

A large extinct marabou stork in African Pliocene hominid sites, and a review of the fossil species of *Leptoptilos*

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Louchart, A., Vignaud, P., Likius, A., Brunet, M., and White, T.D. 2005. A large extinct marabou stork in African Pliocene hominid sites, and a review of the fossil species of *Leptoptilos*. *Acta Palaeontologica Polonica* 50 (3): 549–563.

New fossils of the family Ciconiidae from Pliocene hominid localities in Chad and Ethiopia are described, and several are shown to belong to *Leptoptilos falconeri*, originally known from the late Pliocene of the Siwalik Hills of India. Comparisons with all the hitherto known species of large Ciconiidae, and with an enlarged sample representing extant species, lead to a re-evaluation of some extinct taxa. Several synonyms are proposed, reflecting better the past diversity for this group. *L. pliogenicus* (Pliocene, Ukraine) is equivalent to *L. cf. falconeri*. *Cryptociconia indica* (late Pliocene, Siwalik Hills) belongs to *Leptoptilos*, and is probably either extant *L. dubius* or female *L. falconeri*. *L. siwalicensis*, from the same locality and also tentatively reported from the late Miocene of Northern Pakistan, is better referred to as *Leptoptilini* gen. et sp. indet. We consider the two following species as valid. *L. titan* (Pleistocene, Java) may be a late offshoot of the lineage of *L. falconeri*. *L. richae* (late Miocene, Tunisia) is the size of *L. crumeniferus*, and is distinct from *L. falconeri*. Thus, *L. falconeri* remains the only ascertained extinct Pliocene species in the tribe *Leptoptilini*. It was a widespread “giant” marabou stork, in the Pliocene of southern Asia, as well as northern and eastern Africa where it coexisted with different Pliocene hominids, and probably eastern Europe. It weighed up to about 20 kg, reached 2 m in height, and had probably slightly reduced forelimbs. It became extinct by the end of the Pliocene. *L. falconeri* is an example of a biogeographical link at the species level between the African and Eurasian faunas in the Pliocene. The fossil record indicates the presence of at least one other lineage in Africa since the early Miocene, similar in size to the extant *L. crumeniferus*.

Key words: Aves, Ciconiidae, *Leptoptilos*, Pliocene, Africa, Asia.

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Introduction

The tribe *Leptoptilini* comprises today the genera *Jabiru*, *Ephippiorhynchus*, and *Leptoptilos*. *Jabiru mycteria* is alone in its genus, and lives in South America. *Ephippiorhynchus* comprises *E. asiaticus* (South East Asia and Australasia) and *E. senegalensis* (sub-Saharan Africa). *Leptoptilos* comprises *L. javanicus* (South East Asia), the endangered *L. dubius* (South Asia), and *L. crumeniferus* (sub-Saharan Africa). Since the middle of the 19th century, many Asian and African Neogene localities have yielded fossils of large storks of the tribe *Leptoptilini* (Aves: Ciconiidae), some being very large (Milne-Edwards 1867–71; Wetmore 1940; Rich 1972, 1974; Harrison 1974; Hill and Walker 1979; Harrison and Walker 1982; Weesie 1982; Brodkorb 1985; Ballmann 1987; Miller et al. 1997; Harris and Leakey 2003; Louchart et al. 2004). Fossil *Leptoptilini* were also reported from Europe (Zubareva 1948; Cheneval 1984), and extant species of this tribe from the New

World, the Palearctic and Australasia. In addition, other fossil Ciconiidae were reported from all the continents, including large ones as well (see Haahrhoff 1988 for a review).

Hitherto, the following extinct species have been described and recognized as relevant strictly to the *Leptoptilini*, in chronological order of description: *Leptoptilos falconeri* (Milne-Edwards, 1868) from the Pliocene of India, *Grallavis edwardsi* (Lydekker, 1891) from the early Miocene of France—and the early Miocene of Libya according to Mlíkovský (2003), *Leptoptilos titan* Wetmore, 1940 from the Pleistocene of Java, *Leptoptilos pliogenicus* Zubareva, 1948 from the early Pliocene of Ukraine (MN 15 age after Mlíkovský 2002), *Leptoptilos richae* Harrison, 1974 from the late Miocene of Tunisia, *Leptoptilos siwalicensis* Harrison, 1974 from the Pliocene of India and tentatively the late Miocene of Pakistan, and *Ephippiorhynchus pakistanensis* Harrison and Walker, 1982 from the late Miocene of Pakistan. *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930 from

the Eocene of Egypt is generally considered a Leptoptilini (Rasmussen et al. 1987; Mlíkovský 2003). Many of the extinct taxa were often neglected at the time of the description of others, leading to a biased appreciation of the diversity.

New fossils of large storks from Africa are described here and identified. They were found in the last decade by the MPFT (Mission Paléolithologique Franco-Tchadienne) in Chad and by the MARP (Middle Awash Research Project) in Ethiopia. The fossil record of birds from Africa is currently very poor compared with that of other continents. The Mio-Pliocene vertebrate localities in these two countries are currently adding valuable insights in the paleoavifaunas of the continent (Louchart 2003; Louchart et al. 2004). More data on the living species, with a better appreciation of the important sexual size dimorphism in the large Ciconiidae, along with the information given by the new African fossils, can shed new light on the fossil record, and allow a better appreciation of the past diversity in the tribe Leptoptilini, particularly in the genus *Leptoptilos*.

The systematic order for extant taxa follows Kahl (1972) for the Ciconiidae, and Del Hoyo et al. (1992) for the other taxa. The osteological terminology follows Baumel and Witmer (1993). The measurements are given in millimeters, unless otherwise stated.

Abbreviations and material

Institutional abbreviations.—The repositories of the fossil specimens cited: BMNH, Natural History Museum (London), formerly British Museum (Natural History); CNAR, Centre National d'Appui à la Recherche (N'Djamena, Chad); IZAN, Institute of Zoology, Ukrainian Academy of Sciences (Kiev); KNM-BN, collections of Baringo district, Kenya, housed in the Kenya National Museums (Nairobi); KNM-LT, collections of Lothagam, Kenya, also housed in the KNM; MGSNI, Mining and Geological Survey, Department Netherland Indies (stored at the Quaternary Geological Laboratory, Geological Research and Development Center, Bandung, Indonesia); T, Colorado Tunisian Collection, Service Géologique (Tunis).

The repositories of the Recent specimens cited: FMNH, Field Museum of Natural History (Chicago); IRSN, Institut Royal des Sciences Naturelles de Belgique (Brussels); LAC, Laboratoire d'Anatomie Comparée, Muséum National d'Histoire Naturelle (Paris); MRAC, Musée Royal pour l'Afrique Centrale (Tervuren, Belgium); MVZ, Museum of Vertebrate Zoology, University of California (Berkeley); UCBL, Université Claude Bernard-Lyon 1 (Villeurbanne, France); USNM, National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

Other abbreviations.—The abbreviations for the fossiliferous areas and localities are as follows: KT13, locality 13 of the Koro Toro area (Chad); KB3, locality 3 of the Kossom Bougoudi area (Chad); SAG-VP-1, Vertebrate Paleontology locality 1 of the Sagantole area (Ethiopia); URU-VP-1, Verte-

brate Paleontology locality 1 of the Urugus area (Ethiopia); OMO and F both correspond to the Omo Shungura Formation (Ethiopia).

Material.—The following Ciconiiformes were examined for morphological comparisons with the fossils and for measurements: *Mycteria americana* MVZ 24920, MVZ 58424, MVZ 61014, MVZ 124846; *M. leucocephala* UCBL 06.1973; *Anastomus lamelligerus* MVZ 133407; *Ciconia nigra* UCBL 35.1, UCBL 35.2; *C. abdimii* MVZ 133692; *C. ciconia* UCBL 34.1; *C. c. boyciana* 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, MRAC 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, MRAC 98025A01, MRAC 99049A13; *Scopus umbretta* MVZ 155163, UCBL 2000; *Balaeniceps rex* LAC 1923-504, MVZ 138003. Comparisons were made also with all the extinct species of large Ciconiidae, essentially from the literature.

The specimens from Ethiopia are housed at the National Museum of Ethiopia, Addis Ababa, Ethiopia. The specimens from Chad are housed at the CNAR.

Geological settings of the new African fossils

The locality KB3 in Chad yielded an incomplete tibiotarsus (Fig. 1A₁–A₃). This locality is dated ca. 5 Ma, and the fossil remains are mainly concentrated in sandstones. The paleo-environment is mixed, with forested and wooded components more present than in the more recent Chadian Pliocene localities where savanna becomes predominant. The presence of a perennial calm freshwater component at the time of deposition of the sandstones is well documented, and the other bird taxa are essentially aquatic (Brunet et al. 2000; Louchart et al. 2004).

The distal tibiotarsus OMO-122-76-367 (Fig. 1G₁–G₃) is from the Omo Shungura Formation, Member C8 (Ethiopia), dated at about 2.5 Ma. *Australopithecus aethiopicus* was then present, in a mixed wooded-savanna and rather mesic environment. The pedal phalanx F-516-23 (Fig. 2A₁–A₃) comes from the stratigraphic level G-27 (upper member G of the Shungura Formation of Omo, Ethiopia), dated 1.94 Ma. The hominids present at this time were *A. boisei* and *Homo* sp., and the environment was an open savanna, under xeric conditions. Both members also show an important freshwater component, as illustrated among others by the very large number of hippopotamid fossils (Brown et al. 1970; Howell and Coppens 1974; Heinzelin 1983; Alemseged 2003).

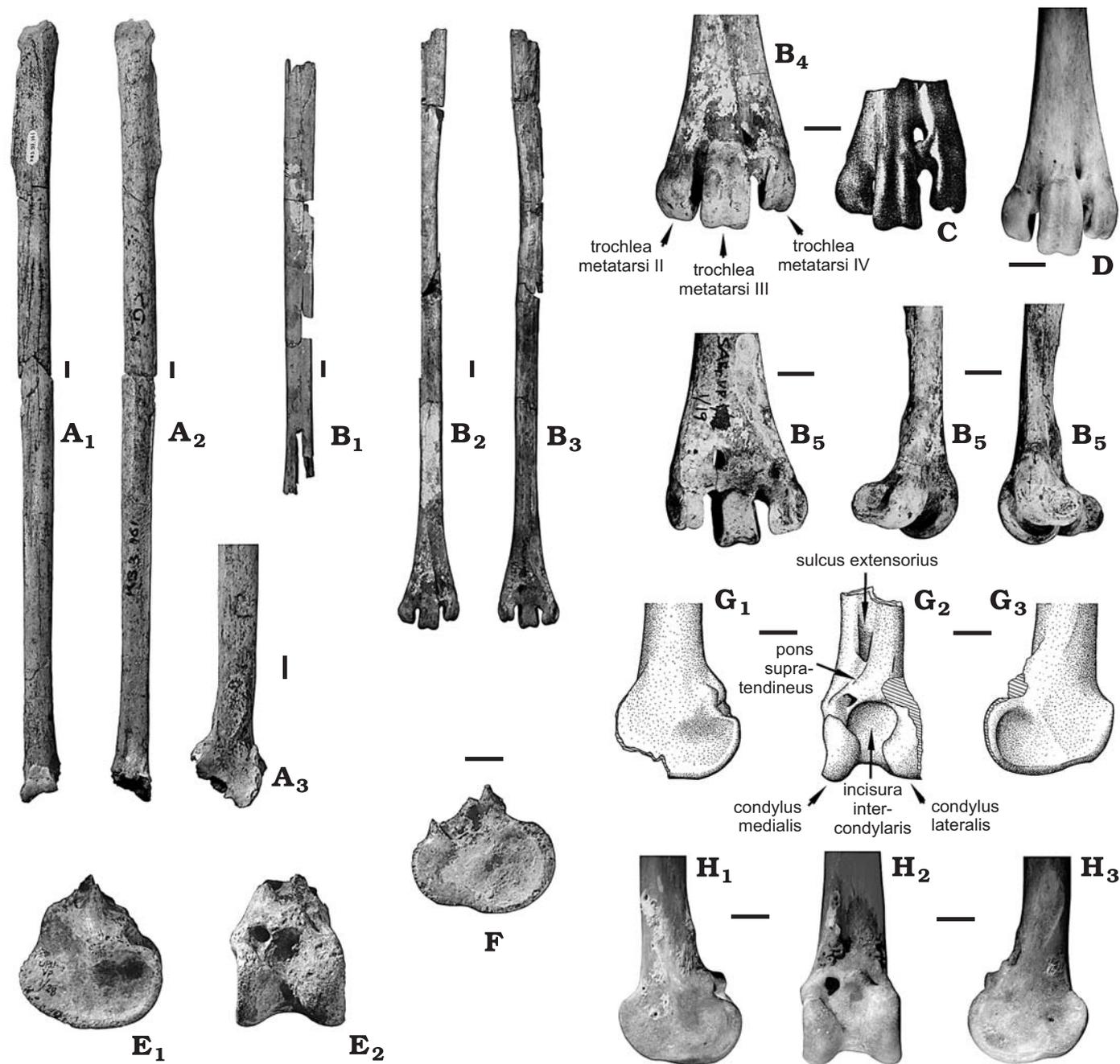


Fig. 1. **A.** *Leptoptilos falconeri*, incomplete left tibiotarsus, KB3-97-161 (Kossom Bougoudi, Chad, ca. 5.0 Ma), comprising part of the distal end and all the shaft; caudal (A_1), cranial (A_2), and lateral (A_3) aspects of the distal part. **B.** *L. falconeri*, SAG-VP-1/19 (Sagantole, Ethiopia, 4.4 Ma); B_1 , part of right tibiotarsus shaft, distal part, cranial aspect; B_2 to B_7 , partial left tarsometatarsus, comprising the distal part and most of the shaft; B_2 , dorsal aspect, B_3 , plantar aspect; the deformation of the shaft visible on B_2 and B_3 is due to diagenetic agents; B_4 , dorsal aspect of distal part; B_5 , plantar aspect of distal part; B_6 , medial aspect of distal part; B_7 , lateral aspect of distal part. **C.** *L. falconeri*, left distal tarsometatarsus, BMNH 39736 (Siwalik Hills of India, 1.8–3.0 Ma), dorsal aspect, from a slightly more lateral point of view compared with B_4 and D ; after Lydekker (1884). **D.** *L. dubius*, FMNH 104387 (Recent), dorsal aspect of the distal part of the left tarsometatarsus. **E.** cf. *L. falconeri*, left distal tibiotarsus, URU-VP-1/28 (Urugus, Ethiopia, 4.4 Ma); medial (E_1) and cranial (E_2) aspects. **F.** cf. *L. falconeri*, right distal tibiotarsus, URU-VP-1/15 (Urugus, Ethiopia, 4.4 Ma), lateral aspect. **G.** *L. falconeri*, left distal tibiotarsus, OMO-122-76-367 (Omo Shungura, Ethiopia, ca. 2.5 Ma); medial (G_1), cranial (G_2), and lateral (G_3) aspects. **H.** *L. dubius*, FMNH 104387 (Recent), left distal tibiotarsus; medial (H_1), cranial (H_2), and lateral (H_3) aspects. Scale bars 10 mm.

Two parts of a single carpometacarpus come from KT13 in Chad (Fig. 2B $_1$, B $_2$, C $_1$, C $_2$). KT13 is a late Pliocene locality (3–3.5 Ma, Brunet et al. 1997) which yielded remains of *Australopithecus* sp. It is contemporaneous with the close lo-

cality KT12, which yielded *Australopithecus bahrelghazali* (Brunet et al. 1995, 1996). The fossils from KT13 were deposited in fine sandstones with little transport. The paleoenvironment is a mosaic of woodland to open savanna, with

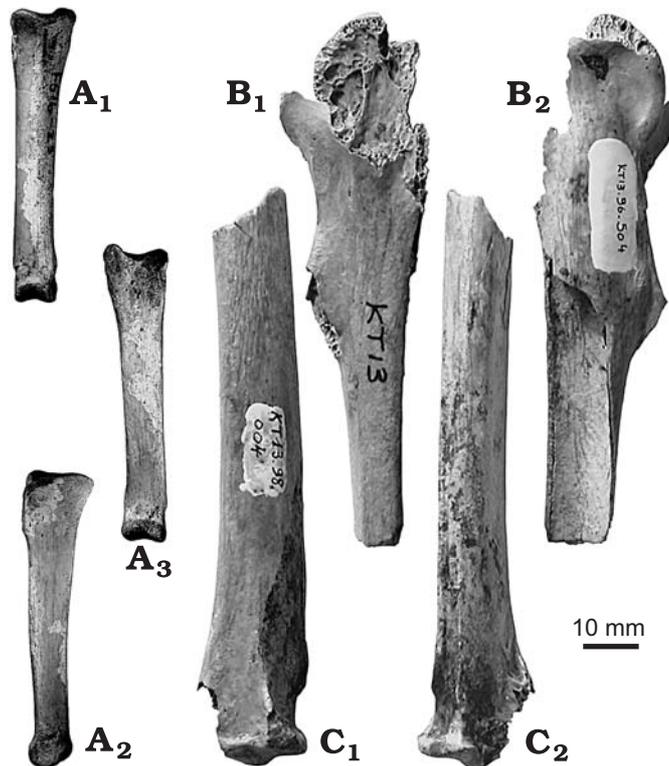


Fig. 2. A. *Leptoptilos falconeri*, right first pedal phalanx of digit II, F-516-23 (Omo Shungura, Ethiopia, 1.94 Ma); dorsal (A₁), lateral (A₂), and ventral (A₃). B. cf. *L. falconeri*, proximal half of left carpometacarpus, KT13-96-504 (Koro Toro, Chad, 3.0–3.5 Ma), with part of the proximal end; ventral (B₁) and dorsal (B₂) aspects. C. cf. *L. falconeri*, distal half of left carpometacarpus, KT13-98-004 (Koro Toro, Chad, 3.0–3.5 Ma), with an almost complete distal end; ventral (C₁) and dorsal (C₂) aspects. KT13-96-504 and KT13-98-004 almost certainly represent together a single carpometacarpus.

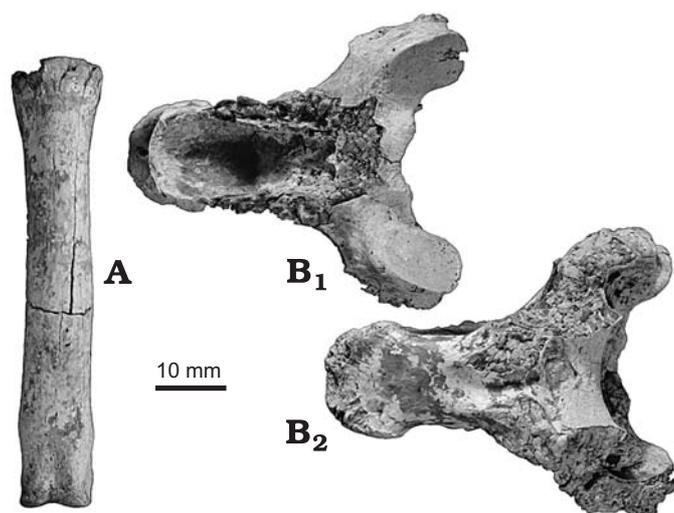


Fig. 3. cf. *Leptoptilos falconeri*, URU-VP-1/45 (Urugus, Ethiopia, 4.4 Ma). A. Left first pedal phalanx of digit III, dorsal aspect. B. Twelfth vertebra, dorsal (B₁) and ventral (B₂) aspects.

an important calm freshwater component. The other bird taxa are essentially aquatic (Brunet et al. 1997; Louchart et al. 2004).

A tibiotarsus shaft and an associated incomplete tarsometatarsus are from the locality SAG-VP-1 in Ethiopia (Fig. 1B₁–B₇). Two distal tibiotarsi (Fig. 1E₁, E₂, and F), a vertebra and a pedal phalanx (Fig. 3A₁–A₃) are from the locality URU-VP-1 in Ethiopia. SAG-VP-1 and URU-VP-1 both belong to the Aramis Member of the Sagantole Formation (Middle Awash), dated at 4.4 Ma, contemporaneous and spatially close to the Aramis localities. The latter yielded *Ardipithecus ramidus* along with a diverse fauna in a largely wooded environment (White et al. 1994; WoldeGabriel et al. 1994; Renne et al. 1999).

Results

Generic allocation within the Ciconiidae.—All the fossil remains discussed or described here correspond morphologically to the living members of the Ciconiidae, which is postcranially an homogeneous and distinctive family. The family Ciconiidae includes all the living storks in a wide sense, distributed in three tribes, six genera and 17 species (Kahl 1972). On the basis of a phenetic analysis of behavioral and skeletal characters, Wood (1984) found a congruence with Kahl (1972) except that he proposed to synonymize *Jabiru* with *Ephippiorhynchus*, and more importantly to remove the latter in its new sense from the Leptoptilini, and to place it in the Ciconiini. This would leave *Leptoptilos* alone in the Leptoptilini. These changes, however, are not supported by Slikas (1997) from molecular evidence. In addition, phenetic analyses are not likely to yield more reliable phylogenetic conclusions than cladistic approaches such as the one by Slikas (1997). Yet, the Leptoptilini appear most probably paraphyletic, and comprise basal species within the family, based on molecular evidence (Slikas 1997). In this study we nevertheless consider the “traditional” tribe Leptoptilini, because it is homogeneous in terms of morphology, osteology, and even behavior (Kahl 1972).

In the Leptoptilini, the limb bones are larger and more robust than in the two other tribes: Mycteriini and Ciconiini. There are in addition a few discrete morphological characters, as well as characteristic inter-segment proportions, separating the Ciconiini, the Mycteriini and the Leptoptilini (e.g., Cheneval 1984; Haarhoff 1988; Olson 1991). Of these characters, only two are useful here because the others are not visible on the preserved parts of the fossils; these are the pneumatization of the carpometacarpus and the ratio of the tibiotarsus length to the tarsometatarsus length. The carpometacarpus from Koro Toro is pneumatized, and considering all the fossils the tibiotarsus is longer than the tarsometatarsus. The remains discussed here thus correspond to the tribe Leptoptilini.

Within the Leptoptilini, several criteria of identification are available. In *Jabiru mycteria* the proportions of the tarsometatarsus and the tibiotarsus are similar to those in *Leptoptilos*. However, its carpometacarpus is stouter than in either *Leptoptilos* and *Ephippiorhynchus* (Tables 1–3). In addition,

the genus being neotropical, it will not be considered further. Between *Ephippiorhynchus* and *Leptoptilos*, the distinction is easy, the tibiotarsus, the tarsometatarsus and some pedal phalanges being more robust in the latter (Tables 2–4, Fig. 4). This is visible on complete fossils as well as incomplete ones comprising a significant part of the shaft, showing muscle scars, limits of crests, changes in width and depth, which can be used as landmarks. The proportions of the distal ends of some long bones are typical in *Leptoptilos* compared with *Ephippiorhynchus* and *Jabiru*, which was noticed by Miller et al. (1997) for the tibiotarsus. The ratio of the depth to the width of the distal end of the tibiotarsus is less in *Leptoptilos* than in *Ephippiorhynchus* (Table 2, Fig. 5). In the distal tarsometatarsus, the ratio of the depth of the middle trochlea (digit III) to its width is greater in *Leptoptilos* than in *Ephippiorhynchus* (Table 3, Fig. 6). These ratios overlap between the genera, but rather moderately so (Tables 2, 3, Figs. 4–6).

A few discrete morphological details have been said to allow separation between *Leptoptilos* and both *Ephippiorhynchus* and *Jabiru*. Miller et al. (1997) reported that on the distal tibiotarsus, the fossa present anteriorly at the base of the condylus lateralis is deeper in *Jabiru* and *Ephippiorhynchus* than in *Leptoptilos*, being almost absent in the latter. We do not confirm such a consistent difference, and rather observe that this fossa is generally well-marked in *Leptoptilos* as well. Cheneval (1984) reported other discrete details separating *Leptoptilos* from *Ephippiorhynchus*, but using only two species, represented by two specimens: one specimen of *L. javanicus* and one of *E. senegalensis*.

Considering the skeletal parts discussed here, according to this author (1) on the tarsometatarsus the area intercotylaris is more hollow in *E. senegalensis* than in *L. javanicus*; the crista medialis hypotarsi is shorter relatively to the crista lateralis hypotarsi in *L. javanicus* than in *E. senegalensis*; the arrangement of the foramina vascularia proximalia and the tuberositas m. tibialis cranialis is different between the two species; the plantar extension of the trochlea metatarsi II is more rounded in *E. senegalensis* than in *L. javanicus*; the fossa metatarsi I is more hollow in *E. senegalensis* than in *L. javanicus*; (2) on the tibiotarsus the tendinal groove is wider in *E. senegalensis* than in *L. javanicus*; a small vascular foramen proximal to the tuberositas retinaculi m. fibularis has a slightly different position in the two species; the epicondylus medialis and lateralis are more developed in *E. senegalensis* than in *L. javanicus*; the sulcus cartilaginis tibialis is more hollow in *E. senegalensis* than in *L. javanicus*; (3) on the carpometacarpus the fossa infratrochlearis bears a foramen in *L. javanicus*, not in *E. senegalensis*; the facies articularis digitis minor is smaller in *L. javanicus* than in *E. senegalensis*; the sulcus between the digital facets is deeper in *E. senegalensis* than in *L. javanicus*. All these discrete details appear unreliable to us with the larger sample of individuals and all the extant species we considered. Moreover, the Chadian and Ethiopian fossils show a slight recent erosion, which obscures the small surface details. These discrete features will therefore not be considered further here,

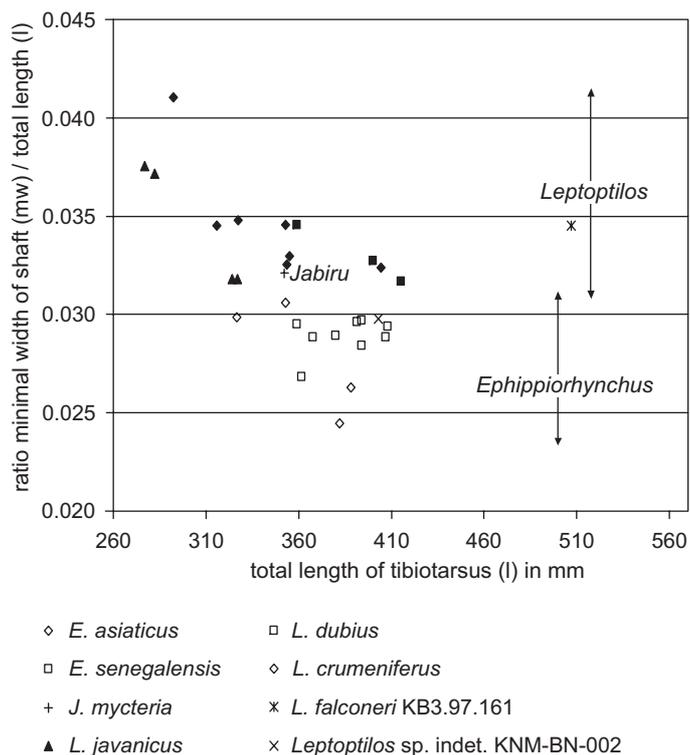


Fig. 4. Diagram showing the ratio of the minimal width of the tibiotarsus shaft to the tibiotarsus total length (without cristae cnemialis and patellaris), for living Leptoptilini and fossil *Leptoptilos*.

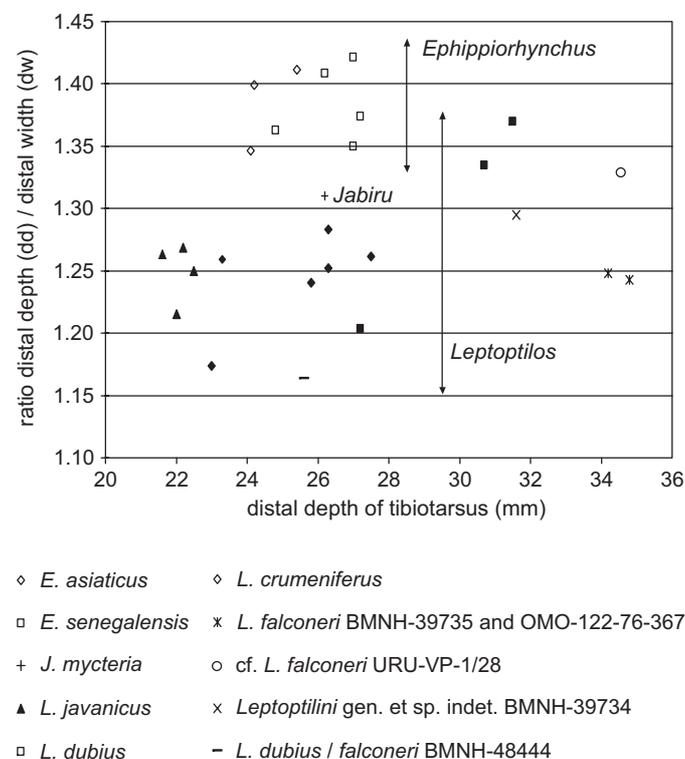


Fig. 5. Diagram showing the ratio of the distal depth of the tibiotarsus to its distal width, for living Leptoptilini and fossil *Leptoptilos*.

Table 1. Measurements (in mm) of the carpometacarpus of the extinct and living Leptoptilini. Abbreviations: l, total length; pw, maximal width of proximal end (cranio-caudally from the end of the processus extensorius to the end of the facies articularis ulnocarpalis); dw, width of distal articular end cranio-caudally; dd, depth of distal articular end dorso-ventrally; mw, minimal width of the os metacarpale majus cranio-caudally. (1): previously *L. pliocienicus* (Zubareva 1948). #, measurements of extant *L. crumeniferus* include independent data from Zubareva (1948). The values are individual measurements, or the minima and maxima separated by “–”; the sample size is given in parentheses. For the ratios, the means are in bold followed by sample size in parentheses. Males are indicated by (M), females by (F), and unsexed by (U). “e” means estimated measurement.

	Species	Specimen	l	pw	dw	dd	mw	mw/l	dw/l	pw/l	dd/l
Fossil	<i>cf. L. falconeri</i>	KT13.96.504; KT13.98.004; Koro Toro (Chad)	197.0 e		15.0		9.40	0.048			0.076
	<i>L. cf. falconeri</i> (1)	IZAN 8060; Odessa (Ukraine)	161.2	31.3		21.5			0.133	0.194	
Recent	<i>E. asiaticus</i> M	IRSN 12386	121.7	24.5	9.5	15.8	5.85	0.048	0.130	0.201	0.078
	<i>E. asiaticus</i> F	IRSN 42167	120.6	24.8	9.0		5.80	0.048		0.205	0.075
	<i>E. asiaticus</i> U	USNM 346193	120.5	24.1	9.7	14.1	5.60		0.117	0.200	0.080
	<i>E. senegalensis</i> M	IRSN 1922	127.2	27.2	10.7		6.55	0.051		0.214	0.084
	<i>E. senegalensis</i> F	IRSN 55843	124.0	25.3	10.7		6.10	0.049		0.204	0.086
	<i>E. senegalensis</i> U	MRAC 91056A01, UCBL 1974	126.8; 132.5	26.9; 27.3	10.1; 10.4	15.7; 16.6	6.10; 6.80	0.050 (n=2)	0.125 (n=2)	0.209 (n=2)	0.079 (n=2)
	<i>J. mycteria</i> U	MVZ 133932	132.8		12.1		8.10	0.061			0.091
	<i>L. javanicus</i> M	IRSN 12392	136.2	28.2	9.7	17.5	6.70	0.049	0.128	0.207	0.071
	<i>L. javanicus</i> F	IRSN 12391	137.0	28.1	10.4	16.8	6.35	0.046	0.123	0.205	0.076
	<i>L. javanicus</i> U	UCBL 1975	127.0	27.3		17.2	6.50	0.051	0.135	0.215	
	<i>L. dubius</i> M	IRSN 12395, FMNH 104387	183.0; 183.0	36.0; 37.5	14.8; 15.0	23.2; 25.0	9.40; 9.55	0.052 (n=2)	0.132 (n=2)	0.201 (n=2)	0.082 (n=2)
	<i>L. dubius</i> F	IRSN 60379	166.5	33.0	13.4	21.4	8.15	0.049	0.129	0.198	0.080
	<i>L. crumeniferus</i> M	IRSN 12396, MRAC 99049A13	149.5; 165.2	30.6; 33.1	13.8	21.8	7.20; 7.75	0.048 (n=2)	0.132	0.203 (n=2)	0.083
	<i>L. crumeniferus</i> F	MRAC 98025A01	141.6	30.4	12.4	19.6	7.35	0.052	0.138	0.215	0.088
<i>L. crumeniferus</i> U	4 specimens after #	128.0–167.5 (n=4)	24.2–31.6 (n=4)		18.0–21.8 (n=4)	6.6–7.9 (n=4)	0.050 (n=4)	0.136 (n=4)	0.186 (n=4)		

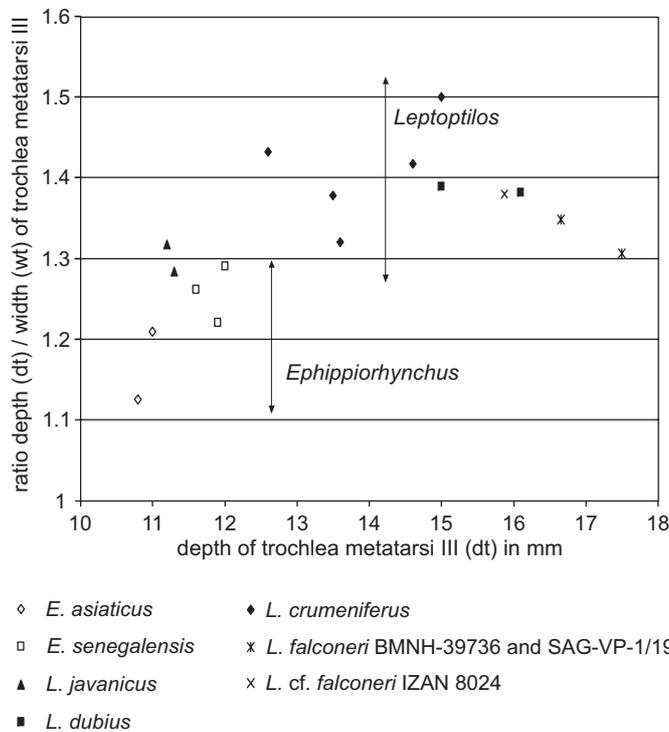


Fig. 6. Diagram showing the ratio of the depth of the trochlea metatarsi III to its width, for living Leptoptilini and fossil *Leptoptilos*.

and we will essentially rely on the intra- and inter-segment proportions.

Within the tribe Leptoptilini, most of the fossils from Ethiopia and Chad correspond in all the characteristics of intra-segment proportions to the genus *Leptoptilos*. One of these, the partial tibiotarsus shaft from Sagantole, can be assigned to the same taxon despite the lack of very distinctive generic features. This is because it belongs to the same individual as the more informative tarsometatarsus. On the other hand, five elements, the carpometacarpus from KT, the two distal tibiotarsi, the vertebra and the phalanx from URU, lack diagnostic generic features that would completely exclude *Ehippiorhynchus*. First, the carpometacarpus is too fragmentary. Secondly, the distal tibiotarsi, the first pedal phalanx of digit III and the vertebra have proportions situated in the interval of overlap between the two genera. These five elements are however tentatively attributed to the same species in the genus *Leptoptilos* because of their complete compatibility with this species, in addition to their close spatial and temporal concomitance with diagnostic remains, while *Ehippiorhynchus* is hitherto unknown there.

Comparisons with the living species.—The postcranial distinctions between species in the genus *Leptoptilos* rely on size. The fossils appear to belong to an extinct species of

Table 2. Measurements (in mm) of the tibiotarsus of the extinct and living Leptoptilini. Abbreviations: l, total length without cristae cnemialis and patellaris; pw, width of proximal articular surface medio-laterally without crista cnemialis lateralis; dw, width of distal end medio-laterally; dd, depth of distal end cranio-caudally; mw, minimal width of shaft medio-laterally; ds, depth of shaft cranio-caudally at the same level. (1): previously *L. falconeri* (Harrison 1974); (2): previously *L. siwalicensis* (Harrison 1974); (3): previously *Cryptociconia indica* (Harrison 1974); (4): previously *Leptoptilos* sp. (Hill and Walker 1979); (5): previously *Leptoptilos* sp. (Harris and Leakey 2003); (6): previously *L. richae* (Harrison 1974). #, measurements of extant *L. crumeniferus* include independent data from Rich (1972); *, measurement from the figures. Remaining conventions are as in Table 1.

	Species	Fossil specimen	l	pw	dw	dd	mw	ds	dd/dw	mw/l	dd/l	dw/l	
Fossil	<i>L. falconeri</i> (1)	lectotype BMNH-39735; Siwalik (India)			28.0	34.8			1.24				
	<i>L. falconeri</i>	KB3.97.161; Kossom Bougoudi (Chad)	507 e				17.50	16.00		0.035			
	<i>L. falconeri</i>	OMO-122-76-367; Omo (Ethiopia)			27.4 e	34.2	17.20		1.25 e				
	cf. <i>L. falconeri</i>	SAG-VP-1/19; Sagantole (Ethiopia)					14.75	14.05					
	cf. <i>L. falconeri</i>	URU-VP-1/15; Urugus (Ethiopia)				35.0 e							
	cf. <i>L. falconeri</i>	URU-VP-1/28; Urugus (Ethiopia)			26.0	34.5				1.33			
	Leptoptilini gen. et sp. indet. (2)	BMNH-39734; Siwalik (India)			24.4	31.6	15.30	13.80	1.30				
	<i>L. dubius / falconeri</i> (3)	BMNH-48444; Siwalik (India)			22.0 *	25.6 *				1.16			
	<i>Leptoptilos</i> sp. indet. (4)	KNM-BN-002; Baringo (Kenya)	403.0 e		23.0 e		12.0 e				0.030		0.057
	<i>Ehippiorhynchus / Leptoptilos</i> sp. (5)	KNM-LT-25106; Lothagam (Kenya)		30.0 e*									
	<i>L. richae</i> (6)	T-1396; Beglia (Tunisia)								1.28 *			
Recent	<i>E. asiaticus</i> M	IRSN 12386	388.0	21.6	17.9	24.1	10.20	10.15	1.35	0.026	0.062	0.046	
	<i>E. asiaticus</i> F	IRSN 42167	382.0	22.2	18.0	25.4	9.35	9.55	1.42	0.024	0.066	0.047	
	<i>E. asiaticus</i> U	LAC 1 specimen, USNM 346193	326.5; 353.0	21.2	17.3	24.2	9.75; 10.80	10.05	1.40	0.030 (n=2)	0.068		
	<i>E. senegalensis</i> M	IRSN 1922, MVZ 140361	407.0; 408.0	23.8; 24.7	19.0; 20.0	27.0; 27.0	11.75; 12.00	10.90; 10.95	1.39 (n=2)	0.029 (n=2)	0.066 (n=2)	0.048 (n=2)	
	<i>E. senegalensis</i> F	IRSN 55843	367.5	20.5	18.2	24.8	10.60	9.50	1.36	0.029	0.067	0.050	
	<i>E. senegalensis</i> U	LAC 1869-89, LAC 1935-193, LAC 1882-421, LAC 1909-62, MRAC 91056A01, UCBL 1974	359.0–394.0 (n=6)	23.4; 24.1	18.6; 19.8	26.2; 27.2	9.70–11.70 (n=6)	10.05; 10.15	1.39 (n=2)	0.029 (n=6)	0.068 (n=2)	0.049 (n=2)	
	<i>J. mycteria</i> U	MVZ 133932	352.0		20.0	26.2	11.30		1.31	0.032	0.074	0.057	
	<i>L. javanicus</i> M	IRSN 12392	324.0	22.2	17.5	22.2	10.30	9.20	1.27	0.032	0.069	0.054	
	<i>L. javanicus</i> F	IRSN 12391	327.0	23.0	18.0	22.5	10.40	9.10	1.25	0.032	0.069	0.055	
	<i>L. javanicus</i> U	UCBL 1975, MVZ 137570	277.0; 282.5	21.5; 21.7	17.1; 18.1	21.6; 22.0	10.40; 10.50	9.00; 9.65	1.19; 1.29	0.037; 0.038	0.078; 0.078	0.061; 0.065	
	<i>L. dubius</i> M	IRSN 12395, FMNH 104387	400.0; 415.0	30.0; 31.0 e	23.0; 23.0	30.7; 31.5	13.10; 13.15	12.10; 12.80	1.33; 1.37	0.032; 0.033	0.074; 0.079	0.055; 0.058	
	<i>L. dubius</i> F	IRSN 60379	359.0	28.1	22.6	27.2	12.40	11.35	1.20	0.035	0.076	0.063	
	<i>L. crumeniferus</i> M	IRSN 12396, MRAC 99049A13	355.0; 292.5	25.3; 26.7	20.8; 21.0	25.8; 26.3	11.70; 12.00	10.75; 10.85	1.25 (n=2)	0.037 (n=2)	0.081 (n=2)	0.065 (n=2)	
	<i>L. crumeniferus</i> F	MRAC 98025A01	327.5	25.5	19.6	23.0	11.40	10.45	1.17	0.035	0.070	0.060	
	<i>L. crumeniferus</i> U	LAC 1884-215, LAC 1909-21, LAC 1997-232, MVZ 134058, and 2 specimens after #	315.8–404.5 (n=4)	25.0	18.5–21.8 (n=3)	23.3–27.5 (n=3)	10.9–13.1 (n=4)	10.60	1.27 (n=3)	0.033 (n=4)	0.074	0.058	

Leptoptilos, even larger than the largest extant one, *L. dubius* of South Asia (Tables 1–4). The integration of a larger sample of the living *Ehippiorhynchus* and *Leptoptilos* species than in earlier works, including both males and females, allows an estimation of both the importance of sexual size dimorphism and individual size variation. For any measurement, $V = [(max\ value\ for\ males - min\ value\ for\ females) / max\ value\ for\ males]$ is a minimum estimate of the variation of this measurement in a species of *Leptoptilos*. There is only a moderate size overlap between sexes. The values of varia-

tion V obtained for the three extant *Leptoptilos* species are about 0.25–0.28 for total lengths, and 0.15–0.20 for the transversal dimensions. These values will help making tentative assignments for some other *Leptoptilos* remains of the Neogene record.

Specific allocation within *Leptoptilos*.—The size (Tables 1–4) allows to identify the Chadian and Ethiopian fossils as *L. falconeri* (Milne Edwards, 1868), initially described from the late Pliocene Siwalik Hills deposits of Uttar Pradesh (In-

Table 3. Measurements (in mm) of the tarsometatarsus of the extinct and living Leptoptilini. Abbreviations: l, total length; pw, width of proximal articular surface medio-laterally; pd, depth of proximal articular surface dorso-ventrally; dw, width of distal end medio-laterally; dd, depth of distal end dorso-ventrally; mw, minimal width of shaft medio-laterally; wt, width of trochlea metatarsi III medio-laterally; dt, depth of trochlea metatarsi III dorso-ventrally. (1): previously *L. falconeri* (Harrison 1974); (2): previously *L. pliogenicus* (Zubareva 1948); (3): previously *L. siwalicensis* (Harrison 1974); (4): previously *L. titan* (Wetmore 1940); (5): previously *L. richae* (Harrison 1974); (6): previously *Leptoptilos* sp. (Hill and Walker 1979). Measurements of extant species include independent data from ## Wetmore (1940) (his minima and maxima), # Zubareva (1948; the two specimens of *J. mycteria* were originally listed erroneously as *Mycteria americana*), and § Rich (1972). *, measurement from figures. Remaining conventions are as in Table 1.

	Species	Specimen	l	pw	pd	dw	dd	mw	wt	dt	dt/wt	pd/pw	dw/l	mw/l	
Fossil	<i>L. falconeri</i> (1)	BMNH-39736; Siwalik (India)				36.0			13.40	17.5	1.31				
	<i>L. falconeri</i>	SAG-VP-1/19; Sagantole (Ethiopia)	405.0 e			36.5	25.6	13.15	12.35	16.65	1.35		0.090	0.032	
	<i>L. cf. falconeri</i> (2)	IZAN 8024; Odessa (Ukraine)	315.0 e			32.2	21.0	13.2	11.50	15.87*	1.38		0.10	0.042	
	Leptoptilini gen. et sp. indet. (3)	BMNH-39741; Siwalik (India)		24.3											
	<i>L. titan</i> (4)	MGSNI 3313; Watoelang (Java, Indonesia)	372.0						12.30						0.033
	<i>L. richae</i> (5)	T-3604; Beglia (Tunisia)										1.31*			
	<i>Leptoptilos</i> sp. (6)	KNM-BN-002; Baringo (Kenya)	345.0 e	27.0 e					11.00 e						0.032 e
Recent	<i>E. asiaticus</i> M	IRSN 12386	352.0	22.2	13.7	24.0	18.4	9.15	9.60	10.8	1.13	0.62	0.068	0.026	
	<i>E. asiaticus</i> F	IRSN 42167	310.0 e; 340.0	21.2	14.0	22.5 e; 24.0	18.6	8.20 e; 8.80	9.20			0.66	0.072 (n=2)	0.026 (n=2)	
	<i>E. asiaticus</i> U	USNM 346193, 1 specimen after #, and 2 specimens after ##	309.0–351.0 e (n=4)	23.1; 23.8 e	13.8	24.0; 24.6 e	18.2	9.10	9.10	11.0	1.21	0.60	0.071	0.027	
	<i>E. senegalensis</i> M	IRSN 1922, MVZ 140361	346.0; 367.5	22.3; 23.3	14.0; 15.0	24.5; 25.9	18.3; 18.3	9.50; 9.75	9.30; 9.50	12.0	1.29	0.64 (n=2)	0.071 (n=2)	0.027 (n=2)	
	<i>E. senegalensis</i> F	IRSN 55843	332.0	20.9	13.2	23.2		8.35	8.80			0.63	0.070	0.025	
	<i>E. senegalensis</i> U	MRAC 91056A01, UCBL 1974, 1 specimen after #, and 2 specimens after ##	318.0–367.0 (n=5)	22.0; 23.5	13.8; 15.6	24.2–25.6 e (n=3)	17.6; 18.3	9.15; 9.15	9.20; 9.75	11.6; 11.9	1.24 (n=2)	0.65 (n=2)	0.069 (n=2)	0.026 (n=2)	
	<i>J. mycteria</i> U	MVZ 133932, 2 specimens after #, and 2 specimens after ##	294.0–349.0 (n=5)	25.5 e; 26.5 e		28.5 e; 29.0		11.50 e; 12.50 e	10.00 e				0.095 e (n=2)	0.040 e (n=2)	
	<i>L. javanicus</i> M	IRSN 12392	253.0	22.6	13.0	26.3	17.5	9.40					0.58	0.10	0.037
	<i>L. javanicus</i> F	IRSN 12391	257.0	21.8	13.8	25.5		8.85	9.60				0.63	0.099	0.034
	<i>L. javanicus</i> U	MVZ 137570, UCBL 1975, and 2 specimens after ##	221.5–287.0 (n=4)	20.5; 21.2	12.5; 13.8	23.8; 24.0	16.0; 18.4	9.25; 9.90	8.50; 8.80	11.2; 11.3	1.30 (n=2)	0.63 (n=2)	0.11 (n=2)	0.043 (n=2)	
	<i>L. dubius</i> M	FMNH 104387, IRSN 12395	326.5; 331.0	27.3; 29.0	17.0; 17.8	30.9; 32.3	23.4; 23.8	11.50; 11.90	11.65; 11.80	16.1	1.38	0.619 (n=2)	0.097 (n=2)	0.036 (n=2)	
	<i>L. dubius</i> F	IRSN 60379	291.5	26.6	16.3	29.1	20.9	10.75	10.80	15.0	1.39	0.61	0.10	0.037	
	<i>L. dubius</i> U	1 specimen after #, and 2 specimens after ##	267.0–335.0 (n=3)			32.0 e			12.00 e					0.098 e	
	<i>L. crumeniferus</i> M	IRSN 12396, MRAC 99049A13	239.0; 283.0	24.8; 24.9	15.7; 16.5	28.3; 28.4	19.7; 21.0	10.30; 10.95	10.00; 10.35	15.0	1.50	0.65 (n=2)	0.11 (n=2)	0.041 (n=2)	
	<i>L. crumeniferus</i> F	MRAC 98025A01	254.0	23.5	14.6	27.4	18.0	10.40	9.80	13.5	1.38	0.62	0.11	0.041	
<i>L. crumeniferus</i> U	MVZ 134058, 2 specimens after #, 2 specimens after ##, and 2 specimens after §	229.0–303.0 (n=5)	23.4	15.3	22.5–29.0 (n=3)	17.0–21.5 (n=3)		8.80–10.80 (n=5)	12.6–14.6 (n=3)	1.39 (n=3)	0.65	0.096 (n=3)	0.038		

dia) (1.8–3.0 Ma, age after Haarrhoff 1988), a species larger than any living Ciconiidae, and morphologically similar to living *Leptoptilos* spp. *L. falconeri* was initially based on two distal tibiotarsi, as well as one proximal and one distal tarsometatarsus (Milne-Edwards 1867–71: 450). Later completed and illustrated by Davies (1880), and Lydekker (1884,

1891), the record of *L. falconeri* was revised by Harrison (1974). *L. falconeri* is from then and hitherto left with the lectotype right distal tibiotarsus BMNH 39735, and four paratypes: the left distal tarsometatarsus BMNH 39736 (Fig. 1C), the left distal femur BMNH 39737, a proximal part of first phalanx of the wing major digit BMNH 39738, and the

Table 4. Measurements (in mm) of the pedal phalanges 1 of digits II and III of the extinct and living Leptoptilini. Abbreviations: pp1II, pedal phalanx 1 of digit II; pp1III, pedal phalanx 1 of digit III; pp1III and pp1IIII, total lengths; pp1IIImw and pp1IIImw, minimal widths medio-laterally. (1): previously *L. pliocenicus* (Zubareva 1948). # Measurements of extant species include independent data from Zubareva (1948). Remaining conventions are as in Table 1.

	Species	Specimen	lpp1II	pp1IIImw	pp1IIImw/ lpp1II	lpp1III	pp1IIImw	pp1IIImw/ lpp1III
Fossil	<i>L. falconeri</i>	F 516.23; Omo (Ethiopia)	53.5	7.00	0.13			
	cf. <i>L. falconeri</i>	URU-VP-1/45; Urugus (Ethiopia)				64.8	9.00	0.14
	<i>L. cf. falconeri</i> (1)	IZAN 6502; Odessa (Ukraine)				72.3	8.40	0.12
Recent	<i>E. asiaticus</i> M	IRSN 12386	48.0	4.65	0.097			
	<i>E. asiaticus</i> F	IRSN 42167	47.0	4.25	0.090			
	<i>E. asiaticus</i> U	USNM 346193	48.4	4.40	0.091			
	<i>E. senegalensis</i> M	IRSN 1922, MVZ 140361	44.7; 49.0	4.35; 4.65	0.096 (n=2)			
	<i>E. senegalensis</i> F	IRSN 55843	46.3	4.15	0.090			
	<i>E. senegalensis</i> U	1 specimen after #				49.5	7.60	0.15
	<i>L. javanicus</i> M	IRSN 12392	50.3	4.70	0.093			
	<i>L. javanicus</i> F	IRSN 12391	45.8	4.20	0.092			
	<i>L. javanicus</i> U	MVZ 137570	36.3	4.20	0.12			
	<i>L. dubius</i> M	FMNH 104387, IRSN 12395	54.5; 57.0	5.55; 5.70	0.10 (n=2)			
	<i>L. dubius</i> U	1 specimen after #				61.0	9.20	0.15
	<i>L. crumeniferus</i> M	IRSN 12396	48.0	5.15	0.11			
	<i>L. crumeniferus</i> U	MVZ 134058	50.2	5.40	0.11	51.0-60.0 (n=3)	6.1-8.5 (n=3)	0.13 (n=3)

left distal humerus BMNH 48435 (Harrison 1974). In addition to its large size, Harrison (1974) listed some morphological characters of *L. falconeri* in comparison with extant species in the genus, including the following for the tarsometatarsus: (1) greater distal extension of the trochlea metatarsi III relatively to the other trochleae; (2) trochlea metatarsi II displaced toward the plantar side. Given the figures (Harrison 1974: fig. 2), the second character does not appear to us to make *L. falconeri* fall outside the variation range of *Leptoptilos* spp. In addition the figure illustrating the first character (Harrison 1974: fig. 1) appears erroneous: the detailed illustration of the same fossil in Lydekker (1884: fig. 14) shows a different relative development of the trochleae, identical to that in extant species as well as in the Ethiopian fossil (Fig. 1B₄, C, D). Therefore, the size of the tarsometatarsus remains the only available criterion. The tarsometatarsus from SAG appears to be the largest known for *L. falconeri*, and so is the tibiotarsus from KB. The tibiotarsus from KB is most probably from a male, while it is more difficult to estimate the sex for the tarsometatarsus from SAG. The latter is associated with a medium sized tibiotarsus shaft for the species, and although the tarsometatarsus/tibiotarsus ratios can show some variation, the individual from KB had probably a substantially larger tarsometatarsus. There is no apparent difference in the robustness of tibiotarsi and tarsometatarsi between males and females of Leptoptilini (Tables 1–4). The carpometacarpus from KT also appears to be large, probably from a male, but is for now only tentatively referred to *L. falconeri*. As suggested above, the length values for the smallest individuals of *L. falconeri* should not be more than 25–30% smaller than in the largest fossils from Chad and Ethiopia, and the width or depth values not more than 15–20% smaller.

These estimations are rough, because the maximal values known for *L. falconeri* are derived from a small sample for now. Some caution is therefore required for specific assignments when the dimensions are not very distinctive.

Estimations of the size of *L. falconeri*.—The minimal circumference of the KB tibiotarsus is 56.8 mm. The equations of Campbell and Marcus (1992) indicate a body weight of about 20 kg corresponding to such a circumference for the category called “long legged” birds, which includes storks. *L. crumeniferus* can weigh up to around 9 kg, less than half the weight of the extinct species. As for the linear dimensions of the bird, the length of the largest bones is 25% (KB tibiotarsus) to 34% (SAG tarsometatarsus) greater than in the largest available *L. crumeniferus*. The latter can stand up to 1.52 m. It can be deduced that *L. falconeri* could stand up to about 2 meters. The KT carpometacarpus (cf. *L. falconeri*) is about 18% larger than the maximum available for *L. crumeniferus*. Thus, the ratios between this wing bone length and the length of the hindlimb bones seem slightly less in *L. falconeri* than in *L. crumeniferus*, suggesting for the former a proportionately slightly reduced wing, from which a minor limitation of its flying abilities can be inferred.

Comparisons with the other extinct Ciconiidae, and re-evaluation of some taxa.—Most of the Neogene fossil record of Ciconiidae consists of isolated fragments of limb elements, especially distal tibiotarsi and tarsometatarsi. Harrison (1974) described a new species (*L. siwalicensis*) and a new genus and species (*Cryptociconia indica*) from the same late Pliocene Siwalik locality as *L. falconeri* (dated 1.8–3.0 Ma, Haarhoff 1988), based on fossils initially attributed to

the latter species. The three resulting taxa were based on a total of only eight remains.

Leptoptilos siwalicensis Harrison, 1974 was based on the left proximal tarsometatarsus BMNH 39741 (holotype) and the paratype right distal tibiotarsus BMNH 39734. Harrison (1974) stated for the tarsometatarsus that in *L. siwalicensis* in comparison with the extant species: (1) the medial side of the proximal end was stouter; (2) the cristae hypotarsi were less elevated “posteriorly” (i.e., toward the plantar side); (3) the “anterior” (i.e. dorsal) ends of the cristae hypotarsi were more abrupt; (4) the muscle attachment situated at the latero-plantar edge of the proximal tarsometatarsus was larger. We find that all these discrete features are actually variable and can be found in extant *Leptoptilos* or *Ephippiorhynchus* species. Our re-identifications therefore rely on the diagnostic limb proportions of *Ephippiorhynchus* and *Leptoptilos* exposed above and on the general size so as to distinguish between species within genera. The holotype tarsometatarsus is attributable to either *Ephippiorhynchus* or *Leptoptilos*, based on its description as well as the illustrations. The paratype distal tibiotarsus is intermediate in proportions between *Ephippiorhynchus* and *Leptoptilos*, eventhough closer to the latter (Table 2). This was noticed by Harrison (1974) as a particular cranial development of the condyles. Therefore this distal tibiotarsus cannot be firmly assigned to *Leptoptilos*. In size, the two fossils can correspond (*contra* Harrison 1974, who had a small comparative sample) to either smaller (female) *L. falconeri*, or *L. dubius* (Table 2). *L. siwalicensis* is thus equivalent to *Ephippiorhynchus/Leptoptilos* sp., because there is no indication for the proximal tarsometatarsus that it is associated with more diagnostic material. *L. siwalicensis* should be referred to as *Leptoptilini* gen. et sp. indet.

Cryptociconia indica Harrison, 1974 was based on the holotype left distal tibiotarsus BMNH 48444. This case is the same as for the tibiotarsus attributed to the preceding species. The new genus *Cryptociconia* was proposed by Harrison (1974) on the basis of the following characters of the fragmentary distal tibiotarsus, in comparison with extant genera in the Ciconiidae: (1) caudal termination of the condylus medialis forming a more abrupt flange onto the shaft; (2) less projecting epicondylus medialis; (3) cranial portion of the condylus medialis relatively narrower. Again, these details show a great variability within large storks. In addition, the fragment is acknowledged by Harrison as damaged and eroded. The morphology of this fossil is not outside the variation range of the genera *Leptoptilos* or *Ephippiorhynchus*, and its proportions are diagnostic of *Leptoptilos* (Table 2). Consequently and on account of its size (Table 2), *Cryptociconia indica* can be considered as equivalent to *L. dubius/falconeri*, or *Leptoptilos* sp.

Fossils of *Leptoptilos dubius* are difficult to recognize because of the probable size overlap with *L. falconeri*. No smaller individual of possible *L. dubius*, which would be too small for *L. falconeri*, is reported in the Siwalik Hills. This

may indicate that most of the fossils would refer to *L. falconeri*, but this is hypothetical.

Leptoptilos pliocenicus Zubareva, 1948, from the early Pliocene of Odessa (Ukraine), was apparently ignored by Harrison (1974). The holotype material consists of an individual represented by mandibular fragments, a quadrate, a humerus, a carpometacarpus, a tarsometatarsus and a first pedal phalanx of the third digit. According to Zubareva (1948), the cranial fragments agree with extant *Leptoptilos* species—*L. crumeniferus* and *L. dubius* were examined—but the beak is narrower and more conical. The humerus shows only a few differences of detail from recent *Leptoptilos* species; however, the ends of the bone are missing, and this specimen is thus of limited interest. The carpometacarpus was said to be more robust, but the measurements show that it is within the variation range of extant species (Table 1). The tarsometatarsus was said to have a less straight shaft and its section to be more rectangular than in extant species. Several details were also reported in the shape of the trochleae, but all are very slight. The tarsometatarsus seems quite robust, from an estimation of its length, but some individuals of extant species reach the same values. The pedal phalanx is longer and more slender than in a small sample of extant *Leptoptilos* as well as in *L. falconeri* from Ethiopia (Table 4). This difference in proportions, however, does not seem to exceed a normal variation, and the large size would well correspond to the range of *L. falconeri*. On the whole, the characteristics of separate bones of *L. pliocenicus* listed by Zubareva (1948), other than size, are either very slight small scale details or better marked characteristics in the proportions, both actually in the variation range of extant species. But since the bones belong to a single individual, it appears that the bird had proportionately much more developed hind limbs than forelimbs, compared with the extant species (Zubareva 1948; Tables 1–4).

The fossils known hitherto for *Leptoptilos falconeri* are only from the hind limbs. This gap now becomes tentatively filled with the carpometacarpus of cf. *L. falconeri* from KT and the Ukrainian individual. The carpometacarpus of KT is not very large, so the African *L. falconeri* seems to have had relatively large hind limb bones. It is therefore most probable that *L. pliocenicus* is a synonym of *L. falconeri*. Zubareva (1948) stated that the two species bear some similarity, but that *L. falconeri* was larger. But since the dimensions of both can actually indicate a single species, considering the important individual and sexual size variability in osteological measurements for the species of *Leptoptilos* as shown above (see Tables 1, 3, 4), nothing precludes considering *L. pliocenicus* as equivalent to *L. cf. falconeri*.

Brodkorb (1985) reported a giant marabou stork of the genus *Leptoptilos* from the Plio-Pleistocene of Olduvai (Tanzania) beside a species similar in size to *L. crumeniferus*. The larger one could well be *L. falconeri*, but the material still needs to be published.

A proximal tibiotarsus from the early Pliocene deposits of Lothagam, Kenya (Apak Member, dated between 4.2 and 5.3

Ma) was identified as a large *Leptoptilos* sp. indet. (Harris and Leakey 2003; Table 2), but it is not clear whether it is distinct from *Ephippiorhynchus*.

In addition, a species close to *Leptoptilos crumeniferus* is present in the late Miocene deposits of Lothagam, northern Kenya (Upper Nawata Member, dated between 5.3 and 6.5 Ma; McDougall and Feibel 2003). Rich (1972, 1974) identified a right distal tibiotarsus and a left distal tarsometatarsus (not right as indicated erroneously in Rich 1972 and Harrison 1974) of a marabou stork from the upper Miocene of the Beglia Formation (Bled ed Douarah, Tunisia) as *L. cf. falconeri*, but these fossils are much smaller than in this species. The morphological peculiarities noticed by Rich (1972) in the shape of both fragments are not diagnostic of *L. falconeri*. Harrison (1974) recognized the inconsistency with the latter, and considered the Tunisian fossils sufficiently different from *L. crumeniferus* to name a new species, *L. richae* (the tibiotarsus being the holotype). The figures in Rich (1972) show that the proportions of these bone ends are typical of *Leptoptilos* as opposed to *Ephippiorhynchus* (Tables 2, 3). *L. richae* Harrison, 1974, however, differs slightly from extant species of *Leptoptilos* in the morphology of the distal tibiotarsus and the distal tarsometatarsus, essentially by two characters (see Rich 1972: figs. 8, 9): (1) the trochlea metatarsi II of the tarsometatarsus in dorsal view is apparently less angular medio-distally (but not as much as on the less accurate figure in Harrison 1974: fig. 1); (2) the distal tibiotarsus shows a torsion, with the condylus medialis displaced cranially relatively to the condylus lateralis in distal view. *L. richae* and *L. crumeniferus* are similar in general size. *L. richae* thus remains a valid species and differs from *L. falconeri* in the proportions of the bone ends and the general size.

Leptoptilos titan Wetmore, 1940 was based on an almost complete tarsometatarsus from the Pleistocene of Watoealang (Java, Indonesia). It clearly belongs to the genus *Leptoptilos*, and is characterized by its large size, exceeding that of the largest extant species *L. dubius*. The deep anterior groove of the shaft and the robustness (Table 3) are not inconsistent with extant *Leptoptilos* species (*contra* Wetmore 1940). The author did not compare the fossil with *L. falconeri*. Both may well represent a single lineage, but given the time difference, and until more material is known, the name *Leptoptilos titan* shall be retained for the Javan specimen.

From the upper Miocene deposits of northern Pakistan, a distal femur was tentatively referred to *Leptoptilos siwalikensis* [sic = *L. siwalicensis*] Harrison, 1974 (Harrison and Walker 1982). This needs to be re-evaluated, and it is not clear whether extant species of *Leptoptilos* or even *Ephippiorhynchus* can be excluded.

From the same deposits was described *Ephippiorhynchus pakistanensis* Harrison and Walker, 1982. Incidentally, the distal tibiotarsus involved and the tentatively referred distal humerus are similar in size and shape to *E. asiaticus*, and the small osteological differences seem unreliable given the variation. *E. pakistanensis* may probably be considered as an

ancestral *E. asiaticus* or as ancestral to both the latter and *E. senegalensis*.

Hill and Walker (1979) described a partial skeleton of a marabou stork from the Miocene (ca. 11.5 Ma) of Ngorora (Baringo, Kenya). The proportions and the morphology point to the genus *Leptoptilos*, but some characteristics make it distinct from all the extant species. The general size is smaller than in *L. falconeri*, larger than *L. crumeniferus*, and the inter-segment proportions differ from those of *L. dubius* (Tables 2, 3). These differences are not surprising given its old age. Hill and Walker preferred to leave it as *Leptoptilos* sp. In addition, the tibiotarsus shaft presents a strong narrowing towards the distal part, which could actually be a pathology. This species is in need of a more precise identification, it may represent a new species, but clearly differs from *L. falconeri*.

Miller et al. (1997) identified a distal tibiotarsus as *Leptoptilos* sp., from Wadi Moghara (early Miocene, Egypt). It is a species similar in size to a small *L. crumeniferus*, and could well be ancestral to it. These authors also indicate that this fossil bears similarities with the corresponding bone from Beglia, now assigned to *L. richae*, especially because of the torsion of the distal end. A close relative of *L. richae* may thus be traced back to the early Miocene, but a more detailed comparison is needed to assess it.

Ballmann (1987) identified a fragment of a coracoid from Sahabi (Mio-Pliocene boundary, Libya) as *Leptoptilos* sp., and found it slightly smaller than *L. crumeniferus*. An ulna shaft and a tibiotarsus shaft, from the Pleistocene of Java, were identified as *L. cf. dubius* by Weesie (1982). Further study and measurements of the Javan remains could probably reveal if these could actually belong to small individuals of *L. titan*.

Several other extinct Ciconiidae have been described, from the Eocene to the Pleistocene (Brodkorb 1963; Olson 1985; Haarhoff 1988; Bocheński 1997; Miller et al. 1997). Most were assigned to extinct genera. Several of them need a re-evaluation. *Ciconiopsis antarctica* Ameghino, 1899 was described from the early Oligocene of Argentina. It requires re-study before it can be accepted as a Ciconiidae (Olson 1985). The holotype of *Amhipelargus majori* Lydekker, 1891, from the lower Pliocene of Samos (Greece), is a distal tibiotarsus. This large Ciconiidae is still smaller than *L. falconeri*, and the genus certainly deserves a re-evaluation. *Prociconia lydekkeri* Ameghino, 1891 from the upper Pleistocene of Brazil, and *Propelargus olseni* Brodkorb, 1963 from the Miocene of Florida, both require revision, and their status as Ciconiidae is not certain (Haarhoff 1988). *Pelargosteon tothi* Kretzoi, 1962 from the lower Pleistocene of Romania was said to be close to *Leptoptilos*, but according to Cheneval (1984) the fragments of sternum and furcula, poorly described and not illustrated, do not allow to establish the relationships with other Ciconiidae. "*Cygnus*" *bilinicus* Laube, 1909 from the lower Miocene of Czech Republic, has been re-identified as a Ciconiidae, but the bad preservation state of the fossils does not allow a more precise identifica-

tion (Mlíkovský and Švec 1989). Moreover, the carpometacarpus illustrated is much smaller (107 mm length) than in *L. falconeri*.

Two extinct genera belong to the Leptoptilini. *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930 from the Eocene of Fayum (Egypt) is the oldest known Ciconiidae. An Oligocene distal tibiotarsus tentatively assigned to the species displays morphological traits that separate it from extant genera (Rasmussen et al. 1987). *Grallavis edwardsi* (Lydekker, 1891), from the early Miocene of France, initially placed in the genus *Propelargus*, and assigned to the new genus by Cheneval (1984), is a Ciconiidae that bears similarities with *Ephippiorhynchus*. It is smaller than *E. senegalensis*, and thus much smaller than *L. falconeri*. Mlíkovský (2003) synonymized *Grallavis* with *Palaeoephippiorhynchus*, on a rather weak basis because little of the skeleton is known simultaneously for both the genera. However, this author still considered the species involved as generically distinct from the living Leptoptilini.

Many species of Ciconiini, thus distinct from the Leptoptilini, have been described in the Old World. In addition, most of them are much smaller than *L. falconeri*: *Ciconia sarmatica* Grigorescu and Kessler, 1977 (upper Miocene of Romania), *C. stehlini* Janossy, 1992 (lower Pleistocene of Hungary), *C. nana* (De Vis, 1888) (late Pleistocene of Australia), *C. minor* Harrison, 1980 (lower Miocene of Kenya), *C. lucida* Kurochkin, 1982 (middle Pliocene of Mongolia) (Grigorescu and Kessler 1977; Harrison 1980; Kurochkin 1982; Haarhoff 1988; Janossy 1992). *C. kahli* Haarhoff, 1988 (early Pliocene of South Africa), is smaller than *L. falconeri*, but for the tarsometatarsus, the size is very close to the smallest individuals of the latter. This indicates that the proportions between the segments differ in the two genera (Haarhoff 1988). Other differences define *C. kahli* as distinct from *Leptoptilos*, and the material includes a partial skeleton, which renders the generic assignment reliable. Haarhoff (1988), however, added that it could be a distinct lineage (an extinct genus) within the Ciconiidae. *C. gaudryi* Lambrecht, 1933 (lower Pliocene of Pikermi, Greece) was based on the holotype humerus figured in Gaudry (1862–67: pl. 59: 12). It actually lies in the range of size of the smallest individuals of *L. falconeri*. However, the illustration is insufficient to ascertain its identification, even as a stork, and the fossil needs to be re-studied. In the New World, all the confidently identified extinct Ciconiidae belong to the tribes Mycteriini or Ciconiini (Olson 1991). In addition, most of them are much smaller than *L. falconeri*. Only the largest species, *Ciconia maltha* Miller, 1910 (late Neogene, North America), reaches a size similar to *C. kahli*. Like the latter, it shows a proportionately larger tarsometatarsus than in *Leptoptilos*. *C. maltha* has a good representation which clearly shows a smaller size (Haarhoff 1988) compared with *L. falconeri*.

The following identifications and synonymies are proposed as follows according to the identification of the new material from Africa and the observations made above.

Systematic paleontology

Class Aves Linnaeus, 1758

Order Ciconiiformes Bonaparte, 1854

Family Ciconiidae Gray, 1840

Tribe Leptoptilini Kahl, 1971

Genus *Leptoptilos* Lesson, 1831

Leptoptilos falconeri (Milne-Edwards, 1868)

pars *Argala Falconeri*; Milne-Edwards 1867–71: 450.

pars *Argala Falconeri*; Davies 1880: 23, 24, 27, fig. 4.

pars *Leptoptilos falconeri*; Lydekker 1884: 139–141, figs. 1, 9, 12, 14.

Argala falconeri; Harrison 1974: 42.

Leptoptilos falconeri; Harrison 1974: 42, 43, 49, figs. 1, 2.

Leptoptilos falconeri; Harrison 1974: 45.

Ephippiorhynchus sp. nov.; Brunet et al. 2000: 207.

very large species of *Jabiru*; Brunet et al. 2000: 205.

Leptoptilos sp. B; Louchart et al. 2004: 413, 414, 418, fig. 7.

Emended diagnosis.—Larger than *L. dubius*, but overlapping with this species for smaller individuals. Morphology and intra-segment proportions otherwise similar to those in *L. dubius* or *L. crumeniferus*. Inter-segment proportions indicating probably more developed hind limbs relative to forelimbs than in extant species.

New material, localities, and age.—An incomplete left tibiotarsus from the early Pliocene of Kossom Bougoudi (Chad), KB3-97-161, comprising part of the distal end and all the shaft (Fig. 1A₁–A₃), probably from a male; a distal part of right tibiotarsus shaft from the early Pliocene of Sagantole (Ethiopia), SAG-VP-1/19 (Fig. 1B₁), associated with a partial left tarsometatarsus, SAG-VP-1/19, comprising the distal end and most of the shaft (Fig. 1B₂–B₇)—these two elements are from a single individual; a left distal tibiotarsus from the late Pliocene of Omo (Ethiopia), OMO-122-76-367 (Fig. 1G₁–G₃), and a right first pedal phalanx of digit II probably from a female, also from the late Pliocene of Omo, F-516-23 (Fig. 2A₁–A₃).

cf. *Leptoptilos falconeri* (Milne-Edwards, 1868)

cf. *Leptoptilos* sp. B; Louchart et al. 2004: 413, 414, 418, fig. 8.

Material, localities, and age.—A proximal half of a left carpometacarpus from the late Pliocene of Koro Toro (Chad), KT13-96-504, with part of the proximal end, and a distal half of a left carpometacarpus, KT13-98-004, with an almost complete distal end (Fig. 2B₁, B₂ and C₁, C₂)—these two elements almost certainly come from a single carpometacarpus, and the total length can be reconstructed; a right distal tibiotarsus from Urugus (early Pliocene, Ethiopia), URU-VP-1/15 (Fig. 1F); a left distal tibiotarsus from Urugus, URU-VP-1/28 (Fig. 1E₁, E₂); a left first pedal phalanx of digit III from Urugus, URU-VP-1/45 (Fig. 3A₁), associated with a 12th vertebra (i.e., 10th after the atlas and axis), URU-VP-1/45 (Fig. 3A₂, A₃)—these two elements are from a single individual. The 12th vertebra URU-VP-1/45 is about 55 mm long and 45 mm wide.

Table 5. A simplified synopsis of the temporal and spatial distribution of the Leptoptilini based on this study and data from Haarhoff (1988), Tyrberg (1998), and Walter Boles (personal communication 11.11.2004).

Age	New World	Palaearctic	Oriental	Ethiopian	Australasian
Holocene / Recent	<i>Jabiru mycteria</i>		<i>Leptoptilos dubius</i> <i>Leptoptilos javanicus</i> <i>Ephippiorhynchus asiaticus</i>	<i>Leptoptilos crumeniferus</i> <i>Ephippiorhynchus senegalensis</i>	<i>Ephippiorhynchus asiaticus</i>
Pleistocene	<i>Jabiru mycteria</i>	<i>Ephippiorhynchus asiaticus</i>	<i>Leptoptilos titan</i> <i>Leptoptilos dubius/titan</i>	<i>Leptoptilos</i> sp.	<i>Ephippiorhynchus asiaticus</i>
Pliocene		<i>Leptoptilos falconeri</i>	<i>Leptoptilos falconeri</i> <i>Leptoptilos dubius/falconeri</i> Leptoptilini gen et sp. indet.	<i>Leptoptilos falconeri</i> Leptoptilini gen et sp. indet.	<i>Ephippiorhynchus asiaticus</i>
late Miocene		<i>Leptoptilos richae</i>	<i>Ephippiorhynchus</i> sp. Leptoptilini gen. et sp. indet.	<i>Leptoptilos</i> sp.	
middle Miocene					
early Miocene		<i>Grallavis edwardsi</i>		<i>Leptoptilos</i> sp.	

Leptoptilos cf. *falconeri*

Leptoptilos pliocenicus; Zubareva 1948: 114–125, 135–136, figs. 1–6.

Material, locality, and age.—All from the early Pliocene of Odessa (Ukraine): upper mandibular fragment IZAN 8025, lower mandibular fragments IZAN 7042 and IZAN 8026, incomplete quadrate IZAN 7042, right humerus without ends IZAN 6939, almost complete left carpometacarpus IZAN 8060, left tarsometatarsus without proximal end IZAN 8024, and first pedal phalanx of the third digit IZAN 6502. All these elements belong to a single individual.

Leptoptilos sp. indet.

Cryptociconia indica; Harrison 1974: 48–49, fig. 4.

Material, locality, and age.—Left distal tibiotarsus from the late Pliocene deposits of the Siwalik Hills of Uttar Pradesh (India): BMNH 48444.

Leptoptilini gen et sp. indet.

Leptoptilos siwalicensis; Harrison 1974: 46, 47, 49, fig. 3.

Leptoptilos siwalikensis; Harrison and Walker 1982: 53, 59, pl. 1: B–F.

Material, locality, and age.—All from the late Pliocene deposits of the Siwalik Hills of Uttar Pradesh (India): left proximal tarsometatarsus BMNH 39741, right distal tibiotarsus BMNH 39734, and left distal femur BMNH 11695.

Discussion

The sexual size dimorphism and individual size variation are important in the living large Ciconiidae, tribe Leptoptilini. The allocation of the new fossil material from Chad and Ethiopia to *L. falconeri*, together with this variation, altogether make it possible to propose some synonymies in this tribe, resulting in a better assessment of the past biological diversity for this group (Table 5). The very large extinct species *L. falconeri* was represented during the Pliocene in the Northern half of Africa, South Asia (Siwalik Hills, India, late Pliocene) and probably also in Ukraine. It was present in Africa from the earliest Pliocene (Kossom Bougoudi, Chad; Sagan-tole, Ethiopia) to the latest Pliocene (Omo, Ethiopia). It is also probably represented in Urugus (early Pliocene, Ethio-

pia), Koro Toro (late Pliocene, Chad), as well as possibly the late Miocene of Kenya. The origin of the species may lie in the middle Miocene. Another species, similar in size to the living *L. crumeniferus*, was already present in the early Miocene of Egypt. Subsequently, at least two species also similar in size to *L. crumeniferus* are present in several African localities, including at least one extinct form, *L. richae*, in the Miocene.

The diversity of the Leptoptilini has been overestimated, and *L. falconeri* appears to remain the only valid extinct species of this tribe in the Pliocene. *L. falconeri* is an example of recent link between Eurasia and Africa, at the specific level. Today, only five non-passerine species of the Ethiopian region also live in the Oriental region. *L. falconeri* is unknown in the southern part of Africa, where another large stork, *Ciconia kahli*, was represented in the Pliocene.

A hypothesis that *L. falconeri* is ancestral to *L. dubius* cannot be completely excluded, the latter being difficult to evidence in the Pliocene. However, the observation of different intersegment proportions between the two species, especially considering the ratio hind limb length/forelimb length, and not only a general body size difference, does not support this hypothesis. With its slightly reduced forelimbs, *L. falconeri* is unlikely to be the direct ancestor of *L. dubius*. The reasons for the extinction of *L. falconeri* remain enigmatic. It is not yet possible to deduce which of the living species is closer to *L. falconeri* in terms of ecology. Today, the species of *Leptoptilos* forage in rather open country, from marshland to dry savanna, and typically need trees and some freshwater in proximity for nesting (Elliott 1992). *L. falconeri* weighed up to 20 kg and probably stood up to 2 m, which makes it one of the largest flying birds. Its probable relatively slightly reduced forelimbs are allometrically congruent with a slight limitation in flight abilities for a bird of large size and mainly terrestrial habits.

Acknowledgements

We are grateful to the participants in the Middle Awash research project for unearthing the bird material of Sagan-tole and Urugus in Ethiopia, and the National Museum of Ethiopia, Addis Ababa. We thank the

Chadian Authorities (Ministère de l'Éducation Nationale de l'Enseignement Supérieur et de la Recherche, Université de N'Djaména, CNAR) for their logistic support. We extend gratitude for their support to the French Ministries, Ministère Français de l'Éducation Nationale et de la Recherche (Université de Poitiers, CNRS), Ministère des Affaires Étrangères (DCSUR, Paris, and SCAC N'Djaména), to the Région Poitou-Charentes, to the Armée Française (MAM and Epervier) for logistic support and to all the participants of the Mission Paléo-anthropologique Franco-Tchadienne for the researches in Chad. We are also grateful to the people in charge of the osteological bird collections examined: Carla Cicero and the late Ned Johnson (MVZ, Berkeley, USA), James Dean (USNM, Washington, D.C., USA), David Willard (FMNH, Chicago, USA), Georges Lenglet (IRSN, Brussels, Belgium), Michel Louette (MRAC, Tervuren, Belgium), and Christine Lefèvre (Anatomie Comparée, Paris, France). We thank Walter Boles and an anonymous reviewer for their comments. A.L. would like to thank Thomas A. Stidham for helpful discussions, F. Clark Howell, and all the Laboratory for Human Evolutionary Studies for their support, and Irina Ivassioutine for her help in translating Ukrainian and Russian articles.

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