

# Avian fossils from the Early Miocene Moghra Formation of Egypt

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**Avian remains from the Early Miocene (~17 Ma) Moghra Formation of Egypt include new records of ‘waterbirds’ (storks, herons, pelicans and allies) and a ratite. Only a single avian fossil has been previously reported from Wadi Moghra and, thus, additional knowledge of the avifauna complements previously documented faunal and floral assemblages and provides a more complete picture of the Early Miocene ecosystem of that locality. The presence of ciconiiforms and pelecaniforms is consistent with the relatively abundant records of ‘waterbirds’ from other African freshwater fossil localities. Moreover, avian fossils from Wadi Moghra provide new insight into the avifaunal composition of the Early Miocene in Africa, a period that is relatively underrepresented in the avian fossil record of that continent.**

**Keywords:** aepyornithoid, Ardeidae, avian evolution, Balaenicipitidae, Ciconiiformes, fossil eggshell

## Introduction

Vertebrates from the Early Miocene Moghra (= Moghara) Formation exposed at Wadi Moghra, Egypt, include a relatively diverse fauna of primates, proboscideans, perissodactyls, artiodactyls, hyaenodontans, carnivorans, fish, turtles and crocodiles (Miller 1996, Sanders and Miller 2002). However, previously reported avian taxa are limited to the isolated distal tibiotarsus of a stork (Ciconiiformes; Miller et al. 1997). Eight additional avian fossils from Wadi Moghra representing at least four avian taxa (Ratitae, Ardeidae, Balaenicipitidae and Ciconiidae) are reported herein. The addition of these taxa to the avifauna of the Moghra Formation provides new details about the ecological composition of that locality and facilitates more detailed comparisons with other African paleofaunas.

Wadi Moghra lies within the Qattara Depression, approximately 60 km south of El Alamein, Egypt (Figure 1). Moghra Formation sediments exposed at this locality include ironstone concretionary lenses, marls and unlithified sand deposits. Those sediments have been interpreted as the result of a mixture of fluvio-marine, estuarine, deltaic and lagoonal depositional settings and the age of the Moghra Formation is estimated at approximately 17–18 Ma (Early Miocene, Burdigalian) based on biostratigraphic correlation with other African localities and with fossiliferous bounding formations (see Said 1990 and Miller 1996 for additional geologic details). The Early Miocene age of the Moghra Formation fauna is congruent with the rise of a land bridge between Afro-Arabia and Europe between 18–20 Ma and the biotic interchange and subsequent faunal changes that resulted have been documented in the mammalian fossil record (Miller 1996).

Avian remains have been reported from Cenozoic African localities ranging in age from Paleocene (e.g. Bourdon et al. 2005, 2008), Eocene (e.g. Andrews 1916, Miller 1997),

Oligocene (e.g. Rasmussen et al. 1987), Middle to Late Miocene (e.g. Rich 1972, Hill and Walker 1979), Pliocene (e.g. Rich 1980, Mourer-Chauviré and Geraads 2010) and Pleistocene (e.g. Brodkorb 1980, Stidham 2010). However, Early Miocene avian fossil localities are comparatively rare on the continent and the quantity of material from those localities is relatively small (though see Rich and Walker 1983, Mlíkovský 2003, Dyke and Walker 2008). Thus, although the fossil remains described herein are fragmentary and isolated, description of avian fossils from Moghra provides new data that helps to fill a temporal gap in our knowledge of the evolution of the African avifauna.

## Materials and methods

In the anatomical descriptions, the English equivalents of the Latin osteological nomenclature summarised by Baumel and Witmer (1993) are primarily used. The terminology of Howard (1929) is followed for features not treated by Baumel and Witmer (1993). Osteological measurements of fossil specimens and extant specimens follow those of von den Driesch (1976), were taken using digital calipers, and were rounded to the nearest 0.1 millimeter. Ages of geologic time intervals are based on the International Geologic Timescale (International Commission on Stratigraphy 2012).

The monophyly of Ciconiiformes and Pelecaniformes remain contentious and relationships among taxa within those proposed clades are not congruent between the results of phylogenetic analyses (Mayr and Clarke 2003, Hackett et al. 2008, see discussion by Smith 2010). For example, morphology-based phylogenetic hypotheses (Livezey and Zusi 2006, 2007, Smith 2010) placed *Balaeniceps* at or near the base of a ‘pelecaniform’ clade

that also includes *Pelecanus*, *Sula*, *Anhinga*, *Fregata* and *Phalacrocorax*. The molecular sequence-based hypothesis of Hackett et al. (2008) placed *Balaeniceps* in a clade that includes *Scopus*, *Pelecanus* and taxa such as *Ardea* and *Ciconia* that are traditionally considered part of the core ciconiiforms. Combined analyses including morphological and molecular sequence data have not been published. The following taxonomic definitions are applied to facilitate discussion herein: Pelecaniformes references the genera *Anhinga*, *Balaeniceps*, *Fregata*, *Morus*, *Pelecanus*, *Phaethon*, *Phalacrocorax*, *Scopus* and *Sula* (i.e. Pelecanimorphae sensu Livezey and Zusi 2007); Ciconiiformes is applied in reference to the genera *Anastomus*, *Ardea*, *Ciconia*, *Egretta*, *Ephippiorhynchus*,

*Jabiru*, *Leptoptilos*, *Nycticorax*, *Plegadis* and *Mycteria* (i.e. Ciconiimorphae sensu Livezey and Zusi 2007).

**Institutional abbreviations:** Duke Lemur Center, Division of Fossil Primates, Durham, North Carolina, USA (DPC); North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA (NCSM); Colorado Tunisian Collection, Service Géologique, Tunis, Tunisia (T); Smithsonian Institution, National Museum of Natural History, Washington, DC, USA (USNM).

**Extant comparative skeletal material:** African Openbill *Anastomus lamelligerus* USNM 291418, 291419; American White Pelican *Pelecanus erythrorhynchos* NCSM 18810; Black-crowned Night-heron *Nycticorax nycticorax* NCSM 17902, 19713; Great Blue Heron *Ardea herodias* NCSM 23290, 17630, 23287, USNM 225156; Greater Flamingo *Phoenicopterus ruber* NCSM 23294; Hamerkop *Scopus umbretta* USNM 345232, 431497, 555705; Jabiru Stork *Jabiru mycteria* USNM 345680; Lesser Adjutant *Leptoptilos javanicus* USNM 430764, 488758; Saddle-billed Stork *Ephippiorhynchus senegalensis* NCSM 21094; Sandhill Crane *Grus canadensis* USNM 431923; Shoebill *Balaeniceps rex* USNM 291364, 344963; Tricolored Heron *Egretta tricolor* NCSM 8508, 23292; White Stork *Ciconia ciconia* USNM 428169, 430430, 605013; Wood Stork *Mycteria americana* NCSM 23188, USNM 19491, 18257. Fossil specimens described herein were also compared to a broad sample of other avian taxa using the synoptic series at USNM.

## Systematic paleontology

**Aves Linnaeus 1758**

**Aves indet. 1**

## Specimen

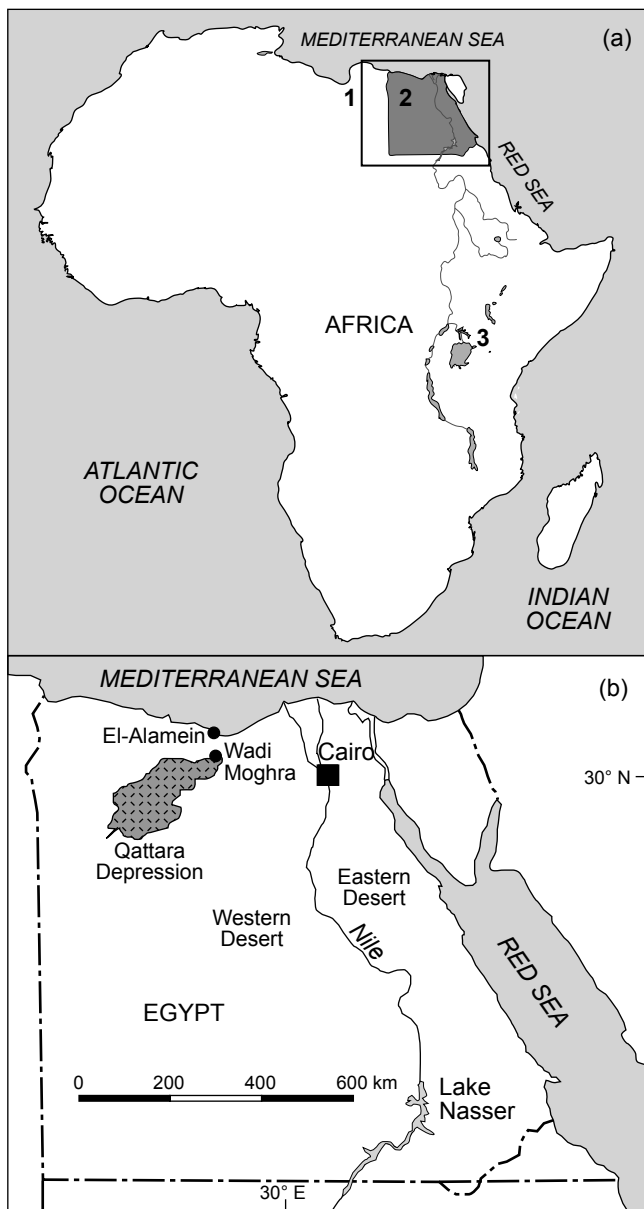
Proximal end of a left tarsometatarsus (DPC 14588; Figure 2a, Table 1).

## Locality

DPC 14588 and the seven other specimens described below were collected from multiple surface exposures of the Early Miocene (17–18 Ma) Moghara Formation at Wadi Moghara, Egypt. The precise horizon within the Moghara Formation from which the specimens were collected is unknown.

## Description

The shaft is hollow with a flattened dorsal face. The dorsal infracotylar fossa is deeply excavated with small paired fossa in the floor of the main fossa (Figure 2b). The medial margin of the shaft is concave, whereas the lateral margin is straight. Fine-scale morphological details of the hypotarsal crests have been obliterated by weathering. A proximal vascular foramen is present just distal to the remains of the hypotarsal crests. The specimen does not possess the pneumatized proximal end (i.e. interconnected infracotylar fossa and vascular foramina) that is characteristic of Pelecanidae and Sulidae. The relative lack of pneumatization and paired foramina of the infracotylar fossa resembles the condition in some specimens of the extant taxa *Ciconia ciconia*, *Balaeniceps rex* and *Scopus umbretta*.

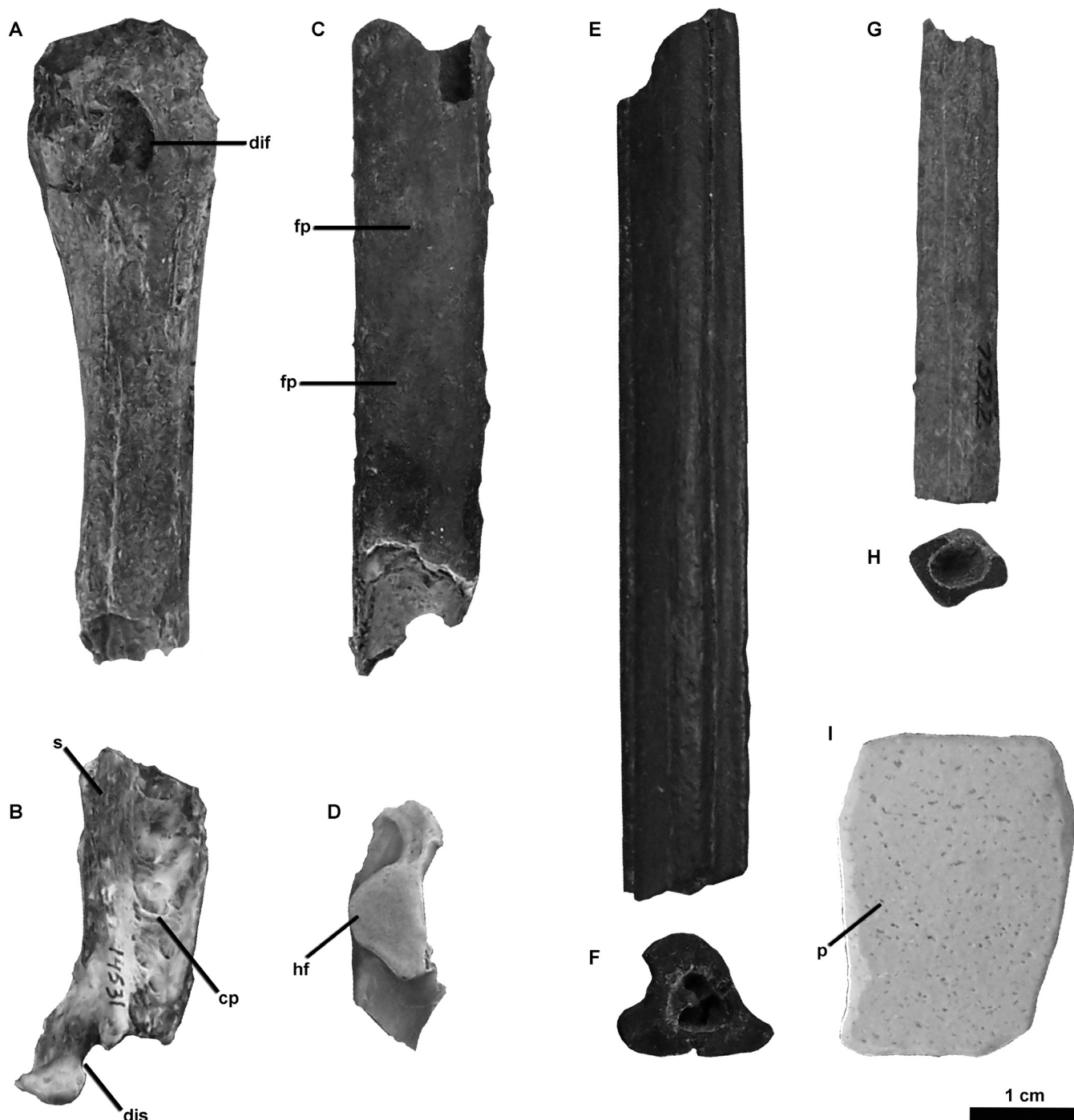


**Figure 1:** Previously reported Early Miocene (i.e. 23–16 Ma) African avian fossil localities (a) and location of Wadi Moghara (b). 1 = Djebel Zelten, Libya; 2 = Wadi Moghara, Egypt; 3 = Rusinga Island, Kenya

### Remarks

There is insufficient morphological detail preserved to allow for more specific referral of DPC 14588 within Aves. However, the relatively large size of the preserved portion of tarsometatarsus (Table 1) is consistent with other

taxa reported herein (e.g. storks; see below). However, because more specific referrals of DPC 3859, DPC 14531 and DPC 14588 are not warranted based on preserved morphology (see below), it cannot be determined if these three specimens represent a single taxon or multiple taxa.



**Figure 2:** Avian fossils from the Early Miocene Moghra Formation. (a) Aves indet. left proximal tarsometatarsus (DPC 14588) in dorsal view; (b) Aves indet. partial pelvis (DPC 14531) in ventral view; (c) Aves indet. right ulnar shaft (DPC 3859) in dorsal view; (d) Ciconiiformes partial left coracoid (DPC 6433) in dorsolateral view; (e–f) cf. Ciconiidae right tibiotarsal shaft (DPC 3860) in anterolateral (e) and proximal cross-sectional views (f); (g–h) cf. Ardeidae right tibiotarsal shaft (DPC 7522) in cranial (g) and cross-sectional views (h); (i) aepyornithoid egg shell fragment (DPC 14570) in exterior view. Anatomical abbreviations: cp = costal processes, dif = dorsal infracotylar fossa, dis = dorsolateral iliac spine, fp = feather papillae, hf = humeral facet, p = egg shell pores, s = synsacrum

The size differences among these indeterminate avian specimens suggest that three distinct taxa are represented. However, size alone is frequently not a reliable indicator of avian diversity (discussed by Stewart 2002, Smith 2011, Smith and Clarke 2011) and the possibility that these specimens could represent an ontogenetic series cannot be excluded. Therefore, each specimen is described under a separate ‘Aves indet.’ heading herein.

Aves indet. 2

Specimen

Partial pelvis (DPC 14531; Figure 2b, Table 1).

Description

Costal (transverse) processes are fused to the ventral surface of the left side of ilium. A small portion of the right side of the ilium is also preserved on either side of a row of fused vertebrae (symsacrum).

Remarks

The size of the bird represented by DPC 14531 is much smaller than the other taxa reported herein (Table 1). However, there is insufficient morphological detail preserved to determine if DPC 14531 represents a juvenile or to allow for more specific referral of this specimen within Aves.

Aves indet. 3

Specimen

Partial right ulnar mid-shaft lacking articular ends (DPC 3859; Figure 2c, Table 1).

Description

The shaft is hollow, with relatively thin-walled cortical bone and a distinctly round cross-sectional shape. Three feather papillae are visible. The cross-sectional width and shape of the shaft, and the size (~2–3 mm in diameter) and spacing (~13 mm apart) of the papillae are consistent with specimens of *B. rex*. The papillae are less distinct than those in *Pelecanus erythrorhychos*; however, damage to the papillae owing to weathering cannot be excluded.

Remarks

As with the two taxonomically indeterminate specimens described above, there is insufficient morphological detail preserved to allow for more specific referral of DPC 3859 within Aves. However, the relatively large size of the preserved portion of ulna (Table 1) is consistent with other

relatively large taxa reported herein (e.g. *Balaeniceps*; see below).

Palaeognathae Pycraft 1900

Ratitae Huxley 1867

Aepyornithoid-type eggshell

Specimen

Eggshell fragment (DPC 14570; Figure 2i, Table 1).

Description

The gently rounded contour of DPC 14570 is consistent with a relatively large egg (e.g. *Struthio*). The thickness (2.1 mm) of the fragment is within the previously reported range for aepyornithoid-type eggshells (1.4–3.05 mm; Saur 1972, 1976, 1978, Saur and Saur 1978, in Bibi et al. 2006). Furthermore, the presence of distinct pores of variable morphology (e.g. long, bent, forked and smaller point pores) in an approximately linear arrangement is consistent with the oological characteristics attributed to the aepyornithoid-type eggshells described by Sauer (1972) and Bibi et al. (2006). The large (4–10 mm) pore complexes or ‘megapores’ characteristic of *Namornis* and *Diamantornis* are absent (Sauer 1972, Stidham 2004, Bibi et al. 2006). Eggshells with the characteristics of DPC 14570 were termed ‘aepyornithoid-type’ eggshells by Bibi et al. (2006), a category that includes the ‘aepyornithoid’ and ‘Type A’ eggshells of Sauer (1972).

Remarks

As indicated by the relatively smooth and undamaged inner and outer surfaces, the original thickness of the shell is preserved. However, as with all of the Wadi Moghra fossils available for study, the eggshell fragment has been rounded and fragmented (likely by transport and weathering, respectively). Insufficient data is available to determine if this damage can be attributed to transport and exposure prior to or at some point after deposition, or if the specimens were weathered *in situ* and reburied. However, the rounding of broken edges in the fragments of fossil eggshell and bones precludes damage owing to recent exposure before collection (i.e. no clean/recent breaks are present).

Aepyornithoid-type eggshell fragments have been reported from Neogene localities across Eurasia and Africa (reviewed by Bibi et al. 2006) and may also be present in the geographically adjacent Early Miocene Jebel Zelten locality in Libya (Mlíkovský 2003). Aepyornithoid-type eggshells have also been reported from Paleogene localities including the Oligocene and Eocene of Mongolia and

**Table 1:** Identification, referral and measurements (mm) of avian fossils from the Early Miocene Moghra Formation. Preserved length or width measurements (denoted by \*) are followed by least width of shaft measurements for tibiotarsi, tarsometatarsi and ulnae, and egg shell thickness for DPC 14570

Taxon	Specimen no.	Side	Portion	Element	Measurements (mm)
Aves indet.	DPC 14588	Left	Proximal	Tarsometatarsus	51.5*/7.7
Aves indet.	DPC 14531	na	Partial	Pelvis	30.3*
Aves indet.	DPC 3859	Right	Shaft	Ulna	54.1*/10.1
Aepyornithoid-type	DPC 14570	na	Partial	Egg shell	26.5* × 19.4* × 2.1
Ciconiiformes indet.	DPC 6433	Left	Omal	Coracoid	22.0*
cf. Ciconiidae	DPC 3860	Right	Shaft	Tibiotarsus	73.2*/8.4
cf. Ardeidae	DPC 7522	Right	Shaft	Tibiotarsus	41.0*/5.7

China respectively (Saur 1972, Bibi et al. 2006). Therefore, the presence of aepyornithoid-type remains in the Early Miocene of Egypt is not surprising. However, as noted by Bibi et al. (2006: 8), “the similarities between eggshells of *Aepyornis*, *Rhea*, *Incognitoolithus* and aepyornithoid-type fossils that are widely dispersed in time and space suggest that the defining characteristics of these eggshells’ morphology may be plesiomorphic for the Ratitae as a whole”. Additionally, aepyornithoid-type eggshells were reported in association with Early Miocene remains of *Struthio coppensi* from Namibia by Mourer-Chauviré et al. (1996). Clearly, the ootaxonomy of fossil Ratitae would benefit from additional discoveries of eggshells with associated osteological remains.

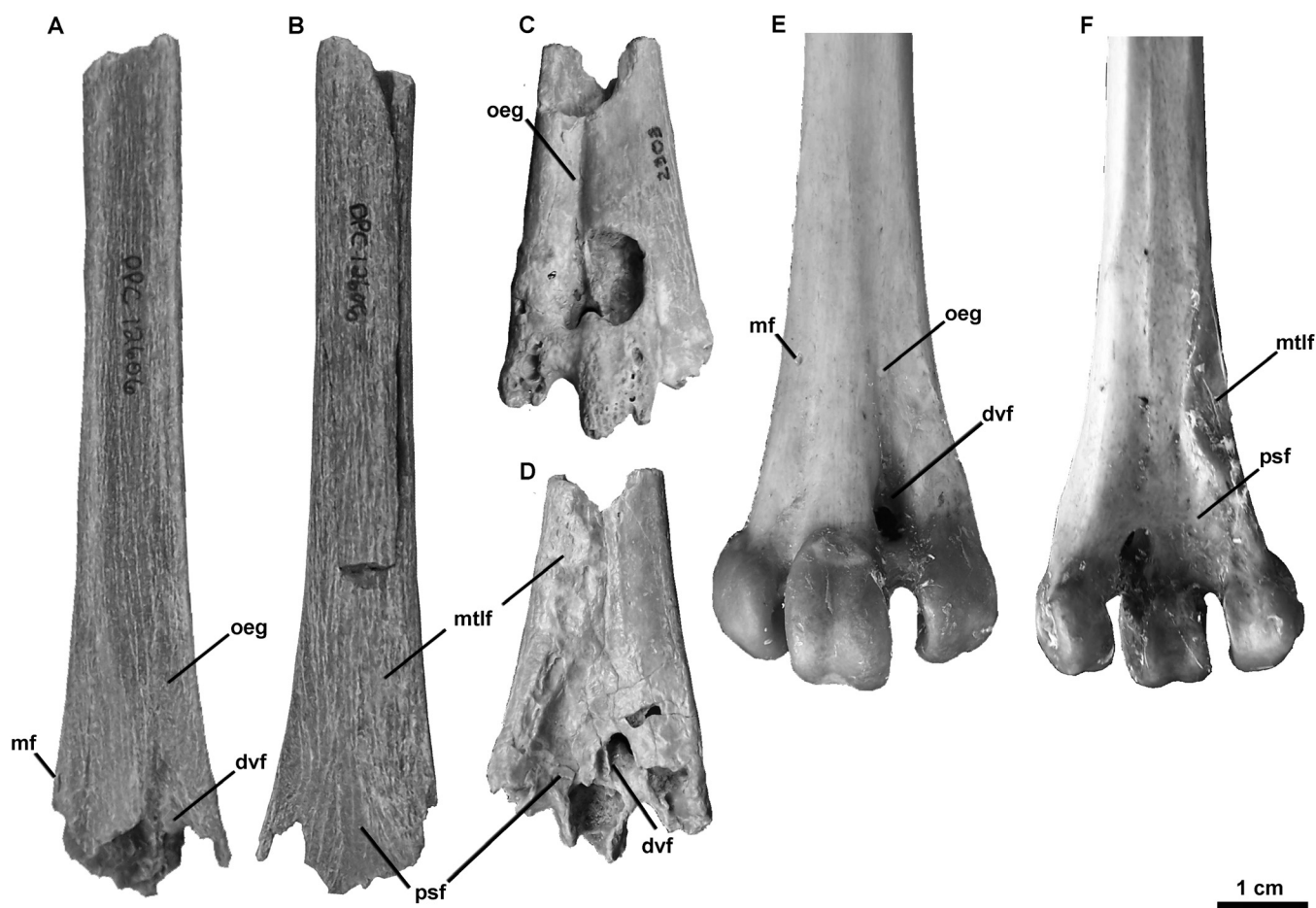
**Neognathae Pycraft 1900**  
**Pelecaniformes**  
**Balaenicipitidae Bonaparte 1853**  
**Balaenicipitidae indet.**

**Specimen**

Distal end of a left tarsometatarsus lacking trochlea (DPC 12606; Figure 3a and b, Table 2).

**Description**

The distal widening of the shaft is consistent with that of Ciconiiformes, which Balaenicipitidae resembles in many characteristics (Rich 1972), and the extreme degree of dorsoplantar compression of the distal-most end of the tarsometatarsus (as compared to the more rounded proximal shaft), the flattened dorsal surface of the shaft (dorsal face of *Ardea* less flattened) is known only in Balaenicipitidae (e.g. *B. rex*). The combination of an extremely flattened distal tarsometatarsal shaft with a deep and relatively wide outer extensor groove leading to a relatively large distal vascular foramen is restricted to Balaenicipitidae. As in *B. rex* and *Ardea* a small foramen is present on the medial surface of the shaft. The foramen is positioned at a level just distal to the fossa demarcating the attachment of metatarsal I in the fossil, but is positioned more proximally in *B. rex*. Furthermore, in the fossil the foramen is positioned on the medial side of the shaft (i.e. the foramen is not clearly visible in dorsal view), rather than on the medial side of the dorsal surface of the shaft as in *B. rex* (foramen not present in *Ciconia*, *Anastomus*, *Scopus* and *Leptoptilos*). The depth and placement of the plantar supratrochlear fossa,



**Figure 3:** Comparison of Balaenicipitidae tarsometatarsi. Balaenicipitidae sp. left distal tarsometatarsus (DPC 12606) in dorsal (a) and plantar (b) views; referred right distal tarsometatarsus of †*Goliathia andrewsi* (DPC 2303) from the Early Oligocene Jebel Qatrani Formation in dorsal (c) and plantar (d) views; left distal tarsometatarsus of extant *Balaeniceps rex* (USNM 344963) in dorsal (e) and plantar (f) views. Anatomical abbreviations: dvf = distal vascular foramen, mf = medial foramen, mtlf = metatarsal I fossa, oeg = outer extensor groove, psf = plantar supratrochlear fossa

**Table 2:** Comparison of Balaenicipitidae tarsometatarsi measurements (mm). Anatomical abbreviations: gL = greatest length, dW = lateromedial width of distal shaft just proximal to trochlea, lwS = least lateromedial width of shaft, ldS = least dorsoplantar width of shaft. Preserved width measurements are denoted by ‘\*’, measurements not available owing to damage are denoted by ‘–’, and extinct taxa are denoted by ‘†’. The distal width value for *P. richae* (T-3606) is from Rich (1972)

Taxon	Specimen no.	Side	Portion	gL	dW	lwS	ldS
<i>Balaeniceps rex</i>	<i>n</i> = 3	NA	Complete	254.7	23.5	10.3	7.3
† <i>Balaenicipitidae</i> sp.	DPC 12606	Left	Distal	86.5*	17.9	9.9	6.2
† <i>Goliathia andrewsi</i>	DPC 2303	Right	Distal	44.5*	24.3	13.7*	5.4
† <i>Paludivavis richae</i>	T-3606	Left	Distal	–	24.6	–	–

the groove that extends to the distal vascular foramen (i.e. the outer extensor groove *sensu* Howard 1929), and the shape, size and position of the fossa demarcating the attachment of metatarsal I are also consistent with that of *B. rex*. However, the plantar side of the shaft of DPC 12606 is more rounded than that of *B. rex*. The trochlea are missing. However, in distal view, the position of the vascular channels are consistent with the lateromedially positioned (i.e. in a relatively straight line) trochlea characteristic of Balaenicipitidae.

**Remarks**

Distal tarsometatarsi from the Early Oligocene (~33 Ma) of Egypt and the Late Miocene (~11–5 Ma) of Tunisia were referred to Balaenicipitidae by Rasmussen et al. (1987) and Rich (1972), respectively. The Tunisian specimen was later referred to †*Paludivavis richae* (Balaenicipitidae) by Harrison and Walker (1982) and the specimen from Egypt was referred to †*Goliathia andrewsi* by Rasmussen et al. (1987). *Goliathia andrewsi* was originally placed in the Ardeidae by Lambrecht (1930) and similarities between the tarsometatarsi of Ardeidae and Balaenicipitidae were discussed by Rich (1972). However, evaluation by subsequent researchers support placement of *G. andrewsi* in Balaenicipitidae (Brodkorb 1980, Rasmussen et al. 1987). The specimen from Egypt (DPC 2303) was not figured by Rasmussen et al. (1987) and is figured herein for the first time (Figure 3c and d).

A small foramen is present on the medial surface of the shaft of DPC 12606 just distal to the fossa demarcating the attachment of metatarsal I. That foramen is not present in DPC 2303 and that area of shaft is not preserved in the *P. richae* specimen from Tunisia (T-3606; Rich 1972). The degree of shaft compression of DPC 12606 is comparable to that of extant specimens of *B. rex*, whereas the shaft of DPC 2303 is flattened to a greater degree. Additionally, the depth of the groove leading to the distal vascular foramen in *B. rex* and DPC 12606 is shallower than that of DPC 2303. Whether or not these are characteristics that differentiate *Goliathia* and *Paludivavis* from other Balaenicipitidae is difficult to determine based on such a small sample of remains. Although the morphology of DPC 2303 and DPC 12606 support referral to Balaenicipitidae, as noted by Rasmussen et al. (1987), the holotype of *G. andrewsi* is an ulna and, therefore, direct comparisons are not possible. The specimen from Moghra (DPC 12606) is, however, smaller (lesser lateromedial width across trochleae) than other species of Balaenicipitidae (Figure 3, Table 2).

**Ciconiiformes Bonaparte 1854**  
**Ciconiiformes indet.**

**Specimen**

Omal end of a left coracoid (DPC 6433; Figure 2d, Table 1).

**Description**

The shape of humeral facet and the adjacent portions of the shaft of the coracoid agree with Ciconiidae and Ardeidae (e.g. *Ardea Herodias* and *Ephippiorhynchus senegalensis*). The humeral facet of Pelecaniformes exhibit more rounded lateral margins (e.g. *Pelecanus erythrorhychos*). The base of the procoracoid process is preserved just distal to the humeral facet along the medial margin of the shaft but the scapular cotyla is not preserved. A distinct acrocoracohumeralis ligament impression is present and compares favourably with that of Ardeidae (e.g. *A. herodias*) and Threskiornithidae (e.g. *Eudocimus ruber*). The acrocoracohumeralis ligament impression of Pelecaniformes such as *Pelecanus*, *Sula*, *Balaeniceps* and *Fregata* are relatively wider lateromedially or not as distinctly bordered by crests along the lateral and medial margins of the impression. The acrocoracohumeralis ligament impression is less deeply excavated in storks including *Mycteria americana*, *E. senegalensis*, *C. ciconia*, *Anastomus lamelligerus* and *S. umbretta*. The furcular facet is not preserved.

**Remarks**

Most of the ventral side of the specimen omal to the base of the procoracoid process is missing and there is insufficient morphological detail preserved to allow for more specific referral of this specimen within Ciconiiformes. The size of the specimen is indicative of a relatively large ciconiiform such as *A. herodias*.

**cf. Ciconiidae Sundevall 1836**

**Specimen**

Fragment of proximal right tibiotarsus shaft (DPC 3860; Figure 2e and f, Table 1).

**Description**

Based on the partial preservation of the fibular crest (apparent as a ‘hooked’ region in the cross-sectional view) and the relatively thicker cortex of the proximal end of the specimen, DPC 3860 appears to be broken just distal to its proximal end (i.e. broken just distal to the surface of articulation with the distal femur). The roughly triangular cross-sectional shape and deep longitudinal grooves along the

shaft agree most with Ciconiidae. Specifically, the relatively deeply grooved cranial surface of the proximal shaft resembles that of *A. lamelligerus*. The medial facet of the shaft is more flattened in Gruidae (e.g. *Grus canadensis*), Phoenicopteridae (e.g. *Phoenicopus ruber*), Ardeidae (e.g. *A. herodias*) and Balaenicipitidae (e.g. *B. rex*).

### Remarks

There is insufficient morphological detail preserved to allow for more specific referral of this specimen within Ciconiidae. However, the presence of a stork is congruent with the relatively widespread geographic and temporal distribution of fossil storks in Africa (reviewed by Miller et al. 1997, Dyke and Walker 2008, Mayr 2009). The oldest remains of a stork are those of †*Palaeohippiorhynchus dietrichi* from the geographically adjacent but considerably older deposits of the Early Oligocene Jebel Qatrani Formation (Lambrecht 1930, Rasmussen et al. 1987). The holotype specimen of *P. dietrichi* is a partial skull and is, therefore, not comparable to DPC 3860. Furthermore, the distal tibiotarsus referred to *P. dietrichi* by Rasmussen et al. (1987) does not preserve the entire shaft and is, thus, not easily comparable to DPC 3860. However, the shaft width of DPC 3860 (8.4 mm, Table 1) appears to represent a stork that was considerably smaller than *P. dietrichi*, which has an approximate distal shaft width of 23 mm (Rasmussen et al. 1987: 16).

Also based on distal tibiotarsi, two fossils storks from Egypt were described by Miller et al. (1997). One specimen (DPC 7689) from the Late Eocene section of the Jebel Qatrani Formation was considered Ciconiidae indet., and the other specimen (DPC 3681) from the Early Miocene deposits at Wadi Moghra was referred to the extant genus *Leptoptilos* (Miller et al. 1997). In general, the lateromedial width across the tibiotarsal condyles of storks is not considerably greater than that of the distal width of the shaft (i.e. the condyles do not lateromedially expand to a great degree in comparison with the width of the shaft). Given the lateromedial width of the distal tarsometatarsi described by Miller et al. (1997; ~18 mm), DPC 3860 likely represents a smaller species of stork than those represented by previously reported remains from Egypt. A partial skeleton from the Middle Miocene of Kenya was also referred to *Leptoptilos* by Hill and Walker (1979). The maximum midpoint tibiotarsal shaft width of that specimen is stated as 15.3 mm (Hill and Walker 1979). As with the other specimens mentioned above, DPC 3860 is likely representative of a smaller form of stork. A distal tibiotarsus from the Late Miocene Beglia Formation of Tunisia was referred to †*Leptoptilos* cf. *falconeri* by Rich (1972) and later designated as the holotype of †*Leptoptilos richae* by Harrison (1974; reviewed by Louchart et al. 2005). The distal shaft width of *L. cf. falconeri* (13.6 mm) is also greater than that of DPC 3860. A distal tibiotarsus with a distal width of 11.2 mm from the late Miocene (~7 Ma) of Chad was referred to cf. *Mycteria* by Louchart et al. (2008). The specimen from Chad was considered to be a juvenile and is, therefore, outside the probable size range of DPC 3860. Material referred to †*Palaeohippiorhynchus edwardsi* from the Early Miocene of Libya by Mlíkovský (2003) and †*Ciconia minor* and *Ciconia* sp. from the Miocene of Kenya by Dyke and Walker (2008) are humeri and a tarsometatarsus and

are, therefore, also incomparable with DPC 3860. *Ciconia minor* and *Ciconia* sp. from the Early Miocene of Rusinga Island, Kenya, and the Middle Miocene of Maboko Island, Kenya, respectively, were described based on a distal femur and a proximal carpometacarpus (Harrison 1980), and are not directly comparable with DPC 3860. However, the size of DPC 3860 is consistent with what might be expected for *C. minor* (i.e. smaller than other known storks) and the possibility that material from Moghra represents that species should be considered further if additional Ciconiidae material is recovered from this locality. Based on measurements reported by Louchart et al. (2005), DPC 3860 is most similar in size to the extant species *Ephippiorhynchus asiaticus*.

### cf. Ardeidae Leach 1820

#### Specimen

Tibiotarsus shaft fragment (DPC 7522; Figure 2g and h, Table 1).

#### Description

The approximately rhomboidal cross-sectional shape of shaft is consistent with that of *Ardea*. The four flattened faces that characterise DPC 7522 is a condition with an extremely limited distribution within the longbones of Aves. Only the tibiotarsi of some Ardeidae (e.g. *Ardea*) are characterised by shafts with a rhomboidal cross-section with all four faces (dorsal, ventral, medial and lateral) without grooves and flattened to the degree present in DPC 7522. The cross-sectional shape of the tibiotarsal shafts of other Ciconiiformes (e.g. *Anastomus*) are more triangular and those of Pelecaniformes (e.g. *Pelecanus*) and Phoenicopteridae (e.g. *P. ruber*) are more rounded on the caudal surface.

#### Remarks

There is insufficient morphological detail preserved to allow for more specific referral of this specimen within Ardeidae. The fossil record of Ardeidae is rather incomplete and in need of revision (reviewed by Olson 1985, Mayr 2009). However, the potential presence of a heron in the Early Miocene deposits at Wadi Moghra is consistent with records of the clade from other Old World localities. The holotype specimen of †*Zeltornis ginsburgi* from the Early Miocene of Jebel Zelten in Libya (Mlíkovský 2003) is a coracoid. †*Xenerodiops mycter* and *Nycticorax* sp. from the Early Oligocene Jebel Qatrani Formation are known from a rostrum and a tarsometatarsus, respectively (Rasmussen et al. 1987). A partial scapula and coracoid from the Late Miocene Baynunah Formation of Abu Dhabi, United Arab Emirates, have also been referred to Ardeidae (Stewart and Beech 2006). Finally, a coracoid from the Middle Miocene of Maboko Island, Kenya, was referred to *Nycticorax* by Dyke and Walker (2008). These other African records of Ardeidae are not considered further because they are not directly comparable to DPC 7522.

#### Discussion

Description of avian fossils from Wadi Moghra provides additional support for the geological interpretation of a deltaic

or estuarine depositional environment at this locality (Said 1990, Miller 1996) and may facilitate additional insights into the study of African biogeography. An estuarine or deltaic interpretation is also consistent with the relatively abundant remains of plants, invertebrates and other vertebrates recovered from Wadi Moghra. The vertebrate fauna of Wadi Moghra now putatively includes at least four avian taxa (Ratitae, Balaenicipitidae, Ciconiidae and Ardeidae), a diverse mammalian fauna (e.g. hyaenodontans, carnivorans, perissodactyls, artiodactyls, primates and proboscideans), fish, turtles and crocodiles (Miller 1996).

Despite the fragmentary and isolated preservation of avian fossils from Wadi Moghra, the association of waterbirds and a ratite in combination with the interpretation of the environment of deposition provides limited means of comparison with other extinct assemblages and extant African avifaunas. Previous compositional evaluation of an avifauna from the Early Oligocene Fayum Depression of Egypt showed that the assemblage from that location most resembled that of the extant avifauna of Uganda in eastern Africa (Olson and Rasmussen 1986). Furthermore, evaluation of the mammalian fauna from Wadi Moghra also suggests a strong biogeographical link with eastern Africa (Miller 1996, Miller et al. 1997, Sanders and Miller 2002). Moreover, associations of herons and storks have been documented from Early Miocene localities in Kenya and Libya (Mlíkovský 2003, Dyke and Walker 2008). Thus, compositionally, the potential association of storks, peleciforms and herons from the Early Miocene of Wadi Moghra is congruent with other African freshwater, aquatic avifaunas, both past and present, and suggests that these taxa have remained relatively widespread on the African continent since at least the Early Miocene.

In contrast to the not wholly unexpected 'waterbird' assemblage, the implications of the presence of Ratitae at Wadi Moghra are less clear. However, it is possible that the eggshell was transported before deposition and it would be premature to draw detailed conclusions based on such limited material. The ratite eggshell from Wadi Moghra does, however, add to the geographically and temporally widespread Old World distribution (Eocene–Pliocene of Eurasia and Africa) of aepyornithoid-type oological remains. Increased knowledge of the avifauna present at Wadi Moghra in the Early Miocene provides a more complete picture of that ecosystem that will only be further clarified by the recovery of additional fossil remains.

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