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GARETH J. DYKE[1] AND CYRIL A. WALKER[2]

ABSTRACT

We present a number of new fossil records of "waterbirds" (encompassing several of the traditional living orders of birds) from three important Miocene deposits in western Kenya. These sites surround Lake Victoria—the Ngorora Formation and sediments at Maboko and Rusinga Islands (Kula Formation)—are well-known hominoid localities, and have yielded a diverse assemblage of contemporary fossil mammals. Previously identified avians from this area include a marabou stork (*Leptoptilos* sp.), the fossil flamingo *Leakeyornis aethiopicus*, as well as a number of additional unidentified phoenicopterid (flamingo) remains. We add records of an anhinga (*Anhinga* cf. *pannonica*), two storks (*Ciconia minor*, *C.* cf. *ciconia/nigra*), a night heron (*Nycticorax* cf. *nycticorax*) and a threskyornithid (the group that includes the ibises and spoonbills) to the known diversity of Kenyan Miocene waterbirds. We also illustrate, for the first time, the holotype and paratype material of the Kenyan Miocene flamingo *Leakeyornis aethiopicus*. Comparisons with other known sites of this age across northern Africa, the Mediterranean and northern Pakistan suggest that Miocene waterbird faunas in this region were very similar in their compositions. While *Anhinga pannonica*, *Ciconia minor,* and *Ciconia ciconia* are documented from other Miocene sites across the region, the osteologically distinct fossil flamingo *Leakeyornis* appears to have been restricted to East Africa. All the avian groups recorded from these Kenyan Miocene sites represent extant genera, in contrast to the described fossil mammals. As has been widely reported from other African sites of this age, fossil birds thus represent a valid mechanism for building hypotheses about palaeoenvironments.

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INTRODUCTION

The Miocene-age (ca. 24–6 mya) avifaunas known from Africa all comprise a considerable number of aquatic or semi-aquatic birds (Rich, 1972; Harrison and Walker, 1982; Rich and Walker, 1983; Olson, 1985a; Louchart et al., 2005a, 2005b). Correlated with the presence of such environments in some parts of Africa at this time, many species of "waterbirds" in the Miocene had a distribution that encompassed an area ranging from northwest Africa and southern Europe into northern Pakistan and northeastern Afrotropical Africa (Howard and Moore, 1984; Blondel and Mourer-Chauviré, 1998). It has been suggested that suitable habitats for such species were more widespread across this broad geographical region, 10–20 mya (Olson, 1985a). In spite of such hypotheses, the literature on Miocene fossil birds from Africa has remained sparse; this area of research has attracted relatively little attention over the last 20 years (but see Louchart et al., 2005a, 2005b; Walker and Dyke, 2006; Leonard et al., 2006). As a result, the background to the present paper justifies a brief synopsis of older literature.

Rich (1972) examined a collection of Middle–Upper Miocene fossil birds from Tunisia and recognised the remains of a fossil anhinga (*Anhinga pannonica* Lambrecht, 1916), originally described from Pannonian Beds (these days regarded as Upper Miocene and not Lower Pliocene) of Hungary (Lambrecht, 1916); a fossil cormorant (*Phalacrocorax littoralis* Milne-Edwards, 1863), first recorded from the Upper Oligocene of southern France; a fossil shoebill stork (subsequently named *Paludiavis richae* by Harrison and Walker, 1982); and a fossil marabou stork (*Leptotilos falconeri* Milne-Edwards, 1868) that was later separated as a new species (*L. richae*) by Harrison (1974). Rich (1974) then recognised a hind limb of this same stork from the Upper Miocene locality of Ngorora, Kenya, which she considered might also be referable to *Leptotilos falconeri*, distinct from *L. richae*. Hill and Walker (1979), however, considered this specimen undiagnostic.

Harrison and Walker (1982) subsequently presented details of an Upper Miocene avifauna from northern Pakistan that included additional fossils of both *Anhinga pannonica* and *Paludiavis richae*. These taxa link this fauna with that described by Rich (1972) from Tunisia. This Upper Miocene collection also included two storks (*Ephippiorhynchus pakistanicus* Harrison and Walker, 1982 and *Leptoptilus siwalikensis* Harrison, 1974), as well as a pelican (*Pelecanus sivalensis* Davies, 1880). These last two species were originally described from the Miocene of northern Pakistan (Davies, 1880; Harrison, 1974).

Representative fossil "waterbirds" that have previously been described from Kenya include the small flamingo *Leakeyornis* (*Phoenicopterus*) *aethiopicus* (Harrison and Walker, 1976; Rich and Walker, 1983) (fig. 1) and the small stork *Ciconia minor* (Harrison, 1980), both from the Lower Miocene of Rusinga Island. Further material indistinguishable from the extant White Stork, *Ciconia ciconia*, is also known from the Middle Miocene of Maboko Island (Andrews et al., 1981). New records of "birds of prey" have also recently been described from these sites (Walker and Dyke, 2006) as well as a small, potentially new species of ostrich (*Struthio* sp.; Leonard et al., 2006).

In this paper we describe a number of new fossil bird specimens from three Miocene localities in western Kenya (Rusinga Island, Maboko Island, and Ngorora) and discuss their significance to our understanding of waterbird evolution in the later part of the Paleogene. For the first time we also illustrate the paratype specimens of the Kenyan Miocene flamingo *Leakeyornis aethiopicus* (fig. 1).

INSTITUTIONAL ABBREVIATIONS: **BMNH S**, Bird Group Collections, Natural History Museum, Tring; **BMNH A**, Department of Palaeontology, Natural History Museum, London; **KNM**, Kenya National Museum, Nairobi; **NMINH**, National Museum of Ireland (Natural History), Dublin.

The fossil specimens discussed in this paper are deposited in the KNM, and were first examined in Nairobi by P. Vickers-Rich in the 1970s, and then by C.A. Walker in 1980. All specimens were subsequently loaned to the BMNH, where they are currently housed. Our use of anatomical terminology follows Baumel and Witmer (1993), with some modifications to English after Howard (1929).
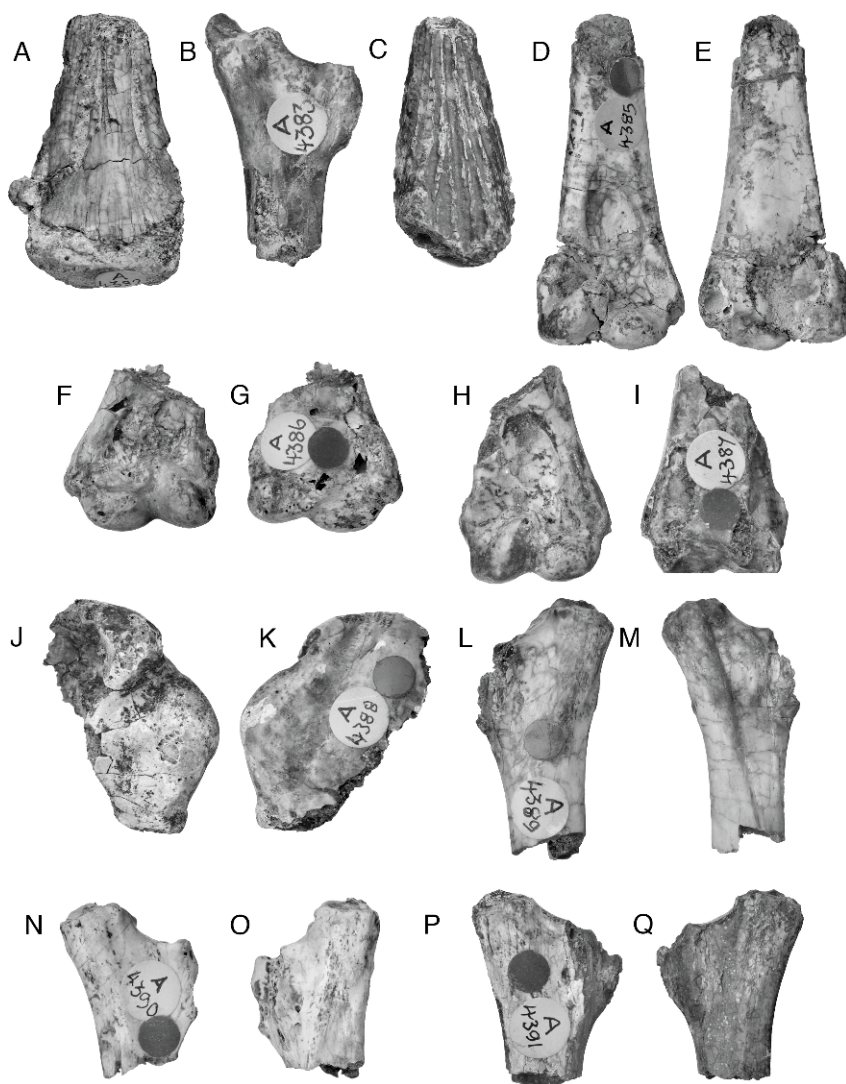
Fig. 1. Fossil material referred to the Lower Miocene Kenyan flamingo *Leakyornis aethiopicus* (see Harrison and Walker, 1976). Not to scale. BMNH A 4382 (holotype)—portion of rostrum in dorsal view (**A**); BMNH A 4383—proximal end of right tarsometatarsus in plantar view (**B**); BMNH A 4384—distal portion of lower jaw in ventral view (**C**); BMNH A 4385—distal end of left humerus in cranial (**D**) and caudal (**E**) views; BMNH A 4386—distal end of right humerus in cranial (**F**) and caudal (**G**) views; BMNH A 4387—distal end of left humerus in cranial (**H**) and caudal (**I**) views; BMNH A 4388—proximal end of left humerus in (**J**) caudal and cranial (**K**) views; BMNH A 4389—proximal end of tarsometatarsus in plantar (**L**) and dorsal (**M**) views; BMNH A 4390—proximal end of tarsometatarsus in dorsal (**N**) and plantar (**O**) views; BMNH A 4391—proximal end of tarsometatarsus in plantar (**P**) and dorsal (**Q**) views.
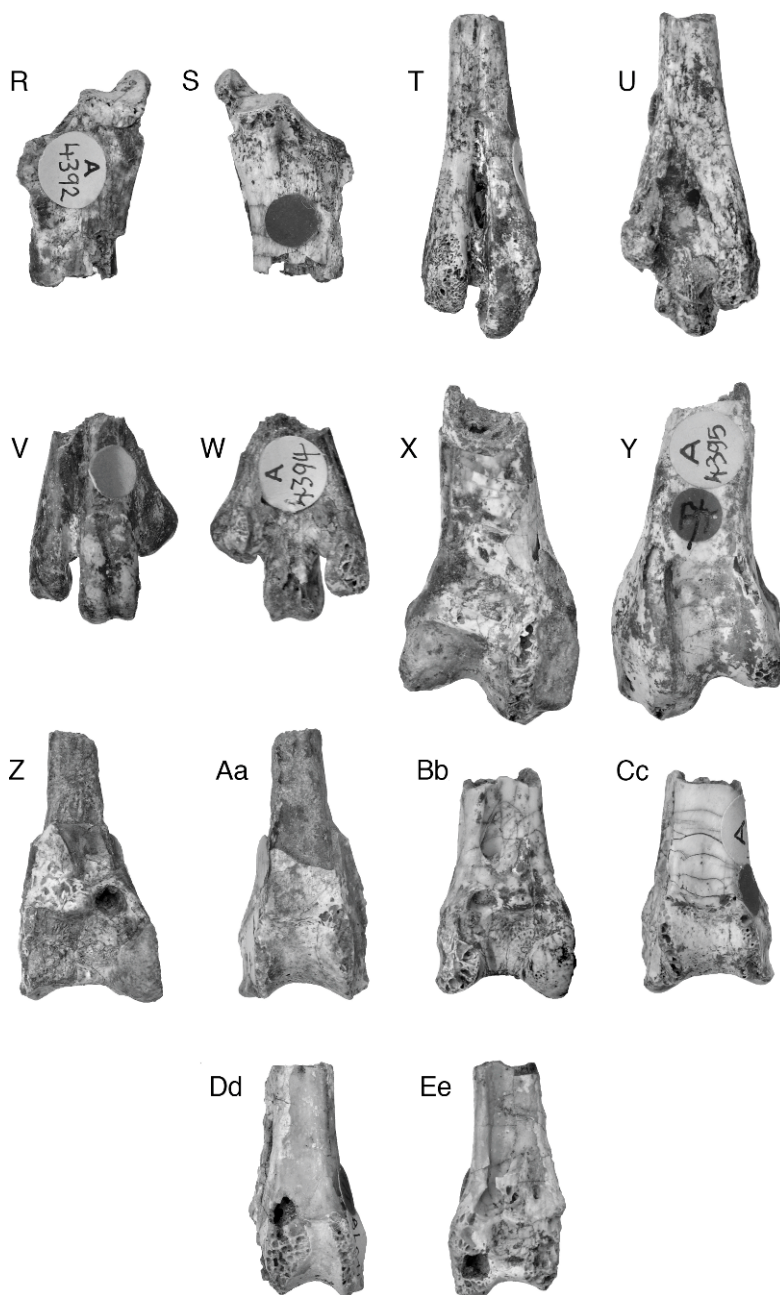
Fig. 1.   (Continued). BMNH A 4392—proximal end of tarsometatarsus in dorsal (**R**) and plantar (**S**) views; BMNH A 4393—distal end of right tarsometatarsus in dorsal (**T**) and plantar (**U**) views; BMNH A 4394—distal end of left tarsometatarsus in dorsal (**V**) and plantar (**W**) views; BMNH A 4395—distal end of right femur in caudal (**X**) and cranial (**Y**) views; BMNH A 4396—distal end of right tibiotarsus in cranial (**Z**) and caudal (**Aa**) views; BMNH A 4397—distal end of left tibiotarsus in cranial (**Bb**) and caudal (**Cc**) views; BMNH A 4398—distal end of left tibiotarsus in cranial (**Dd**) and caudal (**Ee**) views.
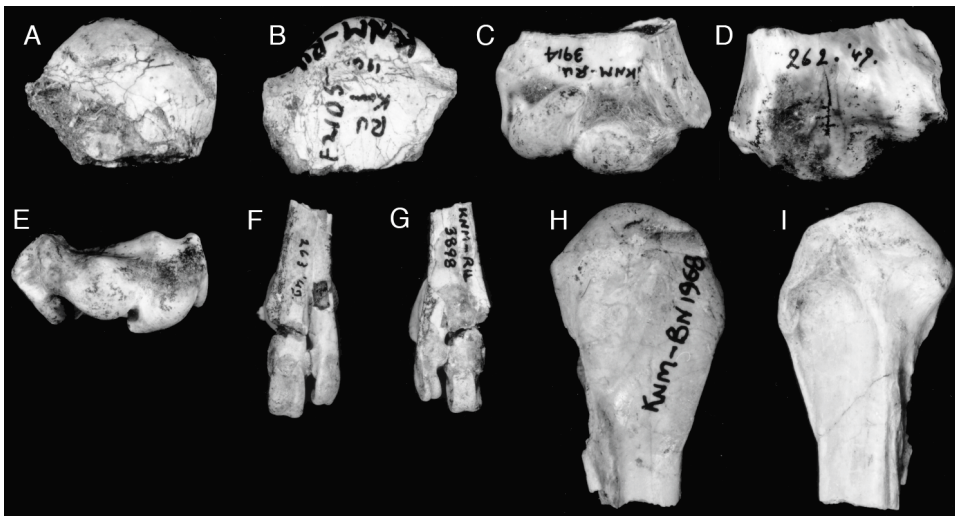
Fig. 2. New records of Miocene Kenyan waterbirds. *Ciconia minor*, incomplete proximal right humerus (KNM RU 3075) in cranial (**A**) and caudal (**B**) views; *Ciconia* sp., distal right humerus (KNH RU 3914) in cranial (**C**), caudal (**D**), and proximal (**E**) views; *Ciconia minor*, distal left tarsometatarsus (KNM RU 3898) in dorsal (**F**) and plantar (**G**) views; *Anhinga* cf. *pannonica*, proximal end of right humerus (KNM BN 1968) in cranial (**H**) and caudal (**I**) views. Not to scale, see text for measurements.

SYSTEMATIC PALAEONTOLOGY

PELECANIFORMES RIDGEWAY, 1887

ANHINGIDAE BRISSON, 1760

Anhinga cf. *pannonica* Lambrecht, 1916

MATERIAL: KNM BN 1968, proximal end of a right humerus (fig. 2).

LOCALITY AND AGE: Ngorora Formation, Middle Miocene of Ngorora, western Kenya. The age of these deposits has been estimated to be 12–10.5 mya; their sedimentology confirms a semi-aquatic environment corroborated by the presence of fish, crocodile, and hippo remains within the formation (Bishop et al., 1971; Pickford, 1981).

DISCUSSION: As many as four species of anhingas (one each from the Americas, Africa, Asia, and Australia) are currently extant (depending on authors; Howard and Moore, 1984; Monroe and Sibley, 1993). However, because these taxa exhibit little morphological variation other than size, there has been much disagreement (especially in older literature) as to how many species should actually be considered valid. Some workers have suggested that anatomical differences represent nothing more than a pattern of geographical

variation and treat these birds within a single species, *Anhinga anhinga* spp., while others accept two—*A. anhinga* in the Americas and *A. melanogaster* in the Old World (see Howard and Moore, 1984). This latter arrangement may be more acceptable on purely anatomical grounds—Harrison (1978) noted a difference in the hypotarsal structure between the Old and New World forms that might justify their specific separation.

The fossil record of the Anhingidae is intermittent (Noriega and Alvarenga, 2002). The earliest apparent example of these birds, *Protoplotus beauforti* Lambrecht (1930), was described from a crushed skeleton found in Eocene deposits on the Island of Sumatra, but it is not until the Upper Miocene that the family becomes abundant in the fossil record, especially in South America (Olson, 1985a; Noriega and Alvarenga, 2002). By this time, however, anhinga osteology is largely indistinguishable from that of the recent genus, thus providing few clues as to the evolution of this group of birds. Outside of South America, in the Old World, three Neogene species are recognised: *Anhinga pannonica*, from the Upper Miocene of Hungary (Lambrecht, 1916); *Anhinga grandis*, from the Upper

Pliocene of North America (Martin and Mengel, 1975); and *Anhinga hadarensis* from the Upper Pliocene of Ethiopia and early Pleistocene of Tanzania (Brodkorb and Mourer-Chauviré, 1982). Of these records, the Hungarian species may have been wide-ranging—Rich (1972) attributed a cervical vertebrae and the proximal portion of a humerus from the Upper Miocene of Tunisia to *A. pannonica*, and Harrison and Walker (1982) added another fragmentary humerus and the distal portion of a tarsometatarsus from the Upper Miocene of Pakistan to this fossil taxon. As an aside, and to complete our discussion of the African fossil record of these birds, it should be noted that the Quaternary species *Anhinga nana* Newton and Gadow (1893) described first from Mauritius and later from Madagascar (Andrews, 1897) was re-identified by Olson (1975) as a cormorant.

Although it is incomplete, KNM BN 1968 closely resembles the known anatomy of both the late Paleogene *Anhinga pannonica* and the extant *A. melanogaster* (which survives in Kenya today; Monroe and Sibley, 1993) (fig. 2). Referral to the former species, however, is supported on the basis of the size and age of this element—its placement within the other African fossil taxon, *A. haddarensis*, is excluded because this species is much stouter and stockier in its limb proportions than any of its kin (Brodkorb and Mourer-Chauviré, 1982). Even though KNM BN 1968 very closely resembles *A. pannonica* in details of its preserved morphology (fig. 2), we make this referral tentatively because of a small comparative sample size of *A. melanogaster* and because of the incompleteness of this fossil. Nonetheless, the new specimen is somewhat larger than all available extant examples of this genus (1.5–3 mm in most dimensions); in this respect KNM BN 1968 may corroborate the arguments of Rich (1972) and Harrison and Walker (1982) regarding material already assigned to *A. pannonica*.

MEASUREMENTS: KNM BN 1968, length across tuberculum dorsale to tuberculum ventrale—20 mm; maximum width of caput—23 mm; cranial extent of crista bicipitalis—22 mm; shaft width and distal termination of crista bicipitalis—13 mm.

CICONIIFORMES BRISSON, 1760

PHOENICOPTERIDAE BRISSON, 1760

Leakeyornis aethiopicus (Harrison and Walker, 1976) Rich and Walker, 1983

MATERIAL: Holotype, BMNH A 4382, basal portion of rostrum. Paratypes, BMNH A 4383, proximal end of right tarsometatarsus; BMNH A 4384, distal portion of lower jaw; BMNH A 4385, distal end of left humerus; BMNH A 4386, distal end of right humerus; BMNH A 4387, distal end of left humerus; BMNH A 4388, proximal end of humerus; BMNH A 4389-4392 proximal ends of tarsometatarsi; BMNH A 4393-4394, distal ends of tarsometatarsi; BMNH A 4395, distal end of right femur; BMNH A 4396-4398, distal ends of tibiotarsi (fig. 1). All collected and presented to the BMNH by L.S.B. Leakey.

LOCALITY AND AGE: Lower Miocene, Rusinga Island (locality RS12), Lake Victoria, Kenya (for locality map and detailed information, see van Couvering and Miller, 1969). This is the oldest of the three sites yielding bird material to be described in this paper; sediments at this locality have been dated to 18–16 mya (van Couvering and Miller, 1969) and again have been interpreted as indicative of floodplain conditions with extensive bodies of standing water (Andrews et al., 1981).

DISCUSSION: Measurements and interpretation of these specimens were presented by Harrison and Walker (1976) and Rich and Walker (1983).

CICONIIFORMES GARROD, 1874

ARDEIDAE VIGORS, 1825

Nycticorax cf. *nycticorax* Linnaeus, 1758

MATERIAL: KNM MB 562, right coracoid lacking ventral portion of sternal end (fig. 3).

LOCALITY AND AGE: Maboko Island, Lake Victoria, western Kenya. The age of these deposits has been estimated to be 16.5–14.5 mya; sediments at Maboko are somewhat older than those exposed at Ngorora and have been inferred to represent a floodplain environment (Andrews et al., 1981).

DISCUSSION: Although the Night Heron (*Nycticorax*) appears to represent a distinct
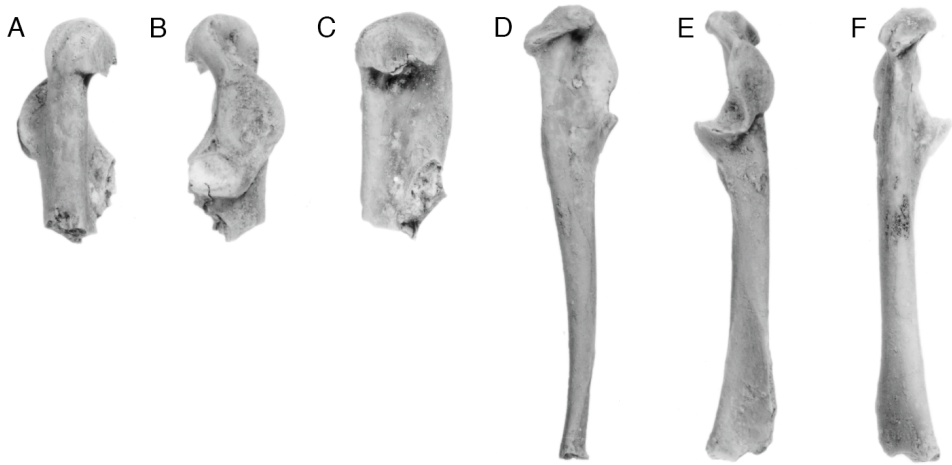
Fig. 3. New records of Miocene Kenyan waterbirds. Indeterminate cranial end of right coracoid referred to Threskiornithidae (KNM MB 563) in ventral (**A**), dorsal (**B**), and medial (**C**) views; *Nycticorax* cf. *nycticorax*, incomplete right coracoid (KNH MB 562) in medial (**D**), dorsal (**E**), and ventral (**F**) views. Not to scale, see text for measurements.

taxon that may have separated early from the other herons (Ardeidae), there is presently little fossil evidence for this. Rasmussen et al. (1987) described a tarsometatarsus from the Jabal Qatrani Formation (Oligocene) in Fayum Province, Egypt, which they considered virtually indistinguishable from the recent Black-crowned Night Heron (*Nycticorax nycticorax*), currently present throughout Africa, southern Europe, and Asia (Monroe and Sibley, 1993). This appears to be the earliest Paleogene record of the genus known to date (Olson, 1985a; Rasmussen et al., 1987).

The coracoid from Maboko Island (KNM MB 562) is typical of *Nycticorax* in that it has a projecting processus acrocoracoideus and a ventrally developed facies articularis clavicularis (fig. 3). The shape of the concavity of the surface between the processus acrocoracoideus and the facies articularis humeralis in this specimen distinguishes it from the neotropical Yellow-crowned Night Heron (*Nyctinyassa violacea*); this concave area also resembles extant specimens of *Nycticorax nycticorax* (fig. 3). Although the dimensions of KNM MB 562 are smaller than comparative material of both these two extant genera (perhaps suggesting specific status for this specimen), we follow Rasmussen et al. (1987) in tentatively referring this fossil to the extant *N. nycticorax*.

MEASUREMENTS: KNM MB 562, preserved length to dorsal lip of facies articularis sternalis—41 mm; maximum medial width of head—9 mm; dorsal thickness of head—4 mm; lateral width to processus procoracoideus—7 mm; dorsal thickness at midshaft—4 mm.

CICONIIDAE GRAY, 1840

Ciconia minor (Harrison, 1980)

MATERIAL: KNM RU 3075, incomplete proximal end of right humerus; KNM RU 3898, distal end of left tarsometatarsus lacking the trochlea for metatarsal II (fig. 2).

LOCALITY AND AGE: Rusinga Island (Kula Beds), Lake Victoria, western Kenya.

DISCUSSION: The first of the two fossil specimens that we refer here to *Ciconia minor* consists of the articulating head of a right humerus broken distal to the sulcus ligamentosus transversus (fig. 2). The caput humeri and tuberculum dorsale of KNM RU 3075 are preserved, however, and present characters that can be used for referral. The caput humeri of this specimen is evenly domed and bears a distinct muscle attachment scar that slants over the cranial side of the tuberculum dorsale as seen typically in extant *Ciconia* (fig. 2). In caudal view, the caput humeri is markedly projected as in *C. minor* (Harrison, 1980) more so than in the

other extant species of this genus. This feature, combined with the presence of numerous foramina distal to the caput humeri, is consistent with species the same size or larger than *C. minor*.

The second specimen referred here (KNM RU 3898) consists of just the distal extremity of a left tarsometatarsus including a small portion of shaft (fig. 2). This specimen is very similar to extant ciconiids we have examined—the dorsal margin of trochlea metatarsal II is prominent and projects distally below the level of trochlea metatarsal III, as in *Ciconia* (fig. 2). KNM RU 3898 corresponds with extant specimens of *C. minor* in its preserved size.

MEASUREMENTS: KNM RU 3075, maximum width across caput to tuberculum dorsale—23 mm; depth of caput humeri—10 mm. KNM RU 3898: total length to trochlea metatarsal III—36 mm; total length to trochlea metatarsal IV—34 mm; width of shaft—30 mm; maximum width of trochlea metatarsal III—4 mm.

Ciconia sp. Brisson, 1760

MATERIAL: KNM RU 3914, distal end of a right humerus (fig. 2).

LOCALITY AND AGE: Rusinga Island (Kula Beds), Lake Victoria, western Kenya (see above).

DICUSSION: Although the two living species of *Ciconia* that fall within the size range of our material, the White Stork (*Ciconia ciconia*) and the Black Stork (*C. nigra*), are strikingly different in their external appearance they are very similar osteologically. Hence, with the exception of some characteristic elements (see above), separation of the two on morphological grounds is often impossible. Harrison (1980), for example, was unable to differentiate a proximal portion of a carpometacarpus from the Miocene of Maboko Island among these two species of *Ciconia*. Because in its size and structure KNM RU 3914 closely resembles the distal humeri of the recent species and even though its epicondylus dorsalis is somewhat more projected (fig. 2), we refrain from more specific assignment here based on such limited fossil material.

MEASUREMENTS: KNM RU 3914, maximum distal width—30 mm; width of shaft proximal to processus supracondylaris dorsalis—24 mm.

THRESKIORNITHIDAE RICHMOND, 1917

Genus and species indeterminate

MATERIAL: KNM MB 563, cranial end of right coracoid (fig. 3).

LOCALITY AND AGE: Maboko Island, Lake Victoria, western Kenya.

DISCUSSION: Rich (in Andrews, 1981) tentatively referred this incomplete and damaged coracoid to the charadriiform family Burhinidae (stone-curlews). However, if this element were from a burhinid then it would pertain to a large bird—approaching the dimensions of *Esacus*, the Great Stone-curlew (Howard and Moore, 1984). However, KNM MB 563 lacks a well-developed processus acrocoracoideus along with the distinct projection on the ventral face of the facies articularis clavicularis that characterises these birds (fig. 3). Our comparisons of this specimen suggest instead that it should be referred to Threskiornithidae (ibises and spoonbills), and more specifically to the ibises.

The fossil record of Old World ibises from similarly aged deposits is, however, poor. Milne-Edwards (1863) described a *Plegadis*-sized ibis, *Actiornis pagana* (see Harrison, 1986 for comments on this genus), from the Upper Oligocene–Lower Miocene of France, and Olson (1985b) described a species, *Geronticus apelex*, and referred an additional specimen to the extant *Threskiornis aethiopicus* (Sacred Ibis). Both these latter taxa have been identified from Early Pliocene sediments in South Africa (Olson, 1985b). KNM MB 563, however, is very fragmentary and we refrain from referring it to a particular genus. In comparison with extant species, this element is larger than corresponding bones from the Glossy Ibis (*Plegadis falcinellus*) and smaller than those of the Sacred Ibis (*Threskiornis aethiopicus*) and the Bald Ibis (*Geronticus calvus*). KNM MB 563 suggests a threskiornithid of similar size to either the Hadada (*Bostrychia hagedash*) or the Madagascan Ibis (*Lophotibis cristata*).

MEASUREMENTS: KNM MB 563, greatest width of sulcus muscularis supracoracoideus—9 mm; width of facies articularis clavicularis—8 mm.

DISCUSSION

Descriptions of new records of fossil waterbirds from Miocene sites surrounding Lake

Victoria allow us to confirm the presence of five families of these birds in the assemblage. Our re-examination of field collections made in the 1980s further augments the list of known taxa, in addition to previous descriptions restricted to specific genera (a stork of the genus *Leptoptilos* and the flamingo *Leakeyornis*)—we have added new records of an anhinga (Anhingidae: *Anhinga* cf. *pannonica*), two distinct size-classes of storks (Ciconiidae: *Ciconia minor*, *C.* cf. *ciconia/nigra*), a night heron (Ardeidae: *Nycticorax* cf. *nycticorax*) and an indeterminate threskyornithid (ibis) to the waterbird faunal list.

The fossil waterbirds thus far identified from these important Kenyan Miocene localities are generalized taxa, clearly not sampling all habitats present in the area at the time of deposition. The absence of a number of key groups of waterbirds commonly found in modern African rivers (e.g., ducks, waders, cormorants, and rails), and known to have been present in the Miocene, may be due to sampling, taphonomic bias or to their actual absence from these areas. A similar bias in the structure of Miocene waterbird assemblages has been noted from other contemporaneous African sites in Tunisia and Egypt (Rich, 1974; Rasmussen et al., 1987). Nevertheless, all of the birds thus far identified from the Kenyan sites sampled around Lake Victoria (this paper; C.A. Walker, unpublished data) are representatives of extant groups. As is also the case with other similar-aged deposits in Egypt, this finding contrasts strongly with descriptions of the fossil mammals from Kenya (Pickford, 1981, 1986), many of which do not sample extant taxa at this time. For this reason, it has been suggested previously that birds should be used preferentially (at least in comparison with mammals) as indicators of paleoenvironmental conditions and habitat preferences in the African Miocene (Harrison and Walker, 1976; Louchart et al., 2005b; Walker and Dyke, 2006; Leonard et al., 2006).

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