Citation for published version:
Field, DJ 2017, 'Preliminary paleoecological insights from the Pliocene avifauna of Kanapoi, Kenya: Implications for the ecology of Australopithecus anamensis', Journal of Human Evolution. https://doi.org/10.1016/j.jhevol.2017.08.007

DOI:
10.1016/j.jhevol.2017.08.007

Publication date:
2017

Document Version
Peer reviewed version

Preliminary paleoecological insights from the Pliocene avifauna of Kanapoi, Kenya: implications for the ecology of *Australopithecus anamensis*

Daniel J. Field[1,2]

[1] Milner Centre for Evolution, Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath, BA2 7AY, UK

[2] Department of Geology & Geophysics, Yale University, 210 Whitney Avenue, New Haven, CT 06511, USA

email: d.j.field@bath.ac.uk

ABSTRACT

Fossil bird remains from the Pliocene hominin-bearing locality of Kanapoi comprise >100 elements representing at least 10 avian families, including previously undescribed elements referred to the 'giant' Pliocene marabou stork *Leptoptilos* cf. *falconeri*. The taxonomic composition of the Kanapoi fossil avifauna reveals an assemblage with a substantial aquatic component, corroborating geological evidence of this locality's close proximity to a large, slow-moving body of water. Both the taxonomic composition and relative abundance of avian higher-level clades at Kanapoi stand in stark contrast to the avifauna from the slightly older (~4.4 Ma vs. 4.2 Ma) hominin-bearing Lower Aramis Member of Ethiopia, which has been interpreted as representing a mesic woodland paleoenvironment far from water. In general, the taxonomic composition of the Kanapoi avifauna resembles that from the Miocene hominoid-bearing locality of Lothagam (though Kanapoi is more diverse), and the aquatic character of the Kanapoi avifauna supports the idea that the environmental conditions experienced by *Australopithecus anamensis* at Kanapoi were markedly different from those experienced by *Ardipithecus ramidus* at Aramis. Additionally, the relative abundance of marabou stork (*Leptoptilos*) remains at Kanapoi may suggest a longstanding commensal relationship between total-clade humans and facultatively scavenging marabous. Additional avian remains from nearby fossil localities (e.g., the Nachukui Formation), ranging in age from 3.26-0.8 Ma, reveal the long-term persistence of an aquatic avifauna in the region.

Keywords: Paleornithology, Paleoecology, *Australopithecus anamensis*, Marabou, Pliocene, Fossil birds

1. Introduction

Deciphering the environmental conditions experienced by Pliocene hominins in East Africa holds important implications for interpreting the lifestyle and selection pressures influencing early human evolution (Olson and Rasmussen, 1986). Collecting efforts over the last ~25 years in the Kenyan Pliocene locality of Kanapoi (4.2 Ma) have revealed a diverse vertebrate fauna comprising fishes, mammals, amphibians, lepidosaurs, turtles, crocodilians, and birds (Harris et al., 2003). However, despite the promising potential of fossil birds as paleoenvironmental indicators (Olson and Rasmussen, 1986; Serjeantson, 2009; Finlayson et al., 2011), to date only 10 total avian specimens have been noted from this important locality, and neither these remains nor their value as environmental proxies have been treated in detail (Harris et al., 2003). Of these previously reported specimens, seven comprise collections of ostrich eggshell fragments (Struthionidae), along with isolated bones from one darter (Anhingidae), one stork (Ciconiidae: *Mycteria*), and a putative duck (Anatidae).

Here, 100 avian specimens from Kanapoi were evaluated, along with 23 additional specimens from more recent deposits located nearby, ranging in age from ~3.26-0.8 Ma. These include specimens collected during the 1990s via surface collection and screen washing, and material collected during the 2000s via surface collection. The entire collection comprises skeletal remains from a minimum of 12 extant avian families (with at least 9 represented from Kanapoi alone), in addition to numerous records of ostrich eggshell. The relatively abundant avian remains from Kanapoi are notable, as the intrinsic fragility and small size of bird bones renders them absent or rare at most East African hominin-bearing assemblages (Louchart et al., 2009). This material enables comparison of the avifaunal composition of Kanapoi with that of the slightly older hominin-bearing locality at Aramis, Ethiopia (Louchart et al., 2009). Although the tetrapod assemblage from Kanapoi was initially interpreted as broadly similar to that from Aramis (Harris et al., 2003), more recent work has indicated divergent ecological settings (Louchart et al., 2009). However, no comparisons between the Aramis and Kanapoi avifaunas have yet been conducted, given the scarce attention avian remains from Kanapoi have thus far received. The present study reveals that both the taxonomic composition and ecological affinities of the Kanapoi avifauna differ markedly from those of Aramis, corroborating other ecological proxies suggesting divergent ecological settings for *Australopithecus anamensis* and *Ardipithecus ramidus* (see other contributions in this special issue).

The vertebrate fossils from Kanapoi predominantly derive from vertic flood-plain paleosols of the Kerio River, overlain by claystones deposited within the early Pliocene Lonyumun Lake (Harris et al., 2003). The avian fossils collected from this locality reflect this general ecological setting, and represent a considerably more aquatic avifauna than that reported for Aramis (Louchart et al., 2009). These differences underscore the utility of fossil birds as sensitive environmental indicators that may help shed light on the environmental conditions experienced by early hominins in East Africa (Olson and Rasmussen, 1986).

2. Materials and methods

2.1 Institutional Abbreviations

Institutional abbreviations used here are: KNM-KP: Kenya National Museum, Kanapoi

Formation; KNM-WT: Kenya National Museum, Nachukui Formation; OB: Kenya National Museum, osteology collection

A complete list of the fossil material examined is provided in the Supplementary Online Material (SOM) Tables S1 and S2.

2.2. Fossil eggshell

Nine specimens comprising multiple eggshell fragments from Kanapoi, discussed by Harris et al. (2003); nine from more recent localities (SOM Table S1 and S2). All exhibit the characteristic 'struthious' pore structure of modern *Struthio* (Sauer, 1972; Harris et al., 2003), and are similar to *Struthio* eggshell reported from Lothagam (Harris and Leakey, 2003; Harris et al., 2003).

2.3. Fossil skeletal remains

One hundred avian specimens from Kanapoi and 23 from more recent nearby localities (principally the Nachukui Formation; see SOM Table S2) were evaluated. These specimens were acquired both by surface collection and by screen washing. All material examined that was collected throughout the 2000s was surface-collected.

2.4. Selected extant comparative material:

Poicephalus meyeri OB 274; *Leptoptilos cruminiferus* OB 35; *Mycteria ibis* OB 49, *Pelecanus onocrotalus* OB 2334; *Alopochen aegyptiacus* OB 1637; *Pterocles exustus* OB 797; *Recurvirostra avosetta* OB 1517; *Alcedo cristata* OB 1117; *Turdus abyssinicus* OB 1693; *Trigonoceps occipitalis* OB 957; *Anhinga rufa* OB 1411; *Apus horus* OB 333

2.5. Ecological analysis

Pliocene avian skeletal remains from Kanapoi (*n*=54) and the more recent localities (*n*=7) were diagnosed to the Family level (Passeriformes were diagnosed to Order), and combined with published data from Aramis (*n*=263) (Louchart et al., 2009). Taxa were divided among three ecological categories according to their general lifestyle habits (Del Hoyo et al., 1992): "aquatic" (i.e., Anatidae, Alcedinidae, Anhingidae, Ciconiidae, Charadriiformes, Pelecanidae), "terrestrial" (i.e., Accipitridae, Columbidae/Pteroclididae, Passeriformes, Psittacidae, Strigidae), and "aerial insectivore" (Apodidae). Results are depicted as pie charts in Fig. 1. Ecological data from Aramis were extracted from Louchart et al. (2009). Data from the more recent localities in the West Turkana region were combined, although these data should be treated with caution as they represent a wide temporal range, from 3.26 Ma in the case of Lomekwi to 0.8 Ma in the case of Todenyang (Brown et al., 2001; McDougall and Brown, 2008). Age estimates for these additional localities are provided in the SOM Table S2.

3. Results

3.1. Ecological analysis

The most frequently represented avian ecologies differ markedly between the skeletal remains from Aramis and the Kenyan localities (Fig. 3). Aramis is dominated by species exhibiting terrestrial/arboreal ecologies (95%; largely parrots, game birds, owls, songbirds, pigeons, and diurnal raptors; Louchart et al., 2009). By contrast, terrestrial birds comprise a much smaller percentage of the avifaunas of both Kanapoi (46%), and the more recent localities (29%). Whereas aquatic taxa and aerial insectivores comprise only a minor component of the Aramis avifauna (4% and <1%, respectively), these groups are comparatively dominant in the localities from the Turkana region, where they combine to represent 54% of the specimens from Kanapoi (30% aquatic and 24% aerial insectivore), and 71% from the more recent localities (all aquatic).

3.2. Taxonomic comparisons

Much like the results of the ecological comparisons (Fig. 4), the taxonomic composition of the Aramis avifauna differs substantially from that of Kanapoi and the more recent localities (Fig. 2). The most abundantly represented groups at Aramis, such as parrots (Psittacidae; 36% of the Aramis skeletal remains), land fowl (Galliformes; 29%), and barn owls (Tytonidae; 8%), are virtually absent from the remains from Kanapoi and the more recent localities, which together yield only a single parrot bone (KNM-KP 58729, likely referable to *Poicephalus*, not *Agapornis*, which is present at Aramis), and no galliforms or tytonids. The most abundantly represented non-passeriform groups at Kanapoi and the more recent localities are swifts (Apodidae; 24% of the Kanapoi avifauna), storks (Ciconiidae; 17% of the Kanapoi avifauna and 29% of the more recent localities), darters (Anhingidae; 6% of the Kanapoi avifauna), and vultures (Accipitridae; 29% of the more recent localities).

3.3. Fossil material examined

Order Struthioniformes

Family Struthionidae

Genus *Struthio*

Material Examined: KNM-KP 36599, KNM-KP 30262, KNM-KP 30490, KNM-KP 32522, KNM-KP 30154, KNM-KP 29300, KNM-KP 30223, KNM-KP 30221, KNM-KP 30154, KNM-WT 14283B, KNM-WT 14278, KNM-WT 14292, KNM-WT 14279, KNM-WT 464, KNM-WT 14235, KNM-WT 479, KNM-WT 424, KNM-WT 3499

Locality and Horizon:

KNM-KP 30490: Kanapoi (close to Wambua's hom, below sand in silt/clay)

KNM-KP 32522: Kanapoi (lower delta sands, below lake beds)

KNM-KP 36599, KNM-KP 30262, KNM-KP 29300, KNM-KP 30223, KNM-KP 30221, KNM-KP 30154: Kanapoi

KNM-KP 29300: Kanapoi (below tuff)

KNM-KP 30154: Kanapoi (below tuff)

KNM-WT 14283B: West Turkana (Kaitio, Detaic)

KNM-WT 14278: West Turkana (Kaitio, in gravels)

KNM-WT 14292: West Turkana (Kaitio, marginal lacustrine/deltaic)

KNM-WT 14279: West Turkana (Kaitio, North, in channel)

KNM-WT 464: West Turkana (Kalochoro, fluvial)

KNM-WT 14235: West Turkana (Lokapetemoe, Below the ?Nariokotome Tuff)

KNM-WT 479: West Turkana (Nachukui; fluvial)

KNM-WT 424: West Turkana (Nachukui; Nariokotome Member, deltaic, in gravels)

KNM-WT 3499: West Turkana (Nachukui, Nariokotome Member, lake margins)

Comparisons:

The following specimens were reported by Harris et al. (2003): KNM-KP 36599, KNM-KP 30262, KNM-KP 30490, KNM-KP 32522, KNM-KP 29300, KNM-KP 30223, KNM-KP 30221, while the following specimens, all consisting of broken *Struthio* eggshell, are reported here for the first time: KNM-KP 30154, KNM-WT 14283B, KNM-WT 14278, KNM-WT 14292, KNM-WT 14279,WT 464, KNM-WT 14235, KNM-WT 479, KNM-WT 424, KNM-WT 3499. As discussed by Harris et al. (2003) and noted above, the ostrich eggshell fragments exhibit the ‘struthious’ pore pattern diagnostic of extant ostriches (Sauer, 1972). Additional, more detailed comparisons between these specimens and other *Struthio* eggshell described from the Neogene of Africa (e.g., Harrison and Msuya, 2005) would be worthwhile, although such comparisons were not undertaken here. Although *Struthio* eggshell is among the most commonly recovered avian fossils from Kanapoi and the more recent Turkana localities, no skeletal material referable to *Struthio* has yet been recovered. Numerous fossils recovered from these localities that had been provisionally referred to *Struthio* are here recognized instead as belonging to marabou storks (*Leptoptilos*).

Order Suliformes

Family Anhingidae

Genus *Anhinga*

Figures: 1D, 1I

Material examined: KNM-KP 53159, KNM-KP 39325, KNM-KP 31743, KNM-WT 14570

Locality and horizon: KNM-KP 53159, KNM-KP 39325, KNM-KP 31743 are from Kanapoi; KNM-WT 14570 is from West Turkana (NC II Photo R16/6)

Comparisons: KNM-KP 53159: Well-preserved distal extremity of right tibiotarsus (lacking spina fibulae and tuberculum retinacula m. fibularis), very fragmentary distal right femur lacking the condylus lateralis, very fragmentary distal extremity of left ulna, exhibiting many broken surfaces, and two other unidentified fragments. Distal extremity of the tibiotarsus agrees in all respects with that of the extant African darter, *Anhinga rufa* OB 1411, but the spina fibulae is not attached along the lateral side of the bone, giving the fossil a superficially narrower appearance. The tibiotarsus is very slightly smaller than extant *A. rufa* OB 1411; the morphology of these elements is otherwise indistinguishable (Fig. 1I). The depressio epicondylaris lateralis and medialis are of comparable depth, with depressio epicondylaris lateralis exhibiting a sharp ridge along its external surface. The pons supratendinius is of the same relative width in both the fossil and OB 1411, and is deflected slightly proximomedially. The shape of the sulcus extensorius is similar in both the fossil and OB 1411; a fairly shallow depression extends from the canalis extensorius towards the proximal end of the bone. In both the fossil and OB 1411, a marked fossa exists on the lateral surface of the epicondylus medialis, and a small pit on the cranial surface of the epicondylus lateralis is positioned in the same place in both. The sulcus m. fibularis is positioned in the same area in both the fossil and OB 1411, and tuberculum retinaculi m. fibularis extends laterally to the same extent in both (although this is somewhat obscured in OB 1411 as the spina fibulae is still attached). Although very little of the femur is preserved, what is there compares closely with *A. rufa* OB 1411. Only the condylus medialis is preserved, but the preserved surface is similar in both the fossil and OB 1411, with a lateral deflection at its cranial terminus. A small nerve foramen enters the caudal surface of the intercondylar space, just above the cranial extent of the articular condyles. The femora exhibit a very shallow fossa poplitea. The tuberculum m. gastroc. lateralis is short, and positioned in the same area of both. On the cranial side, although the sulcus intercondylaris of the fossil is not preserved, the sulcus patellaris of both is extremely shallow. A crest leading from the cranial surface of the medial condyle is a marked ridge in both the fossil and OB 1411. The fossil ulna is very poorly preserved with numerous broken surfaces, but its general size compares well with extant *A. rufa* OB 1411.

KNM-KP 39325: Left humerus. Nearly complete and three dimensionally preserved, missing only the distalmost extremity of the bone. The fossil is indistinguishable from extant *A. rufa* OB 1411 (Fig. 1D).

KNM-KP 31743: Right distal humerus. The fossil compares favorably with the nearly complete fossil humerus KNM-KP 39325; however, the latter specimen is missing the distal-most portion of the bone. Where they can be compared, the tuberculum supracondylare ventrale of KNM-KP 31743 is slightly less pronounced, but this may be the product of weathering of the bone surface. The elements are practically identical in size.

KNM-WT 14570: Omal extremity of right coracoid, virtually indistinguishable from that of *A. rufa* OB 1411 in all respects. The bone surface is slightly weathered, making the articular surfaces more difficult to discern. The facies articularis humeralis, cotyla scapularis, and processus procoracoideus are preserved in their entirety. The cranial-most extent of the processus acrocoracoideus is missing; however, a long articular surface is preserved along the ridge of the processus acrocoracoideus from the facies articularis humeralis to the broken area, as in *A. rufa* OB 1411. The cotyla scapularis is very shallow, and slightly mediolaterally ovoid, as in *A. rufa*. The fossil is very slightly smaller than the corresponding region of the right coracoid of *A. rufa* OB 22. The processus acrocoracoideus appears to be slightly less deflected medially as in *A. rufa* OB 22.

Order Ciconiiformes

Family Ciconiidae

Genus *Leptoptilos cf. falconeri*

Figures: 2 A-J

Material examined: KNM-KP 50804, KNM-KP 50764, KNM-KP 50761, KNM-KP 50760, KNM-KP 50800, KNM-KP 53164, KNM-KP 51011, KNM-KP 56949, KNM-WT 56350, KNM-WT 16081

Locality and horizon: KNM-KP 50804: Kanapoi (lacustrine sequence, delta sands)
KNM-KP 50764: Kanapoi (lacustrine sequence)
KNM-KP 50761: Kanapoi (lacustrine sequence)
KNM-KP 50760: Kanapoi (lacustrine sequence)
KNM-KP 50800: Kanapoi (lacustrine sequence)
KNM-KP 53164: Kanapoi (upper fluvial sequence)
KNM-KP 51011: Kanapoi (lacustrine sequence, delta sands)
KNM-KP 56949: Kanapoi (deltaic)
KNM-WT 56350: West Turkana, Tondenyang (Nariokotome Member, lake margins)
KNM-WT 16081: West Turkana, KLI (Photo R14/3)

Comparisons: KNM-KP 50804: Distal right humerus. The specimen is not especially well preserved, and some surfaces are covered in sediment. Although the specimen is slightly larger than extant *L. crumeniferus* OB 35, it is otherwise indistinguishable–all visible morphology of the fossil humerus and that of OB 35 agrees. KNM-KP 50804 is better preserved than KNM-KP 51011 as the surface is not flattened, and the dorsal edge of the bone is preserved. The specimen compares closely with the the humerus of the Pliocene marabou *Leptoptilos lüi* (Zhang et al., 2012).

KNM-KP 50764: Right wrist region of a large bird. Preserved elements are distal-most right ulna, radiale, ulnare, and proximal-most carpometacarpus in several pieces. The proximal extremity of the carpometacarpus is preserved; it compares with *Leptoptilos crumeniferus* OB 35 in all respects (Fig. 2H). Notably, major pneumatic foramina perforate the proximal carpometacarpus—a diagnostic feature for *Leptoptilos* (Louchart et al., 2005), and are present in the same positions as in extant *L. crumeniferus*. These are on the proximal articular surface, within the fossa infratrochlearis. On the ulna, the position and shape of the shallow depressio radialis is similar in the fossil and OB 35. The angle and position of the condylus dorsalis ulnae is comparable with that of OB 35. A small tubercle projects just medially with respect to the sulcus intercondylaris, and projects to a comparable degree as OB 35. In proximal view, all aspects of the ulnar morphology compares with extant *L. crumeniferus*, including the position and relative size of the substantial pneumatic foramen between the condylus ventralis ulnae and tuberculum carpale. Ulnare: Opposite to the incisura metacarpalis, along the crus breve, a marked depression runs along the length of the bone in both the fossil and extant *L. crumeniferus*. Most of the crus breve is broken off (Fig. 2I). A large pneumatic foramen is present in the middle of the dorsal surface of the modern specimen, with a comparable foramen in that position on the fossil. All visible aspects of the radiale compare well with OB 35. One end of the fossil is broken off (this end exhibits a small pneumatic foramen in OB 35). Several other small fossil bone fragments from this specimen are not definitively attributable to particular elements.

KNM-KP 50761: Phalanx distalis digiti majori of a massive bird. Morphology compares very closely with *L. crumeniferus* OB 35, but the fossil is larger. On its plantar surface, the fossil shows less pronounced excavation and no pneumatization towards the distal end with respect to OB 35. The distalmost extremity of the element is broken.

KNM-KP 50760: Pedal phalanx and radiale of a very large bird. Both are considerably larger than *L. crumeniferus* OB 35, but the morphology is otherwise generally indistinguishable (Fig. 2J).

KNM-KP 50800: Proximal tarsometatarsus including articular surfaces. The plantar surface of the hypotarsus is broken. Compares closely in every way (including size) with extant *L. crumeniferus* OB 35.

KNM-KP 53164: *Leptoptilos* skull. A fragmentary right quadrate is preserved, but extremely poorly. Much of the surface morphology is obscured either by breaks or by surrounding skull/jaw elements being fused to the surface. Very little can be said by way of comparison with extant *L. crumeniferus* at present on the basis of the quadrate due to its poor state of preservation. The neurocranium is crushed fairly flat dorsally. As a result, the caudal surface of the skull (which forms a vertical plane in *Leptoptilos*; Zhang et al., 2012) is greatly compressed. The caudal margin of the skull is sheared rostrally such that much of it lies roughly in the same plane as the dorsal surface of the skull. A prominent crista nuchalis transversa is observed on the left side of the skull that originally would have separated the skull's dorsal surface from its roughly perpendicular caudal surface. As in *L. lüi*, but not extant *L. crumeniferus* (Zhang et al., 2012), the lamina parasphenoidalis is apparently situated lower than the condylus occipitalis, resulting in a marked fossa subcondylaris.

KNM-KP 51011: Distal humerus and some associated shaft fragments. The specimen agrees well in both size and morphology with the distal humerus of *L. lüi* (Zhang et al., 2012).

KNM-KP 56949: Left tibiotarsus shaft and pedal phalanx. The midshaft morphology compares well overall with extant *L. crumeniferus* OB 35, but the diameter is larger in the fossil. The fossil also exhibits a more gradual taper, indicating a wider and longer tibiotarsus than that of OB 35. The bone exhibits one flat surface, and would have been semicircular in cross section. The lateral aspect of the bone is broken and missing, thus the area of attachment of the fibula cannot be assessed. In *L. crumeniferus* OB 35, the distalmost portion of the fibula joins the tibiotarsus, and fuses completely with it. A distal pedal phalanx is also associated with this specimen; other than its very large size, it compares closely with OB 35.

KNM-WT 56350: Distal right humerus of a marabou stork; slightly smaller than the other two distal stork humeri from Kanapoi, meaning it is essentially indistinguishable in size from extant *L. crumeniferus* OB 35. The proximal extension of the dorsal condyle is weathered away, and the dorsal surface of the bone is missing.

KNM-WT 16081: Most of a synsacrum, lacking pelvic elements. Comparable in size and visible morphology to extant *L. crumeniferus* OB 35.

Genus *Mycteria*

Figures: 1B, 1C, IJ

Material examined: KNM-KP 50759, KNM-KP 30231

Locality and horizon: KNM-KP 50759: Kanapoi, lacustrine sequence

KNM-KP 30231: Kanapoi (below tuff)

Comparisons: KNM-KP 50759: Well-preserved proximal right femur. Compares very closely in all respects with same element of *Mycteria ibis* OB 49, although the fossil is slightly larger (Fig. 1J).

KNM-KP 30231: Distal pedal phalanx, fragment of distal left tarsometatarsus, left radiale, near-complete right tibiotarsus (proximal end, distal end, and shaft fragments), unidentified shaft fragments from a long bone, partial fibula. The radiale and distal end of tibiotarsus are well preserved, and are referable to *Mycteria* (Fig. 1B, 1C). This specimen was first noted and diagnosed by Harris et al. (2003).

Order Pelecaniformes

Family Pelecanidae

Genus *Pelecanus*

Figures: 1H

Material examined: KNM-WT 19627

Locality and horizon: West Turkana (NAI Photo R 22/2)

Comparisons: Specimen comprises the distal end of a right humerus, and the distal and proximal ends of a left humerus. The bones are massive and reasonably well preserved, although much of the bicipital and deltopectoral crests are eroded away on the proximal humerus. Apart from these preservational artifacts, the visible morphology of the specimen is virtually indistinguishable from extant *Pelecanus onocrotalus* OB 2334 (Fig. 1H).

Order Psittaciformes

Family Psittacidae

Figures: 1A

Material examined: KNM-KP 50759

Locality and horizon: KNM-KP 50759: Kanapoi, lower fluvial sequence

Comparisons: KNM-KP 58729: Complete left tarsometatarsus. The bone is stout overall, with its proximal articular shelf offset laterally from the main axis of the bone. The squat shape of the bone and its zygodactyl configuration are psittaciform synapomorphies (Ksepka and Clarke, 2012). Although some of the bone surface remains obscured by matrix, including much of the proximal articular surface, all visible morphology agrees with a referral to Psittacidae. The hypotarsus bears a closed bony canal for the tendon of the musculus flexor digitorum longus (furrow/canal no. 1 of Strauch, 1978). The fossil is figured next to *Poicephalus meyeri* OB 274, with which it agrees well despite being slightly larger (Fig. 1A). Matrix obscures part of the plantar region, precluding assessment of whether the lateral foramen vasculare is displaced well proximal of its medial counterpart as in extant parrots (Ksepka and Clarke, 2012).

Order Apodiformes

Family Apodidae

Figures: 1F

Material examined: KNM-KP 53036, KNM-KP 53040, KNM-KP 53041, KNM-KP 53045, KNM-KP 53007, KNM-KP 53008, KNM-KP 53009, KNP-KP 53014, KNM-KP 32825, KNM-KP 30640, KNM-KP 53037, KNM-KP 53034

Locality and horizon: KNM-KP 32825: Kanapoi (microfauna level).

Comparisons: KNM-KP 53036: Left phalanx proximalis digiti majoris; element is robust, and exhibits broken articular surfaces.

KNM-KP 53040. Left proximal half of carpometacarpus exhibiting well-preserved articular surfaces.

KNM-KP 53041: Small left ulna, three-dimensionally preserved, complete and undamaged. Articular surfaces very well preserved. Radial and humeral fossae are both deep. The crests on the distal surface are very deep and well developed.

KNM-KP 53045: Corpus major of right carpometacarpus.

KNM-KP 53007: Omal end of right coracoid; broken along the midshaft just sternal to the procoracoid process. Massive acrocoracoid process completely preserved, with short procoracoid process. Humeral articulation facet is complete and well preserved. Procoracoid nerve foramen present. Cotyla scapularis shallow, directly adjacent to the sternal extremity of the humeral articulation facet (Fig. 1F).

KNM-KP 53008: Distal ends of two left ulnae (practically identical). Very well preserved. From a large swift; articular surfaces clearly demarcated.

KNM-KP 53009: Well-preserved proximal end of left radius; quite slight; agrees in terms of size and general morphology with *Apus horus* OB 333.

KNP-KP 53014: Distal end of right ulna. Relatively poorly preserved, but articular surfaces on distal end are well preserved and prominent. Agrees well with *A. horus* OB 333.

KNM-KP 32825: Right distal ulna of a large swift including part of the shaft; generally poorly preserved but articular surfaces generally clear.

KP 30640: Complete, very well preserved right ulna of a swift. Articular surfaces well preserved.

KNM-KP 53037: Largely complete phalanx proximalis digiti majori; muscle scars and associated crests are obvious, and distal articular surface is well preserved.

KNM-KP 53034: Very well preserved, near-complete right carpometacarpus of a swift (~the size of *A. horus* OB 333). The corpus minor is broken on its distal end, preserving nearly half its length. The rest of the bone is well preserved and complete.

Order Anseriformes

Family Anatidae

Figures: 1G

Material examined: KNM-WT 52128:

Locality and horizon: West Turkana; Nachukui. Deltaic setting within Nariokotome Member

Comparisons: KNM-KP 39326: This proximal left humerus fragment was previously referred to Anatidae, although confusingly also to Charadriiformes (Harris et al., 2003). The specimen is very poorly preserved, and is probably best referred to Aves indet.

KNM-WT 52128: Proximal left femur of a fairly large anatid, slightly smaller than Egyptian goose (*Alopochen aegyptiaca* OB 1637), with which it is compared in Fig. 1G. All aspects of morphology compare well with *A. aegyptiaca*, although much of the proximal surface is eroded away. The dorsal surface of the femoral head is flattened in both the fossil and OB 1637. A low crista trochanteris barely extends above the level of the femoral head.

Families: Columbidae/Pteroclididae?

Material examined: KNM-KP 53043, KNM-KP 53019

Locality and horizon: KNM-KP 53043: Kanapoi

KNM-KP 53019: Kanapoi

Comparisons: KNM-KP 53043: Moderately well preserved right distal humerus; some damage to the surface. The articular surfaces are fairly distinct. The specimen generally compares favorably with Columbidae and Pteroclididae, including *Pterocles exustus* OB 797.

KNM-KP 53019: Very poorly preserved distal end of left humerus; articular surfaces largely absent. Visible morphology agrees with Columbidae and Pteroclididae.

Order Strigiformes

Family Strigidae

Material examined: KNM-KP 30642

Locality and horizon: Kanapoi

Comparisons: Specimen is poorly preserved, and comprises the omal extremity of a right scapula, an ungual phalanx, and three unidentifiable bone fragments from a very small owl; comparable in size to *Glaucidium capense*.

Aves Indet.

Material examined: KNM-KP 53026

Locality and horizon: Kanapoi; “Joseph’s Trench”, Step 4

Comparisons: Distal end of a fairly large avian pedal phalanx. Agrees in general morphology and size with a mid- to small-sized bustard, although a firm diagnosis is not possible based on the limited material.

Order Charadriiformes

Family Recurvirostridae?

Material examined: KNM-KP 53046

Locality and horizon: Kanapoi

Comparisons: Partial proximal left humerus of a charadriiform bird; most of the caput humeri is present. The specimen exhibits a prominent tuberculum ventrale, connected to the humeral shaft via a sharp ridge. The specimen shows a deep and elongate fossa pneumotricipitalis, which, although in-filled with sediment, is clearly of the 'dual type, non-pneumatic' (Baumel and Witmer, 1993). Both the crista deltopectoralis and crista bicipitalis are broken close to the main shaft of the humerus. Caput humeri are separated from the tuberculum ventrale by a deep incisura capitis. In cranial view, a deep, laterally extensive sulcus ligamentum transverus is visible. Although the crista bicipitalis is largely broken, what remains of the intumescentium humeri is broad. There is a deep impressio coracobrachialis, which terminates proximally in a broken edge; thus, the tuberculum dorsale is not preserved. The preserved edge of the crista deltopectoralis suggests that it was considerably longer than the crista bicipitalis (~30%). The sulcus n. coracobrachialis is shallow. Every aspect of the preserved and visible morphology compares with the humerus of *Recurvirostra avosetta* OB 1517.

Order Coraciiformes

Family Alcedinidae?

Material examined: KNM-KP 53061

KNM-KP 53018

Locality and horizon: Kanapoi

Comparisons:

KNM-KP 53061: Left ulna, proximal end. Both radial and humeral articulations are fairly shallow; radial articulation sub-rectangular in shape. Compares in all visible respects, including identical size, with *Alcedo cristata* OB 1117.

KNM-KP 53018: Shaft of a small right tarsometatarsus. Element is relatively stout; the distal trochleae are broken, as is most of the proximal surface of the element. The element is of comparable size to *Alcedo cristata* OB 1117.

Order Passeriformes

Material examined: KNM-KP 53044, KNM-KP 53003, KNM-KP 53005, KNM-KP 53006, KNM-KP 53016, KNP-KP 53021, KNM-KP 53029, KNM-KP 53004, KNM-KP 53017, KNM-KP 53042, KNM-KP 53035, KNM-KP 53033, KNM-KP 53032, KNM-KP 53027, KNM-KP 53023, KNM-KP 53015

Locality and horizon:

KNM-KP 53044: Kanapoi
KNM-KP 53003: Kanapoi
KNM-KP 53005: Kanapoi
KNM-KP 53006: Kanapoi
KNM-KP 53016: Kanapoi “bat site”
KNP-KP 53021: Kanapoi
KNM-KP 53029: Kanapoi
KNM-KP 53004: Kanapoi "Wambua's hominid, Step 3"
KNM-KP 53017: Kanapoi "bat site"
KNM-KP 53042: Kanapoi
KNM-KP 53035: Kanapoi

KNM-KP 53033: Kanapoi

KNM-KP 53032: Kanapoi

KNM-KP 53027: Kanapoi

KNM-KP 53023: Kanapoi "microfauna Nichola dP4-sieve WT 3425"

KNM-KP 53015: Kanapoi

General notes:

KNM-KP 53044: Left distal humerus of a small passeriform; very friable and poorly preserved.

KNM-KP 53003: Complete, three-dimensionally preserved right carpometacarpus; Articular surfaces well preserved.

KNM-KP 53005: Small, very well preserved distal extremity of left humerus; articular surfaces well preserved.

KNM-KP 53006: Small, moderately well preserved distal end of right ulna.

KNM-KP 53016: Tiny, broken proximal end of carpometacarpus.

KNP-KP 53021: Small, very well preserved proximal end of right carpometacarpus.

KNM-KP 53029: Distal end of left tarsometatarsus; tiny and very slender. No phalangeal trochleae are preserved and the element seems unlikely to be further diagnosable.

KNM-KP 53004: Left carpometacarpus from a small passerine, well preserved and nearly complete, corpus minor not preserved.

KNM-KP 53017: Left distal ulna. Small element, generally poorly preserved.

KNM-KP 53042: Tiny, very well preserved omal extremity of a coracoid and much of the shaft. The humeral articulation facet, acrocoracoid process, and procoracoid process all well preserved. The procoracoid process is very short; cotyla scapularis not notably concave; humeral articulation facet elongate and narrow, acrocoracoid process very pronounced and broad.

KNM-KP 53035: Tiny, left distal ulna with much of the shaft preserved.

KNM-KP 53033: Tiny, right distal ulna, with articular surfaces at the wrist well preserved.

KNM-KP 53032: Omal extremity of a very small right coracoid. Agrees well with KNM-KP 53042. The specimen exhibits a negligible procoracoid process, a poorly defined, non-concave cotyla scapularis, and a broad, well-developed acrocoracoid process. The shaft is broken just below the procoracoid process. The humeral articulation facet is preserved in its entirety.

KNM-KP 53027: Generally poorly preserved and very small right distal ulna including some of the shaft.

KNM-KP 53023: Fairly well preserved right distal ulna of a mid-sized passerine.

KNM-KP 53015: Tiny, right distal ulna of a passerine bird. Not well preserved.

Order Accipitriformes

Family Accipitridae

Subfamily cf. Aegypiinae

Figures: 1E

Material examined: KNM-WT 16156, KNM-WT 19983

Locality and horizon: Kanapoi

KNM-WT 16156: West Turkana (Lo. 9).

KNM-WT 19983: West Turkana (Hippo Site)

Comparisons:

KNM-WT 16156: Right distal ulna and some of the shaft from a large raptor; some of the articular surface is preserved. Compares closely with Aegypiinae.

KNM-WT 19983: Complete, three-dimensionally preserved right ulna from a large raptor. The fossil preserves short, poorly defined quill knobs, comparable to those on the ulna of *Trigonoceps occipitalis* OB 957. Although generally similar to the ulna of *L. crumeniferus*, the humerus of *L. crumeniferus* is ~8% longer, has quill knobs that are much more clearly defined, extensive pneumatization at the proximal and distal ends of the bone, a more laterally elongated humeral articulation, a less deeply excavated impressio brachialis, a more sharply pointed tuberculum carpale, and a pronounced and acute tubercle on the distal extremity of the condylus ventralis ulnae.

4. Discussion

While the present study represents a preliminary investigation, the early Pliocene fossil avifauna from Kanapoi clearly represents a diverse taxonomic assemblage. It appears broadly comparable to that described from the Miocene locality of Lothagam (Harris and Leakey, 2003), although the mammalian faunas from these localities differ considerably (Bobe, 2011). Despite the fact that only a comparatively small sample of avian fossils has been examined to date, no fewer than 12 family-level clades are represented between Kanapoi and the more recent Turkana localities. Additionally, at least some of these clades are represented by multiple taxa, including storks (Ciconiidae), which are represented by both *Mycteria* and *Leptoptilos*. Given that additional avian material has been surface collected from Kanapoi and the more recent localities (and thus far been unavailable for examination), it is almost certain that the diversity of this avian assemblage is strongly undersampled. This is underscored by the fact that only a minority of the Kanapoi avian material has thus far proven diagnosable to family, and it is likely that future attention and sampling via surface collection and sieving will shed additional light on the affinities of these remains. A prior survey of the Kanapoi fossil avifauna (Harris et al., 2003) revealed the remains of only four avian taxa in the form of numerous ostrich eggshell specimens, several fragmentary long bones from *Mycteria,* a tentatively-referred fragmentary duck humerus, and a complete *Anhinga* humerus. It seems certain that additional sampling from Kanapoi and the younger West Turkana localities will continue to reveal an interesting diversity of fossil birds with potential to shed light on the paleoenvironment of *A. anamensis*, and the composition of East African Pliocene avifaunas.

4.1. Kanapoi paleonenvironment, and early Pliocene hominin niche partitioning

The avian fossils from Kanapoi and the more recent West Turkana localities reveal an obvious ecological signal. Although the general tetrapod assemblage at Kanapoi was initially described as broadly similar to the comparably aged (though slightly older) assemblage from Aramis, Ethiopia (Harris et al., 2003), more recent work (e.g., Louchart et al., 2009) as well as the present avian dataset stands in stark contrast to this assessment. In addition to producing fossil hominin remains, Aramis represents the most extensively evaluated early Pliocene avifauna from East Africa. A survey of that avifauna (Louchart et al., 2009) yielded at least 370 catalogued avian specimens, representing 29 species and 16 families. Among the 296 diagnosable elements from this avifauna, only 3.8% represented aquatic taxa (Louchart et al., 2009). Most small elements were interpreted to have derived from owl pellets, and collectively, the paleoenvironment at Aramis was determined to represent one dominated by mesic woodlands (Louchart et al., 2009).

By contrast, the broader West Turkana avifauna is comparatively dominated by aquatic taxa, which comprise 27% (Kanapoi) and 71% (more recent localities) of the avian fossils diagnosed to date. The majority of extant waterbird diversity (Aves: Aequorlitornithes) is the product of a large monophyletic radiation uniting, among many other groups, shorebirds (Charadriiformes), storks (Ciconiiformes), darters (Suliformes: Anhingidae), and pelicans (Pelecaniformes: Pelecanidae) (Prum et al., 2015). In addition to these aequorlitornithid representatives, the broader West Turkana avifauna comprises representatives of at least two additional aquatic lineages: waterfowl (Anseriformes: Anatidae), and a probable kingfisher (Coraciimorphae: Alcedinidae). The Kanapoi avifauna is entirely consistent with the idea that *A. anamensis* from this locality lived alongside a large, slow-moving body of water. The stark difference in both the taxonomic composition and comparative abundance of taxa from the Kanapoi and Aramis avifaunas may be suggestive of divergent habitat preferences (if not ecological niche partitioning) among early Pliocene hominins in East Africa.

4.2. Implications for the origins of Africa's extant avifauna

Today, Africa's avifauna is extraordinarily diverse—represented by over 2,500 living species (Brown et al., 1982). However, a relatively sparse avian fossil record has hindered our understanding of the pattern and timing of Africa's avifaunal assembly (Louchart et al., 2005, 2009; Mayr, 2009). As such, the fossil assemblage at Kanapoi may have much to contribute to our understanding of avian evolution in the Pliocene of East Africa. Although the present contribution represents a preliminary assessment, the future incorporation of avian fossils from Kanapoi into detailed character-taxon datasets may yield insights into the precise phylogenetic placement of these specimens. Indeed, these fossils may variously provide useful apical minimum constraints in node-dating divergence time analyses, help illuminate the evolution of African avian biogeography, and shed light on the broader evolutionary history of East African birds. The evolutionary relationships and biogeographic origins of several major clades of African endemic birds have long remained obscure (e.g., turacos; Musophagidae, secretarybirds; Sagittariidae, shoebills; Balaenicipitidae), a product, in large part, of their extremely scarce fossil records. The detailed examination of avian remains from localities like Kanapoi may ultimately help clarify how, when, and where the modern constituents of the East African avifauna came to be.

4.3. Giant extinct marabou storks, and the antiquity of marabou-hominin interactions

One of the most striking aspects of the Kanapoi avifauna is the relative abundance of a giant marabou stork, larger than the extant marabou *L. crumeniferus* (represented by eight specimens from Kanapoi). Although a giant extinct marabou, *L. falconeri*, has been reported from the Pliocene of Chad and Ethiopia (after initially being described from the

Siwalik Hills of Pakistan; Louchart et al.,2005), the occurrence of this taxon in the early Pliocene of Kenya represents an extension of its known geographic range in East Africa. Previously, remains of fossil marabous from Kenya had been reported from only the late Miocene locality of Lothagam, northern Kenya (Upper Nawata Member, between 5.3 and 6.5 Ma (McDougall and Feibel, 1999; Harris and Leakey, 2003; Louchart et al., 2005) and the Miocene locality of Ngorora (Baringo, ca. 11.5Ma; Hill and Walker, 1978; Louchart et al., 2005).

Previous descriptions of *L. falconeri* material comprise only distal tibiotarsi, distal tarsometatarsi, pedal phalanges, a fragmentary carpometacarpus, and a vertebra. The material herein referred to *L.* cf. *falconeri* represents a neurocranium and quadrate, much of the forelimb (portions of the humerus, ulna, os carpi ulnare, os carpi radiale, proximal carpometacarpus and manual phalanx), hindlimb (pedal phalanges, proximal tarsometatarsus, tibiotarsus) and synsacrum. While these remains are fragmentary, scaling equations (e.g., Field et al., 2013) should allow for the future study of body size evolution in Leptoptilini, a subject of current research interest (Louchart et al., 2005; Meijer and Due, 2010; Zhang et al., 2012). Future detailed study of the *Leptoptilos* material recovered from Kanapoi will doubtless shed considerable additional light on the morphology of giant Neogene marabous, despite the fact that the cranial remains are presently in need of additional mechanical preparation. The rarity of fossil *Leptoptilos* crania (Zhang et al., 2012) renders the Kanapoi remains of particular interest, and may enable the future investigation of endocranial morphology and detailed anatomical comparisons with extant marabous using computed tomographic reconstructions (Balanoff et al., 2016). Full descriptions and analysis of the Kanapoi *Leptoptilos* material, which is beyond the scope of the present contribution, promises to reveal many new details about the morphology of this gigantic Pliocene stork.

The scavenging ecology of extant marabous (i.e., their propensity to feed on human refuse), and the relatively frequent co-occurrence of fossil marabous and early human relatives from the Miocene through the Pleistocene (Harris and Leakey, 2003; Louchart et al., 2005, 2008; Zhang et al., 2012) raises the interesting (though presently speculative) possibility of multi-million-year commensalism between marabous and early humans (H. James, personal communication). The occurrence of both *L.* cf. *falconeri* and the earliest-known australopithecines at Kanapoi may lend some support to this idea. Perhaps the association between humans and marabous, which today are abundant around urban areas throughout East Africa, reflects the result of over five million years of acclimation to mutual coexistence.

4.4. Taphonomy of Kanapoi avian remains

The vast majority of the avian remains from Kanapoi and the more recent West Turkana localities are broken and isolated, an observation consistent with sorting by moving water (Louchart et al., 2009; Longrich et al., 2011). In contrast to the small vertebrate remains recovered from Aramis, few or none of the avian remains examined here exhibit obvious signs of feeding by rodents or chewing by mammalian carnivores, underscoring the taphonomic distinctness of these two localities. The relative abundance and damage of many of the small vertebrate remains from Aramis were interpreted to be consistent with their derivation from owl pellets; however, the Kanapoi fossils exhibit little evidence in support of a similar taphonomic history. Sorting due to water transport may in part contribute to the considerable diversity of the Kanapoi avifauna despite the modest number of elements collected and examined to date: in addition to autochthonous bird carcasses that may have been deposited nearby, the assemblage may also reflect allochthonous avian remains transported by water from more distal settings.

5. Conclusion

Louchart et al. (2009) suggest that the fossil avifauna from the *Ardipithecus*-bearing Aramis locality reflected a taphonomic setting where most carcasses were buried, without transport, in a mesic woodland environment far from water. By contrast, the bird fossils from the roughly contemporaneous *A. anamensis*-bearing sites of Kanapoi lack any notable woodland signal, and the presence of a variety of aquatic taxa is instead suggestive of a setting close to water. The paleoecological differences between these sites suggest possible differentiation in environmental preferences between contemporaneous hominin taxa in East Africa, and the presence of the large Pliocene marabou stork *L.* cf. *falconeri* may reflect a long-term commensal relationship between marabous and hominins. In sum, geological, taphonomic, and taxonomic evidence are indicative of an ecological setting in close proximity to a large, slow-moving water body for *A. anamensis* at Kanapoi. This work emphasizes the utility of fossil birds as sensitive environmental indicators (Olson and Rasmussen, 1986), and their potential contribution to paleoecological reconstructions of early hominin paleoenvironments.

Acknowledgements

I am grateful to C. Ward, M. Plavcan, and F. Manthi for the invitation to take part in this research, D. Matthieson for her initial work on the fossil birds from Kanapoi, A. Louchart, M. Plavcan, and C. Ward for helpful and constructive reviews of this manuscript, and C. Brochu (East African birds), H. James (human-marabou commensalism), and S. Frost (small vertebrate taphonomy) for helpful discussions during the course of this study. Funding for this project was provided by NSF BCS-1231749, NSF BCS-1231675, the Wenner Gren Foundation, and the University of Missouri Research Board. DJF is supported by a 50th Anniversary Prize Fellowship at the University of Bath.

Figure Captions

Fig. 1: Selected non-*Leptoptilos* avian fossil material from Kanapoi and West Turkana. Scale bar equals 1cm. 2A: tarsometatarsus of Psittacidae KNM-KP 58729 (left), and extant *Poicephalus meyeri* OB 274 (right), in cranial view; 2B-C: distal right tibiotarsus of stork (Ciconiidae: *Mycteria*) KNM-KP 30231 (right) and extant *Mycteria ibis* OB 49 (left) in cranial (2B) and lateral (2C) view; 2D: left humerus of *Anhinga* KNM-KP 39325 (right) and extant *Anhinga rufa* OB 1411, in dorsal view; 2E: right ulna of vulture (Accipitridae: Aegypiinae) KNM-WT 19983 (right) and extant *Trigonoceps occipitalis* OB 957 (left), in ventral view; 2F: Omal extremity of right coracoid of swift (Apodidae) KNM-KP 53007 (left), and extant *Apus horus* OB 333 (right); 2G: proximal left femur of Anatidae KNM-WT 52128 (right), and extant *Alopochen aegyptiaca* OB 1637 (left), in cranial view; 2H: proximal left humerus of *Pelecanus* KNM-WT 19627 (left) and extant *Pelecanus onocrotalus* OB 2334 (right), in cranial view; 2I: distal right tibiotarsus of

Anhinga KNM-KP 53159 (left) and extant *Anhinga rufa* OB 1411 (right), in cranial view; 2J: proximal right femur of stork (Ciconiidae: *Mycteria*) KNM-KP 50759 (left), and extant *Mycteria ibis* OB 49 (right), in cranial view.

Fig. 2: Selected fossil marabou stork (Ciconiidae: *Leptoptilos*) material from Kanapoi and West Turkana. Scale bar equals 1cm. 1A-C: neurocranium KNM-KP 53164 in dorsal (1A), posterior (1B), and right lateral (1C) view; 1D: synsacrum KNM-WT 16081 in dorsal view (left), modern *L. crumeniferus* OB 35 (right); 1E: proximal tarsometatarsus KNM-KP 50800 in cranial view; 1F: distal right humerus KNM-KP 50804 in cranial view; 1G: distal right ulna KNM-KP 50764 (left), extant *L. crumeniferus* OB 35 (right) in ventral view; 1H: proximal right carpometacarpus KNM-KP 50764 (left), extant *L. crumeniferus* OB 35 (right); 1I: ulnare KNM-KP 50764 (left), extant *L. crumeniferus* OB 35 (right); 1J: radiale KNM-KP 50760 (left), extant *L. crumeniferus* OB 35 (right).

Fig. 3: Dominant avian ecologies represented at Kanapoi and the more recent Turkana localities, compared to the slightly older fossil avifauna from Aramis, Ethiopia (based on skeletal data; Aramis data from Louchart et al., 2009). Aquatic birds and aerial insectivores (swifts) together comprise the dominant avian lifestyles represented at Kanapoi, with aquatic birds dominating at the more recent localities. By contrast, aquatic birds and swifts are extremely rare at Aramis.

Fig. 4: Comparison of the dominant avian taxa represented at Kanapoi, the more recent Turkana localities, and Aramis (Aramis data from Louchart et al., (2009)). The dominant

clades at Kanapoi and the more recent localities, including storks (Ciconiidae), swifts (Apodidae), and songbirds (Passeriformes) are poorly represented at Aramis, where small parrots (Psittacidae), barn owls (Tytonidae), and landfowl (Galliformes; comprising *Francolinus*, *Pavo*, and Numididae) are dominant. Predominantly aquatic taxa (in blue) are extremely scarce at Aramis, but comparatively abundant at Kanapoi and the more recent Turkana localities.

References

Balanoff, A.M., Bever, G.S., Colbert, M.W., Clarke, J.A., Field, D.J., Gignac, P.M., Ksepka, D.T., Ridgely, R.C., Smith, N.A., Torres, C.R., Walsh, S., Witmer, L.M., 2016. Best practices for digitally constructing endocranial casts: examples from birds and their dinosaurian relatives. J. Anat. 229, 173-190.

Baumel, J.J., Witmer, L.M., 1993. Osteologia. In: Baumel, J.J., King, A.S., Breazile, J.E., Evans, H.E., Vanden Berge, J.C. (Eds.), Handbook of Avian Anatomy: Nomina Anatomica Avium. Publications of the Nuttall Ornithological Club, Cambridge, Massachusetts, pp. 45-132.

Bobe, R., 2011. Fossil mammals and paleoenvironments in the Omo-Turkana Basin. Evol. Anthropol.20, 254-263.

Brown, B., Brown, F.H., Walker, A., 2001. New hominids from the Lake Turkana basin, Kenya. J. Hum. Evol. 41, 29-44.

Brown, L.H., Urban, E.K., Newman, K., Woodcock, M., Hayman, P., 1982. The Birds of Africa. Academic Press, London.

Del Hoyo, J., Elliot, A., Sargatal, J., 1992. Handbook of the Birds of the World. Lynx Editions, Barcelona.

Field, D.J., Lynner, C., Brown, C., Darroch, S.A.F., 2013. Skeletal correlates for body mass estimation in modern and fossil flying birds. PLOS ONE 8, e82000.

Finlayson, C., Carrión, J., Brown, K., Finlayson, G., Sánchez-Marco, A., Fa, D., Rodríguez-Vidal, J., Fernández, S., Fierro, E., Bernal-Gómez, M., 2011. The *Homo* habitat niche: using the avian fossil record to depict ecological characteristics of Palaeolithic Eurasian hominins. Quaternary Sci. Rev. 30, 1525-1532.

Harris, J., Leakey, M., 2003. Lothagam birds. In: Leakey, M.G.; Harris, J.M. (Eds.), Lothagam: the Dawn of Humanity in Eastern Africa. Columbia University Press, New York, pp.161-166.

Harris, J.M., Leakey, M.G., Cerling, T.E., Winkler, A.J., 2003. Early Pliocene tetrapod remains from Kanapoi, Lake Turkana Basin, Kenya. Contrib. Sci. 498, 39-114.

Harrison, T., Msuya, C.P., 2005. Fossil struthionid eggshells from Laetoli, Tanzania: Taxonomic and biostratigraphic significance. Journal of African Earth Sciences 41, 303-315.

Hill, A., Walker, A., 1978. A fossil marabou (Aves: Ciconiidae) from the Miocene Ngorora formation, Baringo district, Kenya. Neth. J. Zool. 29, 215-221.

Ksepka, D.T., Clarke, J.A., 2012. A new stem parrot from the Green River Formation and the complex evolution of the grasping foot in Pan-Psittaciformes. J. Vert. Paleontol. 32, 396-406.

Longrich, N.R., Tokaryk, T., Field, D.J., 2011. Mass extinction of birds at the Cretaceous-Paleogene (K-Pg) boundary. Proc. Natl. Acad. Sci. 108, 15253-15257.

Louchart, A., Vignaud, P., Likius, A., Brunet, M., White, T.D., 2005. A large extinct marabou stork in African Pliocene hominid sites, and a review of the fossil species of *Leptoptilos*. Acta Palaeontol. Pol. 50, 549-563.

Louchart, A., Haile-Selassie, Y., Vignaud, P., Likius, A., Brunet, M., 2008. Fossil birds from the Late Miocene of Chad and Ethiopia and zoogeographical implications. Oryctos 7, e167.

Louchart, A., Wesselman, H., Blumenschine, R.J., Hlusko, L.J., Njau, J.K., Black, M.T., Asnake, M., White, T.D., 2009. Taphonomic, avian, and small-vertebrate indicators of *Ardipithecus ramidus* habitat. Science 326, 66e1-66e4.

Mayr, G., 2009. Paleogene Fossil Birds. Springer, Berlin.

McDougall, I., Brown, F.H., 2008. Geochronology of the pre-KBS Tuff sequence, Omo Group, Turkana Basin. J. Geol. Soc. London 165, 549-562.

McDougall, I., Feibel, C.S., 1999. Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift. J. Geol. Soc. London 156, 731-745.

Meijer, H.J., Due, R.A., 2010. A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia). Zool. J. Linn. Soc.-London 160, 707-724.

Olson, S.L., Rasmussen, D.T., 1986. Paleoenvironment of the earliest hominoids: new evidence from the Oligocene avifauna of Egypt. Science 233, 1202-1204.

Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., Lemmon, A.R., 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526, 569-573.

Sauer, E., 1972. Ratite eggshells and phylogenetic questions. Bonn Zool. Beitr 23, 3-48.

Serjeantson, D., 2009. Birds. Cambridge Manuals in Archaeology. Cambridge University Press, Cambridge.

Zhang, Z., Huang, Y., James, H.F., Hou, L., 2012. A marabou (Ciconiidae: *Leptoptilos*) from the Middle Pleistocene of northeastern China. The Auk 129, 699-706.