A MARABOU (CICONIIDAE: *LEPTOPTILOS*) FROM THE MIDDLE PLEISTOCENE OF NORTHEASTERN CHINA

ZIHUI ZHANG,[1,5] YUNPING HUANG,[2] HELEN F. JAMES,[3] AND LIANHAI HOU[1,4]

[1]*College of Life Sciences, Capital Normal University, Beijing 100048, China;*
[2]*School of Archaeology and Museology, Peking University, Beijing 100871, China;*
[3]*Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013, USA; and*
[4]*Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, P.O. Box 643, Beijing 100044, China*

ABSTRACT.—A new species of marabou, *Leptoptilos lüi* sp. nov., is described on the basis of a cranium, distal humerus, and proximal phalanx of the major digit, from the Middle Pleistocene Jinniushan locality, Liaoning Province of northeastern China. Fossil crania of the genus *Leptoptilos* are rare, and that of the new bird is distinct from the crania of its extant relatives. The forelimb elements are the largest and most robust among living and fossil species of *Leptoptilos* and are characterized by autapomorphic characters. *Leptoptilos lüi*, like the African Marabou Stork (*L. crumeniferus*), probably possessed a considerable flight capability and fed mainly on pieces of carrion torn from carcasses by other, sympatric large scavengers. The new stork aids in our understanding of the paleoecology and paleoenvironment of northeastern China in the Middle Pleistocene, helps us characterize the scavenger guild that fed on the Middle Pleistocene megafauna, and shows that the genus *Leptoptilos*, now restricted to the Old World tropics, extended into higher latitudes in the Middle Pleistocene. *Received 7 October 2011, accepted 11 June 2012.*

Key words: biogeography, Jinniushan site, *Leptoptilos lüi* sp. nov., Middle Pleistocene, northeastern China.

Un Marabú (Ciconiidae: *Leptoptilos*) del Pleistoceno Medio del Nororiente de China

RESUMEN.—Describimos una nueva especie de marabú, *Leptoptilos lüi* sp. nov., basados en un cráneo, la parte distal de un húmero y la falange proximal del dígito más grande. La nueva especie proviene de la localidad Jinniushan del Pleistoceno medio, provincia de Liaoning, nororiente de China. Los cráneos fósiles del género *Leptoptilos* son raros y el de la nueva especie es distinto de los cráneos de sus parientes vivos. Los elementos de la extremidad delantera son los más grandes y robustos entre las especies conocidas (vivas y extintas) de *Leptoptilos* y se caracterizan por presentar caracteres autoapomórficos. Tal como *L. crumeniferus*, *L. lüi* probablemente poseía una capacidad de vuelo considerable y se alimentaba principalmente de trozos de carroña arrancados de cadáveres por otras especies simpátricas de grandes carroñeros. Esta nueva ave ayuda a nuestro entendimiento de la paleoecología y el paleoambiente del nororiente de China en el Pleistoceno medio, y a caracterizar el gremio de especies carroñeras que se alimentaban de la megafauna de mediados del Pleistoceno. Además, nos demuestra que el género *Leptoptilos*, ahora restringido zonas tropicales del Viejo Mundo, se extendía hacia latitudes más altas en ese periodo.

THE STORKS (CICONIIDAE) form a well-defined group, with the majority found in the tropics, especially tropical Africa. The family is usually divided into three tribes based on morphological and behavioral characters: Mycteriini, Ciconiini, and Leptoptilini (e.g., Kahl 1972, 1979). Leptoptilini comprises three genera: *Jabiru*, *Ephippiorhynchus*, and *Leptoptilos*. These genera contain six living species, which are generally resident and nonmigratory but can be nomadic in response to rainfall conditions. The Greater Adjutant (*Leptoptilos dubius*), Marabou Stork (*L. crumeniferus*), and Lesser Adjutant (*L. javanicus*) are distributed in tropical Asia

and Africa and feed mainly on carrion. The Jabiru (*Jabiru mycteria*) occurs in Central and South America, and *Ephippiorhynchus* (two species) is found in the Indian subcontinent, New Guinea, Australia, and tropical Africa; members of these two genera forage in shallow water for small fish.

Leptoptilos is well known in the Neogene fossil record. With the exception of *L. patagonicus* from the Late Miocene of Argentina (Noriega and Cladera 2008), all fossils are from the Old World, especially Africa and South Asia, dating from Miocene to Pleistocene. *Leptoptilos falconeri*, originally known from the late Pliocene of the

Siwalik Hills of India (Milne-Edwards 1867–1871), covered a wide geographic range from South Asia to eastern and northern Africa, but became extinct by the end of the Pliocene (Louchart et al. 2005). Two further Pliocene *Leptoptilos* species are *L. pliocenicus* from Ukraine (Zubareva 1948) and *L. siwalicensis* from India (Harrison 1974). Miocene deposits yielded *L. richae* in Tunisia and *Leptoptilos* spp. in Kenya, Lybia, and Egypt (Harrison 1974, Hill and Walker 1979, Ballmann 1987, Miller et al. 1997, McDougall and Feibel 2003). Pleistocene representatives of the genus are *L. titan* and *L. robustus* from Java and Flores of Indonesia, respectively (Wetmore 1940, Meijer and Due 2010). The new species of *Leptoptilos* described here is from the Middle Pleistocene Jinniushan locality, Liaoning Province of northeastern China. The unexpected occurrence of a marabou at this high latitude has implications for understanding the biogeography and diversity of the genus *Leptoptilos*. In addition to the analysis of the mammalian fauna (Jinniushan Lianhe Fajuedui 1976, Rosenberg et al. 2006), the presence of a species of *Torgos* (Zhang et al. 2012) and a parrot (Z. Zhang et al. unpubl. data), the new stork adds information to, and confirms the paleoenvironmental evaluation of, that region in the Middle Pleistocene.

The Jinniushan locality is part of an isolated hill of limestone, located to the west of Xitiantun village, Yingkou county, in Dashiqiao city of Liaoning Province, northeastern China (Fig. 1). It has yielded numerous vertebrate specimens, including many bird remains, and is famous for the discovery of archaic human fossils in the sediments (Lu 2003, Rosenberg et al. 2006). The cave is about 13.5 m long (east–west) and 9.5 m wide (north–south), and its original mouth faces east. The excavation area is about 11×5–5.5 m, with a total area of 55–60.5 m^2. The deposit is divided into eight layers from top to bottom. The upper layers 1–4 consist of sediments of dark brown or brownish yellow sandy clay and breccia; the lower layers 5–8 consist of cemented breccia, brownish red sandy clay, sand, and large pebbles. The specimens reported here were excavated from layer 8, together with the human fossils in 1984, by a group from the School of Archaeology and Museology at Peking University and the Cultural Relics and Archaeology Institute of Liaoning Province.

Methods

Fossils were morphologically and biometrically compared with extant ciconiiform skeletons (M = male, F = female) from the National Museum of Natural History, Smithsonian Institution, USNM: *Letoptilos crumeniferus* 489395F, 489396M, 488128M, 488129F, 430819F, 431231, 631760M; *L. dubius* 429220F, 225988F; *L. javanicus* 223897M, 488758, 430764; *Jabiru mycteria* 429840M, 345680F, 318650F, 320691F, 428619F, 343461, 343462, 343464, 343465, 343466, 343467; *Ephippiorhynchus asiaticus* 19694, 346193;
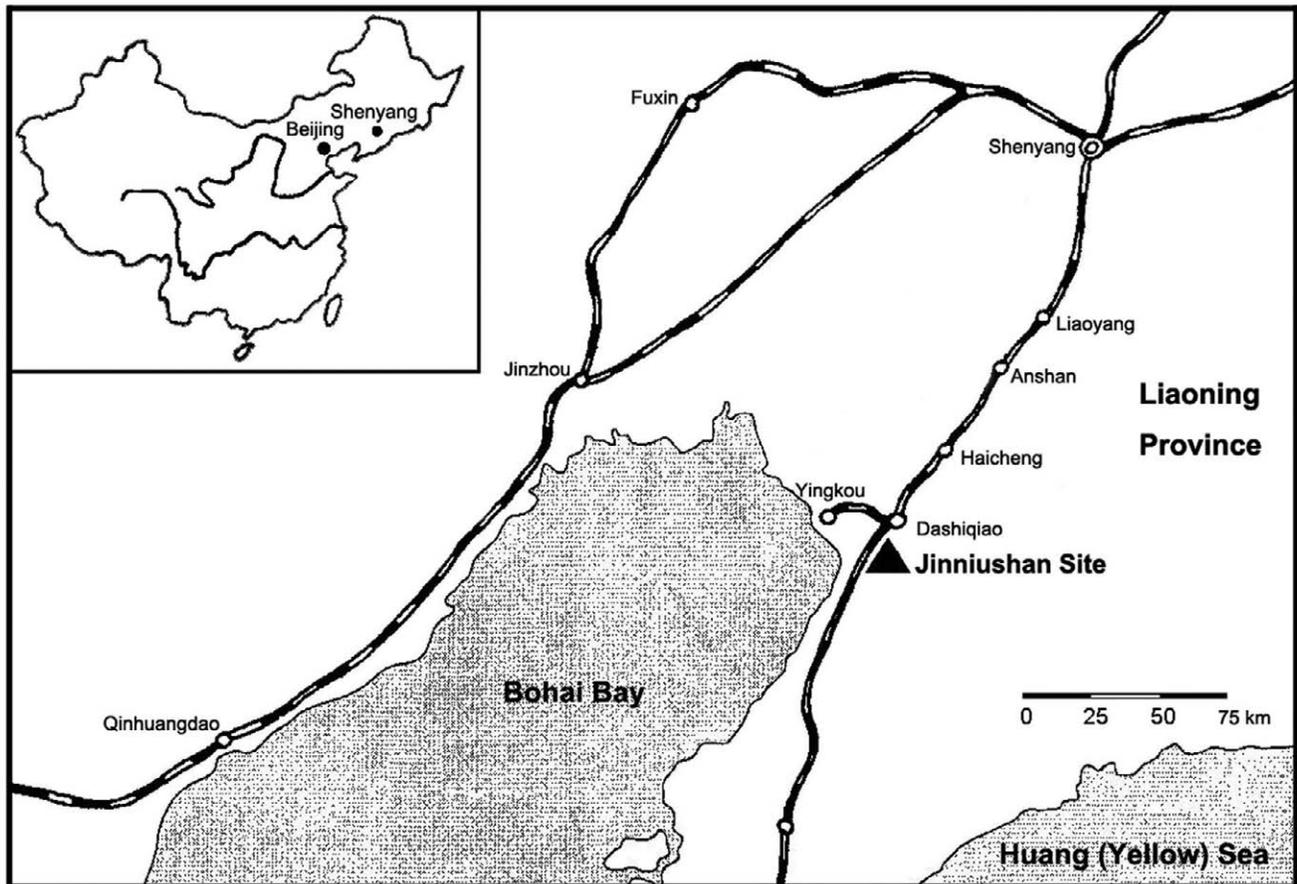

Fig. 1. Geographic location of the Jinniushan site, modified from Lu (2003).

Ciconia maguari 614525M, 614526M, 614528F; *C. ciconia* 605009F, 605011F, 605012, 605013F, 605014, 605016F, 605019, 605020F, 605021F, 430430M, 291559M, 428169M, 18200.

The fossil material is housed in the School of Archaeology and Museology, Peking University, China (SAM). Osteological terminology follows that of Baumel and Witmer (1993). Measurements of the cranium, humerus, and proximal phalanx of the major digit were taken with a caliper to the nearest 0.1 mm. Selected measurements are presented in scatter plots (Figs. 2 and 3).

SYSTEMATIC PALEONTOLOGY

Ciconiiformes Bonaparte, 1854
Ciconiidae Gray, 1840
Leptoptilini Kahl, 1971
Leptoptilos Lesson, 1831

Taxonomic remarks.—The new species can be assigned to the taxon *Leptoptilos* by the combination of the following derived characteristics: large cranium with nearly flat dorsal surface; interorbital area broad, upper border of the orbit presents as an oblique straight line in dorsal view; caudal surface of the skull is in a vertical plane; fossa temporalis small and shallow; distal fusion of processus postorbitalis and processus zygomaticus; robust, long humerus with deep fossa m. brachialis; prominent tuberculum supracondylare ventrale and processus supracondylaris dorsalis.

Leptoptilos lüi sp. nov.

Holotype.—SAM 94. J.VIII-13. C-11 (partial cranium; Fig. 4).
Paratypes.—SAM 94. J.VIII-13. C-11 (left humerus, comprising distal end and most of shaft; Fig. 5A–C). SAM 84.YJAT2-15 (nearly complete right proximal phalanx of major digit; Fig. 5D–F).

Locality and horizon.—The specimen was excavated from the limestone cave at Jinniushan site near the town of Yingkou in Liaoning Province (Fig. 1), northeastern China (40°34′40″N, 122°26′38″E). Middle Pleistocene, 260,000 years ago (Lu 2003, Rosenberg et al. 2006).

Etymology.—In honor of Professor Zun-e Lü, an archaeologist at Peking University, in recognition of his major contributions to the finding of Jinniushan Man (Archaic *Homo sapiens*), and the excavation and scientific research of the Jinniushan site over many years.

Measurements of holotype.—Cranium height, 47.4 mm; least distance between temporal fossae, 50.0 mm; width at postorbital process, 84.0 mm; width at temporal fossa, 57.6 mm; least distance between temporal fossae, 50.0 mm.

Measurements of paratypes.—Humerus: preserved length, 195 mm; midshaft width, 25.5 mm; midshaft depth, 22.2 mm; transverse width of distal end, 56.9 mm; condylus dorsalis length, 25.6 mm; condylus dorsalis depth, 29.1 mm; condylus ventralis depth, 27.9 mm. Phalanx proximalis digiti majoris: length, 67.7 mm; maximal width, 22 mm; proximal width (dorsoventrally), 16.5 mm; distal width (dorsoventrally), 11.1 mm.

Differential diagnosis.—The humerus and the proximal phalanx of the major digit of *L. lüi* are the largest and most robust compared with corresponding elements of extant and fossil species (Figs. 2 and 3). Apart from its large size, the new species is distinguished from extant *Leptoptilos* spp. in having the lamina parasphenoidalis situated lower compared with the condylus occipitalis, the processus postorbitalis and zygomaticus projecting more laterally, and the fossa subtemporalis on the cranium being larger. The humerus is characterized by a ventral enlargement of the epicondylus ventralis, a more pronounced distal projection of
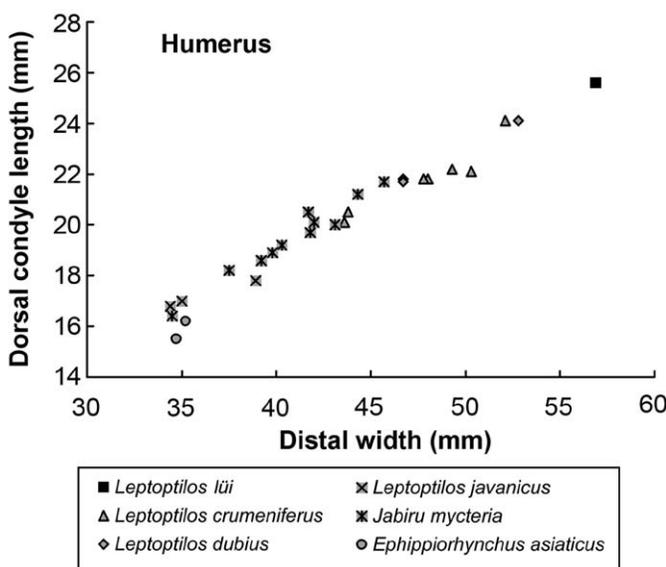

FIG. 2. Scatter plots showing the distal width and dorsal condyle length of the humerus of *Leptoptilos lüi* sp. nov. and extant Leptoptilini.
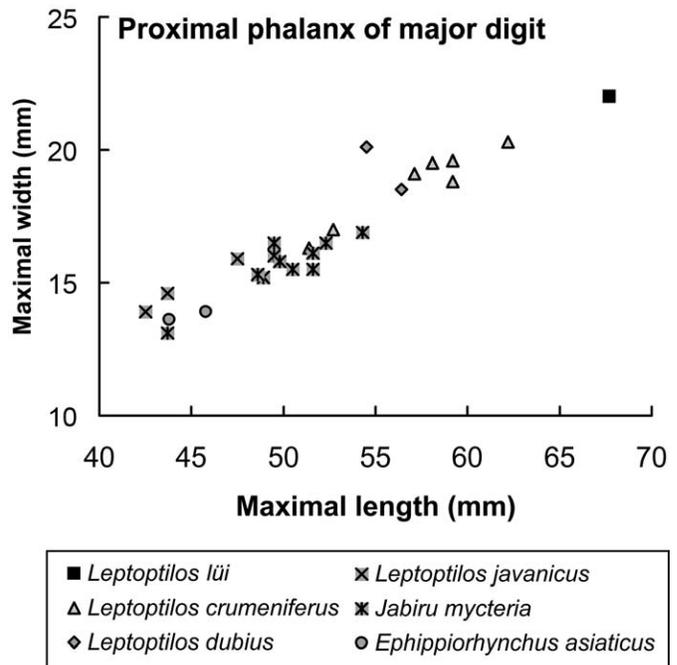

FIG. 3. Scatter plots showing the maximal width and length of the proximal phalanx of the major digit of *Leptoptilos lüi* sp. nov. and extant Leptoptilini.
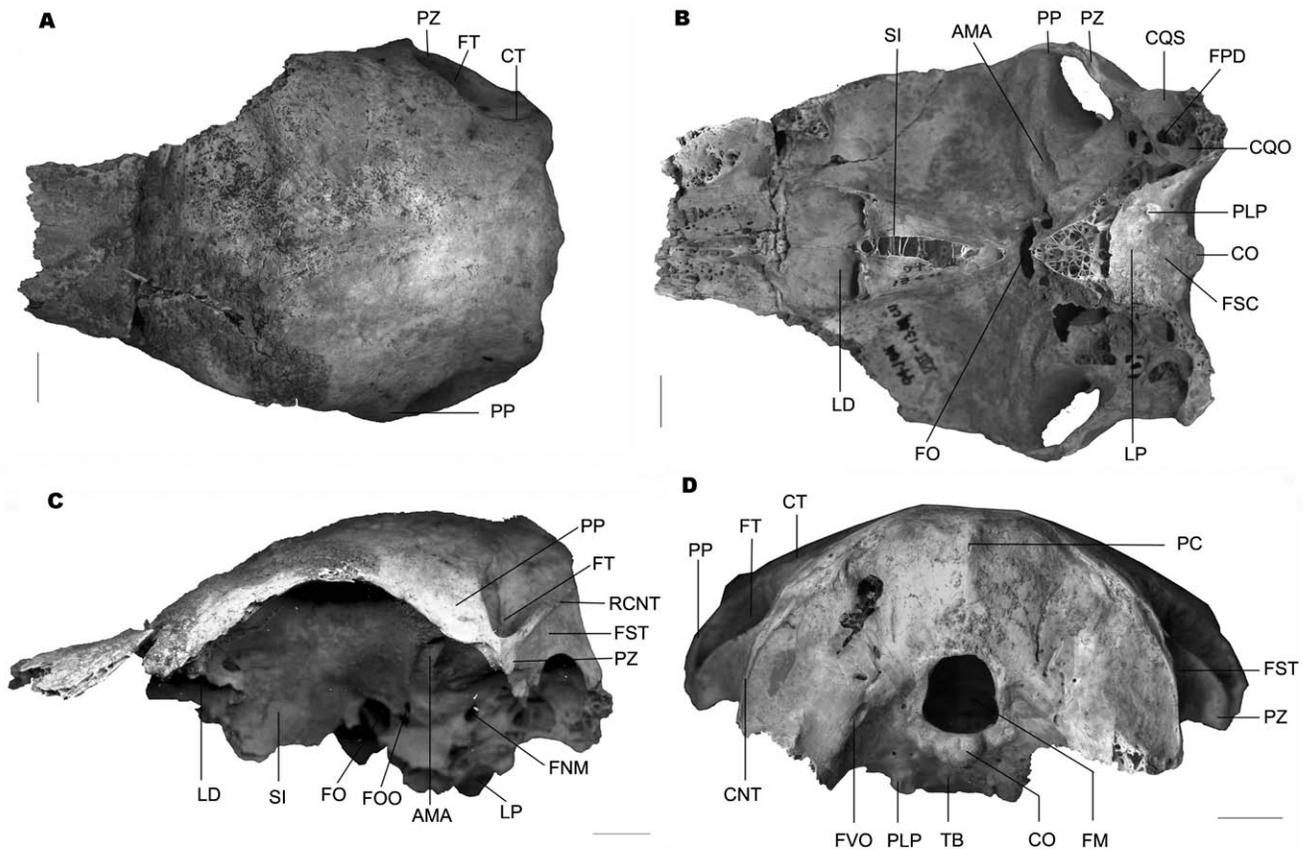
Fig. 4. Cranium of *Leptoptilos lüi* sp. nov. in (A) dorsal, (B) ventral, (C) lateral, and (D) caudal views. Abbreviations: AMA = area muscularis aspera, CNT = crista nuchalis transversa, CO = condylus occipitalis, CQO = cotyla quadratica otici, CQS = cotyla quadratica squamosi, CT = crista temporalis, FPD = foramen pneumaticum dorsale, FM = foramen magnum, FNM = foramen nervi maxillomandibularis, FOO = foramina nervi ophthalmici and nervi oculomotorii, FO = foramen opticum, FSC = fossa subcondylaris, FST = fossa subtemporalis, FT = fossa temporalis, FVO = foramen venae occipitalis externae, LD = lamina dorsalis, LP = lamina parasphenoidalis, PC = prominentia cerebellaris, PLP = processus lateralis parasphenoidalis, PP = processus postorbitalis, PZ = processus zygomaticus, RCNT = rostral branch of crista nuchalis transversa, SI = septum interorbitale, and TB = tuberculum basilare. Scale bars = 1 cm.

the processus flexorius, and a more prominent dorsal edge of sulcus scapulotricipitalis.

In contrast to *Leptoptilos lüi*, the humerus of *L. patagonicus* is less expanded distally, with a much smaller transverse width (46.2 mm); the proximal surface of condylus ventralis seems more convex and the depression between it and the tuberculum supracondylare ventrale is broader; the long axes of the condylus ventralis and condylus dorsalis are nearly the same length. The distal humerus of *L. falconeri*, apart from its small size (transverse width from the tuberculum supracondylare dorsale to the epicondylus ventralis is 52.1 mm), is different from *L. lüi* in having a broader groove between tuberculum supracondylare ventrale and condylus ventralis (Harrison 1974), and the proximal tip of the condylus dorsalis pointing cranioventrally, not ventrally. The phalanx proximalis digiti majoris of *L. falconeri* is much narrower than that of *L. lüi*. The preserved humeral shaft of *L. pliocenicus* cannot be compared directly with *L. lüi*, but the former species is now considered synonymous with *L. falconeri* (Louchart et al. 2005). Comparisons between the new species and the Pleistocene *L. titan* and *L. robustus* are not possible, owing to lack of overlap

in the preserved skeletal elements. We note, however, that, judging from the preserved elements, the new species appears to be larger than *L. titan* and *L. robustus*.

Description.—The roof of the cranium is relatively flat, short, and broad (especially in the interorbital area) in dorsal view (Fig. 4A). The upper border of the orbit is slightly oblique and extends gradually laterally from the rostral to distal end in dorsal view. The lacrimal is not completely preserved but appears to have been flat and joined solidly with the frontal. The ectethmoid is plate-like. The lateral and caudal margins of the lamina dorsalis are strongly raised and are pierced by a large and oval foramen at the corner where the two edges meet. There is no sulcus nervi olfactorii in the upper part of the septum interorbitale. Fonticuli interorbitales are absent. Ventral of the processus postorbitalis, there is a pronounced and well-defined groove between the orbit and the fossa temporalis (Fig. 4B, C). This structure was interpreted as the area muscularis aspera by Baumel and Witmer (1993) or as the orbital and postorbital crests by Zusi and Storer (1969) and can be observed in all storks. The groove is relatively broad, with its cranial border lower and less developed than the caudal crest in *L. lüi*.
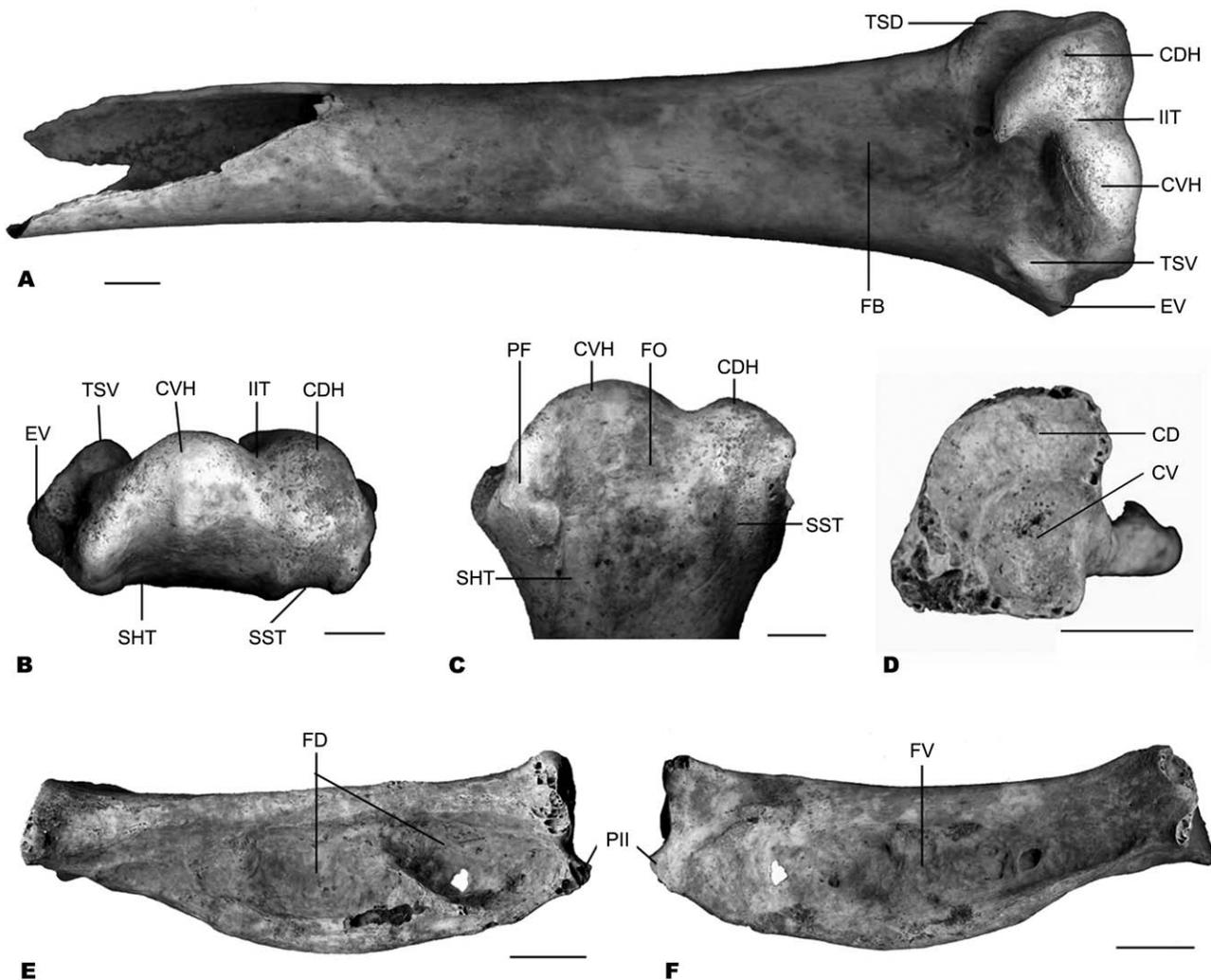
FIG. 5. Humerus of *Leptoptilos lüi* sp. nov. in (A) cranial, (B) distal, and (C) caudal views; and phalanx proximalis digiti majoris in (D) proximal, (E) dorsal, and (F) ventral views. Abbreviations: CD = cotyla dorsalis, CDH = condylus dorsalis humeri, CV = cotyla ventralis, CVH = condylus ventralis humeri, EV = epicondylus ventralis, FB = fossa m. brachialis, FD = fossa dorsalis, FO = fossa olecrani, FV = fossa ventralis, IIT = incisura intercondylaris, PF = processus flexorius, PII = processus internus indicis, SHT = sulcus humerotricipitalis, SST = sulcus scapulotricipitalis, TSD = tuberculum supracondylare dorsale, and TSV = tuberculum supracondylare ventrale. Scale bars = 1 cm.

The foramen nervi maxillomandibularis is large and positioned ~10 mm caudoventral to the base of the area muscularis aspera (Fig. 4C). The cotylae quadraticae otici and squamosi are separated by the large foramen pneumaticum dorsale, and the latter cotyla is larger and more concave than the former (Fig. 4B). Although the base of the cranium is not completely preserved, it is clear that lamina parasphenoidalis is much lower than condylus occipitalis, thus resulting in the presence of a marked fossa subcondylaris (Fig. 4B); these are autapomorphic characters for *L. lüi*. The condition found in extant species of Leptoptilini differs in that condylus occipitalis and lamina parasphenoidalis lies in the same plane, separated by a shallow and small fossa subcondylaris. There is no fossa parabasalis on the external skull base as in all extant storks, so the foramina for cranial nerves IX and X, and for the carotid and ophthalmic arteries, are loosely separated from each other in this region.

The processus postorbitalis is prominent with a blunt distal end, which fuses with the processus zygomaticus (Fig. 4B–D); this derived condition is only found in *Leptoptilos* among extant storks and supports assignment of the fossil to this genus. The processus postorbitalis of *L. lüi* projects more laterally rather than ventrally, and thus results in a broader cranium in dorsal and caudal views, whereas it points nearly ventrally in extant species of *Leptoptilos* (Figs. 4A, D and 6). The fossa temporalis is more restricted and shows less concavity in all the species of *Leptoptilos*, both extant and fossil, than in *Jabiru* and *Ephippiorhynchus*. It is fully or partially exposed in dorsal view in *L. lüi* and *L. dubius*, respectively, and completely concealed in *L. crumeniferus* and *L. javanicus*. The
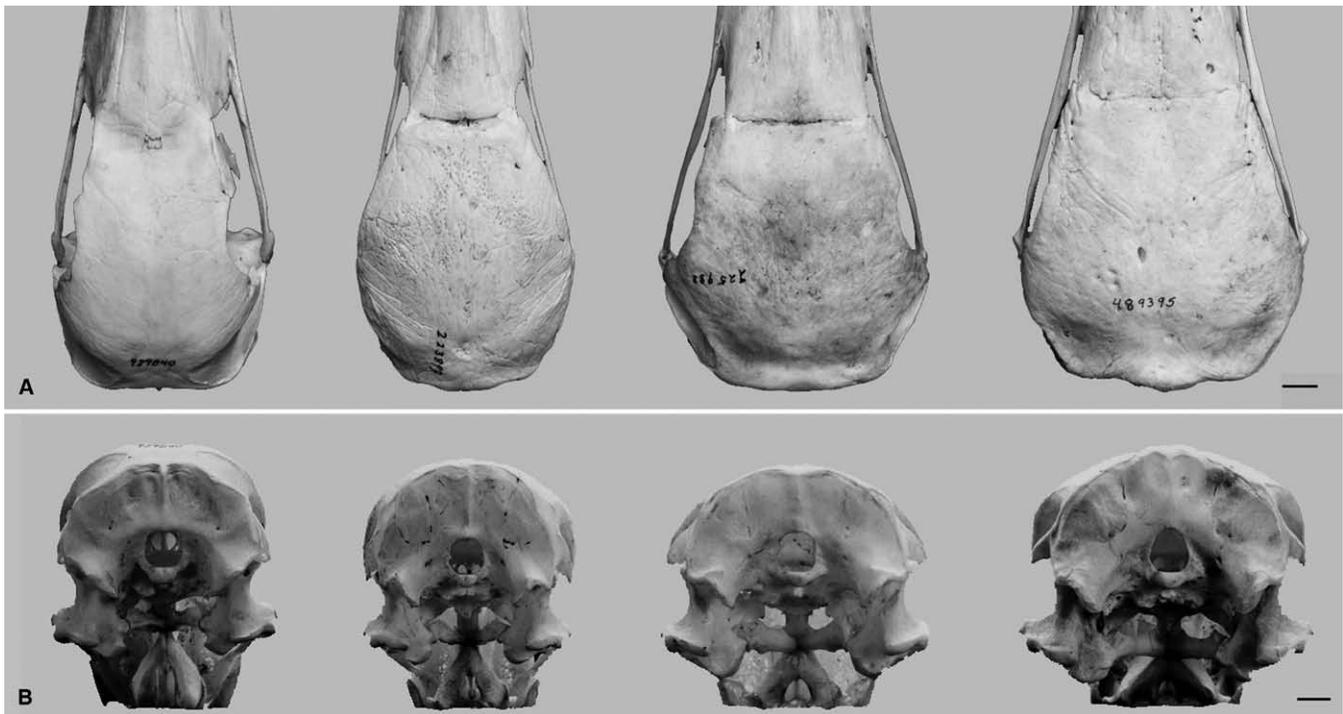
Fig. 6. (A) Dorsal and (B) caudal views of the crania of extant *Leptoptilos* and *Jabiru*. From left to right: *Jabiru, L. javanicus, L. dubius,* and *L. crumeniferus*. Scale bars = 1 cm.

crista temporalis is well separated from the median line of the cranium. In general, the morphology of the temporal area in *L. lüi* is most similar to *L. dubius*. The crista nuchalis transversa is well defined and bifurcates (Fig. 4C). The fossa subtemporalis is shallow, but larger than in extant species of *Leptoptilos*. The processus suprameaticus, although not completely preserved, curves gently as in *L. dubius* and *L. javanicus*. Mainly because of the poorly developed prominentia cerebellaris, the caudal surface of the cranium is roughly flat and lies in a vertical plane; these are apomorphic characteristics for genus *Leptoptilos*.

The distal half of the left humerus (Fig. 5A–C) is well preserved. The fossa m. brachialis is deep, broad, and extends more proximally; caudal to it are several pneumatic foramina. In cranial view (Fig. 5A), the condylus dorsalis tapers gradually from distal to proximal and projects proximo-ventrally, forming an acute angle with the axis of the humeral shaft. Its proximal tip points ventrally and does not reach the caudal border of the fossa m. brachialis. Both the distal humeral width and the dorsal condyle length of *L. lüi* are the largest among the species compared (Fig. 2). The condylus ventralis is oriented dorsoventrally, with its long axis nearly perpendicular to, and slightly longer than, that of the condylus dorsalis. The incisura intercondylaris is shallow and V-shaped in caudal view. The epicondylus ventralis is well developed, extending more ventrally and lying proximally to the epicondylus dorsalis and the condylus ventralis. The tuberculum supracondylare ventrale is larger than in the other species compared and projects more craniodorsally, thus resulting in a deeper depression between it and the condylus ventrale. The epicondylus dorsalis is compressed ventrodorsally, with its caudal surface being coplanar with that of the condylus dorsalis. Proximal to the epicondylus dorsalis, the tuberculum supracondylare dorsale is represented by a strong, craniodorsally projecting crest, which forms a moderate angle with the dorsal margin of the humeral shaft. The scars for the attachment of muscles and ligaments are obvious and deep at the distal end. In caudal view (Fig. 5C), the processus flexorius is an elongated triangle in outline; it is longer than in all extant Leptoptilini, but nevertheless it projects less distally than either of the condyles. The widths of the sulcus scapulotricipitalis and the sulcus humerotricipitalis are nearly the same, but the latter groove is comparatively shallow, continuous with the olecranon fossa. The distal end of the dorsal edge of sulcus scapulotricipitalis is relatively high and protrudes more distally, forming a sharp transition with the caudal surface of epicondylus dorsalis.

The phalanx proximalis digiti majoris of. *L. lüi* (Fig. 5D–F) is distinctly larger than the corresponding bone of living species of Leptoptilini (Fig. 3). The ventral side of its proximal end bears a distinct, large tuberculum, which serves for the insertion of M. flexor digitorum superficialis (Livezey and Zusi 2006). There is a sub-longitudinal, faint groove on its dorsal surface, which projects craniodorsally from proximal to distal. There is also another tendinal groove on the dorsum of the caudal border of this phalanx. Although a processus internus indicis is not completely preserved, it is clear that it projects farther beyond the facies articularis phalangealis as in extant Leptoptilini. The fossa ventralis exhibits several pneumatic foramina at the proximal and central parts. The fossa dorsalis is divided by an oblique bulge into two
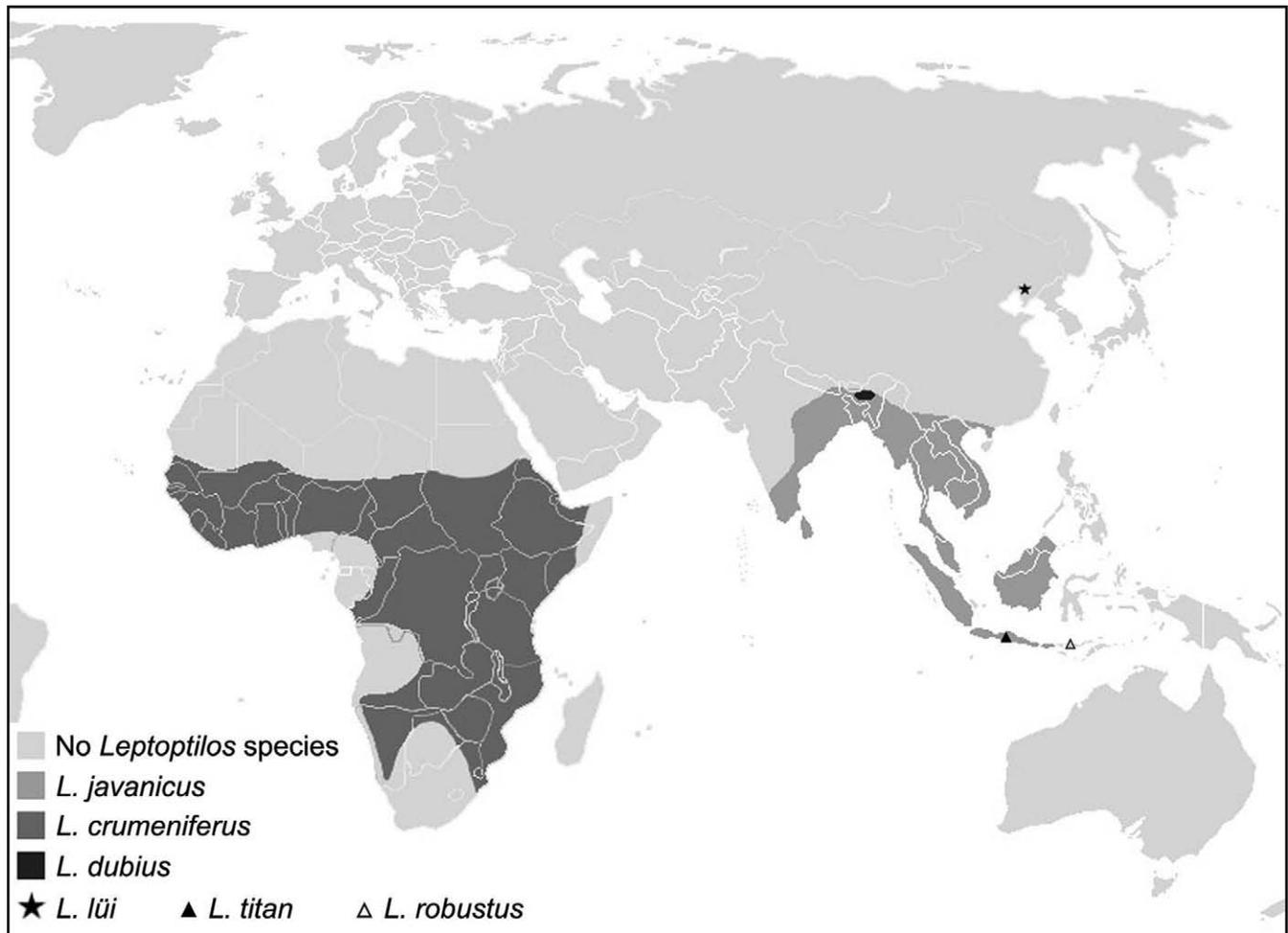
FIG. 7. Distribution map of extant and Pleistocene *Leptoptilos*.

fossae as in other storks; the distal subfossa is smaller and deeper than the proximal one. Facies articularis phalangealis bears a pneumatic foramen in its central part.

DISCUSSION

Unlike the island marabou *L. robustus*, which may have been flightless in response to the insular environment of Flores (Meijer and Due 2010), the large marabou reported here is presumed to have possessed considerable flight capability, similar to living species of *Leptoptilos*, as indicated by well-pneumatized bones and the thin walls of the shaft of the long limb bones (Currey and Alexander 1985).

Sediments and the mammalian fauna indicate that the climate of the Jinniushan site 260,000 years ago was warmer and wetter than at present, and the predominant habitats were woodland to open grassland plain (Jinniushan Lianhe Fajuedui 1976, Rosenberg et al. 2006). These conditions are favorable to the development of thermal air currents that enable some birds to soar for long distances. Like living species of *Leptoptilos* (Kahl 1966, Hancock et al. 1992), *L. lüi* probably relied primarily on soaring or gliding rather than flapping flight for movement and food seeking.

The shallower and more constricted fossa temporalis in *L. lüi* resembles other *Leptoptilos*, but differs from *Jabiru* and *Ephippiorhynchus* and suggests that *L. lüi* was mainly a scavenger, whereas *Jabiru* and *Ephippiorhynchus* forage in shallow water and catch small fish for food. By analogy with modern *Leptoptilos*, *L. lüi* may have been associated with vultures and other scavengers during the non-breeding season, and it possibly fed on carrion of *Equus sanmeniensis*, *Megaloceros pachyosteus*, *Dicerorhinus mercki*, *Bison* spp., *Cervus* spp., and *Gazella* spp. (Hancock et al. 1992). The occurrence of *Trogontherium* reveals the existence of aquatic habitat, where *L. lüi* could have preyed on fish, frogs, and crustaceans during the breeding season, for the essential calcium requirements of the fast-growing young (Hancock et al. 1992).

All living species and reported Pleistocene representatives of *Leptoptilos* are distributed in tropical Africa and Asia (Fig. 7), and none in northern China. Our study of *L. lüi* extends the biogeographic distribution of the genus into higher latitudes, and a different biome, during the Pleistocene. The disappearance of *L. lüi* was likely a result of Pleistocene megafaunal extinctions and climate change to colder and drier conditions.

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