetation. An avifauna closely analogous to that of the Fayum is found today only in a limited area of Uganda, north and west of Lake Victoria, a region of swampland bordered by forest and grasslands that presents marked faunal similarities to the environment inferred for the Egyptian Oligocene.

THE EARLY OLIGOCENE FOSSIL DEposits of the Fayum depression in Egypt are renowned for having produced remains of the earliest known hominoid primates (*1–4*). The importance of these fossils to understanding evolution in the lineage thought to have given rise to *Homo sapiens* has focused interest on the nature of the environment in which these early primates lived, and the deposits have been subject to intensive modern paleontological collecting. Fossils come mainly from two intervals in the Jebel Qatrani Formation known as the upper and lower sequences that are probably early Oligocene in age (*5*, *6*). Two of the Fayum primate genera, *Aegyptopithecus* and *Propliopithecus*, are hominoids possibly ancestral to *Homo* and the modern great apes. The Fayum is the only place yet known where this stage in human ancestry is preserved, and a complete understanding of the Fayum paleoenvironment is thus essential to interpreting the adaptations of these earliest apes.

Controversy has surrounded the nature of the paleoenvironment of the Fayum deposits and its implications for the adaptations of the primates that lived there. Kortlandt (*7*), in attempting to counter the belief that the area was forested and the primates arboreally adapted, argued that the environment consisted of semiarid, almost treeless scrubland, for which reason the Fayum primates must have been terrestrial. These arguments were vitiated by Bown *et al.* (*8*) based on evidence from lithology, sedimentology, fossils of plants, vertebrates, and invertebrates, and finally from the structural adaptations of the primates themselves. They concluded that the Jebel Qatrani Formation was deposited near the coastline of the Tethyian seaway with interdigitating habitats of estuarine mangroves, fresh and brackish fluviatile swamps, and forested floodplains flourishing in a climate "typified by adequate, though probably seasonal rainfall" (*8*).

Fossil birds have hitherto played little part in the reconstruction of the paleoenvironment of the Fayum as only four taxa were recorded in the early collections. Among the modern collections is a greater variety of fossil birds that have recently been studied and identified (*9*). Although the total number of diagnostic avian specimens is only 30, a minute fraction of the total number of vertebrate fossils obtained, some 17 to 19 species are represented, indicating great diversity in the avifauna considering the small sample size. The significance of these specimens for paleoecological studies is greater than their scarcity would imply because

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most of the fossil birds are clearly referable to living families and several may be closely related to living genera. In contrast, all of the more than 37 genera and all but 6 of the 18 families of mammals described in the Fayum fauna are extinct (*4*, *10–12*). For this reason it is difficult to make many direct inferences about the Fayum paleoenvironment from the mammalian fauna.

The only birds in the fauna that cannot easily be referred to living families are two very problematic supposedly ratite-like forms (*Stromeria* and *Eremopezus*), and a distinctive new family of heron-like birds (*9*). The last was probably aquatic, whereas the "ratite" identifications are based on such fragmentary material that nothing can be said about relationships or ecology. The remaining fossil birds, by analogy with living counterparts, provide two kinds of information: (i) the habitat preference of individual species and (ii) the climatic association that can be inferred from the avifauna as a whole. The probable ecological requirements of each of the species of birds known from the Fayum deposits and the most reasonable modern counterpart for each are assessed below.

The most frequently encountered birds in the Jebel Qatrani Formation are jacanas (Jacanidae), with three species in two genera. These occur both in the upper and lower sequences. Jacanas are excellent paleoecological indicators because of their very restricted habitat requirements and because they are nonmigratory, being found only in warm, tropical climates (*13*). They have extremely long toes and associated tarsal specializations for walking on lily pads (Nymphaeaceae) and other floating vegetation. Two of the jacanas from the Fayum are much larger than any living species, implying very large lily pads or very densely matted vegetation. Fossils of Nymphaeaceae (*Nelumbo*) have been reported from the Fayum deposits (*8*). Two species of jacanas, differing mainly in size, occur sympatrically in parts of Africa today (*Actophilornis africanus* and *A. "Microparra" capensis*) and provide modern analogs for the fossils.

Another characteristic member of the Fayum fauna is a shoebilled stork (Balaenicipitidae). The distinctive single living species of shoebill, *Balaeniceps rex*, is confined to east-central Africa in a narrow belt extending from the Sudan to Zambia. These birds forage mainly on dense mats of floating plants from which they capture large fish in the massive bill by "collapsing" forcefully through the vegetation (*14*).

At least two species of herons (Ardeidae) occur in the Fayum deposits, one of which is inseparable from the modern genus of night herons *Nycticorax*, represented in Africa today by *N. nycticorax*. The other is of less certain affinity but a reasonable modern counterpart would be the purple heron, *Ardea purpurea*, a species that frequents well-vegetated areas of freshwater. Both of these species are widely distributed, though scattered, in Africa.

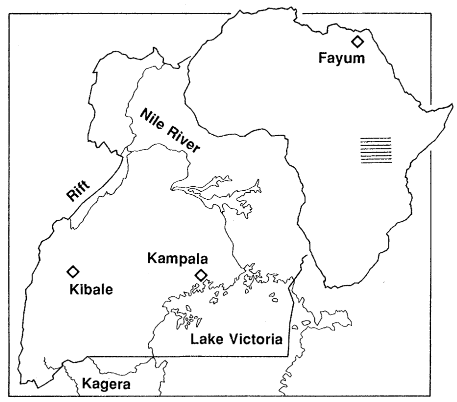

Fig. 1. The ranges of 12 of the 14 modern counterparts of Oligocene fossil birds from the Fayum, Egypt, overlap in the limited area of southwestern Uganda (hatched area in map of Africa on the right) bounded by Lake Victoria, the Nile River, the Kagera River, and the western Rift Valley (enlarged on the left). The fossil bird assemblage indicates that the Fayum during the Oligocene resembled the swamplands bordered by forests and savannas typical of areas that have been studied near modern Kampala and Kibale.

A fossil stork (Ciconiidae) from the Fayum, *Palaeoephippiorhynchus dietrichi*, was originally described as being similar to the modern saddlebill stork *Ephippiorhynchus senegalensis* (*15*), a species that occurs in various freshwater habitats throughout much of Africa. Two species of fossil flamingos (Phoenicopteridae) are present in the Fayum deposits, but these may be more closely related to the extinct genus *Palaelodus*, which had different locomotor and feeding adaptations and probably different habitat requirements than modern flamingos, which are locally abundant at large, shallow lakes in east and east-central Africa.

A small fossil crane (Gruidae) from the Fayum resembles in size the anatomically primitive crowned cranes (*Balearica*), which are widely distributed in moist areas of Africa and require dense swamp or marsh vegetation for nesting. A small rail (Rallidae) from the Fayum is similar to modern forms that occupy a variety of habitats. *Sarothrura rufa*, the most widespread species of its genus and one that preferentially inhabits thick swamp vegetation, provides a reasonable counterpart.

A fossil cormorant (Phalacrocoracidae) from the Fayum is similar in size and morphology to *Phalacrocorax carbo*, a widely distributed extant species found throughout most of eastern and southern Africa. It feeds on fish and other aquatic animals that it captures by diving.

Two fossils from the Fayum are referred to the Pandionidae. The single modern species of this family, the osprey, *Pandion haliaetus*, occurs in Africa almost entirely as a wintering bird from the north, but is widespread. Ospreys are almost entirely piscivorous and feed in both freshwater and marine situations by plunging on their prey from a height. If the habits of the fossil forms were similar, it would imply the presence of some areas of open water. An eagle from the Fayum is most similar to the genus *Haliaeetus*, whose members are also largely piscivorous and occur mainly in the vicinity of aquatic environments. The modern African fishing eagle *H. vocifer* is the only member of the genus in continental Africa and is widespread.

The only true land bird among the Fayum fossils, apart from the supposed ratites, is a turaco or plantain-eater (Musophagidae) closely resembling species of the modern genus *Crinifer* (*sensu stricto*), of which the eastern species, *C. zonurus*, may be taken to represent the fossil form. The modern musophagids are strictly arboreal and are confined to Africa, where most of the species occur in heavily forested areas. Exceptions, however, are the species of *Crinifer* and *Corythaixoides*, which inhabit more arid savanna, woodland or acacia bush.

To find an area today where an avian assemblage most similar to that of the Fayum occurs, we used the maps compiled by Snow (*16*), from which the distributions of all the modern counterparts to the Fayum birds were superimposed. Overlap between the ranges of 12 of the 14 species occurs only in a very restricted area of Uganda, north and west of Lake Victoria, including the north shore of that lake (Fig. 1). It should be noted that among the modern analogs, the taxa of more limited distribution that are the principal cause of the area of overlap being so restricted (*Balaeniceps*, *Crinifer*, and *Actophilornis*) are among those whose fossil counterparts are the most confidently identified. Snow does not report any osprey specimens from this area, but there are sight and breeding records for ospreys from the Ugandan shore of Lake Victoria (*17*, *18*). The only species absent from this area are the flamingos, which require shallow bodies of saline or brackish water, although flamingos do occur in the rift systems that flank Lake Victoria on the east and west, and estuarine environments probably suitable for modern-type flamingos occurred near the site of deposition of the Fayum fossils (*6*, *8*).

The area of Uganda indicated above is recognized as forming a distinctive faunal zone (*19*) bounded by Lake Victoria on the east, the Victoria Nile on the north, the Kagera River on the south, and the western rift system on the west (Fig. 1). The region differs from areas to the south and east of Lake Victoria in having a wetter climate and, until recently, in supporting a belt of continuous forest. The vegetation today includes a variety of moist savanna types, wooded grasslands, patches of forest, swamp, and swamp forest. Despite decades of intensive draining, swamps are abundant and widespread in Uganda, in some regions making up more than 20% of the surface area (*20*). Forest still covers 8% of the country, mostly in the southwest, although much has been cleared for human habitation, cattle grazing, and agriculture.

Eggeling (*21*, *22*) conducted floral and faunal surveys of a virgin swamp bordered by forest near Kampala, Uganda, and identified within the swamp seven successive communities that he named, on the basis of the dominant species, the lily, fringing papyrus, fern and sedge, *Limnophyton*, papyrus, *Miscanthidium*, and palm zones. The ferns and sedges grow on immense floating mats of vegetation. The following birds, among others, were found in this swamp (*21*): musophagids ("*Schizorhis*" = *Crinifer* in part, species not identified), *Balearica*, *Actophilornis*, *Phalacrocorax*, *Ephippiorhynchus*, at least three genera of rails, eight species of herons, including *A. purpurea*, and a variety of diurnal raptors. Thus, the only major groups of Fayum birds not reported in the Ugandan swamp during Eggeling's survey were flamingos and *Balaeniceps*, the last possibly having been locally extirpated. In addition, Eggeling noted three species of primates in the swamp forest. An aerial photograph of such a swamp near Kampala shows areas of floating vegetation, open channels, and papyrus fringes, bordered by extensive forest and patches of grassland (*23*). The forests near Lake Victoria have now been largely removed, but well-studied forested tracts such as Kibale Forest still exist to the west of the lake (*19*, *20*). Kibale supports an anthropoid primate community consisting of two families, five genera, and eight species (*24*), which compares very closely with the two families, four genera, and eight species known from the upper sequence of the Jebel Qatrani Formation.

By analogy with Uganda, the climate of the Fayum region of Egypt during the early Oligocene may be assumed to have been warm, annually stable, and tropical. Near Kampala, the mean monthly low temperatures are about 15°C, and the mean monthly highs are about 25°C, with little variation among months. Rainfall on the Ugandan shores of Lake Victoria averages 1520 to 2030 mm per year, and falls 160 to 170 days per year (*19*, *22*, *25*). At Kibale Forest, 100 km west of the lake, the mean annual rainfall is 1475 mm, and it falls on the average 166 days per year. The daily mean minimum and maximum temperatures at Kibale are 12.7° and 25.5°C (*24*). At both Kampala and Kibale there is only mild seasonality of rainfall, with no severe dry season.

The fossil avifauna provides strong evidence that the paleoenvironment of the Fayum during the Oligocene closely resembled modern Ugandan swamps bordered by forest and open woodland or grassland. This area of Uganda presents other striking parallels with the fauna, flora, and environment known or inferred for the Fayum. Thus, the climate and habitat of the earliest known hominoids may be projected with considerable precision and confidence. The next African hominoids to appear in the fossil record after the Fayum forms are the various species of early Miocene dryopithecines, which are known mainly from the islands and shores of modern Lake Victoria (*1*), suggesting that such environments continued to be important in hominoid evolution.

The Fayum avifauna shows that fossil birds may be an important tool for paleoenvironmental reconstruction providing a relatively direct means of interpretation comparable only to plant megafossils, for which birds provide an independent check. The persistence of Paleogene avian taxa into modern times may permit inferences to be drawn from a few dozen bird fossils that cannot be obtained from examination of thousands of mammalian teeth belonging to extinct families and genera. Paleontologists should be made increasingly aware of this underestimated resource so that avian fossils are no longer consigned to trays of scrap as so often in the past.

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