

Fossil Birds from the
Oligocene Jebel Qatrani Formation,
Fayum Province, Egypt

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ABSTRACT

Rasmussen, D. Tab, Storrs L. Olson, and Elwyn L. Simons. Fossil Birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. *Smithsonian Contributions to Paleobiology*, number 62, 20 pages, 15 figures, 1986.—Fossils from fluvial deposits of early Oligocene age in Egypt document the earliest known diverse avifauna from Africa, comprising at least 13 families and 18 species. Included are the oldest fossil records of the Musophagidae (turacos), Pandionidae (ospreys), Jacanidae (jacanas), and Balaenicipitidae (shoebilled storks). Other families represented are the Accipitridae (hawks and eagles), Rallidae (rails), Gruidae (cranes), Phoenicopteridae (flamingos), Ardeidae (herons), Ciconiidae (storks), and Phalacrocoracidae (cormorants). A highly distinctive rostrum is described as a new family, Xenerodiopidae, probably most closely related to herons. A humerus lacking the distal end is tentatively referred to the same family. Two new genera and three species of large to very large jacanas are described from the distal ends of tarsometatarsi. This Oligocene avifauna resembles that of modern tropical African assemblages. The habitat preferences of the constituent species of birds indicate a tropical, swampy, vegetation-choked, fresh-water environment at the time of deposition.

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Fossil Birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt

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Introduction

Fossils from the Oligocene Jebel Qatrani Formation of Fayum Province, Egypt, provide one of the earliest and most complete records of the continental Tertiary flora and fauna of Africa. The Fayum is best known for its early anthropoid primates, but in addition has yielded 13 other orders of mammals, including the only marsupial known from Africa, turtles, crocodiles, snakes, lizards, sharks and skates, lungfish, bony fishes, and a variety of plants and trace fossils (Bown et al., 1982; Simons and Bown, 1984; Gebo and Rasmussen, 1985).

Despite this diversity of fossil forms, very little has been known of the avifauna. Previously, only four species of birds had been described from the Fayum, all of which were named over 50 years ago (Andrews, 1904; Lambrecht, 1929, 1930). Rich (1974) mentioned, but did not describe, a fifth avian specimen, evidently a humerus belonging to the Pelecaniformes. In 1962, a large tarsometatarsus was recovered from the lower part of the Jebel Qatrani Formation. Moustafa (1974) suggested that this might belong to *Eremopezus* but it was never described and has since been lost. Apart from these few specimens from the Fayum, the only other Paleogene fossil bird hitherto reported from Africa is *Gigantornis eaglesomei* Andrews, based on a sternum from the Eocene of Nigeria belonging to the gigantic pseudo-toothed peleciform birds of the marine family Pelagornithidae (Olson, 1985).

Fossils from the Fayum are usually poorly mineralized and

quickly disintegrate when exposed to surface weathering. In recent years, however, methods have been developed for the efficient recovery of small and delicate fossils from the Jebel Qatrani sandstones (Simons, 1967). This has led to the recovery of a number of specimens of birds, mainly of smaller species than those known previously, that would never have survived normal erosional exposure on the surface. Detailed study of the intrafamilial taxonomic relationships of most of these fossils has not been attempted, as each of the species is represented by only a few fragmentary specimens. Instead, emphasis is placed on the zoogeographical and paleoecological significance of the fossil avifauna.

The 340 m thick Jebel Qatrani Formation consists mainly of variegated sandstones and mudstones deposited as point bars and overbank deposits by several meandering streams or rivers (Bown and Kraus, 1987). These sediments are exposed in a series of escarpments forming the northern rim of the Fayum depression located southwest of Cairo (Figure 1). The Jebel Qatrani Formation conformably overlies the predominantly marine sediments of the late Eocene Qasr el Sagha Formation, and is capped by the Widan el Faras Basalt which has been dated at 31 ± 1 my (Fleagle et al., 1986; see Figure 2), thus providing a minimum age for the very top of the formation (latest early or earliest middle Oligocene). The highest fossil bird and primate localities in the Jebel Qatrani Formation are 100 m below this basalt layer and are separated from it by a major erosional unconformity, making it almost certain that none of the fossils are younger than early Oligocene.

Two main fossil-producing levels occur in the Jebel Qatrani sediments, one near the top of the formation in what is known as the upper sequence, the other near the middle of the lower sequence (Bown and Kraus, 1987; these are the "Upper and Lower Fossil Wood Zones" of previous authors). The upper and lower sequences are separated by a cliff-forming marker

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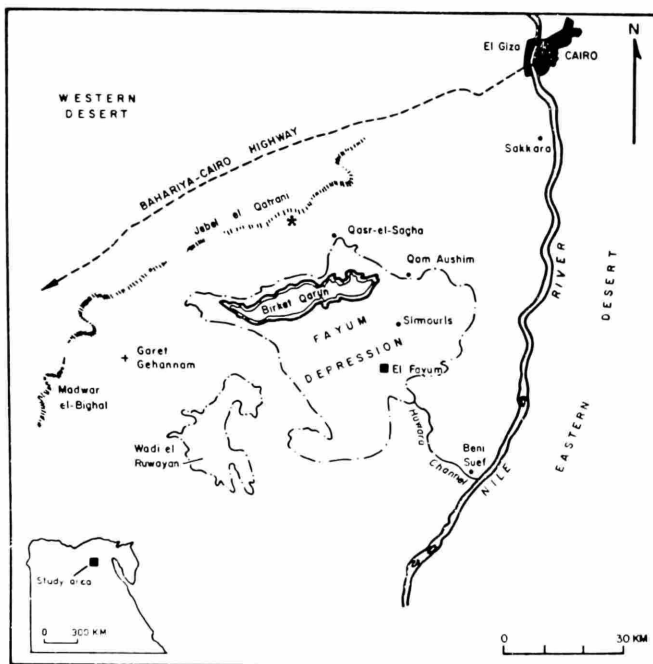


FIGURE 1.—Map of Egypt showing the position of the field camp (asterisk) and the Jebel Qatrani Escarpment in relation to the Fayum Depression and Cairo. The Jebel Qatrani Escarpment is composed of the upper 100 m of the Jebel Qatrani Formation and a resistant overlying basalt. North of the escarpment lies the Miocene Kashab Formation, immediately to the south are exposures of the Oligocene Jebel Qatrani Formation, and farther south is the marine Eocene Qasr el Sagha Formation. Most fossil-producing quarries occur within 5 km of the camp location. Modified from Bown et al. (1982).

bed called the Barite Sandstone (Figure 2).

The four previously described bird specimens from the Fayum were collected during the first decade of this century from what were then called the “fluvio-marine beds” (the fluvial Jebel Qatrani). The early expeditions collected nearly exclusively in the lower sequence, from which all four bird specimens came. When the first of these, *Eremopezus eocaenus* Andrews (1904), was described, the “fluvio-marine beds” were considered to be of late Eocene age, hence the specific name. Andrews’ (1906) list of the vertebrate fauna associated with *Eremopezus* clearly places it in the lower Oligocene, however.

Since 1960, Yale and Duke University expeditions led by Simons, in cooperation with the Egyptian Geological Survey and General Petroleum Company, have collected extensively throughout the stratigraphic range of the Jebel Qatrani Formation. The great majority of the bird bones, as well as the small mammals, come from upper sequence quarries (Figure 2).

Fossils were collected at each of the quarries by surface collecting, excavation, or a special wind-quarrying technique, described elsewhere (Simons, 1967), which is responsible for the recovery of all new bird specimens described here. The fossils were compared with recent and fossil skeletal material in the National Museum of Natural History, Smithsonian

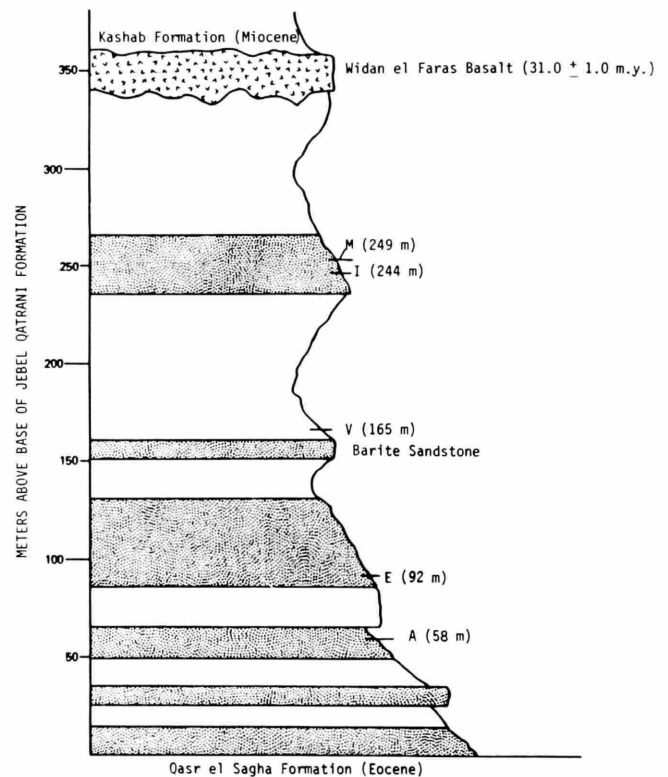


FIGURE 2.—Simplified section of the Jebel Qatrani Formation showing the stratigraphic positions of quarries that have produced birds. The sediments lying above the Barite Sandstone constitute the upper sequence, those below constitute the lower sequence. The vast majority of bird specimens have come from Quarries I and M of the upper sequence. Quarry V has not yet produced any diagnostic bird elements. Quarries E and A have each produced a single diagnostic bone (of a jacanid and accipitrid, respectively). Modified from Bown and Kraus (1987).

Institution (USNM), and the Zoology Department, Duke University. Specimens are cataloged in the collections of the Cairo Geological Museum (CGM) and the Duke University Primate Center (DPC). The sequence of taxa generally follows that in Olson (1985).

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Systematic Paleontology

Order and Family Indeterminate

Eremopezus eocaenus Andrews, 1904

HOLOTYPE.—Distal end of left tibiotarsus, British Museum (Natural History) A843.

TYPE LOCALITY AND HORIZON.—North of Birket Qarun, lower sequence, Jebel Qatrani Formation.

REMARKS.—Andrews (1904, 1906) compared this rhea-sized tibiotarsus with a variety of ratites and concluded that it combined features of several of them, while at the same time it differed widely from all other birds, ratite or carinate. He declined to assign the specimen to any higher level taxon except "Order Ratitae" (Andrews, 1906:258). With considerable doubt, he also referred a pedal phalanx recovered from the same pit to this species. This was "remarkable for the breadth and depth of its proximal end compared with the distal" (Andrews, 1906:260).

Andrews always expressed great uncertainty as to the relationships of *Eremopezus*. Rothschild (1911) placed *Eremopezus* in its own subfamily, Eremopezinae, of the Aepyornithidae, the elephantbirds of Madagascar. This was presumably because of his belief that it was a "general type intermediate between *Aepyornis* and *Struthio*" (Rothschild, 1911:149). The name Eremopezinae is thus attributable to Rothschild (1911), rather than to Lambrecht (1933) as usually cited (e.g., Brodkorb, 1963). Lambrecht (1933) also included *Eremopezus* in its own subfamily in the Aepyornithidae on the basis of deep ligamental pits on the lateral and medial sides of the condyles. See additional remarks on this species below.

Stromeria fajumensis Lambrecht, 1929

HOLOTYPE.—A broken and much worn distal end of a right tarsometatarsus lacking all but the bases of the trochleae; specimen in Munich.

TYPE LOCALITY AND HORIZON.—North of Dimeh, Fayum, Jebel Qatrani Formation.

REMARKS.—The spelling *fajumensis* was used consistently in the original publication (Lambrecht, 1929), the emendation to *fayumensis* (Lambrecht, 1933) being unjustified. Lambrecht assigned this specimen to the Aepyornithidae on the basis of a projecting crest on the plantar surface of the shaft, a feature he considered to be shared with the similarly-sized *Mullerornis betsilei* Milne-Edwards and Grandidier. He found the similarity compelling enough to suggest that *Stromeria* represents a direct ancestor of Malagasy aepyornithids. We feel that such conclusions are not justified by the extremely poor nature of

the specimen. Judging from Lambrecht's (1929) photographs, the plantar crest actually differs considerably in shape and proportions from that of *Mullerornis*.

At no point did Lambrecht (1929, 1933) ever state why *Eremopezus eocaenus* and *Stromeria fajumensis*, known only from noncomparable elements, should belong to different species, genera, and subfamilies. Perhaps this was because the specimen of *Eremopezus* was judged to be markedly different from typical aepyornithids, whereas that of *Stromeria* was not.

The distal width of the tibiotarsus of *Eremopezus* was given as 48 mm (Andrews, 1904) and that of the tarsometatarsus of *Stromeria* as 55 mm (Lambrecht, 1929). In modern cursorial ratites such as *Rhea*, the distal ends of the tarsometatarsus and tibiotarsus are about equal in width, but in other ratites the distal end of the tarsometatarsus may be more expanded. Thus in the Aepyornithidae the distal width of the tibiotarsus is 93–95% of the distal width of the tibiotarsus (data from Andrews, 1904; Milne-Edwards and Grandidier, 1869), and in moas 70–80% (data from Oliver, 1949). Therefore, with the width of the tibiotarsus of *Eremopezus* being 87% of the width of the tarsometatarsus of *Stromeria*, it is entirely conceivable that both may be referable to a single genus or species, particularly given the likelihood of individual and sexual differences in size.

In summary, there is no compelling evidence to suggest that more than one species of ratite-like bird is represented in the Fayum deposits, a point previously noted by Moustafa (1974), and the material is insufficient to determine with confidence anything about the relationships of the bird. As Andrews (1904:170) himself stated, with his characteristic insight: "*Eremopezus* may be merely another instance of retrogressive modification leading to loss of flight and increase of bulk in a group of Carinate birds, such as has occurred in the case of the Stereornithes, the Gastornithes, and probably in most of the early so-called Ratite birds."

Ratites are usually associated with open grassland and savanna, but since this is not true of cassowaries or moas, the supposed ratite of the Fayum tells us nothing about the environment in which it lived.

Order CUCULIFORMES

Family MUSOPHAGIDAE

Genus and Species Indeterminate, aff. *Crinifer*

FIGURES 3, 4

MATERIAL EXAMINED.—CGM 42836, distal end of left tarsometatarsus (Figure 3); CGM 42837, distal end of right humerus (Figure 4).

LOCALITY AND HORIZON.—Both specimens are from Quarry M, upper sequence.

MEASUREMENTS.—Tarsometatarsus CGM 42836: distal width,



FIGURE 3.—Anterior view of distal end of left tarsometatarsus (CGM 42836) of a turaco (Musophagidae) resembling *Crinifer*.

9.4 mm; width and depth of shaft, 4.8×3.2 mm. Humerus CGM 42837: distal width, 14.0 mm; depth of external condyle, 6.9 mm; width and depth of shaft at midpoint, 5.8×5.0 mm.

COMPARISONS.—The tarsometatarsus lacks part of the inner trochlea, and the middle trochlea is somewhat abraded but preserves a deep trochlear groove (Figure 3). The specimen lacks the unusual configuration of the outer trochlea seen in *Musophaga* and to a lesser extent in *Tauraco* and *Corythaeola*. The distal foramen is small and discrete, as in *Crinifer* and unlike the double opening, with the distal foramen partially separated from the intertrochanteric foramen, observed in *Musophaga*. The condition in *Corythaeola* shows an approach to that of *Musophaga*. The fossil is indistinguishable from specimens of the extant genus *Crinifer* except that it is larger than in any modern musophagids except *Corythaeola*.

The humerus is slightly abraded at the distal end but is intact as far as the pectoral crest (Figure 4). The entepicondylar process is large, extending distally well beyond the condyles, the brachial depression is small, and the shaft is distinctly curved. The modern genera of musophagids are not readily distinguished from one another on the basis of characters of the humerus. The fossil is somewhat larger than in any of the extant forms except *Corythaeola* and hence is of a size



FIGURE 4.—Palmar view of distal end of right humerus (CGM 42837) of a turaco (Musophagidae) resembling *Crinifer*.

compatible with being from the same species as the tarsometatarsus.

REMARKS.—Previously, fossils of Musophagidae had been reported from the late Oligocene of Bavaria and the early Miocene of France and Kenya (Olson, 1985). Thus the Fayum fossils provide the earliest record for the family. That they cannot be distinguished generically from extant forms indicates that the humerus and tarsometatarsus of at least some musophagids have probably not evolved appreciably since the Oligocene. The greater resemblance of the fossils to *Crinifer* may only reflect the fact that this genus appears to be the most primitive of modern musophagids in tarsal morphology.

The modern species of *Crinifer* tend to prefer open parkland and woodland as opposed to the mesic, densely canopied forest frequented by most musophagids. Musophagids are among the

most primitive living birds (Olson, 1985), and as Stegmann (1978) has noted, the young are slow in developing and use the wings, which have claws on the alular and major digits, to clamber about in trees. All modern musophagids are strictly arboreal and frugivorous, and the Fayum birds may thus have relied to some extent on the same food sources as the contemporaneous primates.

Order "FALCONIFORMES"

Family ACCIPITRIDAE

Genus and Species Indeterminate, aff. *Haliaeetus*

MATERIAL EXAMINED.—DPC 1652, distal end of left tarsometatarsus.

LOCALITY AND HORIZON.—Quarry A, lower sequence.

MEASUREMENTS.—Distal width, 23.9 mm; distance between distal foramen and external intertrochlear space, 4.6 mm.

COMPARISONS.—This specimen comes from a large accipitrid similar in size and morphology to modern eagles of the genus *Haliaeetus*. The distal foramen is large and situated far distally, and the trochleae are widely spaced, in both of which features the specimen differs markedly from the Old World vultures (Gypaetinae or Aegypiinae auct.). The internal intertrochlear space is wider than in any of the modern genera of Accipitridae examined. There is a distinct muscle scar on the ridge between the facet for metatarsal I and the inner trochlea. This is variably present in some extant genera of Accipitridae, being especially noticeable in *Gypohierax*. The strong buttressing along the lateral edges of the shaft that is characteristic of *Aquila* and buteonine hawks, is absent in the fossil. The overall similarity of the fossil is greatest to modern kites and eagles of the genera *Milvus* and *Haliaeetus*, which are closely related in any case (Olson, 1982), and to the more distantly related African palm-nut vulture, *Gypohierax*.

REMARKS.—The intrafamilial systematics of modern Accipitridae is still very poorly understood and it is hazardous to attempt to determine the closest relationships of isolated fossils of hawks and eagles. The overall morphology of the Fayum fossil suggests that it could be from a fishing eagle allied with *Haliaeetus*, the modern forms of which are hunting and scavenging birds that frequent bodies of fresh water and seacoasts. During deposition of the lower sequence, where this specimen was found, the Fayum was situated much closer to the seacoast than during deposition of the upper sequence (Bown and Kraus, 1987). Similarities to *Gypohierax* may reflect shared primitive characters. The monotypic living genus *Gypohierax* is specialized in its food habits, subsisting mainly on nuts of the oil palm. It may be the sole remnant of a group that was perhaps more diverse and widespread in the past. For example, the early Miocene accipitrid *Palaeohierax* from France has been noted by several authors as being closely related to *Gypohierax* (see Olson, 1985).

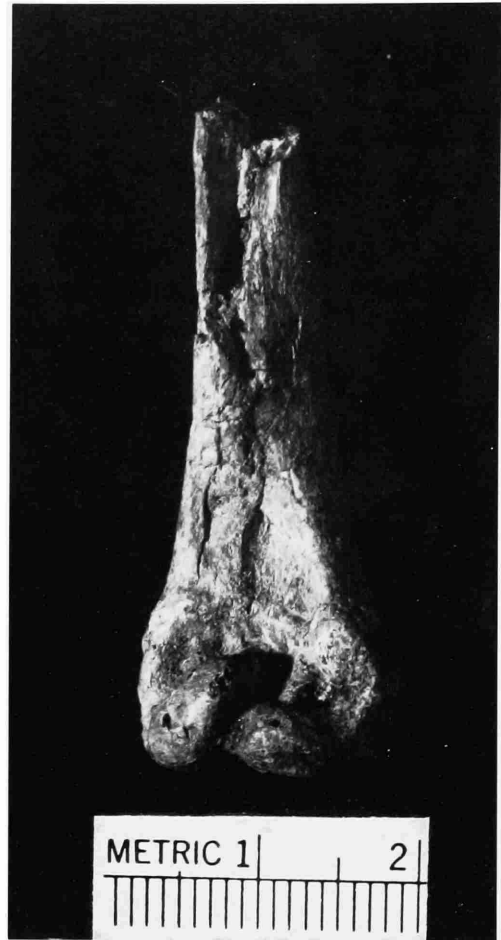


FIGURE 5.—Palmar view of distal end of right humerus (DPC 3082) of an osprey (Pandionidae) resembling *Pandion*.

The Accipitridae are fairly common in the fossil record, which extends at least as far back as the late Eocene or early Oligocene. The present specimen constitutes the first Paleogene record of the family for Africa.

Family PANDIONIDAE

Genus and Species Indeterminate, aff. *Pandion*

FIGURE 5

MATERIAL EXAMINED.—DPC 3082, distal end of right humerus (Figure 5).

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—Distal width, 16.9 mm; depth of external condyle, 10.2 mm.

COMPARISONS.—The skeleton in the Pandionidae differs markedly from that in the Accipitridae, the humerus being of a rather generalized waterbird type that is more similar in some respects to that in certain Pelecaniformes than to the

Accipitridae. The Fayum fossil is most similar to the humerus in *Pandion* and the Phaethontidae, differing from the latter in the shallower, less pronounced olecranal fossa and in details of shape and position of muscle scars (Figure 5). The fossil is essentially identical to the extant species of *Pandion* except for its smaller size, relatively narrower breadth across the brachial depression, and the presence of a small, deep pit between the internal condyle and the attachments of the anterior articular ligament.

REMARKS.—Fossil ospreys, all referable to the extant genus *Pandion*, have been identified from the middle Miocene of California, and the late Miocene and early Pliocene of Florida and North Carolina (Warter, 1976; Becker, 1985; Olson, 1985). The Fayum record is thus the earliest for the family and the first fossil record for Africa. The living osprey is practically cosmopolitan in distribution, although in Africa it occurs almost entirely as a migrant, with only scattered nesting records (Chorley, 1939; Snow, 1978). The osprey subsists almost entirely on fish captured by diving, usually from a considerable height, and because of its diet is necessarily restricted to aquatic and marine environments. If the habits of the fossil form were similar, it would mean that a certain amount of open, relatively shallow water was present near the site of deposition.

?PANDIONIDAE, Genus and Species Indeterminate

MATERIAL EXAMINED.—DPC 1929, damaged right carpometacarpus.

LOCALITY AND HORIZON.—Quarry I, upper sequence.

MEASUREMENTS.—Length, 85.0 mm; width of trochlea, 9.7 mm; breadth of distal articular surface, approximately 10.3 mm.

COMPARISONS.—The very short distal symphysis and the broad, curved, distal base of the minor metacarpal indicate that this specimen is from a raptorial bird. The proximal base of the minor metacarpal is not as offset ventrally from the carpal trochlea as in the Accipitridae, and the facet for digit II is a strong crest rather than a weak protuberance as in the Accipitridae. In both respects the fossil is more similar to the Pandionidae. The specimen is in the size range of the modern osprey, *Pandion haliaetus*, but is slightly more robust and may have come from a species larger than the preceding one.

Order GRUIFORMES

Family RALLIDAE

Genus and Species Indeterminate

MATERIAL EXAMINED.—DPC 3858, distal end of left tarsometatarsus.

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—Distal width, 4.5 mm.

COMPARISONS.—The posterior portions of the inner and

outer trochleae have been lost through abrasion. These two trochleae are shorter than the middle one and are deflected posteriorly, but considerably less so than in the Charadriiformes or in *Turnix*. The middle trochlea has a distinct groove whereas the other two trochleae are smooth and rounded; the distal foramen is large, with a deep tendinal groove. In these features, and in size, this specimen resembles small rails of the genera *Sarothrura*, *Coturnicops*, and *Laterallus*, but the fossil is otherwise much too incomplete to be able to ascertain its relationships within the large and relatively homogeneous family Rallidae.

REMARKS.—Although the Rallidae may well have existed throughout most of the Tertiary, their record prior to the Oligocene is based on very unsatisfactory material that has not been certainly identified. The Fayum specimen is the earliest rail thus far reported from Africa. Although some modern species of rails occur in moist forests or in grasslands, most species inhabit well-vegetated marshes.

Family GRUIDAE

Genus and Species Indeterminate

MATERIAL EXAMINED.—DPC 5330, distal end of left tarsometatarsus and portions of shaft.

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—Distal width, 14.9 mm; depth of middle trochlea, 6.4 mm; approximate shaft depth, 5.6 to 5.9 mm, and shaft width, 5.3 to 5.6 mm.

COMPARISONS.—The trochleae are well preserved except for the proximo-ventral portion of the middle trochlea. The bone is broken and incomplete immediately proximal to the trochleae, but a distal section of shaft 80 mm in length is intact. The second and fourth trochleae are shorter than the middle one and are deflected posteriorly. The specimen resembles gruids (including *Aramus*) and differs from the somewhat similar Phoenicopteridae in the distinct protruding wing at the ventro-distal extremity of the second trochlea, the less deeply furrowed middle trochlea, and the shallower, hollowed ventral area immediately proximal to the trochleae.

The specimen resembles *Balearica* and *Anthropoides* and differs from *Aramus* in the more elevated second trochlea, and in the lateral profile of the middle trochlea, which is slightly compressed dorsoventrally rather than rounded. The tarsometatarsus differs from all modern gruids in two details. The wing on the second trochlea is weaker and more distally produced, rather than being distinctly hooked proximally; and the shaft is as deep or deeper than it is wide. In size, the Fayum fossil is intermediate between the smaller *Aramus* and the larger *Anthropoides virgo*, although closer to *Aramus*.

REMARKS.—The Fayum specimen is the earliest crane recorded from Africa. A diversity of small to medium-sized cranes resembling the crowned cranes of the modern African genus *Balearica* have been reported from Europe and North

America (Olson, 1985). The forms of *Balearica* are smallish cranes that today occur in wet habitats across much of sub-Saharan Africa. They may forage in open grasslands, but nest only in heavily vegetated swamps where the cover is thick and high enough to hide the birds (Johnsgard, 1983). *Balearica*, alone among modern cranes, frequently roosts in trees. The diet includes a diversity of animal and vegetable foods.

Order CHARADRIIFORMES

Family JACANIDAE

The distinctive lily-trotters or jacanas are represented by a diversity of species in the Fayum deposits, all of the elements recovered so far being the distal ends of tarsometatarsi, which are highly distinctive in having the huge distal foramen, broad tendinal groove, and flattened shaft unique to this family.

Modern jacanas are much oversplit at the generic level, with the seven or eight species being placed in six genera. A more realistic classification is that of Strauch (1976), who recognized only two genera based on differences in morphology and plumage of the wing. In *Jacana* (including *Hydrophasianus*) the wings are distinctly patterned, the radius is unmodified, and there is a strong carpal spur. In *Metopidius* (including *Actophilornis*, *Microparra*, and *Irediparra*), the wings are unpatterned, the carpal spur is lacking, and the radius is greatly expanded distally into a unique broad blade. Fry (1983) has noted that *Microparra capensis* is apparently a neotenic form of *Actophilornis*, and although the radius is not greatly expanded in this species, it may secondarily have reverted to the primitive condition. Fry's classification, in which all jacanas are lumped under the genus *Jacana* except for the monotypic genera *Microparra* and *Hydrophasianus*, is at odds with the preceding characters and Fry's own observations. Except for the modifications of the wing, there are no major differences in osteology between the various modern species of jacanas.

Nupharanassa, new genus

TYPE SPECIES.—*Nupharanassa bulotorum*, new species.

DIAGNOSIS.—Differs from all modern Jacanidae in having the distal foramen of the tarsometatarsus much larger, not circular in outline but tapering proximally to produce a tear-drop shape; trochleae more nearly in the same proximo-distal plane, the inner and outer trochleae being more distally produced relative to the middle trochlea; scar for hallux and the opposite lateral portion of the posterior surface of shaft more excavated; anterior portion of shaft lateral to distal foramen more expanded and flattened.

ETYMOLOGY.—Greek *nouphar* (Latin *nuphar*), a waterlily, plus *anassa*, a queen. From the association of jacanas with waterlilies, the large size of the fossil forms relative to modern jacanas, and in allusion to the giant waterlily *Victoria regia*,

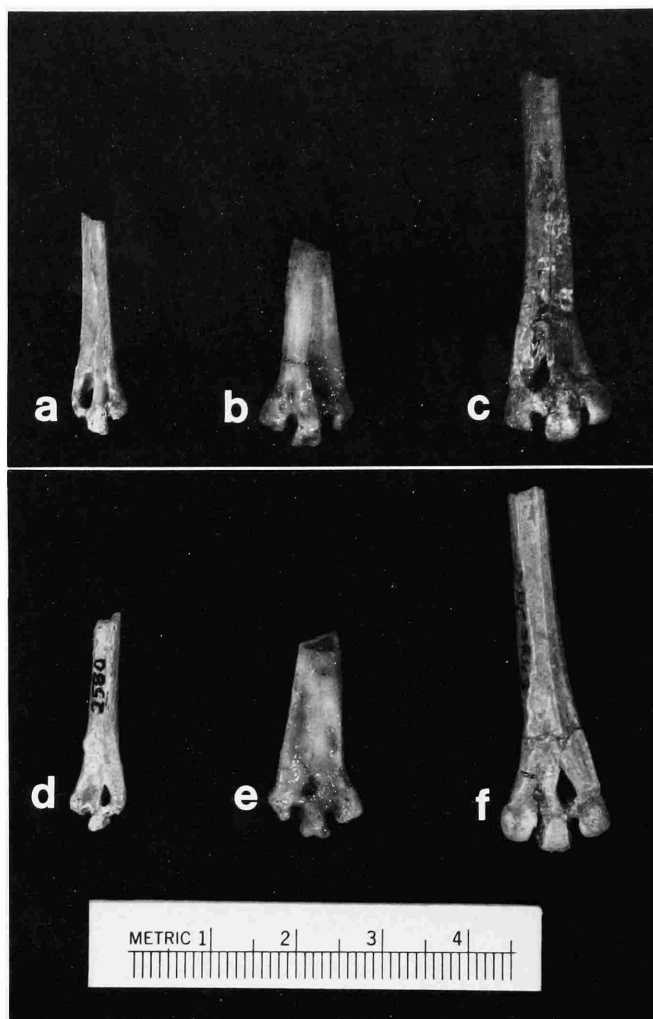


FIGURE 6.—Anterior (top row) and posterior (bottom row) views of distal ends of tarsometatarsi of Jacanidae: a,d, right tarsometatarsus, holotype of *Nupharanassa tolutaria*, new genus and species (DPC 2850); b,e, left tarsometatarsus, holotype of *Janipes nymphaeobates*, new genus and species (CGM 42839); c,f, right tarsometatarsus, holotype of *Nupharanassa bulotorum*, new genus and species (DPC 3848). All to same scale.

also named for a queen. The gender is feminine.

Nupharanassa bulotorum, new species

FIGURE 6c,f

HOLOTYPE.—DPC 3848, distal end of right tarsometatarsus (Figure 6c,f).

TYPE LOCALITY AND HORIZON.—Quarry M, Fayum Province, Egypt. Upper sequence of the Jebel Qatrani Formation, Lower Oligocene. Collected by R.H. Madden.

MEASUREMENTS OF HOLOTYPE.—Width at base of trochleae, 11.4 mm; distal width, 12.2 mm; length of distal foramen, 3.6 mm.

REFERRED SPECIMENS.—DPC 5327, distal end of left

tarsometatarsus lacking the distal portions of the trochleae, from Quarry M; DPC 5328, distal end of left tarsometatarsus lacking lateral portion of shaft and outer trochlea, also from Quarry M.

DIAGNOSIS.—Much larger than any previously known species of Jacanidae, being some 30 to 35 percent larger than a male of *Metopidius indicus*, the largest living species.

ETYMOLOGY.—“Of large lotuses” from Latin, *bu*, large, and the genitive plural of *lotus* (from the Greek *lotos*).

REMARKS.—The referred specimens are smaller than the holotype but probably fall within the size range of the species, given the pronounced sexual dimorphism in size in extant jacanas. In the holotype there is no osseous bridge defining the intertrochlear foramen, so that this opening is continuous with the distal foramen. It is difficult to say whether the absence of this bridge is normal or due to wear, though there is no clear sign of breakage. By contrast, there is a distinct intertrochlear foramen in the referred specimen, DPC 5327.

Nupharanassa tolutaria, new species

FIGURE 6a, d

HOLOTYPE.—DPC 2580, distal end of right tarsometatarsus lacking most of the inner and outer trochleae and part of the middle trochlea (Figure 6a,d).

TYPE LOCALITY AND HORIZON.—Quarry E, Fayum Province, Egypt. Lower sequence of the Jebel Qatrani Formation, Lower Oligocene. Collected by R.F. Kay.

MEASUREMENTS.—Width at base of trochleae, 6.5 mm; length of distal foramen, 2.4 mm.

DIAGNOSIS.—Although badly damaged, the specimen preserves most of the characters distinguishing *Nupharanassa* from other jacanas. The species is much smaller than *N. bulutorum*, falling within the size range of all but the smallest species of modern jacanas.

ETYMOLOGY.—Latin, *tolutarius*, trotting; from the modern name “lily-trotter,” often applied to the jacanas.

REMARKS.—This specimen is significant in that it comes from the lower sequence, about 150 m below the other Fayum fossils of jacanas. Although the mammalian faunas of the upper and lower sequences are broadly similar, few species overlap both levels, and in some cases genera or families present at one level are absent from the other (for example, the propliopithecoid primates occur only in the upper quarries). The two levels thus represent two significantly different temporal and ecological assemblages. The entire 340 m of the Jebel Qatrani evidently represents a period of time on the order of 8–10 million years, 150 m may span 3–4 million years or more, and the presence of a jacana in the lower sequence thus suggests that ecological conditions suitable for jacanas probably persisted throughout at least the major period of fossil deposition in the Jebel Qatrani Formation.

Janipes, new genus

TYPE SPECIES.—*Janipes nymphaeobates*, new species.

DIAGNOSIS.—Differs from *Nupharanassa* and all living jacanas in the proportionately much smaller size of the distal foramen, the relatively broader and more flattened shaft, the slightly wider intertrochanteric notches, and the more excavated anterior and posterior portions of the lateral part of the shaft.

ETYMOLOGY.—“Foot with an arched passageway,” from Latin *janus*, arched passageway, connecting vowel “i,” plus *pes*, foot; for the distinctive shape of the large distal foramen as it passes through the bone. The gender is masculine.

Janipes nymphaeobates, new species

Figure 6b,e

HOLOTYPE.—CGM 42839, distal end of left tarsometatarsus, with abraded trochleae (Figure 6b,e).

TYPE LOCALITY AND HORIZON.—Quarry M, Fayum Province, Egypt. Upper sequence of the Jebel Qatrani Formation, Lower Oligocene. Collected by J.G. Fleagle.

MEASUREMENTS.—Width at base of trochleae, 9.2 mm; length of distal foramen, 1.9 mm.

DIAGNOSIS.—This species exceeds all extant forms in size, but is smaller than *Nupharanassa bulutorum*.

ETYMOLOGY.—Greek, *nymphaia* (Latin stem *nymphae-* plus connecting vowel “o”), waterlily, and *bates*, a walker; again from the habits of jacanas of walking on waterlilies.

REMARKS.—The only Tertiary member of the Jacanidae yet recognized is the much younger *Jacana farrandi* Olson from the late Miocene (latest Clarendonian and early Hemphillian) of Florida (Olson, 1976; J. Becker, personal communication). The Fayum specimens constitute the earliest record of the family and the first for Africa. *Janipes* exhibits derived features that indicate the Oligocene radiation of this family involved more than just size differentiation. Nevertheless, the large size of both upper sequence taxa is remarkable. The only modern species of jacanas that are sympatric are “*Actophilornis*” *africanus* and “*Microparra*” *capensis* in Africa, which differ greatly in size, and *Metopidius indicus* and “*Hydrophasianus*” *chirurgus* in Asia, which belong to the two different groups of jacanas and also differ, though less significantly, in size.

The habitat requirements of jacanas are quite restricted. They are found exclusively in tropical regions on quiet bodies of fresh water with lush floating vegetation, particularly Nymphaeaceae. Their toes are greatly expanded as an adaptation for spreading their weight over a greater area to prevent sinking into the vegetation, which accounts for the extreme specialization of the tarsometatarsus. The Fayum jacanas are similarly adapted, so similar habitats must have been present at the time of deposition. In addition, the much larger size of two of the fossil forms suggests that the

vegetation present was particularly dense or that the species of Nymphaeaceae present were very large.

The value of jacanas as paleoenvironmental indicators is of special interest with regard to *Nupharanassa tolutaria*, which comes from the enigmatic Quarry E. This has yielded a higher proportion of shark teeth and skate plates than other Fayum quarries. The small size and poor condition of other fossils in parts of this quarry appear to indicate that they have been reworked or transported some distance. The occurrence of a strictly fresh-water species such as the jacana, along with skates and sharks, which prefer brackish or salt water, tends to support this conclusion.

Family PHOENICOPTERIDAE

Genus Indeterminate, aff. *Palaelodus*, species 1

FIGURES 7, 8a

MATERIAL EXAMINED.—DPC 5326, abraded distal end of right tibiotarsus (Figure 7). DPC 2646, proximal and distal ends of a left carpometacarpus lacking the intermediate portions of the major and minor metacarpals (Figure 8a). DPC 3083, proximal end of left carpometacarpus.

LOCALITY AND HORIZON.—Carpometacarpus DPC 3083, and tibiotarsus 5326, Quarry M; carpometacarpus DPC 2646, Quarry I; all upper sequence.

MEASUREMENTS.—Carpometacarpus DPC 2646: proximal depth, 11.8 mm; width of trochlea, 4.8 mm; distal depth \times width, 5.9×3.9 mm. Tibiotarsus DPC 5326: distal width 10.8 mm; condylar depth, 10.4 mm (a minimum figure as the condylar edges are abraded).

COMPARISONS.—The tibiotarsus, DPC 5326, has a deep, distinct anterior intercondylar fossa as in the Phoenicopteridae and Ciconiidae (Figure 7). Unlike the latter, the fossa is not round, but rather trapezoidal in shape, and the lateral part of the fossa extends deeply into the proximal part of the external condyle (see Olson and Feduccia, 1980), a feature not present in ciconiids, nor in other Charadriiformes. The distal opening of the tendinal foramen is separated from the intercondylar fossa by a distinct ridge of bone that extends medially to the internal condyle, a distinctive characteristic of flamingos. The anterior intercondylar tubercles, although abraded, appear to have been weak, and the peroneal grooves on the lateral part of the external condyle are absent. In these details the Fayum specimen differs from modern flamingos and more closely matches specimens of *Palaelodus*.

The Fayum tibiotarsus differs from that of *Palaelodus* primarily in the absence of a strong protuberance on the lateral surface of the external condyle, and the slightly smaller size of the tendinal foramen. In size, the fossil closely matches the holotype of *Palaelodus gracilipes* Milne-Edwards.

One of the two carpometacarpi, DPC 3083, is poorly preserved, but so far as can be determined agrees in detail with



FIGURE 7.—Anterior view of distal end of right tibiotarsus (DPC 5326) of a flamingo (Phoenicopteridae) resembling *Palaelodus*. The porous appearance of the condylar edges is due to abrasion that has removed the smooth outer surface.

the other carpometacarpus, DPC 2646, to which all following comments pertain. The fossil resembles the carpometacarpus in the Phoenicopteridae (especially *Palaelodus*) and Podicipedidae in having a straight, splint-like minor metacarpal that runs closely parallel with the major metacarpal, leaving a narrow intermetacarpal space (Figure 8a,b). Other features



FIGURE 8.—Internal views of left carpometacarpi of fossil flamingos (Phoenicopteridae): *a*, middle Oligocene specimen from the Fayum (DPC 2646); *b*, late Oligocene to early Miocene (Aquitanian) specimen of *Palaelodus crassipes* from France (USNM 256086). The shape of the alular metacarpal in the specimen of *Palaelodus* has been altered somewhat by severe abrasion. The length of the Fayum specimen is unknown, but was probably shorter than the specimen of *Palaelodus*, as indicated.

that the fossil shares with flamingos and grebes include the facet for digit III, which is indistinct and proximal to that for digit II, and the long distal symphysis, which is not as extensive as in modern flamingos, but closely resembles the condition

in *Palaelodus*. The Fayum specimen differs further from the Podicipedidae and resembles *Palaelodus* in having the dorsal process of the alular metacarpal much larger and shaped as in the Charadriiformes. It differs from all other phoenicopterids in having a deep excavation on the internal side of the base of the alular metacarpal. The Fayum carpometacarpus is smaller than specimens of *Palaelodus crassipes* Milne-Edwards at USNM, and is about the size expected for *P. gracilipes*. Since the carpometacarpi and tibiotarsi come from the same stratigraphic level, and all are from a bird the size of *P. gracilipes*, it is likely that they represent a single species.

REMARKS.—See account under following species.

Genus Indeterminate, species 2

MATERIAL EXAMINED.—DPC 5513, fragment of left coracoid lacking sternal end, furcular facet, and tip of procoracoid.

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—DPC 5513: medio-lateral width at narrowest point of shaft, 7.1 mm; length and width of glenoid facet, 7.0×6.7 mm.

COMPARISONS.—This specimen has the stout shaft with a marked “waist” and the large medially-projecting perforate procoracoid that distinguishes flamingos from storks and other large waterbirds. It agrees closely with modern flamingos and with the extinct genus *Palaelodus* as well. The procoracoid is slightly smaller and more gracile than in most specimens of *Phoenicopterus* spp., but resembles that in *Palaelodus*. The scapular facet is proportionately smaller than in *Phoenicopterus* or *Palaelodus*. The fossil resembles modern flamingos in the absence of a strong ridge running down a short distance from the furcular facet on the postero-medial side of the head, a feature that is prominent in specimens of *Palaelodus*. The size of the Fayum coracoid matches that of *Palaelodus crassipes* and the living species *Phoeniconaias minor*.

REMARKS.—Flamingos are fairly common in the fossil record, with described species from North America, Europe, Africa, and Australia (Olson and Feduccia, 1980; Olson, 1985). The Fayum specimens are the earliest recorded flamingos from Africa. They evidently represent at least two species—a small one within the size range of *Palaelodus gracilipes* of the European early Miocene (Aquitanian); and a larger species in the range of *P. crassipes*. The morphology of the smaller specimens suggests a rather close affinity with *Palaelodus*, while the generic relationships of the larger species are not evident.

Modern flamingos are normally gregarious birds that prefer open, shallow water, usually saline or alkaline, in which they filter feed for microorganisms. The genus *Palaelodus* has shorter tibiotarsi and shorter, more laterally compressed tarsometatarsi than the modern flamingos, possibly an adaptation for swimming (Olson and Feduccia, 1980). Because the Fayum flamingos cannot be definitely referred to modern genera, their habitat requirements are uncertain, except that

they would not have occurred far from water.

Order "CICONIIFORMES"

The traditional order Ciconiiformes appears to be a polyphyletic assemblage (see Olson, 1979, 1985) and there are considerable uncertainties surrounding the relationships of the herons (Ardeidae) in particular. Even more uncertainty attaches to two additional fossil specimens that we have not been able to refer to any living family of birds. These, a rostrum and most of a humerus, are among the best preserved of the avian

fossils from the Fayum (Figures 9–11). They share more similarities with herons than with any other group of birds, but are so distinctly different that a new family is warranted for them.

The rostrum is very heavily ossified, with the ventral bars of the premaxillae completely fused so that the ventral surface of the rostrum is covered with bone as in the core Ciconiiformes, Ardeidae, and Pelecaniformes. The fossil rostrum differs from all of those groups except the Ardeidae in having large, open nostrils with narrow, well-defined nasal bars. The diagnosis therefore emphasizes the characters

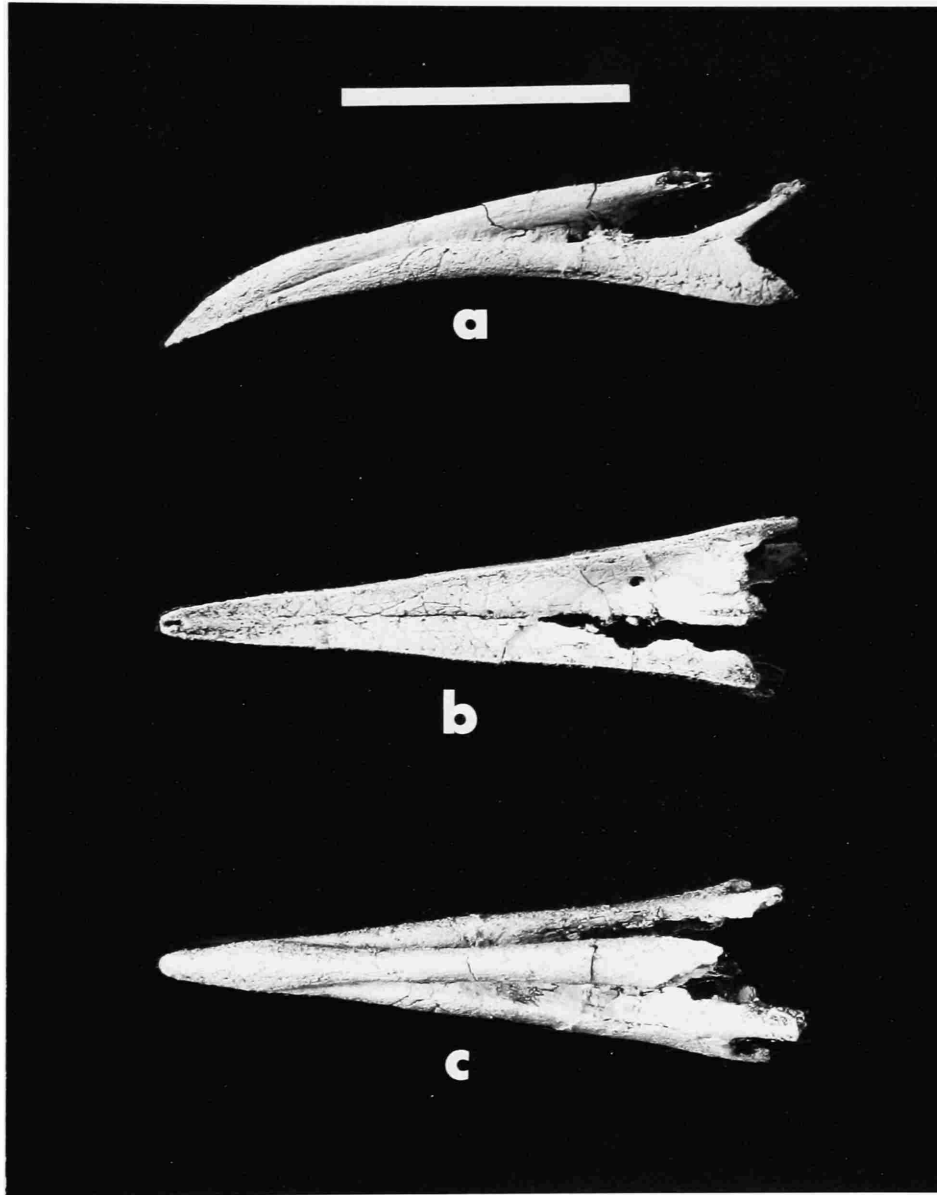


FIGURE 9.—Rostrum (holotype, DPC 3088) of *Xenerodiops mycter*, new genus and species: a, left lateral view; b, dorsal view; c, ventral view. About natural size, bar = 40 mm.

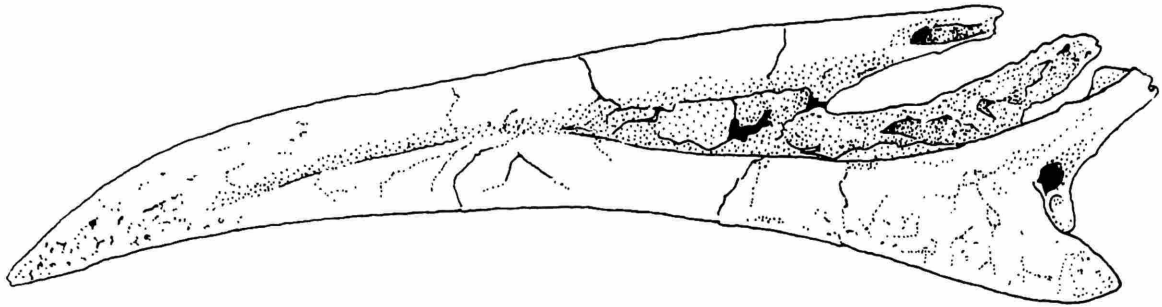


FIGURE 10.—Drawing of the rostrum (holotype, DPC 3088) of *Xenerodiops mycter*, new genus and species, in left lateral view. About five-thirds natural size (total length of specimen, 88 mm).

differentiating the new family from the Ardeidae.

Family XENERODIOPIDAE, new family

TYPE GENUS.—*Xenerodiops*, new genus.

DIAGNOSIS.—The rostrum is heavy and decurved, with well-defined lateral grooves that delimit a somewhat swollen terminus, quite unlike the straight, sharply pointed rostrum of herons. The dorsal bar is narrow and deep, and does not become expanded and flattened posteriorly as in the Ardeidae. It appears that the nasal septum may have been completely ossified (although it is broken posteriorly so this cannot be determined with certainty), whereas in the Ardeidae there is practically no indication of an ossified nasal septum. The nasal bars are thick and almost cylindrical, unlike the thin flattened nasal bars in the Ardeidae. The posterolateral corner of the premaxilla is a large, deep, posteriorly directed flange above which the quadratojugal bar articulates at some distance dorsally; in herons this is a slender process that runs under, and is in contact with, the quadratojugal bar. The humerus is on first appraisal heron-like but more robust, with a more expanded and triangular pectoral crest and a more rounded bicipital crest that is much more distinctly set off from the shaft. Unlike herons or any of the “core” Ciconiiformes, the tricipital fossa is excavated and not pneumatic, although there are a few small foramina around the proximal margin, as in the Phoenicopteridae.

Xenerodiops, new genus

TYPE SPECIES.—*Xenerodiops mycter*, new species.

DIAGNOSIS.—As for the family.

ETYMOLOGY.—Formed from Greek *xenos*, stranger; *erodios*, a heron; and *ops*, countenance; from the very peculiar, though heron-like, appearance of the rostrum. The name is used as masculine in gender.

Xenerodiops mycter, new species

FIGURES 9–11

HOLOTYPE.—DPC 3088, nearly complete rostrum lacking the dorsal portion of the descending process of the right nasal bar and the posterior portion of the dorsal bar and attached parts of the nasal septum; on the ventral surface, the posterior third of the right side is cracked and lacking some bone, and the posterior portion of the premaxilla has been compressed medially, but the left side is intact and appears undistorted (Figures 9, 10).

TYPE LOCALITY AND HORIZON.—Quarry M, Fayum Province, Egypt. Upper sequence of the Jebel Qatrani Formation, Lower Oligocene. Collected by Simons.

MEASUREMENTS OF THE HOLOTYPE.—Length of ventral chord from tip to posterior flange of premaxilla, 86.2 mm; least width of dorsal bar, 4.3 mm; greatest proximal width (measured from left side to midline and then doubled) 26.2 mm; width at most swollen point of tip, 7.1 mm.

PARATYPE.—DPC 2350, left humerus lacking distal end, from Quarry I, upper sequence, Jebel Qatrani Formation, Fayum district, Egypt (Figure 11). Collected by J.G. Fleagle.

MEASUREMENTS OF PARATYPE.—Estimated total length, 120 mm; width and depth of shaft at approximate midpoint, 8.8 × 6.5 mm; width through dorsal and ventral tubercles, 24.1 mm; depth of head, 7.3 mm.

DIAGNOSIS.—As for the family. The humerus indicates a species somewhat smaller than the smallest modern stork, *Ciconia abdimii*, and probably larger than *Ardea alba* and most modern herons except the larger species of *Ardea*. The proportions of the rostrum are so different from those of possible relatives that size comparisons are very difficult, but the width at the base would seem to indicate a species of about the same size as suggested by the humerus.

ETYMOLOGY.—Greek *mykter*, nose, with regard to the most salient attributes of the species. The name is a masculine noun

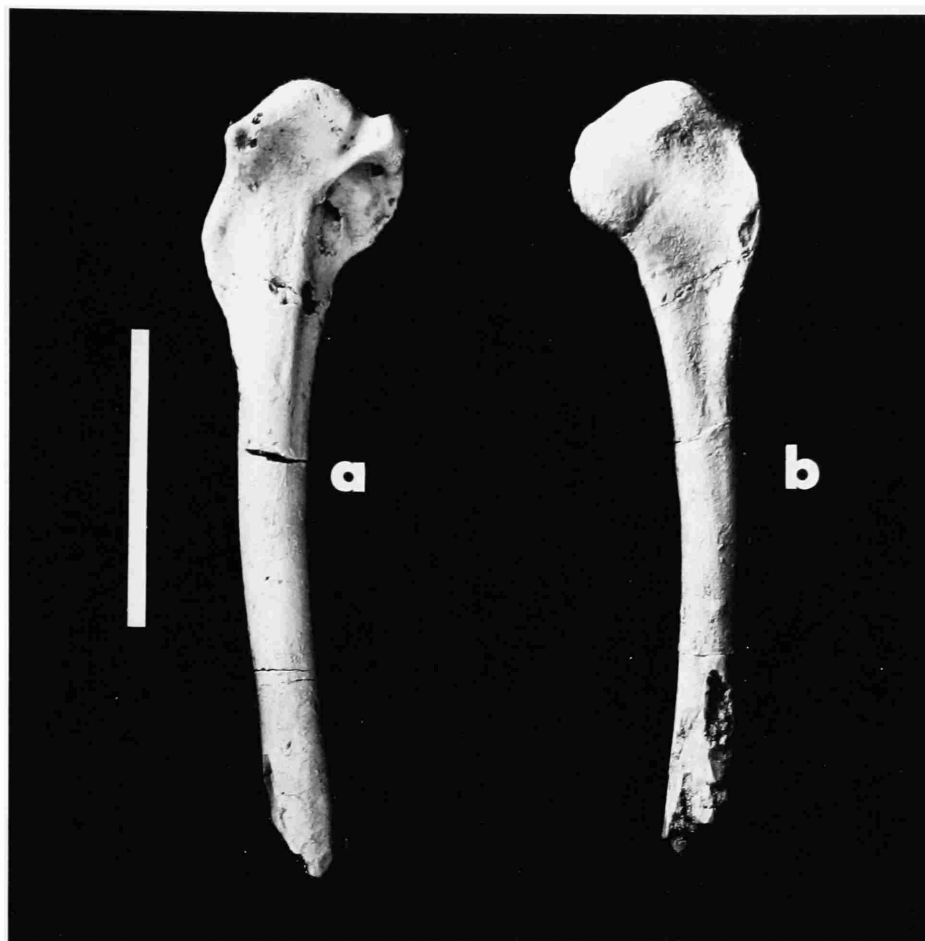


FIGURE 11.—Left humerus (paratype, DPC 2350) of *Xenerodiops mycter*, new genus and species: *a*, anconal view; *b*, palmar view. About natural size, bar = 40 mm.

in apposition.

REMARKS.—The nostril in *Xenerodiops* was holorhinal and the skull highly kinetic. To judge by the remaining portions of the nasal bars, there was a well-developed naso-frontal hinge, probably more like that in storks or *Cochlearius* than that in typical herons. Functionally, as well as morphologically, the bill in *Xenerodiops* was adapted for strong biting, and it appears intermediate between the pointed spearing device such as that typical of herons, and the cylindrical, decurved bill of storks of the genus *Mycteria* (sensu lato), which is adapted for feeding tactilely in turbid or vegetation-choked water by grasping prey on contact with a “bill-snap” reflex (Kahl and Peacock, 1963).

The humerus is assigned to this species because it came from a bird of similar size to the holotype and because it is heron-like but distinctly different from all modern herons. Its referral can only be regarded as tentative at this point. As with the rostrum, the humerus of *Xenerodiops* could be viewed as being intermediate in structure, as the bicipital and pectoral crests are

better developed than in the Ardeidae and not as expanded as in the Ciconiidae. The phylogenetic significance of *Xenerodiops* can be determined satisfactorily only with additional material.

Family ARDEIDAE

Nycticorax sp.

FIGURE 12

MATERIAL EXAMINED.—CGM 42840, nearly complete right tarsometatarsus lacking distal portions of the trochleae and most of the proximal articular surface (Figure 12); DPC 3856, left coracoid lacking the sternal end.

HORIZON AND LOCALITY.—Both specimens are from Quarry M, upper sequence.

MEASUREMENTS.—Tarsometatarsus CGM 42840: approximate length, 74 mm; width and depth at base of trochleae, 6.9 × 3.0 mm. Coracoid DPC 3856: depth at glenoid facet, 7.3 mm.



FIGURE 12.—Anterior view of right tarsometatarsus (CGM 42840) of a night heron, *Nycticorax* sp. (Ardeidae).

COMPARISONS.—The tarsometatarsus is relatively short and robust, with the trochleae short and widely spaced (Figure 12). Proximally, the medial side of the shaft is markedly thin, tapering to a sharp edge. In these respects the specimen differs from all modern genera of herons compared (*Ardea*, *Syrigma*, *Pilherodius*, *Cochlearius*, *Tigrisoma*, *Botaurus*) except *Nycticorax* and *Egretta sacra*. From the last it differs in the morphology of the medial flange. The specimen closely

matches *Nycticorax* in all details, falling well within the range of variation of USNM specimens of *N. nycticorax*. The long, narrow shaft of the fossil coracoid is also characteristic of *Nycticorax* (Olson, 1977) and it is likely therefore that this specimen is referable to the same species as the tarsometatarsus.

REMARKS.—Although we are hesitant to assert the existence of a modern genus of heron in the Oligocene of Egypt, there is no basis for considering these specimens as belonging to anything other than a species of *Nycticorax*. If the unusual tarsometatarsal anatomy of this genus is not primitive for the Ardeidae, it would indicate that the night herons separated from other members of the family at least 31 million years ago. This is the first Tertiary record of the genus. Night herons are crepuscular or nocturnal in habits and feed in aquatic environments.

Genus and Species Indeterminate

FIGURE 13

MATERIAL EXAMINED.—CGM 42838, rostrum lacking posterior portions (Figure 13). CGM 42835, distal end of a left tarsometatarsus of a juvenile individual. DPC 3085, complete but weathered right pedal phalanx 1 of digit II.

LOCALITY AND HORIZON.—The rostrum is from Quarry I, upper sequence; the other two specimens are from Quarry M, upper sequence.

MEASUREMENTS.—Rostrum CGM 42838: width and depth 40 mm from tip, 11.2×6.8 mm. Tarsometatarsus CGM 42835: width and depth at base of trochleae, 8.8×3.7 mm. Phalanx DPC 3085: length, 28.3 mm; proximal width and depth, 7.6×3.7 mm; distal width, 3.6 mm.

COMPARISONS.—The rostrum (Figure 13) is the only reasonably diagnostic element among the above three specimens, all of which are of a size compatible with a medium-sized modern heron such as *Ardea alba* or *Egretta rufescens*. Because there is no good evidence to suggest that more than one species is represented in this material, all the specimens are considered together here, although there is likewise no proof that all come from a single species.

The rostrum is long, narrow, and nearly straight. It is not unlike that in the extant genus *Egretta*, but is more compressed dorsoventrally, with a narrower median ridge, strong rostral grooves, and a more concave ventral surface. This combination of characters distinguishes it from any of the extant species of herons examined.

The juvenile tarsometatarsus is almost completely undiagnostic except that the alignment of the trochleae in the same antero-posterior plane, and the small distal foramen and faint tendinal groove, make it recognizable as coming from a heron. The pedal phalanx has the broad, flat proximal end that is quite characteristic of the basal phalanges in the Ardeidae.

REMARKS.—Although one would expect from their relatively

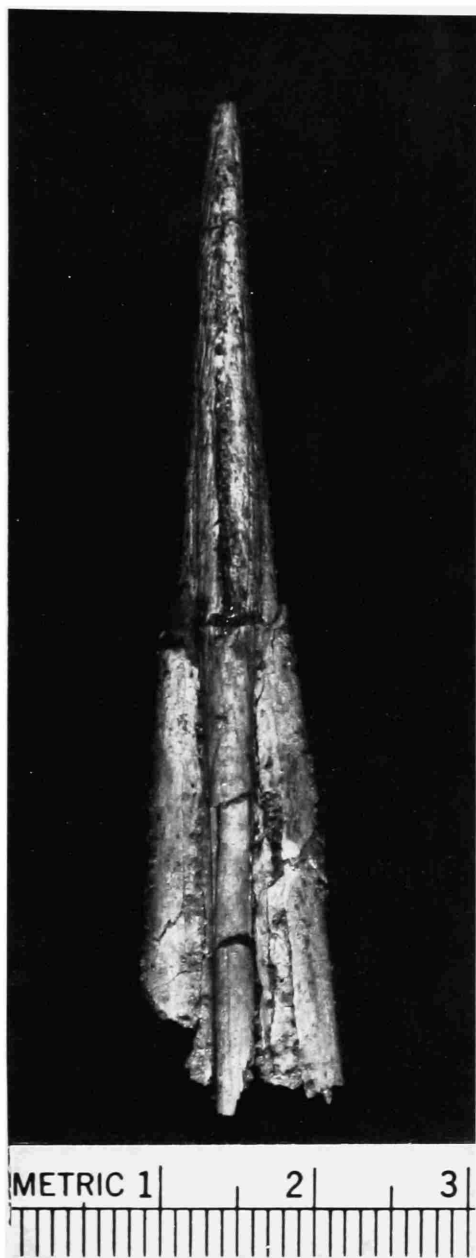


FIGURE 13.—Dorsal view of rostrum (CGM 42838) of a medium-sized heron (Ardeidae).

large size and generally aquatic habits that herons would have a reasonably good fossil record, they are actually quite scarce in Tertiary deposits, many previous records having been based on misidentified specimens (Brodkorb, 1980; Olson, 1985). There are scattered records of true herons beginning in the late Eocene or early Oligocene of France and extending through the remainder of the Tertiary, although the relationships of most of these fossils to living herons have not been firmly established. Hitherto, the earliest record for the Ardeidae in Africa was *Zeltornis ginsburgi* Balouet (1981), known from

an incomplete coracoid from the early Miocene of Libya. The sample of fossil herons from the Fayum provides the earliest representation of the family for the continent.

Family CICONIIDAE

Palaeoephippiorhynchus dietrichi Lambrecht, 1930

HOLOTYPE.—A nearly complete rostrum and mandible with associated occipital region of cranium; specimen in Stuttgart.

TYPE LOCALITY AND HORIZON.—North of Qasr Qarun, Jebel Qatrani Formation.

REMARKS.—See following account.

?*Palaeoephippiorhynchus dietrichi* Lambrecht, 1930

FIGURE 14

MATERIAL EXAMINED.—DPC 2347, distal end of right tibiotarsus.

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—Intercondylar width, 17.9 mm; condylar depth, 24.2 mm.

COMPARISONS.—The specimen is slightly abraded and only a short portion of the shaft is present. It resembles the Ciconiidae and differs from the somewhat similar Balaenicipitidae and Vulturidae in the deep, narrow tendinal groove, and the distinct intercondylar fossa. It differs from recent Ciconiidae in the weak intercondylar tubercle (not just due to abrasion), the relatively greater intercondylar width, the transversely furrowed supratendinal bridge, and the smaller distal tendinal opening. In size it would rank among the larger living storks such as *Leptoptilos* and *Jabiru*, and therefore would presumably have been about the size of *Palaeoephippiorhynchus dietrichi*. That species was described as being most similar in bill morphology to the extant genus *Ephippiorhynchus*, whereas the fossil tibiotarsus shows no particular resemblance to that of any living genus. Thus it cannot certainly be established whether one or two species of storks are represented in the Fayum deposits.

REMARKS.—*Palaeoephippiorhynchus* is the earliest certain ciconiid. Modern storks may either be highly aquatic or may be scavengers that frequent open grassland and savanna. *Ephippiorhynchus* is one of those that is very aquatic in its preferences, so if the similarities in feeding adaptations between it and *Palaeoephippiorhynchus* are any indication, the latter may have been also.

Family BALAENICIPITIDAE

Goliathia andrewsi Lambrecht, 1930

HOLOTYPE.—Complete ulna, British Museum (Natural History), A883.



FIGURE 14.—Anterior view of distal end of right tibiotarsus (DPC 2347) of a large stork (Ciconiidae), possibly referable to *Palaeoephippiorhynchus*.

TYPE LOCALITY AND HORIZON.—Fayum Province, lower sequence, Jebel Qatrani Formation.

REFERRED SPECIMEN.—DPC 2303, distal end of right tarsometatarsus lacking trochleae.

LOCALITY AND HORIZON OF REFERRED SPECIMEN.—Quarry M, upper sequence.

MEASUREMENTS OF REFERRED SPECIMEN.—Width at level of distal foramen, 23 mm (thus matching that in a specimen of *Balaeniceps rex* in the Smithsonian collections).

COMPARISONS.—The specimen shows the distinctive flattened shaft of the Balaenicipitidae, with the remains of the trochleae in the same antero-posterior plane, and the distal foramen situated far distally in a deep, V-shaped tendinal groove.

REMARKS.—The holotypical ulna of *Goliathia andrewsi* was originally described as that of a heron, but Brodkorb (1980) has presented cogent arguments for referring it to the Balaenicipitidae. The validity of this assignment is corroborated by the discovery of an additional fossil from the same

formation that is definitely referable to that family. Because it is unlikely that there were two species of shoebilled storks of the same size present at the time of deposition, it is reasonable to assume that both specimens refer to the same species, or at least a single evolving lineage, as the holotype probably comes from a stratigraphic level considerably lower than that of the referred tarsometatarsus. Whether *Goliathia* can actually be separated generically from *Balaeniceps* remains to be determined.

The only previous fossil occurrence of a shoebilled stork is another distal end of a tarsometatarsus from the late Miocene of Tunisia (Rich, 1972). This specimen is smaller than in modern *Balaeniceps* or the Fayum tarsometatarsus. Rich considers the Tunisian form to be generically distinct from the modern one based on size and the morphology of the trochleae. The lack of trochlear surfaces on the Fayum specimen makes direct comparison impossible.

The only extant species in this family, the shoebill, *B. rex*, is confined to east-central Africa and inhabits fresh-water swamps that are thickly overgrown with vegetation, upon which it walks by means of its large feet. It is structurally and behaviorally highly adapted for capturing large prey in heavy vegetation, most commonly lungfish, catfish, and bichirs (Guillet, 1979). Lungfish and catfish are abundant in the Fayum fauna (Bown et al., 1982). The shoebill, along with the jacanas, provides strong evidence for an environment of fresh-water swamp much overgrown with vegetation.

Order PELECANIFORMES

Family PHALACROCORACIDAE

Genus and Species Indeterminate

FIGURE 15

MATERIAL EXAMINED.—DPC 5658, distal portion of a premaxilla.

LOCALITY AND HORIZON.—Quarry M, upper sequence.

MEASUREMENTS.—Minimum height proximal to swollen terminus, 4.2 mm; width at same point, 4.5 mm.

COMPARISONS.—The palatal surface of the bill is straight along the proximal-distal axis, not recurved as in modern *Phalacrocorax auritus*, *P. olivaceus*, and some others. The bill broadens only gradually towards the base, unlike the robust, distinctly tapering rostrum of *P. atriceps* and some other modern species; nor is the bill distinctly compressed dorsoventrally as in *P. pelagicus*. The terminus has a moderate to strong hook, which differs from the slight hook typical of many modern species. In size, proportions, and shape, the Fayum fossil compares best, out of 20 modern species examined, with *P. bougainvillii*, a medium to large marine cormorant with a proportionately long, narrow bill. The proximal portion of the fossil specimen seems to show the rostral groove opening into



FIGURE 15.—Right lateral view of rostrum (DPC 5658) of a cormorant (*Phalacrocoracidae*).

a nostril, but this may be due to breakage.

The rostral groove of the fossil, and the series of foramina that line the groove, are similar to modern cormorants. In modern species the distal end of the groove curves strongly downward and empties gutter-like to the lateral palatal edge. In the Fayum specimen the rostral groove connects weakly with a more distal and lower groove that ends abruptly past the swollen terminus but does not continue to the lateral edge of the bill. In addition, the fossil preserves a pair of deep sulci running antero-posteriorly across the dorsal surface of the most curved, swollen part of the terminus, which differs from the two shallow grooves that enter small foramina well proximal to the hooked terminus in all modern cormorants. In both of these features—the distal configuration of the rostral groove, and the superior sulci at the hooked terminus—the specimen differs from all modern cormorants but is nearly identical to modern species of *Sulidae*. The Fayum fossil differs completely from *sulids* in other aspects of gross morphology.

REMARKS.—The configuration of the grooves on the distal portion of the rostrum are best interpreted as primitive features reflecting a common ancestry with the *Sulidae*. The Fayum specimen must either predate, or be on a separate lineage from, the common ancestor of modern species of *Phalacrocorax*.

The earliest known cormorant is from the Eo-Oligocene Phosphorites du Quercy, and numerous specimens referred to *Phalacrocorax* have been described from the early Miocene onward in North America and Europe (Olson, 1985). The Fayum specimen is the earliest recorded cormorant from Africa.

Modern cormorants are cosmopolitan in distribution, rang-

ing broadly over coastal and freshwater habitats. They dive in open, calm or flowing water for fish, crustaceans, and other aquatic animals. The Fayum cormorant, along with the ospreys and flamingos, suggests that in addition to the heavily overgrown swampy areas, there were open areas free of vegetation.

Discussion

The environment indicated by the Fayum bird assemblage differs from previous reconstructions in its emphasis on slow current and lentic conditions in association with a great deal of emergent aquatic vegetation. Lithologic characteristics of the Fayum quarries indicate that deposition of most bones occurred on point bars by active current. There is no doubt, however, that swampy areas were developed along certain sections of river, along the river borders, or perhaps in extensive over-bank areas. A variety of mudstones found in the upper sequence, including parts of Quarries I and M, were perhaps deposited in such an environment (Bown and Kraus, 1987). Vegetation-choked swamp may well have been the preferred habitat of some of the large, stocky-bodied mammalian herbivores such as the anthracotheres and giant hyracoids, which are among the most common of the Fayum mammals.

The fossil avifauna of the Fayum doubtless has not sampled all of the habitats present in the area at the time of deposition, but is dominated by birds from a habitat that had not been clearly identified previously. The absence of certain groups commonly found in modern tropical African rivers such as ducks, ibises, shorebirds other than Jacanidae and Phoenicopter-

idae, and certain land birds such as Coraciiformes, Galliformes, and Passeriformes, may be due either to sampling bias or to these taxa actually being absent in northern Africa in the early Oligocene. Ducks and passeriforms, for example, do not appear in European and North American deposits until about the beginning of the Miocene. Rich (1974) noted the unexpected absence of anatids, galliforms, and passerines from the middle to late Miocene Beglia Formation of Tunisia. Otherwise, the Tunisian assemblage includes taxa now typical of sub-Saharan Africa.

From a zoogeographic standpoint, the Fayum avifauna is extremely similar to one that would be expected along a tropical swampy river in central Africa today. The Balaenicipitidae and Musophagidae are now restricted to Africa, although fossil musophagids are known from the Tertiary of Europe. The Fayum fossils belonging to the Pandionidae and Jacanidae are by far the earliest records for these families, both of which are now widely distributed, the Jacanidae in the New and Old World tropics, and the Pandionidae worldwide. The Accipitridae, Rallidae, Gruidae, Phoenicopteridae, Ciconiidae, Ardeidae, and Phalacrocoracidae are represented elsewhere by early Tertiary fossils from the New and Old World, and each is widely distributed today. The avian assemblage from the Fayum corroborates evidence from other localities in the Tertiary of North Africa (Brunet, 1971; Rich, 1972) suggesting that there has been relative stability in some components of the

African avifauna since at least the beginning of the Oligocene. The principal change observed is the retreat of numerous taxa from the northern part of the continent doubtless as a result of the geologically very recent development of the Sahara desert.

All of the birds in the Fayum sample belong to living families except the supposed ratite and *Xenerodiops*. This is in contrast to the fossil mammals, which include numerous forms grossly different from modern African groups, such as anthracotheres, arsinotheres, creodonts, ptolomaiids, giant hyracoids, parapithecids and tarsiid primates, and marsupials. For this reason, the fossil birds are superior to mammals as indicators of past environmental conditions and permit paleoecological inferences to be made with some confidence. In Oligocene times, the Fayum contained a low swampy river, or series of rivers, overgrown in places with papyrus, reeds, and floating vegetation such as *Salvinia* and water lilies (Wing and Tiffney, 1982). Analysis of the fossil birds shows that the most closely analogous modern avifauna exists today only in a limited area of Uganda, north and west of Lake Victoria (Olson and Rasmussen, 1986). This region presents several other striking parallels with the biota and environment known or inferred for the Fayum in the early Oligocene. Our evidence from fossil birds strongly supports the paleoenvironmental reconstruction of Bown et al. (1982), and is at odds with the treeless, arid, sahelian habitat suggested for the Fayum by Kortlandt (1980).

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