

Fossil birds from the Late Miocene of Chad and Ethiopia and zoogeographical implications

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ABSTRACT - Since a review of the Tertiary birds of Africa 30 years ago by Rich (1974), a great wealth of new data and new interpretations have augmented this fossil record, hitherto still relatively poor when compared with that of northern continents. A growing amount of new fossils is coming from hominid localities, now extending as early as the Late Miocene. Recently found bird fossils from the Late Miocene of Chad and Ethiopia are described here. They come respectively from several localities of Toros Menalla (Djurab Desert, Chad), dated ca 7 Ma, several localities of the Western Margin of the Middle Awash (Afar rift, Ethiopia), dated 5.6-5.8 Ma, and a locality of the Central Awash Complex of the Middle Awash, dated ca 5.2 Ma. 19 different taxa in 11 families are identified, essentially aquatic birds except for part of the fossils from one Ethiopian locality, ALA-VP-2. The bird assemblages from the three groups of localities by age and location provide some paleoenvironmental indications. Several taxa are new, or are new to Africa, and several are the earliest fossil records of a modern genus or lineage. Three extinct taxa are represented: the large darter *Anhinga* cf. *A. pannonica*, a new species of a giant saddlebill stork, genus *Ephippiorhynchus*, and a swan *Afrocygnus chauvireae*. Families with an extremely scarce record worldwide are represented here (Pandionidae, Heliornithidae). Comparisons are made which reveal some similarities between the Chadian and Ethiopian sites, as well as with Late Miocene localities in Kenya, Tunisia and Libya. At a larger scale, from the Mio-Pliocene of Africa, *Leptoptilos falconeri* and *Anhinga* cf. *A. pannonica* were also of Eurasian distribution, while *Pavo* sp. and *Heliopais* cf. *H. personata* are now typical of the Oriental Region. These represent important zoogeographical links between Africa and Eurasia at that period, compared with the relations observed today between the non-passereous birds of the Paleotropical (=Ethiopian) and Oriental regions.

Key words: Africa, Aves, Biogeography, Chad, Ethiopia, Late Miocene.

Oiseaux fossiles du Miocène supérieur du Tchad et d'Ethiopie et implications zoogéographiques

- Depuis la synthèse de Rich (1974) sur les oiseaux fossiles du Tertiaire d'Afrique, nombre de nouvelles données et interprétations ont enrichi ce registre, malgré tout encore assez pauvre comparé aux continents de l'hémisphère nord. De nouveaux fossiles d'oiseaux proviennent de sites à hominidés, s'étendant désormais jusqu'au Miocène supérieur. Des fossiles trouvés ces dernières années dans le Miocène supérieur du Tchad et d'Ethiopie sont décrits ici. Ils proviennent respectivement de différentes localités de Toros Menalla (Djourab, Tchad), datées de ca 7 Ma, plusieurs localités de la Marge Occidentale de la région de l'Aouache Moyen (Afar, Ethiopie), datées de 5,6-5,8 Ma, et une localité du Complexe de l'Aouache Central (également dans l'Aouache Moyen) datée de ca 5,2 Ma. Au total 19 taxons différents répartis dans 11 familles sont déterminés. Ce sont essentiellement des oiseaux aquatiques, sauf pour une partie des fossiles d'une localité Ethiopienne, ALA-VP-2. Les assemblages d'oiseaux des trois groupements de localités par âge et localisation, fournissent des informations paléoenvironnementales. Plusieurs taxons sont nouveaux, ou nouveaux pour l'Afrique, et plusieurs sont les plus anciens représentants d'un genre ou d'une lignée actuels. Trois taxons éteints sont représentés: le grand anhinga *Anhinga* cf. *A. pannonica*, une nouvelle espèce de jabiru géant, genre *Ephippiorhynchus*, et un cygne *Afrocygnus chauvireae*. Des familles très rares dans le registre fossile mondial sont représentées aussi (Pandionidae, Heliornithidae). Des comparaisons sont proposées, mettant en évidence des similarités entre les localités Tchadiennes et Ethiopiennes, ainsi qu'avec des localités du Miocène supérieur du Kenya, de Tunisie et de Libye. A plus grande échelle, présents dans le Mio-Pliocène d'Afrique, *Leptoptilos falconeri* et *Anhinga* cf. *A. pannonica* étaient aussi représentés en Eurasie, tandis que *Pavo* sp. et *Heliopais* cf. *H. personata* sont aujourd'hui typiquement des taxons de la région Orientale. En termes de zoogéographie, cela témoigne de liens de continuité importants entre l'Afrique et l'Eurasie à cette période, en comparaison avec les relations actuelles entre les oiseaux non-passereux des régions Paléotropicale (=Ethiopienne) et Orientale.

Mots-clés: Afrique, Aves, Biogéographie, Ethiopie, Miocène supérieur, Tchad.

INTRODUCTION AND GEOLOGICAL SETTINGS

Fossil avifaunas from the Tertiary of Africa are rare, and generally with low numbers of fossils and taxa. Exceptions are the Plio-Pleistocene deposits of Olduvai Gorge, Tanzania (about 30000 fossils; see Brodkorb, 1985) and the Early Pliocene deposits of Langebaanweg, South Africa (see Rich, 1980). Both are still awaiting detailed studies for most

of their bird fossils.

Here we describe the bird faunas of several Late Miocene localities in Chad and Ethiopia (fig. 1), some particular taxa being described in detail elsewhere (Louchart et al., 2005b, c). They are then interpreted, especially as indicators of zoogeographical relations.

In Ethiopia, the Late Miocene localities comprising birds are: ADD-VP-1 (Adu Dora, Vertebrate Paleontol-

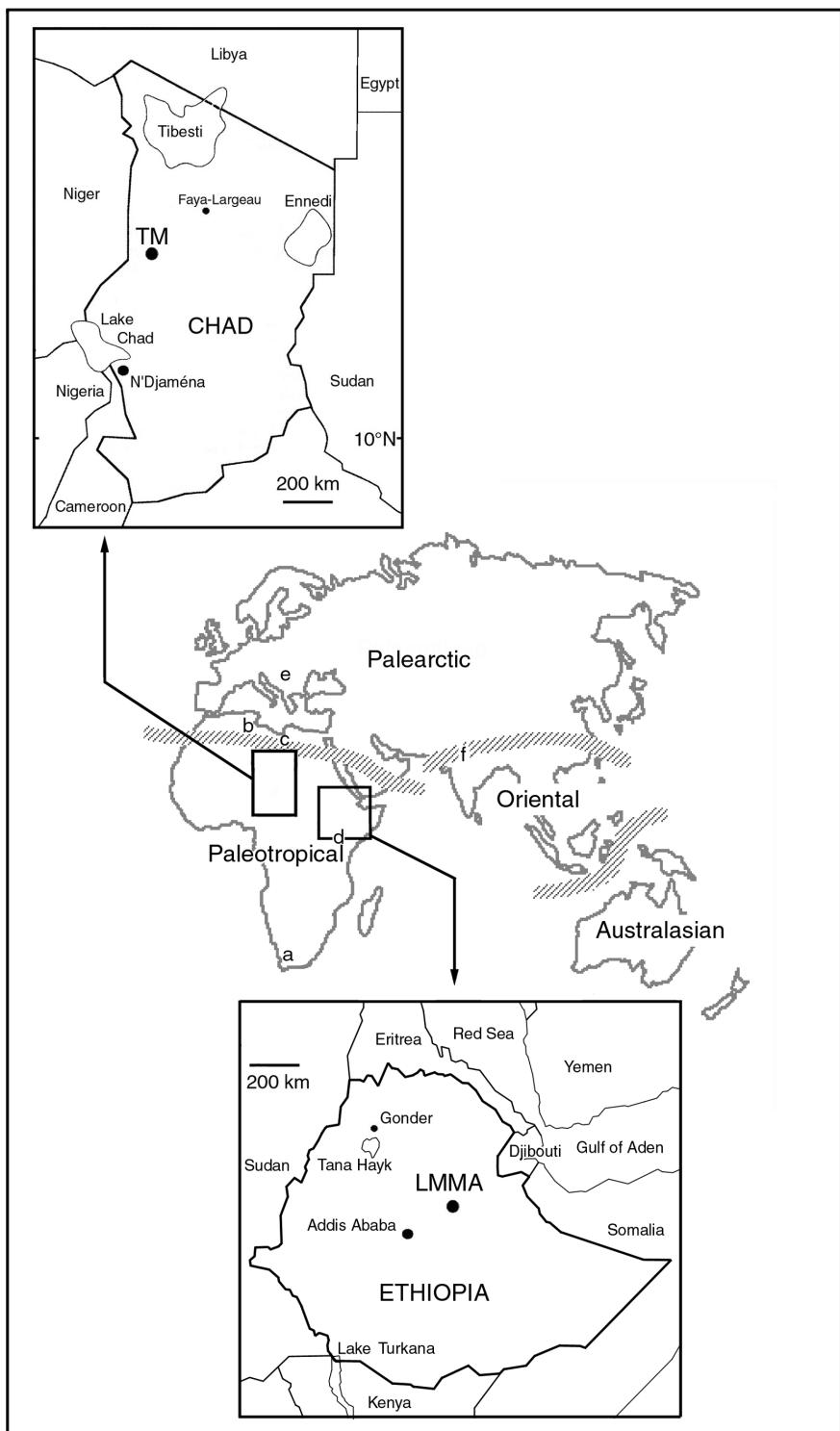


Figure 1 - Map showing the geographical location of the Chadian and Ethiopian sites, in the context of the recent zoogeographical regions of the Old World. TM indicates the localities of the Toros Menalla area (Chad). LMMA indicates the Late Miocene localities of the Middle Awash area (Ethiopia). Other important localities or groups of localities discussed in the text are indicated by lower case letters: a: Langebaanweg (South Africa), b: Beglia (Bled ed Douarah, Tunisia), c: Sahabi (Libya), d: Lothagam (Kenya), e: Pannonian Basin (Hungary-Romania), f: Siwalik Hills of India and Pakistan.

ogy Locality 1), AFD-VP-1 (Ali Ferou Dora), ALA-VP-2 (Alayla), ASK-VP-3 (Asa Koma), DID-VP-1 (Digiba Dora), STD-VP-1 and STD-VP-2 (Saitune Dora). These localities lie along the Western Margin of the Middle Awash, in the Afar depression (fig. 1). They all belong to the Asa Koma Member of the Adu Asa Formation, dated between 5.6 and 5.8 Ma (5.54-5.77 Ma; Haile-Selassie, 2001a, b, Wolde-gabriel et al., 2001, Haile-Selassie et al., 2004a, b). Additionally a single bird fossil comes from the locality AMW-VP-1 (Ambo West), situated in the Central Awash Complex of the Middle Awash. It belongs to the Kuseralee Member of the Sagantole Formation, dated ca 5.2 Ma (5.2-5.6 Ma; Renne et al., 1999, Haile-Selassie, 2001a, b, Wolde-gabriel et al., 2001, Haile-Selassie et al., 2004b). The fossils were deposited in fluvial silty clays. All but Adu Dora and Ali Ferou Dora yielded fossils of the early hominid *Ardipithecus kadabba*. Paleoecological evidence shows that the different localities sampled are essentially forested/wooded or semi-wooded habitats near water (lake or slow river). Compared with later localities of the Middle Awash, the paleoenvironments consisted of « closed, humid, cool and possibly high elevation habitats » (Haile-Selassie, 2001a, b, Wolde-gabriel et al., 2001, Haile-Selassie et al., 2004a, b: p. 547).

In Chad, the Late Miocene localities comprising birds are: TM 09, TM 60, TM 75, TM 89, TM 90, TM 112, TM 242, TM 266 and TM 337. These are all from the Anthracotheriid Unit of the Toros Menalla fossiliferous area. Part of them (the localities TM 247, TM 266 - type locality - and TM 292) yielded the early hominid *Sahelanthropus tchadensis* (Brunet et al., 2002). The Toros Menalla fossiliferous area is located in the intracratonic Chad Basin, about 800 km NE of the present day Lake Chad (fig. 1). The fossils from these different contemporaneous Late Miocene localities were deposited in perilacustrine sands (Vignaud et al., 2002). The Anthracotheriid Unit is dated biochronologically to ca 7 Ma; its different, contemporaneous localities yielded a diverse fauna, comprising aquatic animals such as fish, crocodiles, amphibious mammals, mammals of gallery forest, wooded savannah, grassland and even evidence of desert (Brunet et al., 2002; 2005; Vignaud et al., 2002).

MATERIAL AND METHODS

The fossil specimens from Ethiopia are housed at the National Museum of Ethiopia, Addis Ababa, Ethiopia. The fossil specimens from Chad are housed at the CNAR (Centre National d'Appui à la Recherche), N'Djamena, Chad. The systematic arrangement follows Del Hoyo et al. (1992, 1994, 1996), and Livezey (1996, 1998) respectively within the Anseriformes and the Gruiformes. The osteological nomenclature is that of Baumel & Witmer (1993) unless stated otherwise, or Howard (1929) when necessary.

All the measurements are in mm. Unless stated otherwise, and unlike the definitions used by several other authors, « width » refers here to a measurement orthogonal to the axis of the postcranial bone, and in the follow-

ing direction for every element: medio-lateral for coracoids, dorso-ventral for humeri, ulnae and radii, orthogonal to dorso-ventral (i.e. in the plane of flatness of the bone) for carpometacarpi, and medio-lateral for femora, tibiotarsi, tarsometatarsi and pedal phalanxes; « depth » refers here to the measurement orthogonal to the width and to the axis of the bone.

The list of the recent osteological specimens examined for comparisons and measurements is given in the Appendix. The acronyms for the museums and other institutions are as follows: BMNH: British Museum of Natural History (Bird Group), Tring, UK; CAS: California Academy of Sciences, San Francisco, USA; FMNH: Field Museum of Natural History, Chicago, USA; IPH: Institut de Paléontologie Humaine, Muséum National d'Histoire Naturelle, Paris, France; IRSN: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; LAC: Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle, Paris, France; MVZ: Museum of Vertebrate Zoology, University of California Berkeley, USA; RMCA: Royal Museum for Central Africa, Tervuren, Belgium; UCBL: Université Claude Bernard - Lyon 1, Villeurbanne, France; USNM: Smithsonian Institution, National Museum of Natural History, Washington, DC, USA.

Systematic paleontology

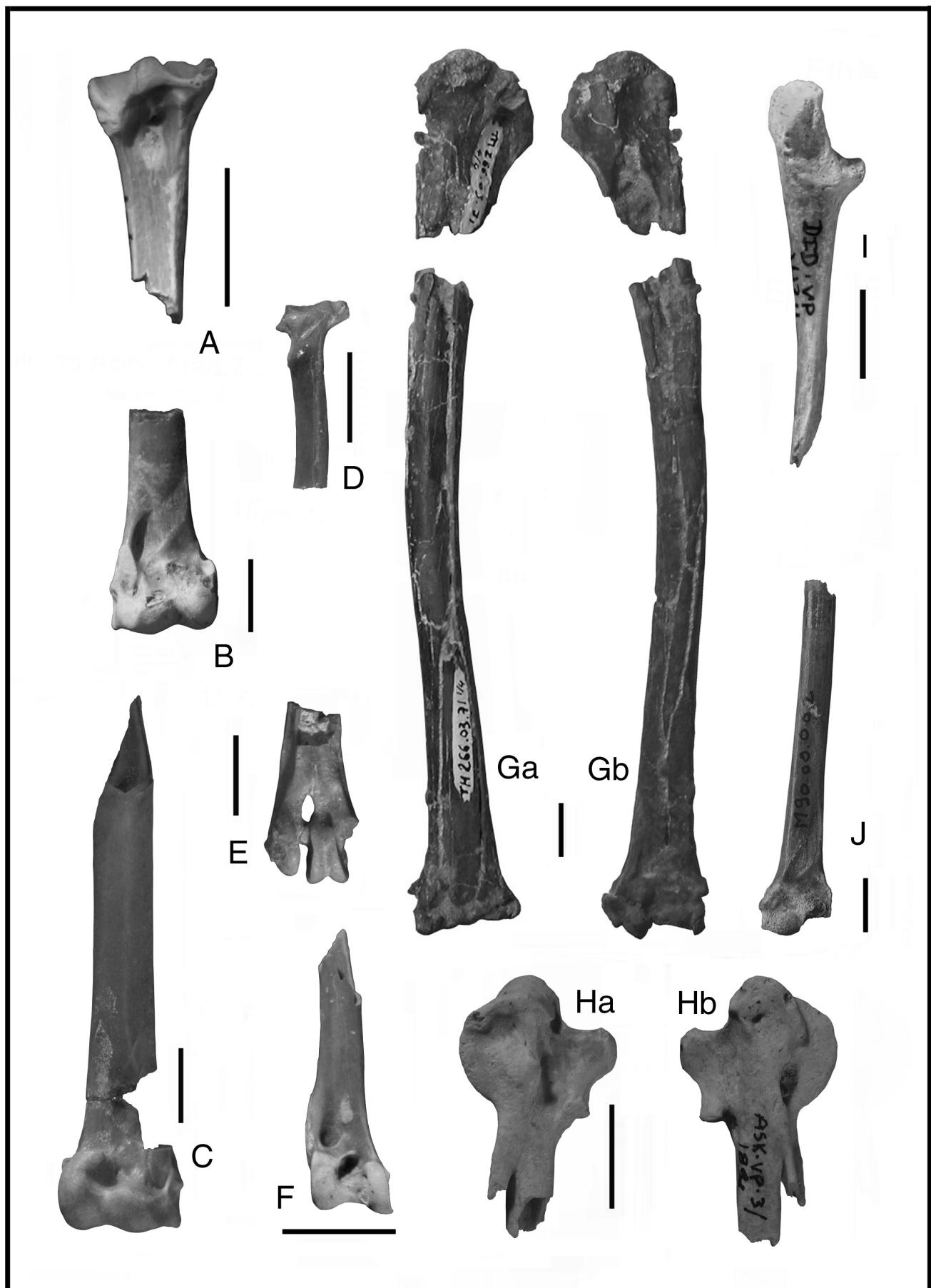
Aves L., 1758
Order Podicipediformes Fürbringer, 1888
Family Podicipedidae Bonaparte, 1831
Genus *Podiceps* Latham, 1787
Podiceps sp. indet., size of small *P. grisegena*

Material: proximal right tarsometatarsus, STD-VP-2/67 (fig. 2A).

Measurements: proximal width: 9.2, proximal depth (including the hypotarsus): 9.7, estimated minimal width of shaft : 3.5.

Localities and age: STD-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: this proximal tarsometatarsus of a grebe shows the generic characters of *Podiceps* as exposed by Bochenksi (1994), and is morphologically similar to the extant species of this genus. Its size is within the variation range of small individuals of recent *P. grisegena*, larger than *P. nigricollis*, and smaller than *P. cristatus* (see measurements in Bochenksi, 1994). This fossil is however too fragmentary to allow a specific identification, or comparison with the several described Mio-Pliocene extinct grebes, especially in Europe (see Bochenksi, 1997). It is identified as *Podiceps* sp., and is the earliest member of this genus so far found in Africa. Two different grebes are known from the Early Pliocene of Langebaanweg (South Africa): a small one referred to the extant species *Tachybaptus ruficollis*, and a larger one identified as *Podiceps* ? sp. (Olson, 1994). The latter spe-



cies is said to display some morphological differences with *Podiceps*, and some similarities with the New World genus *Podilymbus* (Olson, 1994). It is represented by a complete humerus and a distal tarsometatarsus, so that the comparison with the Ethiopian fossil is presently not possible. The South African *Podiceps* ? sp. seems only slightly smaller than the Ethiopian *Podiceps* sp.

Order Pelecaniformes Sharpe, 1891

Family Phalacrocoracidae Bonaparte, 1853

Genus *Phalacrocorax* Brisson, 1760

Phalacrocorax sp., size of *P. africanus*

Material: distal right tibiotarsus AFD-VP-1/5 (fig. 2F).

Measurements: distal width: 7.3, distal depth: 6.8, minimal width of shaft: 3.9.

Localities and age: AFD-VP-1, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene, Ethiopia, 5.6–5.8 Ma.

Remarks: This distal tibiotarsus agrees in morphology with the cormorants, genus *Phalacrocorax* (Phalacrocoracidae), and differs from the closely allied family Anhingidae (genus *Anhinga*) in, among others: condylus medialis more distally situated relative to the condylus lateralis, narrower pons supratendineus, and absence of a pit at the proximal base of the condylus lateralis, cranially. Within the genus *Phalacrocorax*, the size of the fossil corresponds to a small species, and falls within the range of 14 individuals of the subsaharan African species *P. africanus* that provide the following intervals (measurements and specimens from Brodkorb & Mouer-Chauviré, 1984, and C. Mouer-Chauviré, pers. com.): distal width: 6.3–7.6, minimal width of shaft: 3.8–4.5. It is also similar in size to other species, such as one individual of the South Asian *P. niger* (measurements and specimens from Brodkorb & Mouer-Chauviré, 1984, and C. Mouer-Chauviré, pers. com.): distal width: 7.0, minimal width of shaft: 3.9. Therefore, the specific identity of the cormorant from AFD remains unknown.

It is smaller than the described extinct African cormorants: *P. tanzaniae* Harrison & Walker, 1979 (from some localities of the Lower Pleistocene of Olduvai Gorge; Harrison & Walker, 1979, Brodkorb & Mouer-Chauviré, 1984), *P. owrei* Brodkorb & Mouer-Chauviré, 1984 (from the

Lower Pleistocene of Olduvai Gorge, Tanzania; Brodkorb & Mouer-Chauviré, 1984), and *P. kuehneanus* Schlüter, 1991 (from the presumably Upper Pliocene of Minjingu, Tanzania; Schlüter, 1991). Incidentally these three forms would need detailed comparisons between each other, and with extant species such as *P. capensis* and *P. fuscicollis*, in order to clarify their validity, relationships and the real diversity of Plio-Pleistocene East African medium-sized cormorants.

Phalacrocorax cf. *P. carbo* (L., 1758)

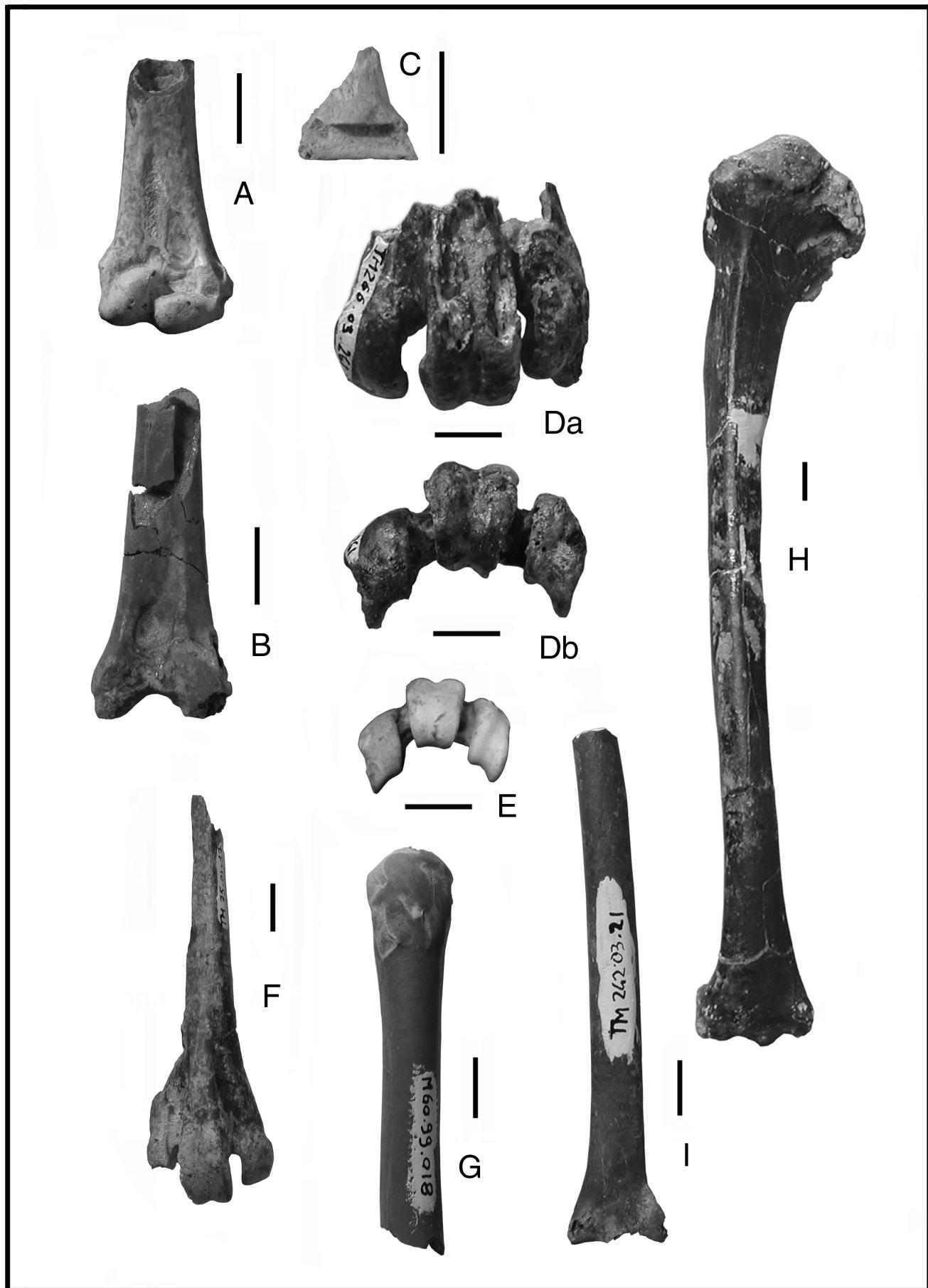
Material: humeral part of left coracoid STD-VP-1/59, humeral part of left coracoid STD-VP-2/90, distal left humerus STD-VP-1/24 (fig. 2B), distal right humerus ADD-VP-1/20 (fig. 2C), distal right ulna ASK-VP-3/157, distal left ulna ASK-VP-3/183, distal left ulna STD-VP-1/7, distal right ulna STD-VP-2/870, proximal left radius ADD-VP-1/19 (fig. 2D), distal left tarsometatarsus STD-VP-2/871 (fig. 2E), and tentatively shaft of left humerus DID-VP-1/104, distal left carpometacarpus ASK-VP-3/484, trochlea metatarsi IV of right tarsometatarsus ASK-VP-3/500, and pedal phalanx STD-VP-2/872.

Measurements: coracoid STD-VP-1/59: greatest width of humeral end: 11.5; coracoid STD-VP-2/90: minimal width of shaft: 5.7; humerus ADD-VP-1/20: distal width: 15.7, distal depth: 11.3, minimal width of shaft: 7.6; humerus STD-VP-1/24: distal width: 14.3, minimal width of shaft (estimated): 7.4; ulna ASK-VP-3/157: distal width: 8.6, orthogonal distal depth: 7.7, greatest diagonal distal depth: 9.9; ulna ASK-VP-3/183: distal width: 8.8, orthogonal distal depth: 8.3, greatest diagonal distal depth: 11.15, minimal width of shaft: 6; ulna STD-VP-1/7: distal width (estimated): 8.1, orthogonal distal depth: 7.6, greatest diagonal distal depth: 9.8, minimal width of shaft: 5.3; ulna STD-VP-2/870: distal width: 9.3, orthogonal distal depth: 7.6, minimal width of shaft: 4.9; radius ADD-VP-1/19: greatest diagonal proximal depth: 5.9; tarsometatarsus STD-VP-2/871: minimal width of shaft: 6.9.

Localities and age: ADD-VP-1, ASK-VP-3, STD-VP-1 and STD-VP-2, and tentatively DID-VP-1, all localities in the Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene, Ethiopia, 5.6–5.8 Ma.

Remarks: These fossils are all morphologically identical with recent species of the genus *Phalacrocorax*.

Figure 2 - A: *Podiceps* sp., size of a small *P. griseogena*, proximal right tarsometatarsus, STD-VP-2/67, dorsal aspect. B: *Phalacrocorax* cf. *P. carbo*, distal left humerus, STD-VP-1/24, cranial aspect. C: *Phalacrocorax* cf. *P. carbo*, distal right humerus lacking the ventral part of the distalmost shaft, ADD-VP-1/20, cranial aspect. D: *Phalacrocorax* cf. *P. carbo*, proximal left radius, ADD-VP-1/19, caudal (interosseous) aspect. E: *Phalacrocorax* cf. *P. carbo*, distal left tarsometatarsus lacking the trochlea metatarsi II, STD-VP-2/871, plantar aspect. F: *Phalacrocorax* sp., size of *P. africanus*, distal right tibiotarsus, AFD-VP-1/5, cranial aspect. G: *Anhinga* cf. *A. pannonica* (Lambrecht, 1916), almost complete left humerus, partly crushed, and lacking fragments of the crista pectoralis, the proximal part of the shaft and fragments of the distal end, TM 266-03-071, a: caudal aspect, b: cranial aspect. H: *Anhinga* cf. *A. melanogaster*, proximal left carpometacarpus, ASK-VP-3/184, a: ventral aspect, b: dorsal aspect. I: *Anhinga* cf. *A. melanogaster*, pars humeralis of left coracoid lacking the processus acrocoracoideus, DID-VP-1/124, dorso-lateral aspect. J: *Anhinga* cf. *A. melanogaster*, distal left humerus lacking condylus dorsalis, TM 90-00-062, cranial aspect. Scale bars equal approximately 1 cm.



The distal width of one of the fossil humeri falls within the variation range of this measurement in recent *P. carbo sinensis* (Central and Southern Europe east to India and China) provided by Ericson & Hernandez-Carrasquilla (1997), which is 15.1-18.0 mm (n=109 adult males and females), while the other (STD-VP-1/24) is slightly smaller than the smallest females. For all the other measurements of other elements most of the fossils listed above are similar in size to smaller individuals of European *P. carbo* examined (see Appendix), while a few are still slightly smaller (essentially STD-VP-1/59, STD-VP-2/90, ADD-VP-1/19). All this is consistent with the fossils representing a single population on average slightly smaller than *P. carbo sinensis* and thus similar in size to the recent African subspecies *P. carbo lucidus*, which is slightly smaller than *P. c. sinensis*, and inhabits today inland East Africa, as well as coastal Western and Southern Africa (Del Hoyo et al., 1992). Given the fragmentary nature of the fossils, their assignment to *P. carbo* remains tentative. This is the earliest record of fossils referable to *P. carbo* in Africa. The fossil listed in Harris & Leakey (2003) for Lothagam is actually said to come most probably from Galana Boi (Holocene).

Family Anhingidae Ridgway, 1887

Genus *Anhinga* Brisson, 1760

Anhinga cf. *A. melanogaster* Pennant, 1769

Material: distal left humerus TM 90-00-062 (fig. 2J), humeral part of left coracoid DID-VP-1/124 (fig. 2I), proximal left carpometacarpus ASK-VP-3/184 (fig. 2H).

Measurements: humerus TM 90-00-062: distal width (estimated): 14.7, distal depth: 9.2, minimal width of shaft: 6.4; coracoid DID-VP-1/124: minimal width of shaft: 4.6; carpometacarpus ASK-VP-3/184: proximal width: 15, proximal depth: 7.1, minimal width of os metacarpale majus: 4.

Localities and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma. DID-VP-1 and ASK-VP-3, both in the Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: These fossils are identical in morphology and size with the recent Old World species *A. melanogaster* (see tabl. 1, and Bordkorb & Mourer-Chauviré, 1982). Given their fragmentary nature, this assignment remains tentative. These are among the oldest records in Africa of a darter (here

used in the same sense as ‘anhinga’) similar in size to the living Old World species, together with records from the Lower and Upper Nawata Members of the Nawata formation of Lothagam, Kenya (respectively 6.5-7.4 Ma and 5-6.5 Ma, Harris & Leakey, 2003, McDougall & Feibel, 2003). Interestingly, a darter close in size to *A. melanogaster* was identified (as *Anhinga* sp.) from the Late Miocene (ca 6 Ma +/- 3 Ma) of Abu Dhabi (United Arab Emirates, Arabian Peninsula) by Stewart & Beech (2006).

Anhinga cf. *A. pannonica* (Lambrecht, 1916)

Material: almost complete left humerus (fig. 2G) and distal part of right humerus with diaphysis, TM 266-03-071.

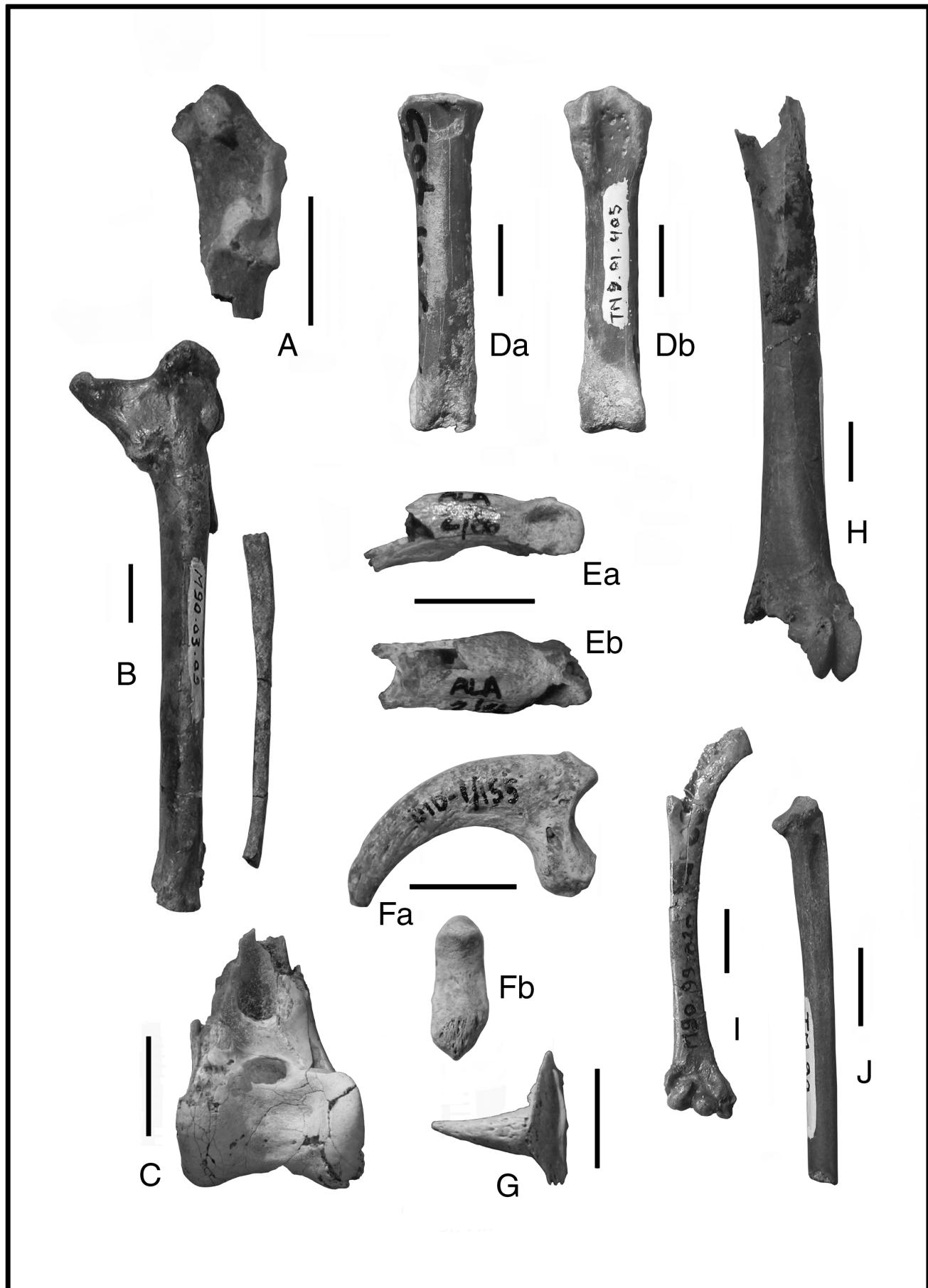
Measurements: left humerus: estimated total length: 167, proximal width without the crista pectoralis: 24.3, distal width (estimated): 21, minimal width of shaft: 9.4; right humerus: distal width (estimated): 19.2, minimal width of shaft: 8.7.

Localities and age: TM 266, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: The humeri of this individual from TM 266 match morphologically the genus *Anhinga*, which comprises today two species: the Old World *A. melanogaster* (including the subspecies *melanogaster*, *rufa*, *vulsini* and *novaehollandiae*), and the New World *A. anhinga* (two subspecies). The latter species is slightly smaller than *A. melanogaster*, and shows morphological differences in many elements (e.g. Harrison, 1978, Brokorb & Mourer-Chauviré, 1982, Becker, 1986, Louchart et al., 2004). However, no useful criterion applies to the humeri from TM, which in addition are crushed, therefore making some minute details difficult to appreciate. Thus these humeri can only be said to belong to the genus *Anhinga*. Their size, however, exceeds distinctively that of corresponding bones in modern *A. melanogaster* and a fortiori *A. anhinga* (tabl. 1).

Rich (1972, 1974) identified a seventh cervical vertebra and a proximal humerus of a darter as *Anhinga* cf. *A. pannonica* (Lambrecht, 1916) in the deposits of Bled Ed Douarah (Beglia Formation, Tunisia, age MN9 after Mlikovsky, 2002). This species was initially described from the Late Miocene (MN10) of Tatarus-Brusturi, Romania (Lambrecht, 1916, Mlikovsky, 2002), on the basis of a sixth cervical vertebra (holotype), with a carpometacarpus as a referred specimen. The humeri from Chad can be compared with the Tunisian humerus, and the relative size of other elements can

Figure 3 - A: *Ardea* sp., size of *A. alba*, distal right humerus, ALA-VP-2/105, cranial aspect. B: *Ardea* sp., size of *A. alba*, distal left humerus lacking all the condylus ventralis, TM 90-04-024, cranial aspect. C: cf. Ardeidae indet., size of *Egretta garzetta*, angulus medialis part of left coracoid, ASK-VP-3/513, dorsal aspect. D: *Ephippiorhynchus tchoufour*, sp. nov., holotype distal left tarsometatarsus, slightly eroded at angles, TM 266-03-261, a: dorsal aspect, b: distal aspect. E: *Ephippiorhynchus senegalensis*, recent specimen for comparison, distal left tarsometatarsus, LAC-1869-89, distal aspect. F: *Ephippiorhynchus/Leptoptilos* sp. A, small, distal right tarsometatarsus, TM 75-01-017, dorsal aspect. G: *Mycteria/Ciconia* sp., size of *M. ibis*, proximal left femur lacking head, TM 60-99-018, lateral aspect. H: *Afrocygnus chauvireae*, complete left humerus, TM 112-00-196, caudal aspect. I: *Afrocygnus chauvireae*, distal part of right ulna lacking the condylus ventralis and the distalmost condylus dorsalis, TM 242-03-021, caudo-ventral aspect. Scale bars equal approximately 1 cm.



help estimating the ratio for humeri between *A. pannonica* and *A. melanogaster*. Lambrecht (1916) did not clearly explain what features made the fossil carpometacarpus he attributed to « *A. pannonica* (?) » closer to *Anhinga* than to *Phalacrocorax*. Rich (1972) estimated that this fossil needed re-examination; however the illustration (Lambrecht, 1916: fig. 7) closely matches modern *Anhinga* morphologically and clearly differs from *Phalacrocorax*. The size of the Romanian carpometacarpus slightly exceeds the upper limit of five recent *A. melanogaster* (respectively 73.0 against 68.5-71.0 mm, after data in Lambrecht, 1916 and Brodkorb & Mourer-Chauviré, 1982), and is 10-15 % larger than in *A. anhinga*. Rich (1972, 1974; see also Brodkorb & Mourer-Chauviré, 1982) listed a number of morphological details making the fossil proximal humerus from Bled ed Douarah different from modern species of *Anhinga*. However, the examination of a larger sample of recent specimens of *Anhinga* than in previous studies of Old World Miocene darters, especially for the living Old World species *A. melanogaster* (regrouping the subspecies from Africa and Madagascar to SE Asia and Australasia, that were formerly considered separate species), reveals that these small details are highly variable intraspecifically, and that the Tunisian humerus matches modern darters morphologically. Its size remains the only characteristic as a distinct species, although it seems close to the upper limit of *A. melanogaster* (tabl. 1). The sixth vertebra from Romania and the seventh vertebra from Tunisia cannot be compared with the species represented in Chad, but information from their size can be useful. In linear dimensions, the sixth vertebra of *A. pannonica* is 20-25 % larger than in *A. anhinga* (Lambrecht, 1916, Rich, 1972), and the seventh vertebra from Tunisia is 5-15 % larger than *A. anhinga* on average (Rich, 1972). *A. melanogaster* is generally 5-10 % larger than *A. anhinga* in linear dimensions of bones (e.g. tabl. 1; see also Brodkorb & Mourer-Chauviré, 1982), which implies that the cervical vertebrae of *A. pannonica* would show a range of dimensions roughly from 5 to 20 % larger than in *A. melanogaster*.

For the humeri, it is also interesting to use the data in Ballmann (1987) who reported a large darter from the Mio-Pliocene of Sahabi (Sahabi Formation, Libya, Mio-Pliocene boundary, i.e. ca 5.3 Ma, after Bernor & Scott, 2003). Among the fossils assigned to this darter, *Anhinga* sp., the author provides measurements for the humerus (tabl. 1). When taken together, the humeri of Toros Menalla, Bled

ed Douarah and Sahabi can be interpreted as representing a single species, on average larger than *A. melanogaster*, and in large part exceeding the maximum for the latter. The linear dimensions of these African Late Miocene humeri taken together are on average 15-20 % larger than in *A. melanogaster*, which is in accordance with the range for *A. pannonica*. The variation range for these fossil humeri, as appreciated from the extremes, remains compatible with a single species. We identify here the fossils of darter from Sahabi as *Anhinga* cf. *A. pannonica*.

It is most probable that a volant (as testified by the full sized wing bones) species of darter such as *A. pannonica* in the Miocene had a larger distribution than Europe, and the presence of a similar sized darter in Africa in the Late Miocene is best interpreted as representing the same lineage. Apart from *A. pannonica*, the only other valid extinct darter known in the Old World is *A. hadarensis* Brodkorb & Mourer-Chauviré, 1982 (see Louchart et al., 2004, and references cited therein; in addition ‘*A. laticeps*’ from the Pleistocene of Australia was recognised as junior synonym of *A. melanogaster novaehollandiae* by Mackness & Van Tets, 1995). *A. hadarensis* is smaller than or similar in size to *A. melanogaster*. A number of extinct, mostly large and sometimes giant darters are by contrast known from the Lower Miocene to the Plio-Pleistocene of South America (and one in the Late Miocene of southern North America). These are: *Meganhinga chilensis* Alvarenga, 1995, from the Lower Miocene of Chile (Alvarenga, 1995); *Macranhinga paranensis* Noriega, 1992, from the Late Miocene Argentina (Noriega, 1992, 2001, 2002, see also Noriega & Alvarenga, 2002); *Anhinga grandis* Martin & Mengel, 1975, from the Late Miocene of Nebraska and Florida and the Middle Miocene of Colombia (Martin & Mengel, 1975, Becker, 1987, Rasmussen & Kay, 1992); *A. fraileyi* Campbell, 1996, from the Mio-Pliocene of SW Amazonia (Campbell, 1996); *Macranhinga ranzii* Alvarenga & Guilherme, 2003 (the largest known darter) and *Anhinga minuta* Alvarenga & Guilherme, 2003 (the smallest known darter), both from the Mio-Pliocene of SW Amazonia (Alvarenga & Guilherme, 2003); *Giganhinga kiyuensis* Rinderknecht & Noriega, 2002, from the Plio-Pleistocene of Uruguay (Rinderknecht & Noriega, 2002); and cf. *Giganhinga* sp. from the Late Miocene of Argentina (the largest known specimen of darter; Areta et al., 2007). These extinct taxa show the morphology of ‘New World’ *Anhinga*, and seem to represent a mini-radiation es-

Figure 4 - A: Small Anatinae indet., humeral end of right coracoid STD-VP-2/913, medial aspect. B: cf. *Plectropterus* sp., size of *P. gambensis*, complete left carpometacarpus, TM 90-03-009, dorsal aspect, with os metacarpale minus shown shifted on the right. C: cf. *Plectropterus* sp., size of *P. gambensis*, distal right tibiotarsus, ALA-VP-2/144, cranial aspect. D: Accipitridae indet., large, left pedal phalanx 1 of digit III, TM 09-01-405, a: dorsal aspect, b: plantar aspect. E: Falconiformes indet., distal fragment of pedal phalanx, ALA-VP-2/339, a: lateral / medial aspect, b: dorsal aspect. F: *Pandion* sp., size of *P. haliaetus*, right pedal phalanx 5 of digit IV (claw), DID-VP-1/155, lacking distalmost end and slightly corroded, a: medial aspect, b: proximal aspect. G: *Francolinus* sp., spur of right tarsometatarsus with small part of shaft, ALA-VP-2/296, latero-plantar aspect. H: *Balearica* sp., shaft with part of distal end of right femur lacking the condylus medialis, TM 89-99-001, caudal aspect. I: *Heliopais* cf. *H. personata*, incomplete right humerus, TM 90-99-020, cranial aspect. J: Rallidae/Heliornithidae indet., proximal right ulna lacking the olecranon, TM 90 (no number yet), cranial aspect. Scale bars equal approximately 1 cm.

sentially in South America. Additionally *A. subvolans* (Brodský, 1956), from the Early Miocene of Florida, is said to share morphological characteristics of darters from the New World and the Old World, but can be separated as well from all the material referred to *A. pannonica* here in being similar in size to *A. melanogaster* (Becker, 1986). *A. pannonica* may be the only thus far known Old World « equivalent » of the New World Neogene large darters.

The assignment of the new Chadian fossils to *A. pannonica* is well supported; however, cervical vertebrae being unavailable for comparisons, this assignment remains tentative. Nevertheless, the assignment of African Late Miocene large darter fossils to *A. pannonica* is particularly reinforced by the fossils from Toros Menalla, highly distinctive by their large size, possibly representing larger individuals within the intraspecific variation, compared with the fossils of Bled ed Douarah for instance. Therefore, the species seems to have been present in Europe (Romania, and also Götzendorf, Austria, see Mlikovsky, 2002), Libya, Tunisia and Chad in the Late Miocene. Additionally it had been identified by Harrison & Walker (1982) in the Late Miocene of the Siwaliks of Pakistan (age ca 7-10 Ma, John Barry, pers. com.).

Anhinga sp.

Material: distal left humerus TM 90-05-001, distal right humerus TM 112-03-012.

Measurements: humerus TM 90-05-001: distal width: 16.3, distal depth: ca 9.8; humerus TM 112-03-012: distal width: 16.7.

Localities and age: TM 90 and TM 112, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: These distal humeri are intermediate in size between *A. melanogaster* and the measurements diagnostic of the larger individuals of *A. pannonica* (tabl. 1). They are therefore difficult to assign to one or the other species.

Family Ardeidae Vigors, 1825, incertae sedis

Genus *Ardea* L., 1758

Ardea sp., size of *A. alba*

Material: distal right humerus ALA-VP-2/105 (fig. 3A), and distal left humerus TM 90-04-024 (fig. 3B).

Measurements: humerus TM 90-04-024: distal width (estimated): 18, minimal width of shaft (estimated): 9.6; humerus ALA-VP-2/105: distal width: 18.7, distal depth: 10.

Localities and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma, and ALA-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: These distal humeri belong to a member of the Ardeidae and match morphologically the species in

the genus *Ardea*. They are very similar to each other, and fall in the variation range of *A. alba* (distal width of humerus : 17.3-20.0, n=11, after Kellner, 1986). However, the species cannot be ascertained, because several other herons in Africa and other parts of the world are the size of *A. alba*.

cf. Ardeidae indet., size of *Egretta garzetta*

Material: angulus medialis fragment of left coracoid ASK-VP-3/513 (fig. 3C).

Localities and age: ASK-VP-3, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: This fragmentary fossil can only be assigned to the family Ardeidae, but not to a particular genus. In size, it corresponds to a species smaller than the previous, and about the stature of *Egretta garzetta* for example.

Order Ciconiiformes Bonaparte, 1854

Family Ciconiidae Gray, 1840

Genus cf. *Mycteria* L., 1758

cf. *Mycteria* sp.

Material: distal right tibiotarsus TM 90-04-033.

Measurements: distal width: 11.2.

Locality and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: This distal tibiotarsus shows the proximal incision of the external condyle typical of the genus *Mycteria* (Olson, 1991). This fossil is probably from a juvenile bird, as shown by the fibrous bone surface visible on some parts without sandstone matrix and without erosion. The small size of this tibiotarsus compared with modern *M. ibis* is therefore due to this juvenile status. Storks of the genus *Mycteria* such as the living African *M. ibis* nest in trees, and the presence of a juvenile tends to indicate a wooded component of the paleoenvironment of TM 90.

Mycteria / Ciconia sp., size of *M. ibis*

Material: two fragments of a right coracoid TM 90-00-018, and proximal left femur lacking the head TM 60-99-018 (fig. 3G).

Measurements: femur TM 60-99-018: proximal depth: 13.8, minimal width of shaft: 9.6, minimal circumference of shaft: 31.1.

Localities and age: TM 60 and TM 90, both in the Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: These fossils correspond in morphology to the genera *Mycteria* and *Ciconia* (see Gruber, 1990). Their generic assignment thus remains unprecise. They correspond in size to the recent African *M. ibis*, for instance. In four recent *M. ibis*, measurements of the femur are: proximal depth: 13.6-15.5, minimal width of shaft: 9.2-10.4.

Genus *Ephippiorhynchus* Bonaparte, 1855

Ephippiorhynchus tchoufour, sp. nov.

Holotype: distal left tarsometatarsus TM 266-03-261 (fig. 3D).

Etymology: Name in apposition, from the Goran word *tchoufour*, meaning ‘large bird’, because of the very high stature inferred for the species, which was among the tallest birds encountered by the earliest Chadian hominids.

Type locality: Locality TM 266, Anthracotheriid Unit, fossiliferous area of Toros Menalla (Djurab, Chad, Africa).

Type horizon: Late Miocene, ca 7 Ma (Vignaud et al., 2002).

Distribution: Type locality.

Material: Holotype.

Diagnosis: Linear dimensions of the tarsometatarsus larger by ca 50 % than the maxima in all other species of *Ephippiorhynchus*.

Measurements: holotype: distal width: 37.3, distal depth: 24, width of trochlea metatarsi III: 13.9, depth of trochlea metatarsi III: 17.1.

Remarks: This tarsometatarsus belongs to the distinctive family Ciconiidae, and matches morphologically the large representatives of the traditional tribe Leptoptilini, which comprises today *Leptoptilos*, *Ephippiorhynchus* and the New World *Jabiru*. The proportions of this element reveal that it belongs to *Ephippiorhynchus* and differs from the other genera. The ratio of the depth of the trochlea metatarsi III to its width is greater in *Leptoptilos* than in *Ephippiorhynchus* (Louchart et al., 2005a), with ranges respectively of 1.30-1.50 and 1.13-1.29. In the fossil from TM 266 this ratio has a value of 1.23, typical of *Ephippiorhynchus*. The dimensions of the fossil exceed by ca 50% the maxima for the two extant species *E. senegalensis* and *E. asiaticus*, (tabl. 2). They also exceed by far the dimensions that can be inferred for the extinct *E. pakistanensis* Harrison & Walker, 1982 (Late Miocene of the Siwalik Series of the Potwar Plateau, northern Pakistan; tarsometatarsus not known), the latter being similar in size to *E. asiaticus* based on other elements (Harrison & Walker, 1982). Incidentally, it is not clear whether *E. pakistanensis* can be confidently separated from *E. asiaticus* based on the morphology of available elements. *E. tchoufour* sp. nov. was therefore a very large representative of the tall and slender saddlebill storks, roughly 50% larger in linear dimensions than the maxima for the extant species, making it one of the tallest non-Ratite birds, possibly up 2 m – 2.20 m height standing upright on the ground.

Ephippiorhynchus/Leptoptilos sp. A, small

Material: proximal left tarsometatarsus TM 266-05-039 with incomplete proximal end, distal right tarsometatarsus TM 75-01-017 (fig. 3F).

Measurements: tarsometatarsus TM 266-05-039: minimal width of shaft: 9.7; tarsometatarsus

TM 75-01-017: distal width: 24.7, width of trochlea metatarsi III (estimated): 9.6, depth of trochlea metatarsi III (estimated): 12.5.

Localities and age: TM 75 and TM 266, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: The proportions of the trochlea metatarsi III (see above) do not allow us to assign the distal tarsometatarsus of a large Ciconiidae to a precise genus. In the fossil, the ratio of the depth of the trochlea metatarsi III to its width is 1.30, which is close to the limit between the genera *Ephippiorhynchus* and *Leptoptilos*. The incomplete proximal tarsometatarsus, showing the same pneumatism as in extant Leptoptilini, is not assignable to a genus either. The size of these tarsometatarsi is similar to that in *E. senegalensis*, and much smaller than in *Ephippiorhynchus tchoufour* sp. nov. above, or in *Ephippiorhynchus/Leptoptilos* sp. B below.

Ephippiorhynchus/Leptoptilos sp. B, large

Material: distal right radius TM 90-04-066, incomplete left tibiotarsus (distal part + shaft) TM 90-01-070, distal left tarsometatarsus TM 90-04-032. From a single individual: distal right ulna, right ulnare carpal and proximal right carpometacarpus TM 90-01-076. Left pedal phalanx 1 of digit III TM 90-00-061, proximal fragment of right pedal phalanx 1 of digit III TM 90-00-023, and proximal fragment of right pedal phalanx 1 of digit III TM 90-01-029.

Measurements: radius TM 90-04-066: distal width: 24.0; tibiotarsus TM 90-01-070: estimated total length: 469, estimated distal depth: 32.8, minimal width of shaft: 15.5; tarsometatarsus TM 90-04-032 : distal width: 33.3; ulna TM 90-01-076: distal width: 26.6, orthogonal distal depth: 25, greatest diagonal distal depth: 29.5, minimal width of shaft: 17.3; ulnare carpal TM 90-01-076: greatest length: 30.5; carpometacarpus TM 90-01-076: proximal depth: 17.9; pedal phalanx 1 III TM 90-00-061: total length: 65.8, proximal width: 12.3, minimal width of corpus: 6.75; pedal phalanx 1 III TM 90-00-023: proximal width: 13, minimal width of corpus: 7.5; pedal phalanx 1 III TM 90-01-029: proximal width: 11.4, minimal width of corpus: 7.5.

Localities and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: These fossils belong to one or more large species of the family Ciconiidae, and morphologically match the species in the traditional tribe Leptoptilini. On the tibiotarsus, the ratio of the minimal width of shaft to the total length is greater in *Leptoptilos* than in *Ephippiorhynchus* (Louchart et al., 2005a): respectively 0.032-0.038 and 0.024-0.030. In the fossil from TM 90, this ratio has an estimated value of 0.033. In one specimen of *Jabiru mycteria*, this ratio is of 0.032. Therefore, the TM 90 tibiotarsus is close to the limit for *Leptoptilos* and *Ephippiorhynchus*, and given its large size, an allometrically increased robustness would not be surprising, so that it cannot be ascertained to which of the genera it belongs. The distal tarsometatarsus is broken on

edges of the trochleae, and estimated dimensions seem to indicate proportions near the limit between *Ephippiorhynchus* and *Leptoptilos* (see Louchart et al., 2005a). These fossils are assigned here to *Ephippiorhynchus/Leptoptilos* sp. B, large. The other fossils of probably the same species of very large stork at TM 90 are not sufficiently diagnostic to precise the genus. They are also referred to *Ephippiorhynchus/Leptoptilos* sp. B, large. All might correspond to *Ephippiorhynchus tchoufour* sp. nov. of TM 266, or to a giant *Leptoptilos* like *L. falconeri* (see Louchart et al., 2005a), and more material would be useful to make more precise identifications.

cf. Ciconiiformes indet., small/medium

Material: pedal phalanx DID-VP-1/105.

Localities and age: DID-VP-1, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6–5.8 Ma.

Order Anseriformes (Wagler, 1831)

Family Anatidae Leach, 1820

Subfamily Anserinae Vigors, 1825

Tribe Cygnini (Vigors, 1825)

Genus *Afrocygnus* Louchart et al., 2005b

Afrocygnus chauvireae Louchart et al., 2005b

Material: complete left humerus TM 112-00-196 (fig. 3H), and fragment of distal right ulna lacking the distalmost part TM 242-03-021 (fig. 3I).

Measurements: humerus TM 112-00-196: total length: 234, minimal width of shaft: 12.9; ulna TM 242-03-021: greatest diagonal distal depth (estimated): 18, minimal distal width of shaft: 7.6, width of shaft in the middle: 8.6.

Localities and age: TM 112 and TM 242, both in the Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: This species and genus were based on the holotype complete humerus, and they are also represented in the Latest Miocene of Sahabi, Libya (Louchart et al., 2005b). The fragmentary ulna matches the ulna of small swans (genus *Cygnus* s.l.). It is about the size of the distal ulna in *C. atratus*, the latter species having a humerus similar in size to that of *Afrocygnus chauvireae*. The distal ulna is often poorly diagnostic, and it is not surprising that no morphological characteristic seems to differentiate it from *Cygnus*, unlike the humerus. Therefore, it is most likely that these two elements, both indicating a swan-sized bird, represent a single species for the Anthracotheriid Unit of Toros Menalla, *A. chauvireae*, given that this is the only swan of this size thus far known in Africa. Swans are absent from subsaharan Africa today, and *Afrocygnus* is close to *Cygnus*, represented worldwide outside Africa (Louchart et al., 2005b).

Subfamily Anatinae Vigors, 1825

Genus cf. *Plectropterus* Stephens, 1824

cf. *Plectropterus* sp., size of *P. gambensis*

Material: shaft of right humerus TM 112-00-164, complete left carpometacarpus TM 90-03-009 (fig. 4B), proximal left carpometacarpus TM 337-03-002, and distal right tibiotarsus ALA-VP-2/144 (fig. 4C).

Measurements: humerus TM 112-00-164: estimated total length: 178, minimal width of shaft: 12; carpometacarpus TM 90-03-009: total length: 99, proximal width: 26.5; carpometacarpus TM 337-03-002: proximal width: 26.5; tibiotarsus ALA-VP-2/144: distal width: 19.

Localities and age: TM 90, TM 112 and TM 337, all three in the Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma, and ALA-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6–5.8 Ma.

Remarks: These fossils are identical in morphology and size to the corresponding bones of recent *Plectropterus gambensis*. Measurements of elements in two recent individuals (one female and one – larger – male) of the latter from the BMNH are: humerus: total length: 145.3, 193.3, minimal width of shaft: 9.9, 12.0; carpometacarpus (female individual only): total length: 77.3, proximal width: 20.1; tibiotarsus (female individual only): distal width: 16.6. The fossils from Chad probably represent a male, given the large size, as well as probably the tibiotarsus from Ethiopia. These fossils are the earliest assignable to the genus *Plectropterus*, and might represent the ancestor of the extant *P. gambensis*. A left carpometacarpus illustrated in Harris & Leakey (2003: fig. 4.37) from the Upper Nawata Member of the Nawata Formation of Lothagam, Kenya (5–6.5 Ma, McDougall & Feibel, 2003) and identified as Anatidae indet., is very similar to the Chadian fossils and seems to be assignable to cf. *Plectropterus* sp. as well.

Small Anatinae indet.

Material: distal right tibiotarsus AMW-VP-1/143, proximal right coracoid STD-VP-2/913 (fig. 4A), proximal right coracoid STD-VP-2/915, proximal right radius STD-VP-2/914, and distal left carpometacarpus STD-VP-2/912.

Measurements: tibiotarsus AMW-VP-1/143: distal width: 8.7, distal depth: 9.3, minimal width of shaft: 4.0; coracoid STD-VP-2/913: greatest width of humeral end: 8.5; radius STD-VP-2/914: greatest diagonal proximal depth: 5.6; carpometacarpus STD-VP-2/912: distal width: 7.5, distal depth: 4.7.

Localities and age: AMW-VP-1, Kuseralee Member, Sagantole Formation, Central Awash Complex (Ethiopia), ca 5.2 Ma, and STD-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6–5.8 Ma.

Remarks: These fossils might represent a single indeterminate species. They are different from and smaller than cf. *Plectropterus* sp., and they match the size of a large *Anas platyrhynchos* for instance.

Anatidae indet.

Material: humeral end fragment of left coracoid ASK-VP-3/510 and sternal end fragment of right coracoid ASK-VP-3/511.

Localities and age: ASK-VP-3, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: These fossils are too fragmentary for a more precise identification.

Order Falconiformes Sharpe, 1874

Family Accipitridae Vieillot, 1816

Accipitridae indet., large

Material: complete pedal phalanx 1 of left digit III TM 09-01-405 (fig. 4D).

Measurements: total length: 47.2, minimal width of corpus: 7.45.

Localities and age: TM 09, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: Among the birds of prey examined, this phalanx resembles that in *Aegypius monachus*, except that it is more elongated. More comparisons will probably allow a more precise identification.

Family Pandionidae Bonaparte, 1854

Genus *Pandion* Savigny, 1809

Pandion sp., size of *P. haliaetus*

Material: right pedal phalanx 5 (claw) of digit IV, DID-VP-1/155 (fig. 4F).

Measurements: maximal dorso-plantar height near the articular surface, including the processus flexorius: 12.2, maximal medio-lateral width at the same level: ca 4.8-5.0 (uncertain because of corrosion).

Localities and age: DID-VP-1, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: This claw shows the extremely slender, sharp and curved shape, typical of the genus *Pandion*, alone in the family Pandionidae. This shape had probably evolved in relation with the function of grasping fish, the diet of ospreys. The shape of the processus flexorius is also distinctive in its more proximal development than in the other birds of prey, as well as in being more compressed medio-laterally. In its dimensions, it is within the range of four recent individuals of *P. haliaetus*: articular dorso-plantar height measured as above: 11.1-13.0; medio-lateral width measured as above: 5.1-5.7.

Fossils of the family Pandionidae are extremely rare worldwide. Two extinct species in the genus *Pandion* have however been named from Miocene deposits of North America (Becker, 1985), but their claws are unknown. They display a few morphological differences with *P. haliaetus*,

but are of similar general size. *P. haliaetus* is today one of the few truly cosmopolitan bird species, and extinct species of osprey may well have been such as well. A claw of a Falconiformes was described from the Early Oligocene of Germany. This claw, a 4th of the digit III, shows the osprey morphology (Schindler & Mayr, 2004) and was assigned to the Pandioninae (i.e. Pandionidae in the systematics adopted here) by Mayr (2006). The fossil claw from Digiba Dora cannot be assigned to the living species rather than to an extinct species of *Pandion*, and is identified here as *Pandion* sp., size of *P. haliaetus*.

Rasmussen et al. (1987) reported a distal humerus of an osprey close to *Pandion* (aff. *Pandion*) from the Oligocene Jebel Qatrani Formation of Fayum (Egypt). There are no other fossils of Pandionidae known from Africa. Ecologically, ospreys require open bodies of water with an abundant resource of live fish. Today *P. haliaetus* is widespread in Africa including Ethiopia, where it is essentially a Palearctic winterer.

This claw presents a corrosion that might be due to the digestion by a mammalian Carnivore.

Falconiformes indet.

Material: proximal fragment of right tarsometatarsus ALA-VP-2/322, distal fragment of pedal phalanx ALA-VP-2/339 (fig. 4E).

Localities and age: ALA-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: These fossils of a Falconiformes differ from the Pandionidae, seem not to belong to a Falconidae, and may belong to the Accipitridae, but they are too fragmentary to allow a more precise and firm identification. They are of medium size among diurnal birds of prey.

Order Galliformes Temminck, 1820

Family Phasianidae Horsfield, 1821

Genus *Francolinus* Stephens, 1819

Francolinus sp.

Material: spur of right tarsometatarsus with small part of shaft ALA-VP-2/296 (fig. 4G).

Measurements: length of spur from base: 4.9.

Localities and age: ALA-VP-2, Asa Koma Member, Adu Asa Formation, Middle Awash Late Miocene (Ethiopia), 5.6-5.8 Ma.

Remarks: This spur is well developed and pointed, and thus differs from spurs observed in the guineafowl genus *Agelastes*. The other genera of guineafowl have no spurs, or only small, rounded bumps. The fossil has the size and shape of spurs present in several species of *Francolinus* s.l., a very diverse genus in Africa, comprising the (sub)genera *Francolinus*, *Peliperdix*, *Scleroptila* and *Pternistis*. A more precise assignment is not possible without more material. This francolin is the earliest reported thus far in the fossil record.

Order Gruiformes (Bonaparte, 1854)
Family Gruidae Vigors, 1825
Genus *Balearica* Brisson, 1760
Balearica sp.

Material: shaft with part of distal end of right femur TM 89-99-001 (fig. 4H).

Measurements: minimal width of shaft: 10, minimal circumference of shaft: 32.5.

Localities and age: TM 89, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: This fragment of femur is identical in morphology and size with the femora in the two extant species of crowned cranes, genus *Balearica* (measurements of minimal width of shaft in *B. regulorum*: 9.7; in *B. pavonina*: 9.1, 10.0, 10.6). These two species are morphologically very close to each other, allopatric (roughly northern and southern Africa respectively), and were formerly considered conspecific (Del Hoyo et al., 1996). The Chadian fossil is certainly closely related to the taxon that gave rise to the two extant species. This is the oldest record of the genus in Africa, where it is endemic today.

Family Heliornithidae G. R. Gray, 1841
Genus *Heliopais* Sharpe, 1893
Heliopais cf. *H. personata* (G. R. Gray, 1849)

Material: incomplete right humerus TM 90-99-020 (fig. 4I).

Measurements: estimated total length: 63.5, minimal width of shaft: 4.35.

Localities and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: This fossil, described elsewhere (Louchart et al., 2005c), is the second fossil record in the world for the family Heliornithidae, and belongs to the genus *Heliopais*. It is identified as *Heliopais* cf. *H. personata*, a species with a South East Asian distribution today.

Ecologically it is indicative of a open freshwater body (lake or slow river) bordered by abundant, overhanging and partly wooded vegetation.

Family Rallidae / Heliornithidae
Rallidae / Heliornithidae indet.

Material: proximal right ulna TM 90 (no number yet) (fig. 4J).

Measurements: greatest proximal width: 6.7, minimal width of shaft: 3.9.

Localities and age: TM 90, Anthracotheriid Unit of the Toros Menalla fossiliferous area (Chad), ca 7 Ma.

Remarks: This proximal ulna could belong to either the Heliornithidae of TM 90, above, or to a Rallidae the size of *Fulica atra*.

Aves indet.

A few fossils from localities of both Chad and Ethiopia could not be identified, even at the ordinal level.

DISCUSSION

The taxa identified in the Late Miocene localities of Chad and Ethiopia generally belong to modern genera, except the swan *Afrocygnus chauvireae* (Louchart et al., 2005b). For some of these taxa, the species represented is similar in size and morphology to a modern species (*Phalacrocorax* cf. *P. carbo*, *Anhinga* cf. *A. melanogaster*, cf. *Plectropterus* sp., size of *P. gambensis*, *Heliopais* cf. *H. personata*) or to two closely allied modern species (*Balearica* sp.). In the case of *Phalacrocorax* cf. *P. carbo*, *Anhinga* cf. *A. melanogaster*, cf. *Plectropterus* sp., and *Heliopais* cf. *H. personata* (Louchart et al., 2005c), the Late Miocene fossils, although of fragmentary nature, are similar to the living species *P. carbo*, *A. melanogaster*, *P. gambensis*, and *H. personata* respectively, and other species can be excluded, extant or extinct. Therefore it is a likely hypothesis that they are ancestral to these living species, although more material will be needed to confirm it or to reveal that they may represent closely related, extinct lineages. In the case of *Balearica* sp., the Late Miocene fossil represents either the ancestor of both living species, the ancestor of one of them, or an extinct species very close to both. The smaller cormorant *Phalacrocorax* sp., size of *P. africanus*, and the osprey *Pandion* sp., are not referable to a particular species.

Beside *Afrocygnus chauvireae*, two other species are extinct: *Anhinga* cf. *A. pannonica* and *Ephippiorhynchus tchoufour* sp. nov. Both are large extinct representatives of genera that comprise today only smaller species. In the case of *A. cf. A. pannonica*, it is the first case in the Old World of two contemporaneous and possibly sympatric species of darters (the second species being *A. cf. A. melanogaster*). The other taxa are not assignable to a particular lineage. Some of the taxa are the earliest African records (at their particular level of identification): *Podiceps*, *Phalacrocorax* cf. *P. carbo*, *Ephippiorhynchus*, cf. *Plectropterus*, *Pandion*, *Francolinus*, *Balearica* and *Heliopais* cf. *H. personata* (the latter being the second record of the Heliornithidae worldwide).

Ecologically, there are several categories of birds represented here. Most of the taxa are aquatic birds that depend on open bodies of water, with fish and aquatic vegetation, for the Chadian as well as for the Ethiopian localities (tabl. 3). From the different, contemporaneous localities of Toros Menalla, the two darters, the two Anatidae, and the finfoot indicate a lake or a slow river. The finfoot precisely points to thick overhanging vegetation and partly forested edges (Louchart et al., 2005c). From the different, contemporaneous (5.6-5.8 Ma) localities of Ethiopia, the grebe, the two cormorants, the darter, the two Anatidae and the osprey indicate a lake or a slow river in the vicinity. From Amba West (ca 5.2 Ma) the single bone of Anatinae indet. indicates

only the presence of a humid setting, without precisions. Then there are birds living primarily in swamps, marshes, humid grasslands, river or lake edges, with at least patches of rather open vegetation to allow foraging for the larger taxa (the large storks). From the Chadian localities these are the heron, the different storks, and the crowned crane. The juvenile smaller stork cf. *Mycteria* sp. is indicative of trees. From the Ethiopian localities at 5.6-5.8 Ma, this category includes the two herons. Third, the birds of prey other than the osprey are ubiquitous. They are the Accipitridae indet. from Chad, and Falconiformes indet. from Ethiopia, and they do not provide useful paleoecological information. Finally, the single exception to these essentially aquatic birds assemblages is *Francolinus* sp. from the Ethiopian locality ALA-VP-2. This is the only dry land bird represented in the localities studied here. This locality further differs from all the other Ethiopian contemporaneous ones in yielding the only non-strictly open water birds (Falconiformes, Ardeidae). To summarise, the paleoecological information is rather similar for the Chadian and Ethiopian Late Miocene localities: presence of open water bodies, lake or slow river, with fish and aquatic vegetation, bordered by partly open vegetated humid edges, and at least for Toros Menalla also partly closed, locally forested edges. In addition, a dry land bird is represented at ALA-VP-2, but does not give precise paleoecological indications.

Some differences in the composition of the fossil avifauna between Chad and Ethiopia are visible (tabl. 3), mainly in that: grebes, cormorants, ducks, osprey and francolins are absent from the Chadian sites, while large storks and Gruiformes are absent from the Ethiopian sites. In the detail there are other differences in composition, but it is difficult to infer from them some differences in paleoenvironment or total avifaunal composition (zoogeography). They may be due to 1) the effect of rather small samples, 2) different sedimentary contexts and probably different taphonomic processes. On the other hand, the Chadian and Ethiopian sites have in common three taxa at the species level or just over: *Anhinga* cf. *A. melanogaster*, *Ardea* sp., and cf. *Plectropterus* sp. (of the same size respectively in each case).

A few interesting similarities can be noticed between these faunas and those of Late Miocene localities of Kenya, Tunisia and Libya. *Anhinga* cf. *A. melanogaster* is recorded in deposits of similar age at Lothagam, Kenya, as well as apparently an Anatidae referable to *Plectropterus*. *Anhinga* cf. *A. pannonica* is recorded in the Late Miocene of Bled ed Douarah, Tunisia, and we tentatively assign fossils from Sahabi, Libya (Latest Miocene) to this species. In the latter locality, *Afrocygnus* is also represented (Louchart et al., 2005b). By comparison, there is no such similarity between both the Chadian and Ethiopian Late Miocene avifaunas and that of the Early Pliocene of Langebaanweg, despite the fact that the latter is very rich, with abundant fossils, unlike the other localities cited above. Nevertheless, the fossil birds of Langebaanweg still require a detailed study for many of the taxa preliminarily listed by Rich (1980). A

difference in composition already seems to exist between the Early Pliocene of Langebaanweg and the Mio-Pliocene of Chad and Ethiopia, however: in the first site the extinct stork *Ciconia kahli* Haarhoff, 1988 is the only large stork, while in the Chadian and Ethiopian sites the large storks discovered thus far belong to the tribe Leptotilini (genera *Leptoptilos* and *Ephippiorhynchus*).

On a larger scale, when using for comparisons the extensive European Mio-Pliocene fossil bird record, the African fossils discussed here do not appear assignable to any of the extinct European birds of these periods, except for *Anhinga* cf. *A. pannonica*. This species constitutes a link between the Late Miocene of Chad and the Middle to Late Miocene of Europe and North Africa, as well as probably of the Siwalik Hills of Pakistan. This link, probably at the species level, is reminiscent of the case of *Leptoptilos falconeri*, a species in common between the northern half of Africa and the Siwalik Hills of India, as well as probably Europe, during the Pliocene (Louchart et al., 2005a). Taxonomic comparisons with the Miocene and Pliocene fossil record from the remaining sites of the Oriental region (East and South-East Asia including Indonesia) are not presently possible. Many of the fossil birds from these areas and periods are still unstudied. Others were studied only preliminarily, some of which were named but without comparisons with the European record for instance (Rich et al., 1986). The few available descriptions are thus generally insufficient for useful comparisons.

A few of the Mio-Pliocene taxa from Africa are today absent from this continent, but present in the Oriental Region. Fossils of peafowl *Pavo* spp. were found in the Early Pliocene of Ethiopia and Kenya as well as Europe (Louchart, 2003, Pickford et al., 2004), while this genus is now restricted to South East Asia. Similarly, the finfoot *Heliopais* cf. *H. personata* in the Late Miocene of Chad is an Oriental element now restricted to South East Asia (Louchart et al., 2005c). Today, considering only the non-passerines, the Paleotropical (=Ethiopian) and Oriental regions share a rather small number of taxa: five to eight at the species level (0.6 to 0.9 % of the non passerine Paleotropical bird species including the regular non breeding), 11 to 15 at the genus level (4.3 to 6 % of the genera), and two at the family level (3.4 % of the families) (Louchart, in prep.). Therefore, the four non passerine bird taxa listed above from the Late Miocene or Early Pliocene of Ethiopian and Chadian localities, that show Oriental (two) or Eurasian (two) affinities - one at the species level, two probably so, and one at the genus level – already appear as important links of continuity between the Paleotropical region and primarily the Oriental region at that time. From probably still continuous then, such links became discontinuous, leading to the typically disjunct distributions of many shared taxa observed today between the Paleotropical and Oriental regions. Several of these distributions are very disjunct, between the tropical rainforests of Central or West Africa and those of South East Asia (e.g. Olson, 1973, 1979, Dinesen et al., 1994, Fjeldsa & Kiure,

2003). The latitudinal regression of Old World tropical biomes and taxa from northern latitudes toward the equator during most of the Cenozoic, due to phases of global cooling, is likely to be the general cause for these patterns, given the geometry of landmasses and the geographical distance over the Indian Ocean between equatorial Africa and equatorial Asia. Finally, *Afrocygnus chauvireae* attests to the past presence of swans in Africa, although it is premature to link it to a taxon of swan from a particular region of the rest of the world (Louchart et al., 2005b).

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APPENDIX. LIST OF THE RECENT SPECIMENS EXAMINED.

Podicipedidae *Podiceps cristatus* UCBL 5.1 to UCBL 5.11; *Podiceps grisegena* IPH (1 indiv.); *Podiceps auritus* UCBL 7.2; *Podiceps nigricollis* UCBL 8.1; *Tachybaptus ruficollis* UCBL 9.1 à UCBL 9.5. Phalacrocoracidae: *Phalacrocorax carbo* UCBL 19.1, UCBL 19.2; *Phalacrocorax aristotelis* UCBL 20.2. Anhingidae: *Anhinga anhinga* BMNH 1896.2.16.17; LAC-1934.541; *A. melanogaster* BMNH 1848.10.31.7; LAC-1882-612, LAC-1886-176,

Taxon	Reference	Total length	Proximal width (from tuberculum dorsale to most ventral extremity of crista bicipitalis)	Distal width	Minimal width of shaft
Living	<i>Anhinga anhinga</i>	BM 1896.2.16.17	124.0	19.2	14.8
	<i>Anhinga anhinga</i>	LAC-1934.541	121.5 (e)	18.5	15.2
	Extremes for <i>A. anhinga</i> including data from Rich (1972) and Ballmann (1987)		120-135 (n=14)		
	<i>Anhinga melanogaster</i>	LAC-1882-612	135.4	19.1	15.0
	<i>Anhinga melanogaster</i>	LAC-1886-176	133.5	20.15	15.25
	<i>Anhinga melanogaster</i>	LAC-1883-543	133.1	18.8	15.75
	<i>Anhinga melanogaster</i>	LAC-1884-193	137.0	20.0	15.3
	<i>Anhinga melanogaster</i> , Japan	BM 1848.10.31.7	140.9	19.6	15.2
	<i>Anhinga melanogaster rufa</i> , Madagascar	BM S/1952.1.87			15.4
	<i>Anhinga melanogaster rufa</i> , captive	B 12295	128.7	18.5	15.4
Fossil	<i>Anhinga melanogaster</i>	4 individuals (Ballmann, 1987)	137.0-142.0 (n=4)		
	<i>Anhinga melanogaster</i>	12 individuals (Becker, 1986)		18.1-21.6 (n=12)	
	Extremes for <i>A. melanogaster</i>		128.7-142.0 (n=11)	18.1-21.6 (n=19)	15.0-16.1 (n=8)
	<i>Anhinga cf. A. pannonica</i> , Bled ed Douarrah	T-3605		> 20.4	
	<i>Anhinga cf. A. pannonica</i> , Toros Menalla	TM 266-03-071	167.0 e	24.3	21.2 e
	<i>Anhinga cf. A. pannonica</i> , Toros Menalla	TM 266-03-071			19.2 e
	<i>Anhinga cf. A. pannonica*</i> , Sahabi	several specimens (Ballmann, 1987)	155.0 e		
	<i>Anhinga cf. A. pannonica*</i> , Sahabi	1P109A			17.0 **

Table 1 - Measurements of the humerus in recent specimens of *Anhinga melanogaster* and *A. anhinga*, and in *Anhinga cf. A. pannonica* from Chad, Tunisia and Libya. All measurements in mm. *: new identification, e: estimated, **: after illustration.

LAC-1883-543, LAC-1884-193; *A. melanogaster rufa* BMNH S/1952.1.87, IRSN 12295, IRSN 22452. Ardeidae: *Botaurus stellaris* UCBL 32.1, UCBL 32.2; *Ixobrychus minutus* UCBL 31.1 to UCBL 31.7; *Nycticorax nycticorax* UCBL 30.1 to UCBL 30.3; *Butorides striatus* LAC (1 indiv.); *Ardeola ralloides* UCBL 28.1 to UCBL 28.5; *Bubulcus ibis* UCBL 29.1 to UCBL 29.4; *Egretta garzetta* UCBL 26.1 to UCBL 26.6; *Ardea alba* LAC (1 indiv.), IPH (1 indiv.); *Ardea cinerea* UCBL 24.1 to UCBL 24.6, UCBL 24.8 to UCBL 24.15; *Ardea purpurea* UCBL 25.1 to UCBL 25.7, UCBL 25.9, UCBL 25.10. Ciconiidae: *Mycteria americana* MVZ 24920, MVZ 58424, MVZ 61014, MVZ 124846; *M. ibis* RMCA 91066A07, RMCA 92008A01, RMCA 93114A46, RMCA 93114A47; *M. leucocephala* UCBL 06.1973; *Anastomus lamelligerus* MVZ 133407; *Ciconia nigra* UCBL 35.1, UCBL 35.2; *C. abdimii* IRSN 55366, IRSN 55367; *C. episcopus* IRSN 64632; *Ciconia ciconia* UCBL 34.1; *C. c. boyiana* MVZ 136568; *Ephippiorhynchus asiaticus* LAC 1 specimen, IRSN 12386, IRSN 42167, USNM 346193; *E. senegalensis* LAC 1869-89, LAC 1882-421, LAC 1909-62, LAC 1935-193, IRSN 1922, IRSN 55843, MVZ 140361, RMCA 91056A01, UCBL 1974; *Jabiru mycteria* MVZ 133932; *Leptoptilos javanicus* IRSN 12391, IRSN 12392, MVZ 137570, UCBL 1975; *L. dubius* FMNH 104387, IRSN 12395, IRSN 60379; *L. crumeniferus* LAC 1884-215, LAC 1909-21, LAC 1997-232, IRSN 12396, MVZ 134058, RMCA 98025A01, RMCA 99049A13. Scopidae: *Scopus umbretta* MVZ 155163, UCBL 2000. Balaenicipitidae: *Balaeniceps rex* LAC 1923-504, MVZ 138003. Threskiornithidae: *Geronticus eremita* BMNH 1867.7.8.9 (Vel. Cat. N° 1393 A), UCBL 1974.1, UCBL 1991.3; *Plegadis falcinellus* IPH (1 indiv.); *Platalea leucorodia* LAC (1 indiv.), BMNH S/1952.1.113, BMNH 1859.2.10.5, BMNH S/1952.3.148. Anatidae: *Cereopsis novaehollandiae* MVZ 137569; *Anser fabalis* LAC 1890.2007, UCBL 45.1; *Anser anser* LAC 1993.93, UCBL 42.1 to UCBL 42.4; *Anser albifrons* MVZ 70321, MVZ 70322; *Anser indicus* MVZ 136143; *Anser caerulescens* MVZ 120301; *Anser rossii* MVZ 133859; *Branta canadensis* MVZ 132955; UCBL 50.1; *Branta bernicla* MVZ 160649; UCBL 48.1; *Coscoroba coscoroba* CAS 85150, MVZ 140776; *Cygnus (Chenopis) atratus* BMNH 1905.2.4.1, BMNH S/1952.3.77, IRSN 29386, MVZ 141910, MVZ 141911, MVZ 143290, MVZ 143291, MVZ 143292, MVZ 143293, MVZ 154271, UCBL 02.2001; *C. (Chenopis) melanocorypha* BMNH 1857.12.21.3, BMNH 1862.11.10.14, IRSN 22424, UCBL 03.2001; *C. (Cygnus) olor* MVZ 115621, UCBL 41.1 to UCBL 41.6; *C. (Olor) buccinator* MVZ 120361, MVZ 137246; *C. (Olor) columbianus columbianus* CAS 57459, CAS 57631, CAS 87609, MVZ 151609; *C. (Olor) c. bewickii* IPH 1465; *C. (Olor) cygnus* MVZ 66973, UCBL 39.1; *Sarkidiornis melanotos* FMNH 338942 (= GW 4148); *Dendrocygna bicolor helva* CAS 58337; *D. arcuata* CAS 57841; *Alopochen aegyptiacus* BMNH 1847.12.11.12, IRSN 72311; *Plectropterus gamben-*

umbretta MVZ 155163, UCBL 2000. Balaenicipitidae: *Balaeniceps rex* LAC 1923-504, MVZ 138003. Threskiornithidae: *Geronticus eremita* BMNH 1867.7.8.9 (Vel. Cat. N° 1393 A), UCBL 1974.1, UCBL 1991.3; *Plegadis falcinellus* IPH (1 indiv.); *Platalea leucorodia* LAC (1 indiv.), BMNH S/1952.1.113, BMNH 1859.2.10.5, BMNH S/1952.3.148. Anatidae: *Cereopsis novaehollandiae* MVZ 137569; *Anser fabalis* LAC 1890.2007, UCBL 45.1; *Anser anser* LAC 1993.93, UCBL 42.1 to UCBL 42.4; *Anser albifrons* MVZ 70321, MVZ 70322; *Anser indicus* MVZ 136143; *Anser caerulescens* MVZ 120301; *Anser rossii* MVZ 133859; *Branta canadensis* MVZ 132955; UCBL 50.1; *Branta bernicla* MVZ 160649; UCBL 48.1; *Coscoroba coscoroba* CAS 85150, MVZ 140776; *Cygnus (Chenopis) atratus* BMNH 1905.2.4.1, BMNH S/1952.3.77, IRSN 29386, MVZ 141910, MVZ 141911, MVZ 143290, MVZ 143291, MVZ 143292, MVZ 143293, MVZ 154271, UCBL 02.2001; *C. (Chenopis) melanocorypha* BMNH 1857.12.21.3, BMNH 1862.11.10.14, IRSN 22424, UCBL 03.2001; *C. (Cygnus) olor* MVZ 115621, UCBL 41.1 to UCBL 41.6; *C. (Olor) buccinator* MVZ 120361, MVZ 137246; *C. (Olor) columbianus columbianus* CAS 57459, CAS 57631, CAS 87609, MVZ 151609; *C. (Olor) c. bewickii* IPH 1465; *C. (Olor) cygnus* MVZ 66973, UCBL 39.1; *Sarkidiornis melanotos* FMNH 338942 (= GW 4148); *Dendrocygna bicolor helva* CAS 58337; *D. arcuata* CAS 57841; *Alopochen aegyptiacus* BMNH 1847.12.11.12, IRSN 72311; *Plectropterus gamben-*

Taxon	Distal width	Width of trochlea metatarsi III	Depth of trochlea metatarsi III
Living <i>Ephippiorhynchus senegalensis</i>	21.6-25.9 (n=10)	8.25-9.75 (n=9)	10.4-12.0 (n=6)
Living <i>E. asiaticus</i>	22.5-24.6 (n=5)	9.1-9.6 (n=3)	10.8-11.0 (n=2)
Fossil <i>E. tchoufour</i> sp. nov., TM 266-03-261	37.3	13.9	17.1
Ratio TM 266-03-261 / maximum for living species	1.516	1.448	1.555

Table 2 - Measurements of the distal tarsometatarsus in recent specimens of the two extant species of *Ephippiorhynchus*, and in *E. tchoufour* sp. nov.

Family / Order	Taxon	Common name	ca 5.2 Ma Ethiopia	5.6-5.8 Ma Ethiopia	ca 7 Ma Chad
Podicipedidae	<i>Podiceps</i> sp. size of small <i>P. grisegena</i>	grebe		X	
Phalacrocoracidae	<i>Phalacrocorax</i> sp., size of <i>P. africanus</i>	smaller cormorant		X	
	<i>Phalacrocorax</i> cf. <i>P. carbo</i>	cormorant		X	
	<i>Anhinga</i> cf. <i>A. melanogaster</i>	darter		X	X
Anhingidae	<i>Anhinga</i> cf. <i>A. pannonica</i> *	large darter			X
	<i>Anhinga</i> sp.	darter		x	
Ardeidae	<i>Ardea</i> sp., size of <i>A. alba</i>	heron		X	X
cf. Ardeidae	cf. Ardeidae indet. size of <i>Egretta garzetta</i>	cf. heron		X	
	cf. <i>Mycteria</i> sp.	stork			X
	<i>Mycteria/Ciconia</i> sp., size of <i>M. ibis</i>	stork		x	
Ciconiidae	<i>Ephippiorhynchus tchoufour</i> sp. nov. *	large saddlebill stork			X
	<i>Ephippiorhynchus/Leptoptilos</i> sp. A, small	large stork			X
	<i>Ephippiorhynchus/Leptoptilos</i> sp. B, large	larger stork		x	
cf. Ciconiiformes	cf. Ciconiiformes indet., small/medium			X	
	<i>Afrocygnus chauvireae</i> *	swan			X
Anatidae	cf. <i>Plectropterus</i> sp., size of <i>P. gambensis</i>	cf. spur-winged goose		X	X
	Small Anatinae indet.	duck	X	X	
	Anatidae indet.			x	
Accipitridae	Accipitridae indet., large	diurnal raptor			X
Pandionidae	<i>Pandion</i> sp., size of <i>P. haliaetus</i>	osprey		X	
Falconiformes	Falconiformes indet.	diurnal raptor		X	
Phasianidae	<i>Francolinus</i> sp.	francolin		X	
Gruidae	<i>Balearica</i> sp.	crowned crane			X
Heliornithidae	<i>Heliopais</i> cf. <i>H. personata</i>	finfoot			X
Rallidae / Heliornithidae	Rallidae / Heliornithidae indet.	rail / finfoot			x

Table 3 - Synoptic table showing the Late Miocene birds of Chad and Ethiopia. All the large crosses correspond to different taxa. The small crosses represent taxa possibly referable to a taxon marked with a large cross within the same group of localities (columns). *: extinct taxon.

sis BMNH 1898.5.9.15, BMNH S/1952.3.109, LAC; *Cyanochen cyanopterus* FMNH 338883; *Tadorna ferruginea* UCBL 53.1; *T. tadorna* UCBL 52.4; *Anas penelope* UCBL 59.1; *A. strepera* UCBL 58.1, UCBL 58.2; *A. crecca* UCBL 55.1 to UCBL 55.3; *A. platyrhynchos* UCBL 54.1 to UCBL

54.6; *A. acuta* IPH (1 indiv.); *A. querquedula* UCBL 57.1, UCBL 57.2; *A. clypeata* UCBL 61.1, UCBL 61.2; *Marmaronetta angustirostris* BM S/1952.1.157 (captivité), IPH (1 indiv.), UCBL 56.1, UCBL 56.2; *Netta rufina* UCBL 63.1, UCBL 63.2; *Aythya ferina* UCBL 64.1 to UCBL 64.6; *A.*

nyroca UCBL 65.1 to UCBL 65.5; *A. fuligula* UCBL 66.1 to UCBL 66.4; *Somateria mollissima* UCBL 76.1; *Clangula hyemalis* UCBL 70.1; *Melanitta nigra* UCBL 73.1, UCBL 73.2; *Bucephala clangula* UCBL 68.1; *Mergellus albellus* IPH (1 indiv.); *Mergus serrator* UCBL 80.1, UCBL 80.2; *Oxyura leucocephala* IPH (1 indiv.). Accipitridae: *Gypaetus barbatus* BM 1845.1.12.1, BM 1876.8.7.7; *Gyps africanus* USNM 430826; *G. rueppellii* USNM 346395; *G. fulvus* BM 1861.3.24.6, BM 1954.30.55; *Aegypius monachus* BM Vel Cat 4 A, BM 1872.10.25.5, BM 1848.3.8.2, UCBL 84.1; *Torgos tracheliotus* IRSN 3875, RMCA 91012A01; *Aquila verreauxii* BMNH 1860.4.23.7; *Aquila wahlbergi* BMNH 1904.10.29.21; *Polemaetus bellicosus* BMNH S/1957.9.1; *Lophoætus occipitalis* BMNH 1850.8.15.61, BMNH S/1955.4.6; *Spizaetus cirrhatus* BMNH S/2002.45.1; *Stephanoætus coronatus* BMNH S/1954.30.42. Pandionidae: *Pandion haliaetus* UCBL 109.1 to UCBL 109.4. Phasianidae: *Alectoris graeca* UCBL 126.1; *Ammoperdix heyi* FMNH 348117; *Francolinus pintadeanus* CAS 61093; *Peliperdix sephaena* USNM 558463; *Pternistis squamatus* squamatus FMNH 93388; *P. leucoscepus* USNM 430614; *P. erckelii* USNM 556785; *Perdix perdix* UCBL 129.2; *Coturnix deleorguei* IRSN 37319, IRSN 37320; *Excalfactoria adansonii* IRSN 37605, IRSN 37606; *Ptilopachus petrosus* IRSN 37318, IRSN 48162; *Pavo cristatus* BMNH S/1952.2.131, BMNH S/1973.66.68, BMNH S/1952.2.132, BMNH S/1987.14.1, BMNH 1859.9.6.421, CAS 42736, RMCA 93137A05, UCBL 455.2; *P. muticus* BMNH S/1966.52.37, BMNH S/1998.41.1, BMNH S/1952.2.34, BMNH 1847.12.11.13, BMNH 1869.10.19.26; *Afropavo congensis* BMNH S/1989.19.16, BMNH S/1977.20.1, BMNH S/1975.16.1, UCBL 1988.1; *Agelastes niger* BMNH S/1961.3.1, IRSN 41605; *Numida meleagris* BMNH S/1999.43.66, RMCA A2 014 A01, UCBL 453.1 to UCBL 453.3; *Guttera plumifera* FMNH 313049, RMCA (QA01)-86337; *G. pucherani* BMNH S/1971.4.5, CAS 86157, RMCA 83364; *Acryllium vulturinum* RMCA 98025 A12, RMCA 98025 A07, RMCA 89049 A08. Turnicidae: *Turnix suscitator* MVZ 133111, MVZ 133103; *T. varia* MVZ 154111. Gruidae: *Balearica regulorum* RMCA 37432; *B. pavonina* RMCA 89049A09,

RMCA 98025A02, RMCA 93143A62; *Anthropoides virgo* RMCA « Archeo » Tell Beydar, UCBL 134.1; *A. paradisea* RMCA 99049A12, RMCA 93143A58; *Bugeranus carunculatus* IRSN 2760.B; *Grus rubicunda* IRSN 41154; *Grus grus* RMCA 93143A60, RMCA 93143A61, UCBL 133.1, UCBL 133.2; *Grus monacha* RMCA 93143A59. Rallidae: *Rallus aquaticus* UCBL 135.1, UCBL 135.2; *Porzana porzana* UCBL 136.1 to UCBL 136.3; *Gallinula chloropus* UCBL 140.1 to UCBL 140.9; *Porphyrio porphyrio* UCBL 141.1; *Fulica atra* UCBL 142.1 to UCBL 142.8. Heliornithidae: *Podica senegalensis* BMNH S/1955.2.1; *Heliopais personata* USNM 534558; *Heliorhynchus fulica* BMNH 1891.7.20.262, MVZ 126568, MVZ 126569. Jacanidae: *Jacana spinosa* MVZ 85598, MVZ 85599. Rostratulidae: *Rostratula benghalensis* MVZ 120048, USNM 613012. Haematopodidae: *Haematopus ostralegus* UCBL 147.1, UCBL 147.2. Ibidorhynchidae: *Ibidorhyncha struthersii* USNM 292766. Recurvirostridae: *Himantopus himantopus* UCBL 190.1 to UCBL 190.3; *Recurvirostra avosetta* UCBL 191.1 to UCBL 191.3. Burhinidae: *Burhinus oedicnemus* UCBL 194.1 to UCBL 194.6. Glareolidae: *Cursorius cursor* UCBL 197.1; *Glareola pratincola* UCBL 195.1. Charadriidae: *Vanellus vanellus* UCBL 149.1 to UCBL 149.8; *Charadrius hiaticula* UCBL 150.1 to UCBL 150.3; *Pluvialis squatarola* UCBL 153.1 to UCBL 153.4. Scolopacidae: *Arenaria interpres* UCBL 157.1 to UCBL 157.5; *Gallinago gallinago* UCBL 158.1 to UCBL 158.7; *Scolopax rusticola* UCBL 161.1 to UCBL 161.4; *Numerius arquata* UCBL 163.1 to UCBL 163.4; *Limosa limosa* UCBL 166.1 to UCBL 166.7; *Tringa totanus* UCBL 171.1 to UCBL 171.3; *Calidris canutus* UCBL 178.1; *C. alba* UCBL 186.1, 186.2; *C. alpina* UCBL 184.1 to UCBL 184.6; *Philomachus pugnax* UCBL 189.1 to UCBL 189.4. Phalaropodidae: *Phalaropus fulicaria* UCBL 192.1, 192.2. Thinocoridae: *Thinocorus orbignyanus* USNM 290109. Chionidae: *Chionis alba* USNM 489489. Stercorariidae: *Catharacta skua* UCBL 198.1; *Stercorarius parasiticus* UCBL 200.1. Laridae: *Larus ridibundus* UCBL 212.1 to UCBL 212.13. Sternidae: *Sterna sandvicensis* UCBL 226.1, 226.2. Alcidae: *Alca torda* UCBL 227.1.