



A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia)

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Fossils of the genus *Leptoptilos* from the Pleistocene of Liang Bua, Flores, Indonesia, belong to a new species of giant marabou stork, *Leptoptilos robustus* sp. nov. This giant bird, estimated at 1.80 m in length, was similar in dimensions to extant *Leptoptilos dubius*, except for the tibiotarsus. The thick cortical bone wall of the tibiotarsus and the estimated weight of 16 kg imply a reduced flight capability. Osteological and biometric characters suggest that *L. robustus* is most closely related to *L. dubius*. An evolutionary lineage is proposed in which a volant *L. dubius*-like ancestor in the Middle Pleistocene evolved into the Late Pleistocene *L. robustus* on Flores, with a concomitant reduction of the ability to fly and an increase in body size. The large body size and terrestrial lifestyle of *L. robustus* are responses to an unbalanced, insular environment with abundant prey items and a lack of mammalian carnivores, and emphasize the extraordinary nature of the *Homo floresiensis* fauna.

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ADDITIONAL KEYWORDS: extinction – fossil bird – *Homo floresiensis* – island fauna – South-East Asia.

INTRODUCTION

The Liang Bua cave on the island of Flores, Indonesia, has yielded numerous vertebrate fossils of a limited number of genera from the Late Pleistocene and Holocene, including a large number of bird bones. The cave received worldwide fame through the finding of a new species of diminutive hominin, *Homo floresiensis* Brown *et al.*, 2004 (see also Morwood *et al.*, 2004, 2005). The remains of *H. floresiensis* are associated with the dwarfed proboscidean *Stegodon florensis insularis* Van den Bergh *et al.*, 2008, the giant rats *Papagomys armandvillei* (Jentink, 1892) and *Papagomys theodorverhoeveni* Musser, 1981, smaller rats, macrochiropterans, Komodo dragon *Varanus komodoensis* Ouwens 1912, and birds (Van den Bergh *et al.*, 2009). Both *H. floresiensis* and *S. florensis insularis* are only present in the Pleistocene deposits of the cave, and are

conspicuously absent from the Holocene sediments (Morwood *et al.*, 2005).

Separated from the continental Sunda shelf by a deep body of water at all times, Flores has always been hard to reach. The isolated position of the island is not only reflected in the limited number of species present, but is also evident from the unbalanced nature of the vertebrate fauna, which contains only some of the clades found on the mainland, and lacks specific groups such as perissodactyls and mammalian carnivores (Van den Bergh *et al.*, 2009; De Vos, Van den Hoek Ostende & Van den Bergh 2007). Typical changes in morphology ensued, the most prominent being the dwarfing and gigantism of large and small mammals, respectively, that is, they follow the ‘island rule’ (Foster, 1964; Van Valen, 1973; Lomolino, 1985). In view of the highly endemic nature of the Pleistocene fauna, Flores is considered a hotspot of insular evolution.

The Liang Bua sequence is unique in that it covers 95 000 years of insular evolution in South-East Asia,

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including the Pleistocene–Holocene transition. Avian fossils are distributed throughout the sediments (Van den Bergh *et al.*, 2009) and thus provide a unique sequence of the Late Pleistocene to Holocene avifauna. In this paper, we present the first description of avian fossils from Liang Bua, representing an endemic species of giant marabou stork that formed part of the natural environment of *H. floresiensis* and illustrates the extraordinary nature of Late Pleistocene Flores.

GEOLOGICAL SETTING

Liang Bua is a limestone cave in western Flores, Indonesia (Fig. 1A, B). It is located approximately 13 km north-west of Ruteng, the capital of the Manggarai Regency. The cave (Fig. 1C) is 30 m wide and 25 m high at the entrance, and was formed in Miocene limestone as an underground cavern by karst dissolution (Morwood *et al.*, 2004).

Within the cave, 11 sectors (I–XI in Fig. 1C) have been excavated. Sectors VII and XI were excavated until bedrock was reached at a depth of approximately 11 m (Morwood *et al.*, 2005). An overview of the stratigraphy of sectors VII and XI is given in Figure 2; for a more detailed analysis, see Westaway *et al.* (2010) and Roberts *et al.* (2010). The uppermost 3.7 m of Sector XI constitute a complex of Holocene deposits, indicated by Layers A–M in Figure 2. These layers document the arrival of *Homo sapiens* at 11 kya and a number of faunal introductions (pigs, macaques, civet cats, and cattle), as well as local extinctions (Van den Bergh *et al.*, 2009). The Holocene deposits are separated from underlying Pleistocene sediments by a distinctive layer of tuffaceous silts, indicated as Layers Na–d in Figure 2. The layers of tuffaceous silts are dated at 17–11 kya (Morwood *et al.*, 2004; Van den Bergh *et al.*, 2009) and are volcanic in origin. The Pleistocene sediments, indicated by Layers O–X in Figure 2, were deposited in pools of standing water and show uncommon evidence of strong flow (Morwood *et al.*, 2005). Evidence for *S. florensis insularis* and *H. floresiensis* occurs throughout the Pleistocene sequence until just below the tuffaceous silt layers. Recent excavations at Liang Bua have indicated an upper age limit for the *H. floresiensis* fauna of 17 kya and that its disappearance coincided with a volcanic eruption (Van den Bergh *et al.*, 2009).

MATERIAL AND METHODS

Sectors were excavated by removing sediment from 100 mm spits (or by stratigraphical unit, whichever was smaller), and the positions of all bones, stone artefacts, pieces of pottery, and charcoal samples were plotted. Large bones found by the excavators were

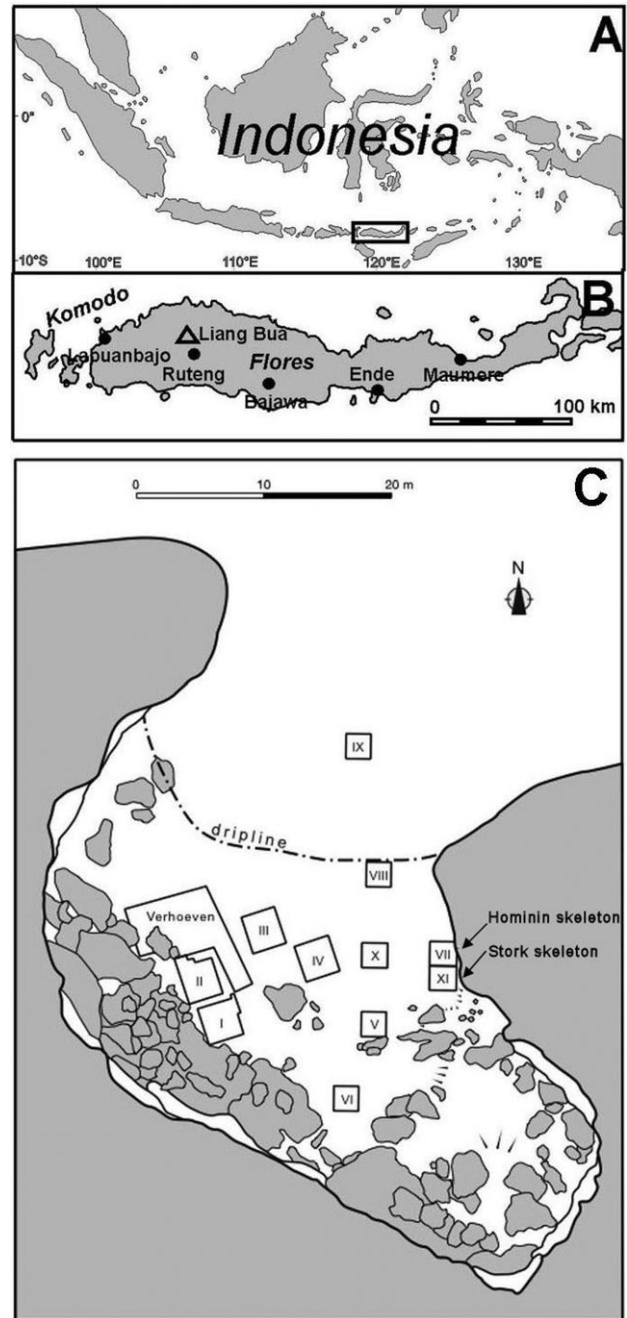


Figure 1. Map of South-East Asia, showing (A) the location of Flores within Indonesia and (B) the location of Liang Bua Cave in western Flores. (C) is a map of the excavated sectors within Liang Bua. Sector VII/XI is located against the eastern wall of the cave. A and B adapted from van den Hoek Ostende *et al.* (2007), C is taken from Morwood *et al.* (2005) and reprinted with permission.

recorded in three dimensions to permit accurate spatial and temporal distributions to be determined throughout the deep stratigraphical sequences. All the deposits were first dry-sieved and subsequently

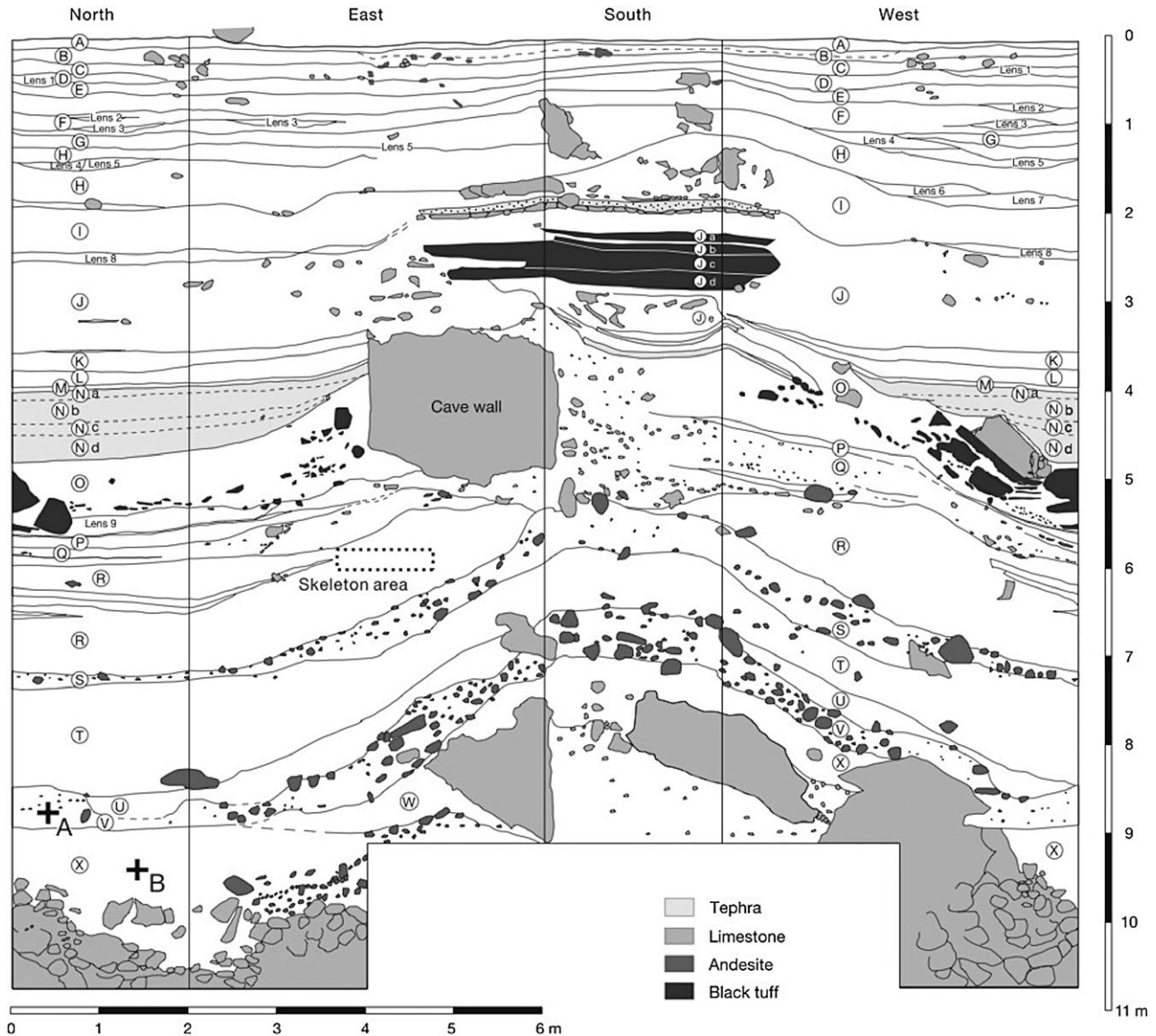


Figure 2. Stratigraphical sequence of the Sector VII/XI trench. Remains from *Leptoptilos robustus* sp. nov. were retrieved from Sector XI, spits 43–47, which correspond to Layers O–P. The white tuffaceous layer is indicated by Na-d and has been dated at 11–17 kya. From Morwood *et al.* (2005), reprinted with permission.

wet-sieved at a mesh width of 2 mm. Faunal remains were then placed in plastic bags, and labelled with spit and stratigraphical information. The vertebrate collection is stored at the National Centre for Archaeology, Jakarta, Indonesia. Parts of the vertebrate collection are under study in the Nationaal Natuurhistorisch Museum Naturalis, Leiden, and papers have appeared on the *Stegodon* remains (Van den Bergh *et al.*, 2008) and the fossil insectivores (Van den Hoek Ostende, van den Berg & Due, 2007; Zijlstra, Van den Hoek Ostende & Due, 2008).

The avian remains documented herein were retrieved from Sector XI, which is directly adjacent to

Sector VII (Fig. 1C) and lies near the east wall of the cave. The bones were collected from a depth of 4.25–4.70 m (spits 43–47), which corresponds to Layer O of the Pleistocene sediments (Fig. 2), a slanted horizon of clayey silts that is located below the tuffaceous silts. All the bones were found within the same sector and are of the same body size. No remains of other large-bodied birds have been found within the same sector. Therefore, the remains in all likelihood belong to one individual. Spits 42, 43, and 46 have yielded bone remains of *H. floresiensis* (Morwood *et al.*, 2005). Thus, the avian remains are directly associated with the *H. floresiensis* fauna.

The avian remains belong to a large ciconiiform bird, and consist of a distal left ulna, proximal left carpometacarpus, distal left tibiotarsus, and a left femur. The ossified pons supratendineus, the fusion of the astragalus to the tibia, and the smooth surface of the bones indicate that the material comes from an adult individual. The bones were morphologically and biometrically compared with representatives of all extant species of *Leptoptilos* and *Ephippiorhynchus* from the Nationaal Natuurhistorisch Museum Naturalis in Leiden (prefix RMNH), the Institut Royal des Sciences Naturelles de Belgique in Brussels (prefix IRSN) and the Natural History Museum in London (prefix NHM) (Appendix 1), including *Ephippiorhynchus asiaticus asiaticus* (Latham, 1790) (RMNH 106117), *Ephippiorhynchus asiaticus* (Latham, 1790) (RMNH 5528, IRSN 12385, IRSN 12386, IRSN 12388, IRSN 12389, IRSN 42165, IRSN 42167, IRSN 42249, NHM 1854.4.6.4, NHM 1859.5.29.2), *Ephippiorhynchus senegalensis* (Shaw, 1800) (NHM 1868.3.21.26), *Leptoptilos crumeniferus* (Lesson, 1831) (RMNH 5995, RMNH 4334, IRSN 12396, IRSN 17115, IRSN 1711Y, IRSN 41570, IRSN 55844, NHM 1866.12.30.23, NHM S/1952.3.133, NHM S/1952.3.182), *Leptoptilos dubius* (Gmelin, 1789) (RMNH 106118, IRSN 12394-95, IRSN 60379, NHM 1851.11.10.53, NHM 1845.1.12.290, NHM S/1952.1.104), and *Leptoptilos javanicus* (Horsfield, 1821) (RMNH 106120, RMNH 1061119, IRSN 12391-93, IRSN 18523, IRSN 48289). Because of sexual dimorphism in size, care was taken to include both males and females of each species in the sample. *Jabiru mycteria* (Lichtenstein, 1819) is not included in the analysis because of its distinctively different geographical range from South America to Mexico.

Comparisons with fossil material (Appendix 2) were made with *L. cf. dubius* from the Pleistocene of Java (RMNH 1490 and RMNH 1491), *Leptoptilos falconeri* (Milne-Edwards, 1868) from the Pliocene of Siwalik, India (NHM 39735 and NHM 39737), *Leptoptilos siwalicensis* Harrison, 1974 from the Pliocene of Siwalik, India (NHM 39734), and *Leptoptilos* sp. from the Pliocene of Siwalik, India (NHM 48444). Louchart *et al.* (2005) identified *L. siwalicensis* as *Leptoptilini* gen. et sp. indet. However, *L. siwalicensis* is retained here because of the observed differences between the two tibiotarsi from the Siwalik that justify separation at the species level. No comparison could be made with *Leptoptilos titan* Wetmore 1940, from Java. This species is known from a tarsometatarsus only. Because this element is unknown for the Flores marabou stork, direct comparisons between these huge stork species are impossible.

All measurements were taken with sliding callipers according to Von den Driesch (1976). Selected measurements are presented in scatter plots (Figs 4, 6, 8,

10). Morphological nomenclature follows Baumel & Witmer (1993). External and internal diameters of bones in cross-sections were measured using ImageJ (version 1.41, <http://rsbweb.nih.gov/ij/index.html>, National Institutes of Health).

The following characters identify the tibiotarsus, femur, ulna, and carpometacarpus from Liang Bua as representative of *Leptoptilini* within *Ciconiidae*: the large size, the straight tibiotarsal shaft, the medial location of the sulcus extensorius and pons supratendineus on the tibiotarsus, a prominent tubercle laterodistal of the pons supratendineus on the tibiotarsus, and the pneumatic foramen on the cranial side of the proximal femur. The family *Ciconiidae* has been traditionally defined on the basis of several morphological and behavioural traits of recent birds (Kahl, 1971, 1972; Wood, 1984) and is comprised of three tribes, that is, the *Leptoptilini*, *Ciconiini*, and *Mycteriini*. Several authors have described skeletal characters as well as inter-segment proportions as criteria for distinguishing the three tribes (Cheneval, 1984; Wood, 1984; Haerhoff, 1988; Louchart *et al.*, 2005). However, a study by Slikas (1997) on mitochondrial cytochrome *b* sequences and nuclear DNA–DNA hybridization suggests that the *Leptoptilini* constitute a paraphyletic group. The discrepancy between molecular and morphological data calls for a thorough systematic revision of the *Ciconiidae* combining internal and external morphology with molecular datasets. As such, a revision goes beyond the goal of our contribution, and we provisionally adopt the traditional arrangement of the *Ciconiidae* in three tribes.

DESCRIPTION AND COMPARISON

CARPOMETACARPUS

The left carpometacarpus (LBA-XI-01; Fig. 3) consists of the proximal half of the os metacarpale majus and the trochlea carpalis. Greatest length = 75.1 mm; proximal width = 25.6 mm; proximal depth = 18.2 mm. The os metacarpale alulare with processus extensorius and os metacarpale minus are missing. Ventrally within the shallow fossa infratrochlearis lies a distinct and large (diameter of 2 mm) pneumatic foramen. In comparison with recent *Leptoptilini*, we found such a foramen only to be present in the genus *Leptoptilos*. The processus pisiformis is damaged. The trochlea carpalis is cranially very shallow, almost flat, but deepens caudally. In dorsal view, the ventral rim of the trochlea carpalis protrudes more from the shaft of the bone than the dorsal one and fuses with the central shaft more distally than the dorsal rim. The fovea carpalis caudalis at the distal end of the trochlea carpalis is

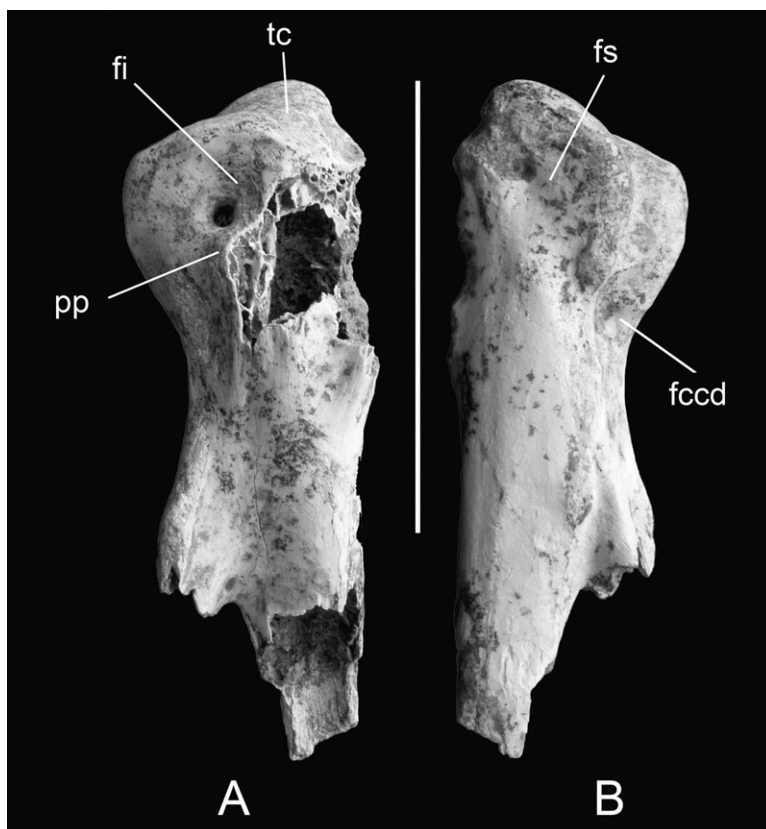


Figure 3. *Leptoptilos robustus* sp. nov., proximal left carpometacarpus (LBA-XI-01). A, ventral view; B, dorsal view. Abbreviations: fccd, fovea carpalis caudalis; fi, fossa infratrochlearis; fs, fossa supratrochlearis; pp, processus pisiformis; tc, trochlea carpalis. Scale bar = 50 mm. Photographs by E. Kruidenier.

marked, although not very deep. The morphology of the trochlea carpalis was similar to that observed in extant Leptoptilini.

Figure 4 shows the proximal width and the proximal depth of the Liang Bua specimen and carpometacarpus of extant Leptoptilini. Note that the proximal width of the Liang Bua carpometacarpus is lower because the processus extensorius is missing. The proximal depth of the Liang Bua carpometacarpus falls within the range of the largest species of extant Leptoptilini, *L. dubius* (Fig. 4), suggesting that the carpometacarpus is as a whole likely to be similar in size to *L. dubius*.

ULNA

The fragment of the left ulna (LBA-XI-02) consists of the distal articulation and a small part of the shaft (Fig. 5). Greatest length = 120.5 mm; distal width = 24.8 mm; distal depth = 21.9 mm; minimum width of the shaft = 14.4 mm; minimum depth of the shaft = 15.3 mm. In dorsal view, a distinct foramen is present in the incisura tuberculi carpalis between the

tuberculum carpalis and the condylus ventralis ulnae. A similar foramen was observed in all extant *Leptoptilos* species, but not in *Ephippiorhynchus*. The tuberculum carpalis is pronounced and rectangular in ventral view. In comparison with recent *Leptoptilos* and *Ephippiorhynchus*, the tuberculum carpalis attains a triangular shape in the latter, whereas a more elongated and rectangular shape was observed in *Leptoptilos*. The condylus ventralis ulnae is pointed and projects further distally than the condylus dorsalis ulnae, which is flattened and wide. In extant *Leptoptilos*, the tuberculum ventralis ulnae is similarly pointed, although less elevated, whereas in extant *Ephippiorhynchus* the tuberculum ventralis ulnae is even less pronounced. The external ridge of the condylus dorsalis ulnae is marked and rounded, and extends well onto the dorsal side of the bone. The depressio radialis is distinct. Two papillae remigales are visible and their interpapillar space measures 15.6 mm.

In Figure 6, the minimum width and minimum depth of the Liang Bua ulna is compared to those of extant Leptoptilini, as well as to an ulna (RMNH 1491)

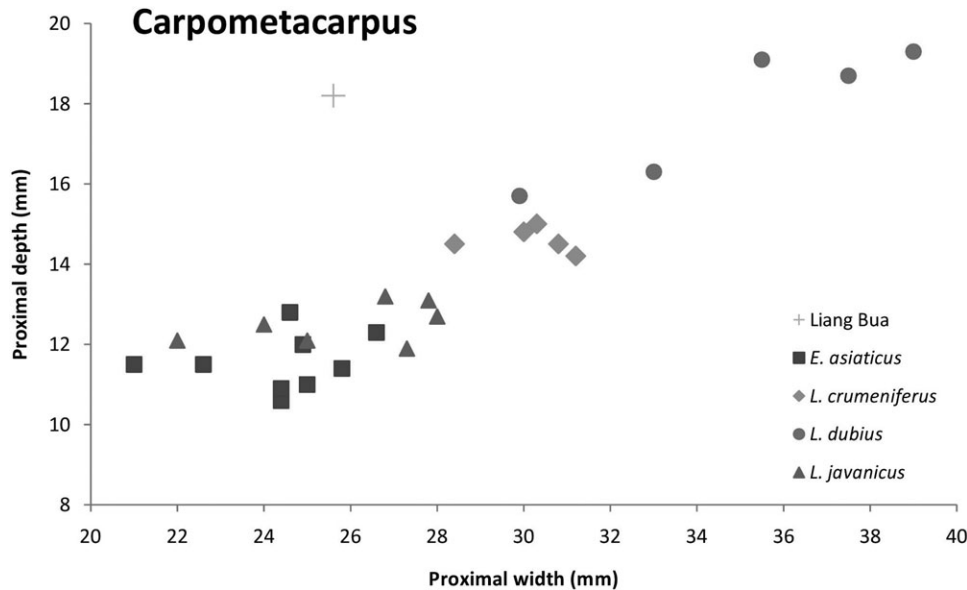


Figure 4. Graph showing the proximal width and proximal depth of the carpometacarpus of *Leptoptilos robustus* sp. nov. and extant Leptoptilini.

identified as *L. cf. dubius* from the Pleistocene of Trinil, Java (Weesie, 1982). The Liang Bua ulna is distinctly larger than the corresponding bone of *Ephippiorhynchus*, *L. javanicus*, and *L. crumeniferus*, as well as the fossil *L. cf. dubius* (RMNH 1491) from Java, and is within the upper size range of *L. dubius* (Fig. 6).

FEMUR

The femur (LBA-XI-03; Fig. 7) is nearly complete, but broken in two and lacks the caput femoris. Greatest length = 140.5 mm; distal width = 34.2 mm; distal depth = 33.4 mm; minimum width of the shaft = 21.5 mm; minimum depth of the shaft = 18.9 mm; proximal width = 32.3 mm; proximal depth = 21.2 mm. The bone is slightly concave on the facies cranialis, but is caudally convex. Proximally, the trochanter femoris is well developed, elevated from the shaft, and curved inwards so that the apex is located along the central axis of the bone. The facies articularis antitrochanterica is orientated at an angle of 25° with respect to the bone's central axis. On the facies cranialis, and approximately 10 mm below the top of the crista trochanteris, lies a distinct subcircular depression (3 mm in diameter) without visible pneumatic foramina. Ballman (1969), however, referred to this depression as a pneumatic foramen. The pneumatic foramen in the Liang Bua femur is similar to the foramina observed in *Leptoptilos* and *Ephippiorhynchus*. Distal of this depression and along the entire width of the bone lies a rugose area (indicated by dotted lines in Fig. 7) that may have served as the origin for large muscles such as the

Musculus femorotibialis. The muscle scars are less pronounced or even absent in extant Leptoptilini. On the facies cranialis, the linea intermuscularis cranialis is distinct and appears to run along the entire length of the shaft, although the specimen is damaged at the distal end. Both the linea intermuscularis cranialis and linea intermuscularis caudalis (on the facies caudalis) attain more central positions on the shaft of the bone in extant *Leptoptilos* and *Ephippiorhynchus* than in the fossil femur, in which they attain a more lateral and medial position, respectively. Distally on the facies caudalis, the fossa poplitea is deep and extends only 10 mm proximally. The condylus medialis is proximally bordered by the fossa poplitea, resulting in a straight mediolateral edge of the condylus medialis. The condylus lateralis is much more rounded proximally and extends further proximally than the condylus medialis, but not beyond the fossa poplitea. The incisura intercondylaris on the facies caudalis is narrow and deep just below the fossa poplitea, but widens distally. On the condylus lateralis, the impressio anae m. iliofibularis is broken off. The trochlea fibularis is still visible and extends distally along the condylus. Apart from the position of the intermuscular lines on the shaft, the Liang Bua femur is similar in morphology to extant Leptoptilini as well as *L. falconeri*. Despite slight damage at both the proximal and distal articulation, the Liang Bua femur agrees in length with recent *L. dubius* and is only slightly smaller in distal width than the distal left femur of *L. falconeri* (NHM 39737) from the Siwalik Hills, India. In the minimum width and minimum depth of

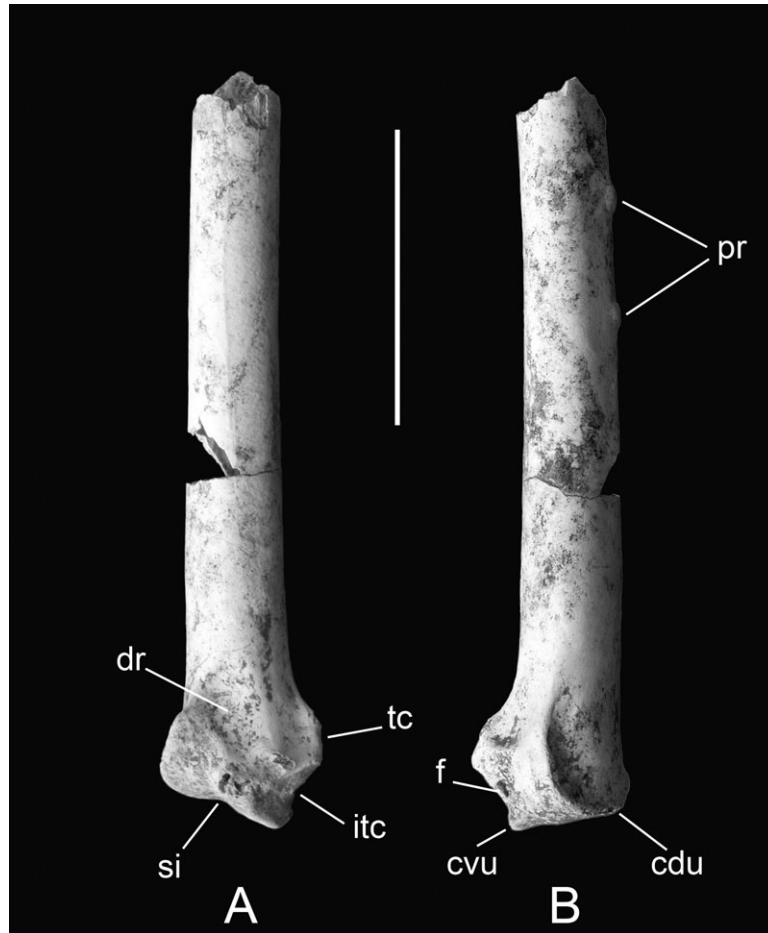


Figure 5. *Leptoptilos robustus* sp. nov., distal part of left ulna (LBA-XI-02). A, ventral view; B, dorsal view. Abbreviations: cdu, condylus dorsalis ulnae; cvu, condylus ventralis ulnae; dr, depression radialis; f, foramen; itc, incisura tuberculi carpalis; pr, papillae remigales; si, sulcus intercondylaris; tc, tuberculum carpale. Scale bar = 50 mm. Photographs by E. Kruidenier.

the shaft (Fig. 8), the Liang Bua femur falls within the range of extant *L. dubius*.

TIBIOTARSUS

The tibiotarsus (LBA-XI-04; Fig. 9) consists of three fragments of the shaft and the distal end, but is lacking the distal condyles. Greatest length of the segments together = 328.5 mm; greatest lengths of separate segments = 144.2, 99.8, and 84.5 mm; minimum width of the shaft = 15.2 mm; minimum depth of the shaft = 14.0 mm. The shaft is long and straight and lacks the lateral rotation of the shaft along the long axis of the bone observed in extant *Leptoptilos* and *Ephippiorhynchus*. In cross-section, the bone attains a sub-triangular shape with the facies caudalis of the shaft rounded, whereas the facies cranialis is flattened. The cortical bone wall of the tibiotarsus (visible at the fracture surface, indi-

cated in Fig. 9 by cs) measures 3.0–4.3 mm, whereas the bone itself has a maximum diameter of 15.1 mm. The ratio of internal to external diameter of a bone, or the relative thickness of the bone wall, is referred to as K. In the Liang Bua tibiotarsus, K is 0.48–0.55. For *L. dubius*, K is 0.69–0.73. For the specimens of the fossil species *L. falconeri* (NHM 39735) and *L. siwalicensis* (NHM 39734), K is 0.69–0.78 and 0.65–0.74, respectively. Note that the latter species was re-classified as Leptoptilini gen. et spec. indet. by Louchart *et al.* (2005), but is here treated as a separate species. Thus, the bone wall of the Liang Bua tibiotarsus is thicker than the largest species of extant *Leptoptilos*, *L. dubius*, as well the fossil species *L. falconeri* and *L. siwalicensis* (Fig. 10). Distally on the facies cranialis, the sulcus extensorius lies on the medial half of the bone. The sulcus extensorius extends for approximately 20 mm proximally of the pons supratendineus. Here, the Liang Bua tibiotarsus differs markedly from

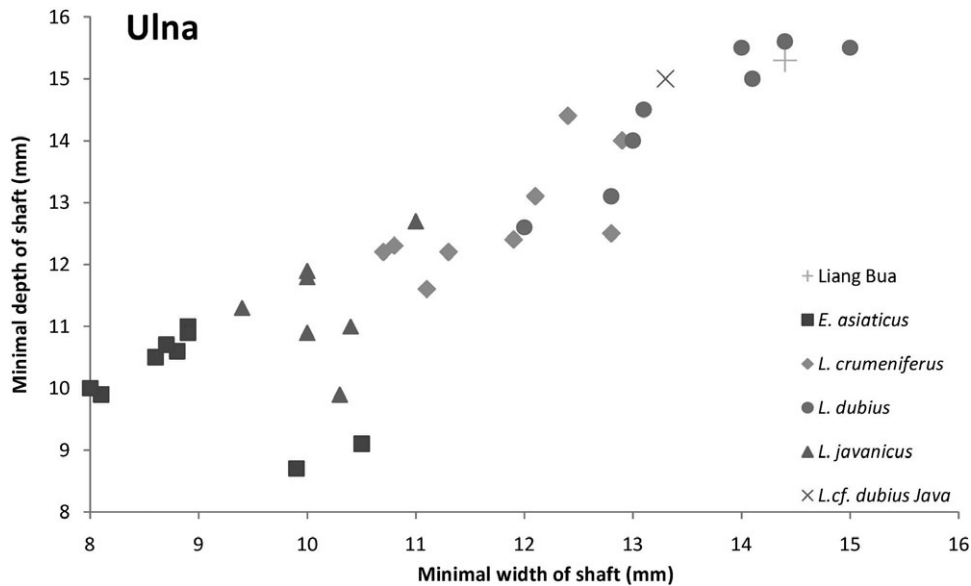


Figure 6. Graph showing the minimum width and minimum depth of the shaft of the ulna of *Leptoptilos robustus* sp. nov., and extant and fossil Leptoptilini.

L. falconeri in that the sulcus extensorius is wider, more deeply excavated and attains a more central placement on the shaft in the latter. In *L. siwalicensis*, the sulcus extensorius is also deep and ends abruptly proximally, whereas, in the Liang Bua specimen, the sulcus extensorius is shallower and proximally merges smoothly with the shaft. The shape and size of the sulcus extensorius in the Liang Bua specimen is more similar to those of extant *L. dubius* than to those of the extinct *L. falconeri* and *L. siwalicensis*. Lateral of the sulcus extensorius gnawing marks are visible. These gnawing marks fit the incisors of the medium- to large-sized rats *Paulamys*, *Komodomys*, and *Papagomys*, all of which were present in the Late Pleistocene of Liang Bua. The pons supratendineus is proximodistally wide (9 mm) and the distal opening of the canalis extensorius is located more medially than its proximal opening. Laterodistal of the pons supratendineus lies a prominent tubercle. This tubercle was not named by Baumel & Witmer (1993), but was referred to as 'prominent tubercle latero-distal to pons supratendineus' by Mayr & Clarke (2003) and 'intercondylar tubercle' by, amongst others, Rasmussen, Olson & Simons (1987). The tubercle itself is damaged, but its well-developed and wide base is still visible. It is located lateral and slightly proximal of the distal opening of the canalis extensorius, and placed centrally on the long axis of the bone, similar to the condition observed in extant *L. dubius*. In *L. falconeri*, there is a deep pit proximolateral of the distal opening of the canalis extensorius, which is absent in the Liang Bua specimen as well as in *L. siwalicensis* and extant Leptoptilini.

Figure 11 shows the dimensions of the Liang Bua tibiotarsus (minimum width and minimum depth of the shaft). In contrast to the carpometacarpus, ulna, and femur, the tibiotarsus is distinctly larger than any other extant Leptoptilini species. The Liang Bua tibiotarsus lies well outside the size range of both sexes of *L. dubius* and, and is similar in size to *L. siwalicensis*, yet smaller than *L. falconeri*.

In conclusion, considering the combination of above described osteological characters in which the Liang Bua bones differ from extant and fossil members of the Leptoptilini, and the large dimensions and thick cortical bone wall of the tibiotarsus, we feel justified in assigning the fossil remains from Liang Bua to a new species of extinct Leptoptilini, *L. robustus* sp. nov.

SYSTEMATIC PALAEOLOGY

CLASS AVES LINNAEUS, 1758

ORDER CICONIIFORMES BONAPARTE 1854

FAMILY CICONIIDAE GRAY 1840

TRIBE LEPTOPTILINI KAHL 1971

GENUS *LEPTOPTILOS* LESSON 1831

***LEPTOPTILOS ROBUSTUS* SP. NOV.**

Holotype: Associated partial skeleton with wing and leg bones (Figs 3, 5, 7, 9), consisting of the proximal half of a left carpometacarpus (preliminary registration nr LBA-XI-01) and the distal part of a left ulna (LBA-XI-02), an almost complete left femur (LBA-XI-03), and the distal part of a left tibiotarsus (LBA-XI-

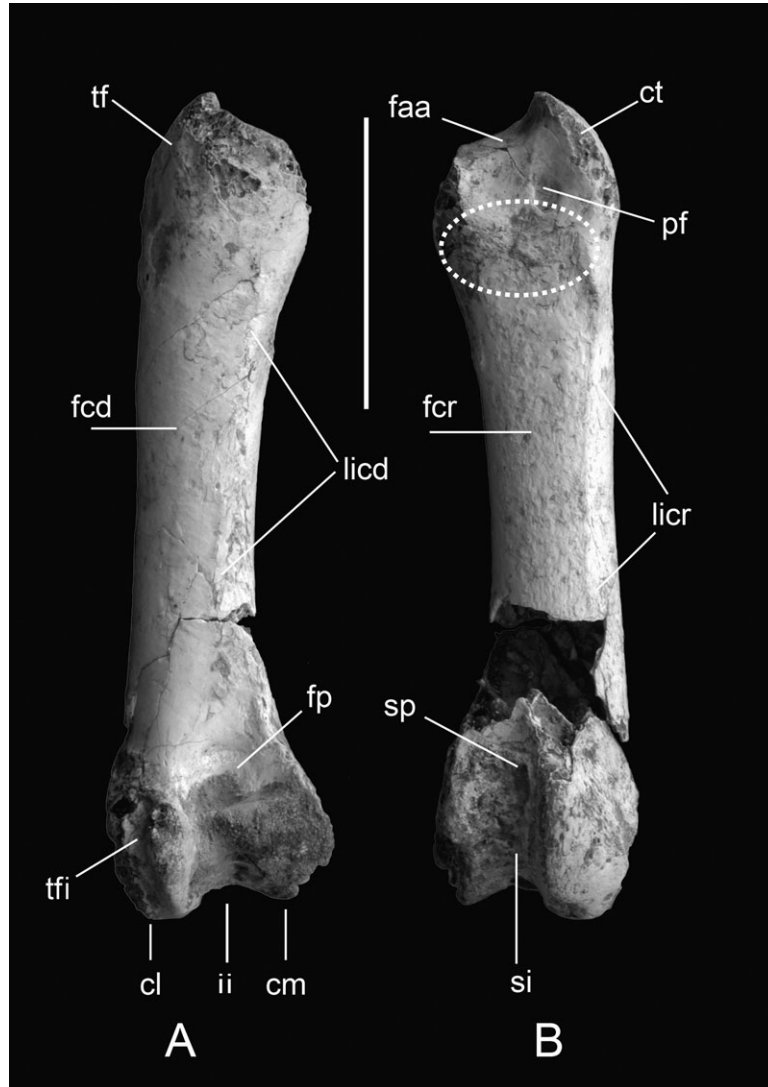


Figure 7. *Leptoptilos robustus* sp. nov., left femur (LBA-XI-03). A, caudal view; B, cranial view. Abbreviations: cl, condylus lateralis; cm, condylus medialis; ct, crista trochanteris; faa, facies articularis antitrochanterica; fcd, facies caudalis; fcr, facies cranialis; fp, fossa poplitea; ii, incisura intercondylaris; licd, linea intermuscularis caudalis; licr, linea intermuscularis cranialis; pf, pneumatic foramen; sp, sulcus patellaris; tf, trochanter femoris; tfi, trochlea fibularis. Scale bar = 50 mm. Photographs by E. Kruidenier.

04). The bones are stored at the National Centre for Archaeology in Jakarta (Indonesia).

Etymology: From the Latin *robustus* meaning 'strong, robust', and referring to the large tibiotarsus and the thickness of its cortex.

Type locality: Liang Bua cave, Manggarai Province, Flores, Indonesia at 08°31'50.4"S, 120°26'36.9"E.

Type horizon and age: Sector XI at Liang Bua (Fig. 1) at a depth of 425–470 cm in layers of brown clayey

silts (Layer O in Fig. 2) and Late Pleistocene in age (Morwood *et al.*, 2005).

Diagnosis: A large species of extinct *Leptoptilos* resembling *L. dubius* in dimensions of the femur, carpometacarpus, and ulna, but with a tibiotarsus wider and deeper than any living *Leptoptilos* and yet smaller than *L. falconeri*, and with the following unique combination of characters: pneumatized carpometacarpus with a distinct foramen in the fossa infratrochlearis; femur with well-pronounced muscle scars on proximocranial surface; linea intermuscularis cranialis and linea intermuscularis caudalis

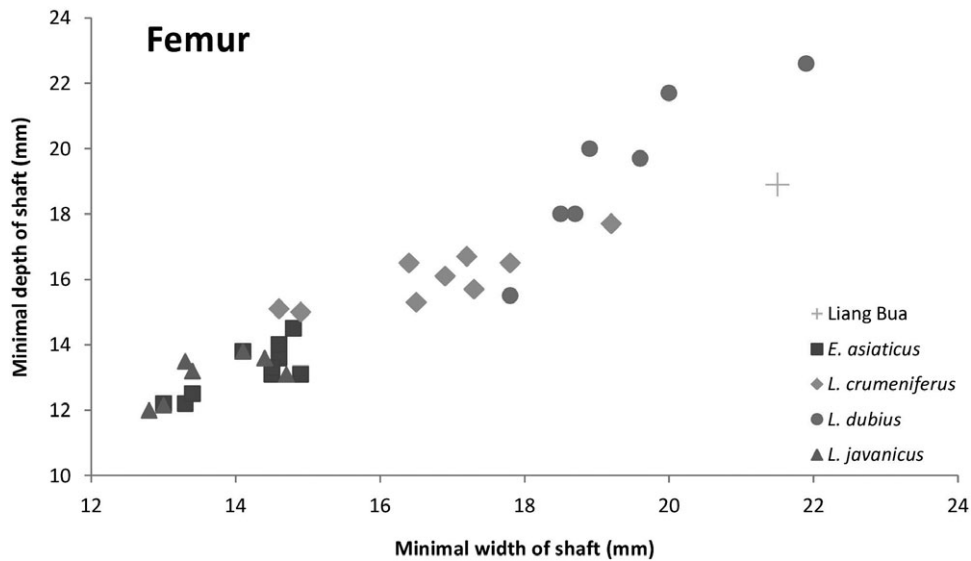


Figure 8. Graph showing the minimum width and minimum depth of the shaft of the femur of *Leptoptilos robustus* sp. nov. and extant Leptoptilini.

with a more lateral and medial location on the shaft, respectively, than extant Leptoptilini; condylus ventralis ulnae pointed, elevated, and projecting distally; tuberculum carpale rectangular in ventral view; foramen in incisura tuberculi carpalis; tibiotarsus with straight shaft and bone wall thicker than any species of *Leptoptilos*; sulcus extensorius shallow, narrow, and located on medial half of bone.

Apomorphies for the genus *Leptoptilos* are the pneumatized carpometacarpus with a distinct foramen in the fossa infratrochlearis and the pointed condylus ventralis ulnae. Autapomorphic characters for *L. robustus* sp. nov. are its large size, the thickening of the cortical bone wall of the tibiotarsus, the absence of a rotation in the tibiotarsal shaft, the elevated and distal projection of the pointed condylus ventralis ulnae, pronounced muscle scars on the proximocranial surface of the femur, and a more lateral and medial location of the linea intermuscularis cranialis and linea intermuscularis caudalis on the femur shaft.

DISCUSSION

From the circumference of the tibiotarsus (48 mm), it can be inferred that *L. robustus* sp. nov. had a body weight of approximately 16 kg (Campbell & Marcus, 1992). This is substantially heavier than any extant species of *Leptoptilos*, which reach maximally 9 kg (Louchart *et al.*, 2005). Louchart *et al.* (2005) estimated a weight of approximately 20 kg and a length of 2 m for *L. falconeri* from Chad. Hence, *L. robustus* is estimated to have reached a height of approxi-

mately 1.80 m, intermediate between those of *L. falconeri* and *L. dubius*. This implies that it must have towered over the tiny *H. floresiensis* standing only 1 m tall (Brown *et al.*, 2004) (Fig. 12). The question as to whether or not *L. robustus* was completely incapable of flight cannot be resolved based on the remains found so far; the fragmentary nature of the ulna and carpometacarpus do not allow for an estimation of the wingspan. Nevertheless, the fact that *L. robustus* is similar in dimensions to *L. dubius* except for the tibiotarsus suggests that *L. robustus* had slightly reduced forelimbs.

A remarkable feature of *L. robustus* is the thick-walled tibiotarsus, which constitutes the thickest bone wall of all living and extinct Leptoptilini. Even the larger *L. falconeri* has a bone wall that is thinner than *L. robustus*. In flying birds, selection for minimum mass has resulted in thin-walled bones. The low K value in the tibiotarsus of *L. robustus* implies a different mode of locomotion; the tibiotarsus was adapted to resist mechanical forces during bending and local blows to the bone. A lifestyle with a reduced ability for flight and a greater reliance on terrestrial locomotion would subject a bone to such mechanical loading. Whereas the higher K values of *L. dubius*, *L. siwalicensis*, and *L. falconeri* all agree with flying birds, the K values for the tibiotarsus of *L. robustus* are comparable to those of flightless birds and terrestrial mammals. For ostrich and moa, Currey & Alexander (1985) reported K values of 0.68 and 0.57, respectively. Such K values are typical for all bones of land mammals (Currey & Alexander, 1985). Recently flightless Galapagos cormorants

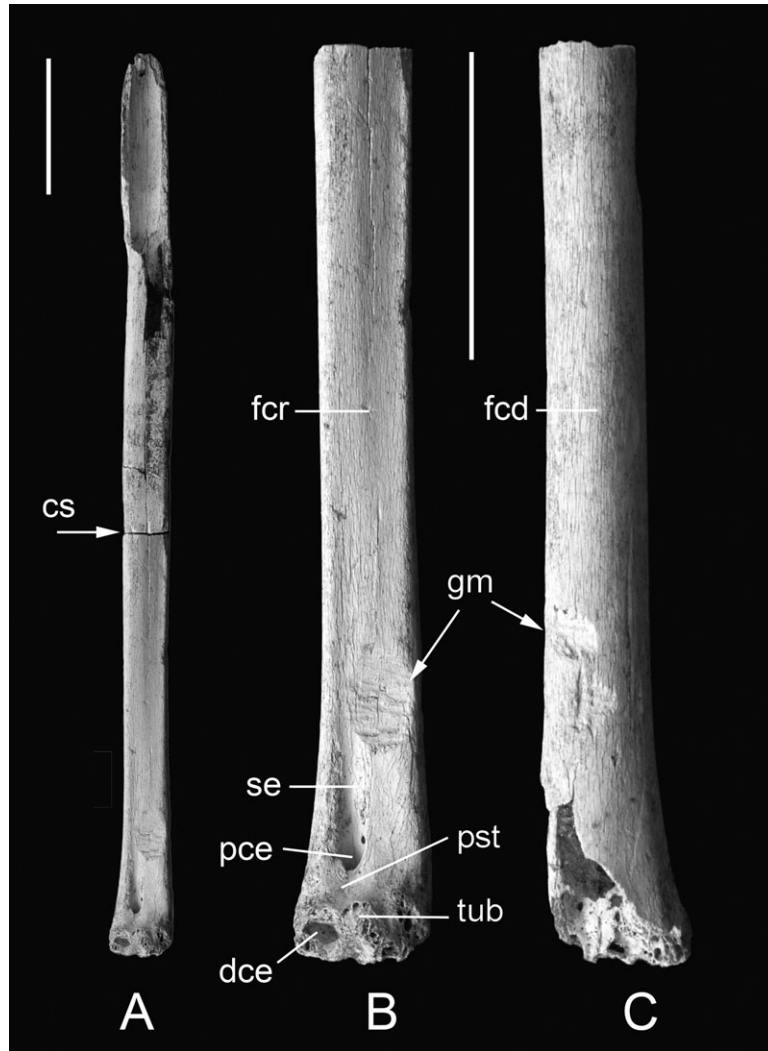


Figure 9. *Leptoptilos robustus* sp. nov., distal left tibiotarsus (LBA-XI-04). A, anterior view of specimen; B, anterior view of distal fragment; C, posterior view of distal fragment. Abbreviations: cs, location of natural fracture at which cross-section is visible; dce, distal opening of canalis extensorius; fcd, facies caudalis; fcr, facies cranialis; gm, gnawing marks; pce, proximal opening of canalis extensorius; pst, pons supratendineus; se, sulcus extensorius; tub, tubercle laterodistal of the pons supratendineus. Scale bars = 50 mm. Photographs by E. Kruidenier.

(*Phalacrocorax harrisi*) were shown to have a marked thickening of the femoral wall (Habib & Ruff, 2008). The extremely thick-walled tibiotarsus and lack of torsion in the shaft in combination with the high inferred body mass indicate that *L. robustus* had adopted a different mode of locomotion from closely related species as it relied less on aerial locomotion.

This conclusion has consequences for the evolution of *L. robustus* sp. nov. Given its ground-bound lifestyle, *L. robustus* must have evolved *in situ* on the island from a flying ancestor. Despite various findings of fossil Leptoptilini in Africa, Central Europe, Central Asia, and even South America (see for example, Milne-Edwards, 1868; Harrison, 1974; Har-

risson & Walker, 1982; Mlíkovský, 2002; Louchart *et al.*, 2005; Noriega & Cladera, 2008), the scant fossil record of birds in South-East Asia leaves it difficult to trace the evolutionary history of *L. robustus*. So far, only Java has yielded fossil Leptoptilini, including *L. cf. dubius* from the Middle Pleistocene of Trinil (Weesie, 1982) and *L. titan* from the Late Pleistocene of Watualang (Wetmore, 1940). In Central Asia, remains of *L. falconeri* were described from the Pliocene of the Siwalik Hills in India (Milne-Edwards, 1868; Lydekker, 1884). Findings of *L. falconeri* in Central Asia, Africa, and central Europe indicate that it was widespread in the Pliocene. The wide range of *L. falconeri* could suggest that *L. robustus* is

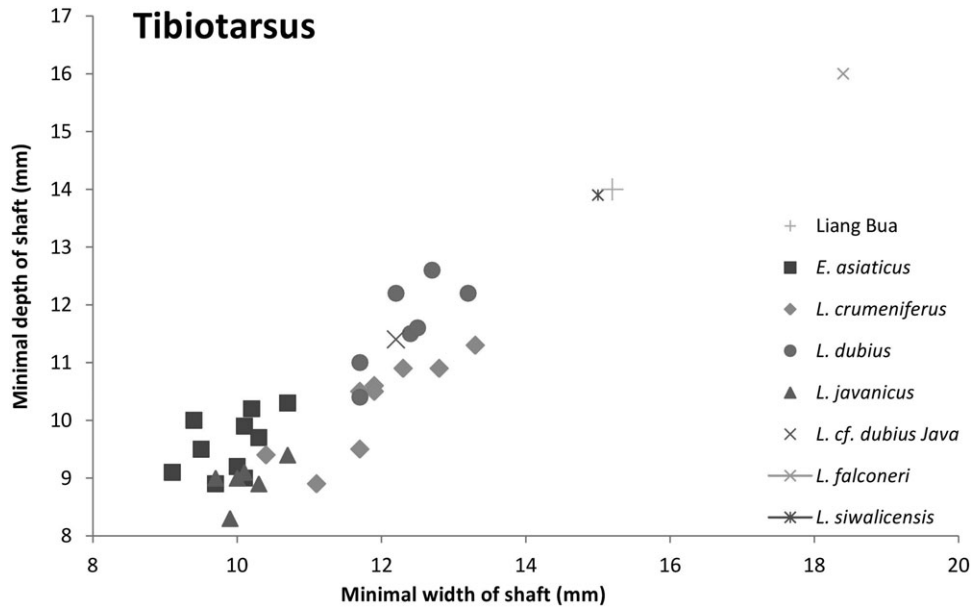


Figure 10. Graph showing the minimum width and minimum depth of the shaft of the tibiotarsus of *Leptoptilos robustus* sp. nov. and extant and fossil Leptoptilini.

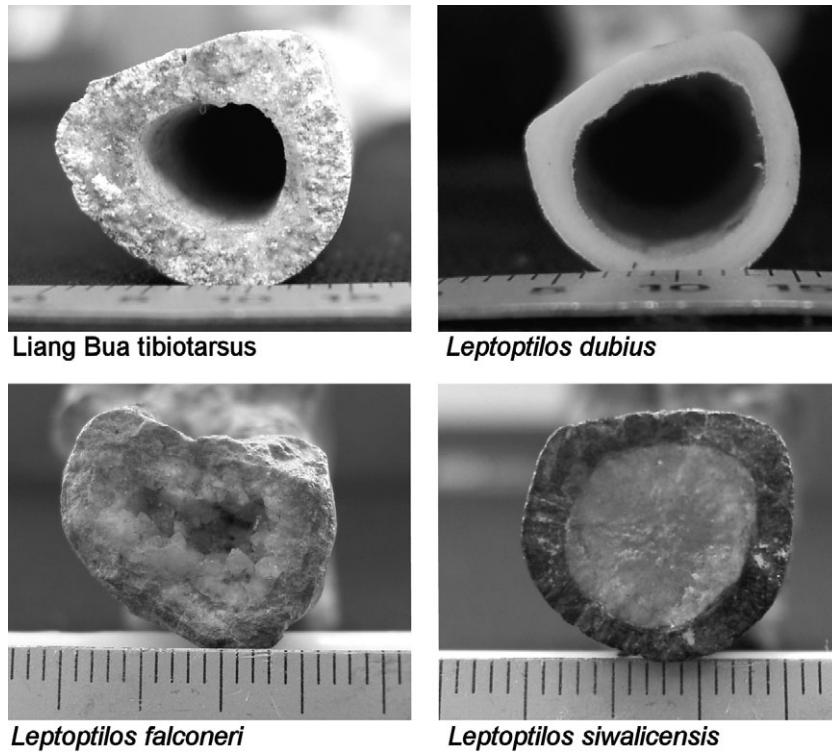
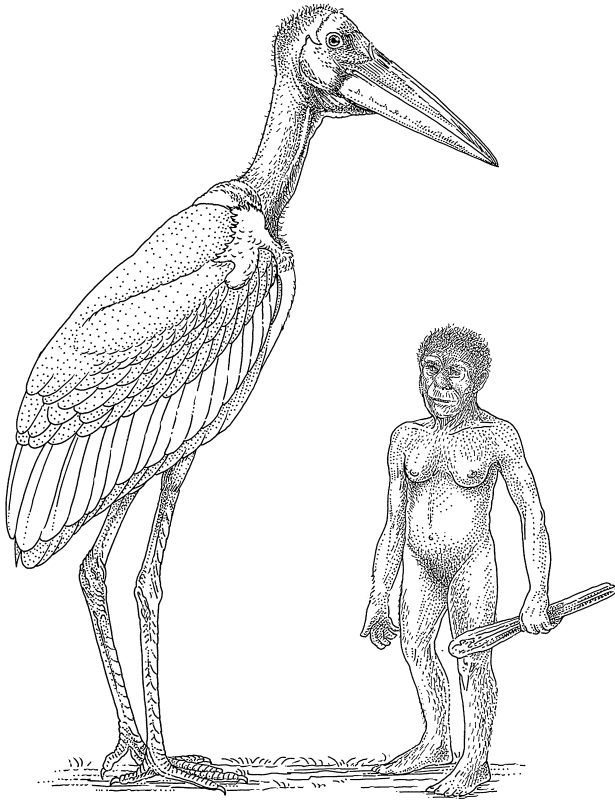


Figure 11. Cross-sections through tibiotarsi of fossil and extant Leptoptilini to show the thickness of the cortical bone wall in *Leptoptilos robustus* sp. nov. To enhance comparison of the bone wall, the images are scaled to be roughly the same size and do not represent the actual sizes of the tibiotarsi.



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Figure 12. Artist's impression of the size of *Leptoptilos robustus* sp. nov. (estimated at 1.8 m) compared to *Homo floresiensis* (estimated at 1.0 m). Drawing by I. van Noortwijk.

conspecific with, or at least descended from it, as both are large-bodied representatives of the genus in Asia. However, conspecificity is ruled out considering the morphological differences between them. So far, *L. falconeri* is not known from any Pleistocene deposits and Louchart *et al.* (2005) supposed that this species became extinct at the end of the Pliocene. It is therefore considered unlikely that *L. falconeri* was ancestral to *L. dubius*.

Osteological characters (size and shape of the sulcus extensorius, shape of the condylus ventralis ulnae, and dimensions of the carpometacarpus, femur, and ulna) suggest that *L. robustus* is closely related to *L. dubius*, which implies that they share a common ancestor. The presence of *L. cf. dubius* in the Trinil beds of Java indicates that this species was already present in South-East Asia by the Middle Pleistocene and may have been widespread (Mees, 2006, pointed out the similarities between the recent avifaunas of Flores and Java). This lends support to the hypothesis that a *L. dubius*-like stork may have been ancestral to

L. dubius, *L. javanicus*, and *L. robustus*. Possibly, *L. titan* from Java may have been part of this clade as well, although there is currently no firm evidence to support this. Note that a lack of corresponding elements prevents a comparison between *L. robustus* and *L. titan*, the latter being based on only a single tarsometatarsus. However, given the reduced flight capabilities of *L. robustus* we regard it unlikely that it was conspecific with *L. titan*. Louchart *et al.* (2005) suggested that *L. cf. dubius* from Java represented additional material of *L. titan*. Measurements of the ulna (RMNH 1491) (Fig. 6) show, however, that this specimen falls within the range of extant *L. dubius*. The *L. titan* tarsometatarsus is 32% larger in length than the corresponding bone of *L. dubius*. Assuming that the former species had similar proportions to its extant relatives, we would expect a much larger ulna for *L. titan*. Therefore, it is improbable that the ulna from Trinil belongs to *L. titan*.

Pleistocene Flores hosted a highly endemic and insular biota lacking mammalian carnivores (Van den Bergh *et al.*, 2009). A (flying) ancestral species of *Leptoptilos* colonizing the island must have been subjected to evolutionary forces very different from those on the continent. Carrion forms an important part of the diet for most *Leptoptilos* species. In mainland ecosystems with mammalian predators, scavenging birds compete for food with mammalian carnivores such as lions and hyenas. In the absence of such competition, food is more abundant. In combination with an abundance of middle and large-sized rats as well as juvenile Komodo dragons, a year-round food supply is provided, which favours habitat fidelity. The decreased interspecific competition for carrion and abundance of prey items would have reduced the need to fly large distances for food. As a consequence, the selection pressure on the flight apparatus was released, a well-known phenomenon in insular biotas (McNab, 1994).

The insular nature, that is, the isolation and an unbalanced fauna lacking in mammalian carnivores, of Pleistocene Flores gave rise to the flightlessness and large body size of *L. robustus*. The increase in body size in an insular setting implies an effect of the 'island rule', which, in contrast to mammals, has received far less attention in birds (for example, Foster, 1964; Van Valen, 1973; Sondaar, 1977; Lomolino, 1985; Meiri, Cooper & Purvis, 2008, for mammals: and Grant, 1965a, b; Blondel, 2000; Clegg & Owens, 2002, for birds). This is despite noticeable changes in body size in fossil insular birds, such as the dodo on Mauritius, Haast's eagle in New Zealand, and fossil insular birds in the Mediterranean (Ballman, 1973, 1976, Weesie, 1988; Alcover *et al.*, 1992), as well as from Cuba (Arredondo, 1976), the Bahamas (Olson & Hilgartner, 1982), Jamaica (Olson

& Steadman, 1977, 1979), and New Zealand (Worthy & Holdaway, 2002). Typically, the most dramatic increase is shown by birds of prey (Accipitriformes) and owls (Strigiformes) (Alcover *et al.*, 1992). Changes in body size and proportions are believed to have taken place in response to the size of their prey items on islands; most insular large birds of prey and owls are likely to have fed on giant rodents, small deer or, in the case of Haast's eagle, even moas (Alcover *et al.*, 1992; Worthy & Holdaway, 2002). The peculiar horns of the insular artiodactyl *Hoplitomeryx matthei* Leinders from the Gargano palaeo-archipelago have even been interpreted as a defence against birds of prey (Leinders, 1984).

The evolution of the large-bodied *L. robustus* from a smaller sized *L. dubius*-like ancestor in the presence of abundant prey items may point towards insular gigantism. A similar case of insular gigantism in the flightless ibis of Jamaica (Olson & Steadman, 1977, 1979) indicates that Ciconiiformes, in addition to diurnal and nocturnal raptors (Accipitriformes and Strigiformes), may increase in body size in response to an insular environment. The absence of mammalian predators on islands clearly offers new opportunities for carnivorous birds.

Leptoptilos robustus sp. nov. constitutes a new species of giant marabou stork and is the first fossil bird to be described from the island of Flores, Indonesia. *Leptoptilos robustus* had a terrestrial lifestyle and formed part of the Late Pleistocene endemic *H. floresiensis* fauna that became extinct at the end of the Pleistocene. Despite being one of today's hotspots of biodiversity (Myers *et al.*, 2000), Wallacea's fossil record of birds is very poor. The finding of *L. robustus* contributes to the fossil record of birds in this region, and sheds light on the evolution and biogeography of storks in South-East Asia.

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APPENDIX 1
LIST OF SPECIMENS AND MEASUREMENT OF EXTANT SPECIES USED IN THIS STUDY

Species	Carpometacarpus		Ulna		Femur		Tibiotarsus		Minimum depth of shaft	unsexed female male	unsexed female male	unsexed female male			
	Proximal width	female male	Proximal depth	unsexed female male	Minimum width	unsexed female male	Minimum depth of shaft	unsexed female male					Minimum width of shaft	unsexed female male	
															female
<i>Ephippiorhynchus astaricus</i> (Latham, 1790)	23.5; 25.4; 24.4; 25.0 (N = 5)	23.9; 24.4; 24.4 (N = 2)	11.5; 10.6; -12.8 (N = 5)	11.7; 12.2; 10.3; -12.3 (N = 4)	9.0; 7.9; -10.5 (N = 5)	8.8; 8.0; -8.9 (N = 4)	8.8; 10.8; 8.7; -10.5 (N = 5)	13.8; 14.6; 13.0; -14.9 (N = 4)	13.9; 13.9; 13.4; -14.5 (N = 2)	12.8; 13.8; 12.3; -13.8 (N = 4)	13.8; 13.8; 13.1; -14.5 (N = 4)	13.9; 12.9; 12.3; -13.3 (N = 2)	9.6; 9.8; 8.9; -10.3 (N = 4)	9.1; 9.5; 9.0; -10.2 (N = 2)	
<i>Ephippiorhynchus senegalensis</i> (Shaw, 1800)	24.6			10.9	8.1	9.6	13.0	12.7	10.4					9.2	
<i>Leptoptilos cramentiferus</i> (Lesson, 1831)	29.6; 28.4; -30.3 (N = 3)	31.4; 29.7; -33.0 (N = 5)	14.8; 14.5; -15.0 (N = 3)	14.6; 14.0; -15.8 (N = 5)	12.0; 11.1; -12.8 (N = 3)	12.4; 11.6; -13.1 (N = 3)	16.2; 14.6; -17.2 (N = 4)	17.2; 14.9; -19.2 (N = 6)	15.9; 15.1; -16.7 (N = 4)	15.9; 15.1; -16.7 (N = 4)	16.0; 14.8; -17.7 (N = 6)	16.0; 14.8; -17.7 (N = 6)	11.9; 11.1; -12.8 (N = 3)	10.1; 8.9; -10.9 (N = 3)	
<i>Leptoptilos dubius</i> (Gmelin, 1789)	33	39.0; 29.9; -37.5 (N = 6)	16.3; 19.3	17.2; 15.7; -19.1 (N = 6)	14.0	13.6; 12.0; -15.0 (N = 6)	18.7; 21.9; 17.8; -20; -15.6 (N = 5)	19.0; 18.0; -21.7 (N = 5)	18	22.6	19.0; 15.5; -21.7 (N = 5)	19.0; 15.5; -21.7 (N = 5)	12.4	11.5; 11.7; -12.7 (N = 5)	11.6; 10.4; -12.6 (N = 5)
<i>Leptoptilos javanicus</i> (Horsfield, 1821)	27.3; 26.8; -27.8 (N = 2)	24.8; 22.0; -28.0 (N = 4)	13.1; 13.1; -13.2 (N = 2)	11.9; 12.4; 12.1; -12.7 (N = 4)	10	10.8; 9.4; -10.4 (N = 4)	14.4; 14.1; -14.7 (N = 2)	13.1; 12.8; -13.4 (N = 4)	13.4; 13.1; -13.8 (N = 2)	13.6	12.7; 12.0; -13.5 (N = 4)	12.7; 10.3; -10.7 (N = 4)	10.1	9.2; 8.9; -9.4 (N = 2)	8.8; 8.3; -9 (N = 4)

APPENDIX 2

LIST OF SPECIMENS AND MEASUREMENTS OF FOSSIL SPECIES USED IN THIS STUDY

Species	Specimens	Description
<i>Leptoptilos cf. dubius</i>	RGM 1491	Diaphysis of left ulna, Pleistocene of Trinil, Java, Indonesia
	RGM 1490	Diaphysis of left tibiotarsus, Pleistocene Trinil, Java, Indonesia
<i>Leptoptilos falconeri</i> (Milne-Edwards, 1868)	NHM 39735	Distal right tibiotarsus, Pliocene of Siwalik, India (lectotype)
	NHM 39737	Distal left femur, Pliocene of Siwalik, India
<i>Leptoptilos siwalicensis</i> Harrison, 1974	NHM 39734	Distal right tibiotarsus, Pliocene of Siwalik, India (paratype & paralectotype)
<i>Leptoptilos</i> sp.	NHM 48444	Distal left tibiotarsus, Pliocene of Siwalik, India