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A Review of the Australian Fossil Storks of the Genus *Ciconia* (Aves: Ciconiidae), With the Description of a New Species

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ABSTRACT. Only a single species of stork, the Black-necked Stork *Ephippiorhynchus* (= *Xenorhynchus) asiaticus*, occurs in Australia today, and is known from several fossil localities from the Early Pliocene. Two species of smaller fossil storks are also known, one previously named and one described here. The former, found in the Darling Downs, southeastern Queensland, was named *Xenorhynchus nanus* De Vis, 1888. Some later authors suggested that this species should be transferred to the living genus *Ciconia*; this decision is confirmed here, the name for this species becoming *Ciconia nana*. The second species of small stork comes from several Late Oligocene and Early Miocene sites at Riversleigh, northwestern Queensland. This taxon is referred to the genus *Ciconia* and distinguished as a new species, *C. louisebolesae*. It constitutes the earliest record of the Ciconiidae from Australia.

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The classification of living storks (Ciconiidae) by Kahl (1979) admitted 17 species in six genera in three tribes, whereas that of Hancock *et al*. (1992) recognized 19 species in six genera in two tribes. The family is represented in Australia by a single living species, the Black-necked Stork, or Jabiru, *Ephippiorhynchus* (= *Xenorhynchus* auct.) *asiaticus* (Latham, 1790).

Storks are rather well represented in the world fossil record, although no comprehensive review of them has been attempted. The earliest records come from the Late Eocene of Egypt (Ciconiidae gen. and sp. indet. and *Leptoptilos* sp. indet.) (Miller *et al*., 1997). After taxa incorrectly referred to this family were removed (Olson, 1985), the earliest named species became *Palaeoephippiorhynchus dietrichi* Lambrecht, 1930 (Late Oligocene; Egypt). The identity of the older *Eociconia sangequanensis* Hou, 1989 (Middle Eocene; China) as a stork needs to be confirmed (Unwin, 1993). Other Tertiary-aged storks are known from North America, Europe and Asia (references in Olson, 1985; Bickart, 1990). Quaternary-aged palaeospecies are known for several extant genera.

The fossil record of this family in Australia has not been studied in detail. Much of the Australian fossil stork material is comparable in size and morphology to *E. asiaticus*. Specimens assigned to this species are known from Pliocene and Pleistocene localities in northeastern and southeastern Queensland and northeastern South Australia (Archer, 1976; Baird, 1991a; Boles & Mackness, 1994; Molnar & Kurz, 1997; Vickers-Rich, 1991).

The first stork reported from Australia was described by C.W. De Vis, who named several species (De Vis, 1888, 1892, 1905); however, all but *Xenorhynchus nanus* are now known to have been misidentified to family (amended family identifications summarized by van Tets & Rich, 1990). Material of a new species of stork from Oligo-Miocene deposits at Riversleigh, northwestern Queensland, was mentioned briefly in the literature with little elaboration (Boles, 1991, 1997; Vickers-Rich, 1991). It is the purpose of this study to review *X. nanus* and the undescribed Riversleigh stork. Both are here considered to belong to the extant genus *Ciconia*. This genus has an extensive fossil record. Three of the living species of *Ciconia* have been recorded from Quaternary deposits (Brodkorb, 1963). Several fossil taxa have been assigned to *Ciconia*, but many are based on single specimens. A large, but unnamed species of *Ciconia* from the Late Miocene-Early Pliocene of Arizona is known from numerous skeletal elements (Bickart, 1990), as is another large form, *C. maltha* L. Miller, 1910, from the Quaternary of North America and Cuba (Miller, 1910; Howard, 1942; Feduccia, 1967). Other palaeospecies include *C. stehlini* Jánossy, 1992 (Early Pleistocene, Hungary, tarsometatarsi, tibiotarsi, ulna, phalanges), *C. gaudryi* Lambrecht, 1933 (Late Pliocene of Greece, humerus), *C. minor* Harrison, 1980 (Late Miocene, Kenya, distal femur) and *C. sarmatica* Grigorescu & Kessler, 1977 (Late Miocene, Romania, proximal carpometacarpus). Lambrecht (1933) cited records of indeterminate species of *Ciconia* from the Pleistocene of California and Late Pliocene of France, and Olson & Rasmussen (2001) recorded two indeterminate species from North Carolina, one Middle Miocene in age, the other Early Pliocene. Late Pleistocene or Quaternary reports of this genus include those by Ono (1984; Honshu, Japan; *Ciconia* sp.), Steadman *et al.* (1994; northeast Mexico; *Ciconia* sp. or *Mycteria* sp.) and Suarez & Olson (2003; Cuba; *Ciconia* sp.).

Species of *Ciconia* and *Mycteria* are rather generalized in their morphology compared to the large, long-legged *Ephippiorhynchus* and *Jabiru*, the heavy-bodied *Leptoptilos* and somewhat aberrant *Anastomus*. Any fossil stork remains not exhibiting characters of these more distinctive genera were frequently allocated to one of the more "typical" ones. The problem of deciding whether a fossil form based on single or fragmentary elements has been correctly assigned to genus is compounded by the heavy reliance by the current taxonomy on behavioural (Kahl, 1972, 1979; Slikas, 1998) or molecular characters (Slikas, 1997).

Materials and methods

Taxonomic nomenclature follows Kahl (1979). Osteological terminology follows Baumel & Witmer (1993), except that as terms of position and direction anterior is used rather than rostral or cranial and posterior rather than caudal. Most of the measurements follow the methods of Steadman (1980) or van den Driesch (1976), and were made with digital calipers and rounded to the nearest 0.1 mm.

Several factors hamper the ease of using the fossil record of storks from elsewhere for evaluating that of Australia. Generic-level taxonomy of the Ciconiidae has changed substantially, with several formerly monotypic genera now merged with others. New palaeogenera were often based on material that exhibited some morphological intermediacy between two nominal genera that have since been synonymised; this is particularly so in the expanded concept of *Ciconia*. The more inclusive generic concepts result in a broader morphological range across the constituent species, into which the palaeospecies may fit comfortably. Published diagnoses of such fossil forms must be assessed with caution because some of the characters may no longer apply to the genus *sensu lato*.

Another difficulty is that many of the species of fossil storks have been based on isolated fragments, confounding comparison between nominal taxa for which common osteological elements are not known. Moreover, many extant taxa are poorly represented in skeletal collections and of those specimens that do exist, individuals from zoos form a high proportion. In addition to any developmental abnormalities the latter may have, most likewise lack provenance and are frequently unsexed.

Osteological diagnosis of Ciconiidae

The skeletal elements can be recognized as belonging to this family on the basis of the following suites of characters. Diagnoses are restricted to those portions of the elements represented by the fossils, both here for the family and subsequently for generic level taxa in the respective species accounts.

Cranium. The lateral indentations at the orbits are shallow (in dorsal view); fossae glandulae nasalis are absent. The processus postorbitalis is long, and the temporal fossae well defined and rather extensive posteriorly. There is a single small circular fontanelle orbitocranialis situated at the posterior border of septum interorbitalis where it joins the braincase.

Quadrate. The anterior and posterior borders of the blade-like processus orbitalis are straight or slightly tapering through most of its length. The process is more or less straight (in posterior view) but not strongly flattened, with the distal end somewhat inflated; it is not incised posteriorly, twisted nor inflected medially or ventrally. The processus oticus is broad and not compressed laterally; the processus mandibularis is deep mediolaterally (in ventral view). The condylus medialis and combined condyli lateralis and caudalis are long and thin, and converge laterally at an acute angle; the sulcus intercondylaris is moderately large, particularly on its medial half. The short, broad projection of the condylus lateralis extends anteriorly along the lateral side, at its anterior end supporting the cotyla quadratojugalis, which is located just above the posteroventral border of the element; the part of the projection between the cotyla and the posterior end of the quadrate comprises about half of its length.

Humerus. The element has a pronounced sigmoid curvature, with a particularly marked anterior bend in the distal end (in dorsal view). *Proximal end*. In anterior view, the long axis and distal border of the caput humeri are oriented dorsodistally-ventroproximally; the caput humeri is moderately short. The sulcus ligamentum transversus and incisura capitis are deep. The tuberculum dorsale is distinct and triangular. The fossa pneumotricipitalis is large. The distal margin of the crista bicipitalis forms a nearly right angle with the shaft. The intumescentia humeri is inflated, particularly distally. The crista deltopectoralis is prominent, with its apex more or less level with the distal end of the crista bicipitalis. *Distal end*. The fossa musculus brachialis is large and deep, particularly ventrodistally, and is angled sharply dorsoproximally-ventrodistally relative to the shaft. The tuberculum supracondylare ventrale is elongate and situated along a prominent ridge. The epicondylus ventralis is strongly produced as a triangular projection. The epicondylus dorsalis and processus flexorius are rudimentary. The ventral side of the distal end is flat (in anterior view) with the processus supracondylare dorsalis prominent, angling moderately to very abruptly to shaft. The fossa olecrani is broad and shallow, and extends proximally from, and dorsoventrally across, the condylus ventralis humeri.

Ulna. *Proximal end*. The proximal end is straight in relation to the shaft, i.e. there is no inflection from the midline of the shaft. The margins of the impressio m. brachialis are pronounced, with the anterior margin the more extensive distally. The tuberculum lig. collateralis ventralis is slightly bulbous but does not overhang the impressio m. brachialis and has a relatively short distal extension along its border. The incisura radialis is more proximodistally oval (narrower, longer) than circular and the impressio m. scapulotricipitalis is small with little distal extension.

Tibiotarsus. *Proximal end*. The proximal end is deeper than wide because the region level with the incisura tibialis between the cristae cnemialis and the facies articularis is elongated. The surface is mostly level, with a small to at most moderate rise towards the cristae cnemialis. The cristae cnemialis are not strongly developed proximally, but are rather broad (in proximal view). They form a more or less 90° angle, and from this junction, the crista cnemialis lateralis is about twice the length of the crista cnemialis cranialis. The crista cnemialis cranialis is situated towards, but not at, the medial edge, with only a slight indentation separating them; it is long distally, angling smoothly into the shaft (in medial view). There is an expanded articular surface at the end of the crista cnemialis lateralis with a flattened anterolateral face, which projects both anteromedially and posterolaterally (in proximal view). *Distal end*. The shaft is long, thin and straight, with the posterior surface rounded and the anterior surface flattened for most of its length, taken up by a very broad and shallow sulcus extensorius, which deepens for a short extent just proximal of the pons supratendineus. There is a large, prominent papilla for M. tibialis cranialis centred directly proximal to the area intercondylaris and level with the distal border of the pons supratendineus. The pons supratendineus is restricted to the medial half of shaft, with its distal border strongly developed into a ridge. The scar on the lateral face of the shaft is large and proximodistally elongated. The sulcus m. fibularis is moderately deep. The distal end of the element has little mediolateral expansion, and the medial border of the shaft does not flare strongly outwards proximal to the condylus medialis. The condyli lateralis and medialis are more or less parallel and directly distal to the respective borders of the shaft, are longer anteroposteriorly than proximodistally, and have about the same distal extension; the condylus lateralis extends further proximally. The condylus medialis is notched distally. The area intercondylaris is a deep circular pit centred on the midline of shaft, extending between the pons supratendineus and the condylus medialis. The sulcus intercondylaris is deep (in distal view) and the trochlea cartilaginis tibialis is shallow with prominent borders.

Tarsometatarsus. *Proximal end*. The eminentia intercotylaris is narrow, with the lateral border abrupt and the medial one sloping (in dorsal view). In proximal view, the rims of the cotylae are rounded and (in dorsal view) the medial rim of cotyla medialis is blunt or rounded. The hypotarsi comprises two parallel cristae hypotarsi separated by a single large sulcus hypotarsi, which is deep throughout its length; it is centred mediolaterally on the plantar face. There is no small secondary groove within the sulcus hypotarsi. *Distal end*. The sulcus extensorius occupies the greater part of the length of the anterior surface, making the distal third of the shaft relatively flat, and then angling from the midline of the shaft to the lateral side at the distal end, extending into the foramen vasculare distale but not beyond that into the incisura intertrochlearis lateralis. The fossa metatarsi I is a long proximodistally elongated oval, terminating distally on a ridge extending towards the trochlea metatarsi II. The fossa supratrochlearis plantaris is markedly excavated lateral to this ridge. The trochleae are not inflated proximally nor do they join the shaft abruptly; the shaft bulges laterally just proximal to the trochlea metatarsi IV, meeting it with relatively little demarcation. The trochleae form a shallow but obvious curve (in distal view). The trochleae metatarsi II and IV are more or less equal in length and shorter than trochlea metatarsi III.

Genus *Ciconia* Brisson, 1760

Ciconia Brisson (1760). *Ornithologia sive Synopsis Methodica*, 1: 48, 361—type species: *Ciconia* = *Ardea ciconia* Linnaeus, 1758.

In the original concept of *Ciconia*, the genus comprised two species, *C. ciconia* Linnaeus, 1758 (Eurasia, Africa) and *C. nigra* Linnaeus, 1758 (Eurasia, Africa). The generic limits were expanded by Kahl (1979) and Wood (1983, 1984) to incorporate three species that were long kept in monotypic genera: *(Sphenorhynchus) abdimii* Lichtenstein, 1823 (Africa), *(Dissoura) episcopus* Boddaert, 1783 (Africa, southern Asia), and *(Euxenura) maguari* Gmelin, 1789 (South America). This has considerably expanded the size range of the species in both directions and added variability in the morphology.

The represented elements can be diagnosed as *Ciconia* and separated from those of other genera of storks by the following suites of characters:

Cranium. Most of the characters on which a generic diagnosis might be based are missing in the fossil. It does permit separation from *Ephippiorhynchus* by having the fossae temporalis moderately shallow and moderately concealed by the cristae temporalis, rather than deep and unconcealed (in dorsal view); the nuchal area (supraoccipital) is slightly convex around the prominentia cerebellum, rather than somewhat concave; and the crista nuchalis transversus is low and does not project posteriorly beyond the extent of the prominentia cerebellum. In these characters, the fossil agrees with *Ciconia*.

Quadrate. The processus oticus is thin (in lateral view). The processus orbitus is thin. The sulcus between the processus mandibularis and condylus pterygoideus is moderately deep. The processus mandibularis is markedly longer mediolaterally than anteroposteriorly, the condyli form an acute angle and the sulcus intercondylaris is relatively narrow.

Humerus. The tuberculum ventrale is situated distal to the caput humeri. The fossa pneumotricipitalis does not extend proximally well beyond the attachment for M. scapulohumeralis caudalis nor as far distally past the midpoint of the crista bicipitalis. The intumescentia humeri is moderately inflated distally. There is a slight notch where the distal end of the crista bicipitalis joins the shaft, but the sulcus nervus coracobrachialis is obsolete. The impressio m. coracobrachialis is flat, not depressed. The dorsal edge of the crista deltopectoralis is generally straight, not concave. The attachment for M. scapulohumeralis cranialis is situated at the proximal end of the linea m. latissimus dorsi rather than ventral to it and directly distal to the fossa pneumotricipitalis. In dorsal view, the dorsal side of the shaft posterior to the condylus dorsalis is shallow, with the anterior and posterior sides straight and roughly parallel, forming a rectangular surface; the anterior face of the shaft meets anteroproximal corner of the processus supracondylaris dorsalis gradually; and the tuberculum supracondylare dorsale is not strongly developed. The epicondylus ventralis is moderately produced (in anterior view). The scar for M. pronator profundus is moderately short and shallow and that for M. flexor carpi ulnaris is moderately small; thus the area of the ventral side distal to the epicondylus ventralis is not markedly excavated (in ventral view) and the epicondylus ventralis is less undercut (in anterior view). The sulcus humerotricipitalis is moderate in width. The condylus ventralis humeri extends further distally relative to the condylus dorsalis humeri (in anterior view); in distal view, its posterior surface faces more posteriorly and less distally. The ventrodistal corner, distal to the epicondylus ventralis, is only slightly to moderately excavated.

Ulna. The condition of the ulnar fragment considered in this study is not suitable for useful comparisons between taxa. This element is not diagnosed further.

Tibiotarsus (taken in part from Howard, 1942 and Olson, 1991). There are limited characters of the proximal end that are useful in separating the genera of storks, and most of these are related to the angles and extent of the cristae and articular surfaces. On the distal end, the tuberculum retinaculi m. fibularis proximal to the condylus lateralis forms a prominent triangular ridge, which is pointed proximally and broadens distally (prominent papilla in *Ephippiorhynchus*); the proximomedial corner of the condylus lateralis is not incised by expansion of the area intercondylaris; the proximomedial border of the condylus medialis lacks a prominent round fossa; the posterior sides of the condyli extend prominently and are more oval than circular (in lateral view); the distal border of pons supratendineus is horizontal (tilted or arched in *Ephippiorhynchus*); the distal opening of the canalis extensorius is moderately to strongly horizontally elongate (rounded in *Ephippiorhynchus*); and the incisura intercondylaris is broad and relatively flat at its base (in distal view).

Tarsometatarsus (taken in part from Howard, 1942). The hypotarsus is slender relative to the proximal width of the cotylae and to the length of crista hypotarsi lateralis, the longer of the cristae; the cristae hypotarsi are slender. The eminentia intercotylaris is situated on the proximodistal midline rather than medial to it, and the lateral side of its base is only slightly excavated, if at all. The area between the cotylae and the hypotarsus consists of a gradual drop with a pit of moderate depth proximal to the cristae hypotarsi. The ridge leading to the distal end of the hypotarsus is generally low and broad. The cotyla lateralis is elongate; the cotyla medialis much more circular (in proximal view). The trochlea metatarsi II is situated dorsally and is little rotated laterodorsally-medioplantarly. The fossa metatarsi I is flush with the surface of the bone or only slightly elevated.

Ciconia nana (De Vis, 1888)

Fig. 1

Xenorhynchus nanus De Vis, 1888. *Proc. Linn. Soc. N.S.W.* 3: 1287, Qld: Darling Downs: Condamine River: Chinchilla.
Ciconia nana (De Vis, 1888). Rich & van Tets, 1982: 306A; van Tets, 1984: 470; van Tets & Rich, 1990: 166; Vickers-Rich, 1991: 752.

De Vis (1888) based *Xenorhynchus nanus* on material from the Condamine River, near Chinchilla, in the Darling Downs of Queensland. The material comprised a distal tibiotarsus, collected by J. Daniels, and a proximal ulna, a later acquisition but described at the same time. Subsequently De Vis (1905) reported this species from Wurdulumankula, Cooper Creek, South Australia, based on a distal tibiotarsus, collected by Professor J. Gregory. The original tibiotarsal fragment was designated as the lectotype by Brodkorb (1963). Similarities in size and shape to species of *Ciconia* were noted by Rich & van Tets (1982), who provisionally transferred this form to this genus, where it has been listed in subsequent reviews (e.g., van Tets, 1984; van Tets & Rich, 1990; Vickers-Rich, 1991), although no detailed comparisons had been made.

The Darling Downs, southeastern Queensland, feature deposits of two discrete periods. Pleistocene deposits occur on the east side of the Condamine River (26°48'S 150°41'E), producing the Darling Downs Local Fauna (Molnar & Kurz, 1997). The older, Pliocene-aged assemblage, the Chinchilla Local Fauna, which yielded the holotype of *X. nanus*, comes from the fluviatile Chinchilla Sands along the western banks of the Condamine River, near Chinchilla. On the basis of closer faunal resemblances of this fauna to the Early Pliocene Bluff Downs Local Fauna than to the Pleistocene Darling Downs Local Fauna, its age has been put at Early to Middle Pliocene (T. Rich *et al.*, 1991).

Many important specimens from Gregory's trip along Cooper Creek have their locality listed as Wurdulumankula, although no similar place name has been found on Gregory's maps (Gregory, 1906), and the exact location of this site is uncertain (Tedford & Wells, 1990). It is considered to be located in the Piranna Soakage of Cooper Creek, in the eastern Lake Eyre basin, South Australia, and to be one of a number of sites from which fossils of the Malkuni Fauna have been recovered, one of two faunas in the fluviatile deposits of the Katipiri Formation (Tedford & Wells, 1990).

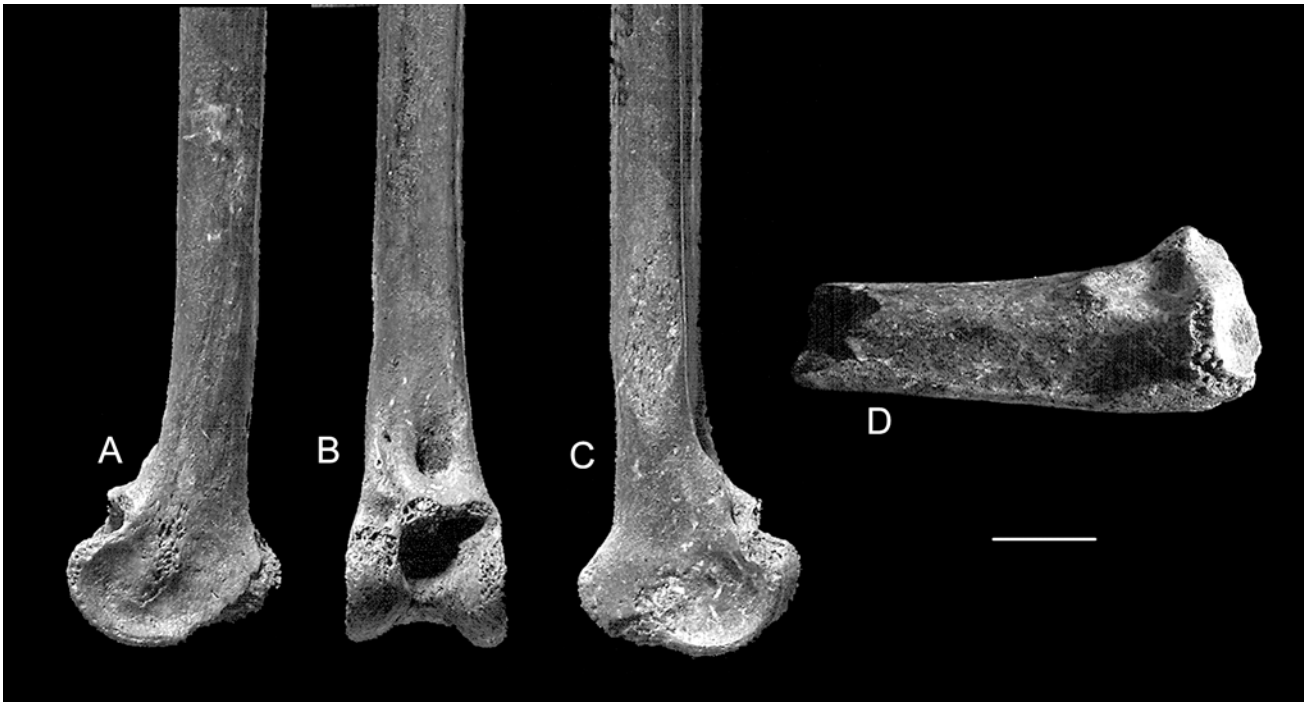

Fig. 1. Specimens of fossil stork *Ciconia nana*. (*A–C*) lectotype (QM F1131), distal right tibiotarsus; (*A*) anterior view; (*B*) lateral view; (*C*) medial view; (*D*) paralectotype (QM F5514), proximal right ulna, anterior view. Scale = 10 mm.

These assemblages represent fluviatile/lacustrine faunas in the Great Artesian basin that predate the formation of inland dunes and are probably Late Pleistocene in age (Woodburne *et al*., 1985). The fossils are found as "float" or in place.

Lectotype. Distal tibiotarsus (QM F1131; Fig. 1a–c; Brodkorb, 1963).

Type locality. North bank of the Condamine River, 5 km from Chinchilla, Darling Downs, Queensland.

Paralectotype. Proximal ulna (QM F5514, Fig. 1d).

Etymology. *Nanus* (Latin, a dwarf), in reference to the small size of this bird in comparison with its putative congener, *E. (X.) asiaticus*.

Diagnosis. *Ciconia nana* is diagnosed from other living species in the genus by the following combination of characters: the anterior extension of the condylus lateralis relative to the condylus medialis is greater; the ridge from the papilla for M. tibialis cranialis to the condylus medialis is only slightly incised by a furrow; and the tuberculum retinaculi m. fibularis is nearly confluent with the lateral border of the shaft (in anterior view).

Of the fossil forms, few can be compared with *C. nana* for lack of common elements. *Ciconia maltha* was much larger (Table 1), as was the unnamed Mio-Pliocene species from Arizona, which Bickart (1990) characterized as a "giant, equalling in size large individuals of the extant *Jabiru mycteria*". The somewhat younger *Ciconia stehlini* had a tibiotarsus of comparable proximal width to *C. nana*. Jánossy (1992) did not provide any characters that serve to separate these species morphologically. Of living species, *C. ciconia* and *C. nigra* are similar to *C. nana* in proximal width of the tibiotarsus but the condyli of *C. nana* are deeper.

Referred material. Distal tibiotarsus (QM F5513), Wurdulumankula, Cooper Creek, South Australia.

Measurements. Table 1.

Description

De Vis' (1888) description of the original tibiotarsus (QM F1131) was detailed, and identified diagnostic characters at family, generic and specific levels. Descriptions of the other specimens amounted to just a few adjectives. The second tibiotarsus "adds nothing to our information about the smaller Jabiru than that it attained a rather larger size than the tibia already described". Its distal width was greater and "all parts of the bone are proportionately larger" (De Vis, 1905). About the ulna De Vis (1888) remarked only that it was of compatible size with the first tibiotarsus but "unfortunately its worn condition unfits it for description".

Tibiotarsus. The lectotypical tibiotarsal fragment QM F1131 consists of the distal end with the shaft broken distal to the crista fibularis (length 118.6 mm as preserved). It is abraded on the proximal borders of both condyli, the cristae of trochlea cartilaginis tibialis, the epicondylus medialis and the papilla for M. tibialis cranialis. The anterior face of the shaft is flattened, with the linea extensorius developed into a low ridge along its distal end. The posterior face is strongly rounded. The tuberculum retinaculi m. fibularis is confluent with the lateral border of the anterior face of the shaft; a nutrient foramen is proximal to this. There is a large, broad, elongate scar on the lateral face of the shaft; the distal end is level with the tuberculum. The tuberositas retinaculi extensorius on the linea extensorius is small but obviously elongate. The sulcus extensorius is of uniform depth, not deepening markedly proximal to the pons supratendineus. The distal border of the pons supratendineus is developed

Table 1. Measurements (mm) of the tibiotarsus of *Xenorhynchus nanus* and other fossil and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). † indicates fossil taxa; values for *Ciconia stehlini* and *C. maltha* from Jánossy (1992) and Howard (1942), respectively. *QM*, Queensland Museum, Brisbane.

	distal width across condyli	**depth, condylus lateralis**	**depth, condylus medialis**
† *Ciconia nana*			
QM F1131 (lectotype)	14.3	19.5	18.5
QM F5513	16.1	20.6	20.5
Ciconia ciconia	15.3; 0.7	18.5; 0.8	18.1; 1.0
	14.5–16.2 (4)	17.4–19.2 (4)	16.6–18.9 (4)
Ciconia nigra	14.8 (1)	18.4 (1)	17.5 (1)
Ciconia maguari	18.2; 1.3	21.8; 1.0	21.7; 0.7
	17.0–19.5 (3)	20.9–22.9 (3)	20.9–22.3 (3)
Ciconia episcopus	11.6; 0.5	13.5; 0.8	13.4; 0.7
	11.0–12.0 (3)	12.3–14.2 (3)	12.4–13.6 (3)
Ciconia abdimii	10.9; 0.8	12.6; 0.6	12.7; 0.7
	9.7–12.1 (6)	11.8–13.7 (6)	11.8–13.9 (6)
† *Ciconia stehlini*	14.5	—	—
† *Ciconia maltha*	18.0–21.5	—	—
Anastomus lamelligerus	11.3; 0.6	13.0; 0.5	13.0; 0.5
	10.6–11.8 (3)	12.6–13.5 (3)	12.7–13.6 (3)
Anastomus oscitans	10.8 (1)	11.8 (1)	12.0 (1)
Mycteria ibis	13.3; 0.5	17.1; 0.6	17.2; 1.0
	12.6–14.2 (6)	16.1–18.3 (6)	16.2–18.9 (6)
Mycteria leucocephala	13.1; 0.4	16.6; 1.4	16.9; 1.0
	12.7–13.4 (3)	15.3–18.1 (3)	16.0–18.0 (3)
Mycteria cinerea	13.2 (1)	18.1 (1)	18.0 (1)
Mycteria americana	13.5; 0.6	17.0; 1.2	16.9; 1.4
	12.6–13.8 (4)	16.0–18.5 (4)	15.6–18.6 (4)
Leptoptilos dubius	20.3; 0	26.5; 0.4	25.9; 0
	20.3 (2)	26.2–26.8 (2)	(2)
Leptoptilos javanica	16.4 (1)	20.5 (1)	19.6 (1)
Leptoptilos crumeniferus	19.1; 0.8	23.4; 0.8	23.8; 0.6
	18.1–20.1 (4)	22.3–23.7 (4)	22.9–24.3 (4)
Jabiru mycteria	21.1; 0.2	27.4; 0.1	28.4; 0.3
	20.9–21.3 (3)	27.3–27.5 (3)	28.1–28.7 (3)
Ephippiorhynchus senegalensis	18.1; 1.1	25.0; 1.6	25.4; 1.3
	17.1–19.5 (4)	23.7–27.3 (4)	24.5–27.3 (4)
Ephippiorhynchus asiaticus	17.1; 0.9	23.0; 1.5	22.9; 1.2
	15.6–18.4 (9)	21.5–25.2 (9)	21.6–24.8 (9)

anteriorly into a strong ridge. The condyli are similar in shape and size, with the condylus medialis extending slightly further distally and more markedly anteriorly. The depressio epicondylus lateralis is deeper and more extensive than the depressio epicondylus medialis; both have prominent rims anteriorly. Despite abrasion, the cristae of the trochlea cartilaginis tibialis are prominent, extending well away from the shaft. Measurements, Table 1.

The other tibiotarsal fragment, QM F5513, is slightly larger and has less abrasion of the distal end. It retains about half the length of the shaft, as does the lectotype (length 62.6 mm as preserved) and the medial half is missing for much of this. It agrees closely with the lectotype in morphology other than that the sulcus extensorius is slightly deeper, the tuberositas retinaculi extensorius is more raised, the tuberculum retinaculi m. fibularis is a small distance from the lateral border rather than confluent with it, and the distal opening of the canalis extensorius is somewhat larger and rounder.

Ulna. Specimen QM F5514 consists of the proximal end of a right ulna. It is rather damaged, with the olecranon missing, and moderate to heavy abrasion on the cotyla dorsalis, facies articularis radialis and crista intercotylaris. It is broken distal to the proximalmost papilla. The impressio m. brachialis is long, moderately deep proximally and shallow distally. It is bounded posteriorly by a broad, rounded tuberculum lig. collateralis ventralis and anteriorly by a heavy ridge, which separates it from a prominent incisura radialis. Although, because of the abrasion, measurements of this element cannot be compared directly with those of other taxa, overall the specimen is slightly smaller than the ulna of *Ciconia ciconia*. The measurements of the specimen as preserved are, length 46.0 mm; proximal width 16.6 mm; proximal depth 11.8 mm.

De Vis (1888) placed this species in the same genus as the living *Ephippiorhynchus asiaticus*, "noting further its strong resemblance to the Jabiru's tibia in the massiveness, direction, and sculpture of the bridge traversing the intercondylar space, we cannot but admit congeneric affinity between the two". A comparison of the distal tibiotarsal fragments with other living species of the Ciconiidae, and *E. asiaticus* in particular, demonstrates that De Vis' generic allocation for these specimens is not supported. The comparative material available to De Vis was limited to selected taxa, almost all of Australian origin. Thus, his placement of the fossil specimens in the same genus as the only Australian species is not surprising; it is doubtful that he had access to osteological representatives of any other genera of storks.

De Vis (1888) noted size differences between the fossil tibiotarsus and that of *E. asiaticus*: "the fossil tibia … is in the mean two-ninths less in its dimensions than the recent bone, indicating a bird but little more than half the bulk of the jabiru of the present day". The morphological differences he mentioned were that "the rotular channel is shallower; there is considerably less intercondylar space behind the posterior edge of the bridge, the canal under the bridge is relatively much wider, the ectocondylar tubercle is not prominent, and the double flexure inwards and forwards apparent in the living jabiru between the shaft and the articular end is scarcely appreciable". Most of these are either actually differences between *Ciconia* and *Ephippiorhynchus* or have no generic significance.

The condition of the ulnar fragment is not suitable to permit a useful comparison. The shallow, round impressio m. scapulotricipitalis may be of generic significance but it is also likely that the possible slight morphological differences between the fossil and recent specimens are due to abrasion.

Riversleigh stork

The presence of a new species of stork from Oligo-Miocene deposits at Riversleigh, was briefly mentioned by Vickers-Rich (1991). Boles (1991) noted that it "was not close to the living … *Xenorhynchus*" without further elaboration, and subsequently (Boles, 1997) stated that the material was "probably referable to *Ciconia*". This taxon is described below.

The Riversleigh deposits are located 5 km west of the Riversleigh homestead (19°02'S 138°45'E), 200 km north of Mt Isa, northwestern Queensland, where they occur as an outcrop of Tertiary limestone overlying the Cambrian Thorntonia Limestone. There are now over 200 named Oligo-Miocene deposits at Riversleigh. An informal system of grouping has been used (Systems A–C). These systems are "regionally clustered sites that appear to be superpositionally-related (differing in age but not significantly in position) and/or space-related (spatially isolated but approximately contemporaneous)" (Archer *et al*., 1989). The principal accumulations are thought to have occurred in several episodes involving large lakes, shallow pools and cave deposits. Undoubted stork material has been recovered from three sites and a referred specimen comes from a fourth.

White Hunter Site, Hal's Hill Sequence, D-Site Plateau, is considered to be part of System A, of Late Oligocene/ Early Miocene age (Creaser, 1997; Myers & Archer, 1997). The White Hunter Local Fauna also contains other birds, including the small casuariid *Emuarius gidju* (Patterson & Rich, 1987) (Boles, 1992), the dromornithid *Barawertoris tedfordi* Rich, 1979, a flightless rail (Boles, 2005) and several passerines. Wayne's Wok Site is in the central section of the D-Site Plateau. Its age is still unclear, but may be System A or B (?Early to Middle Miocene) (Black, 1997; Cooke, 1997a; Creaser, 1997). Birds found here also include *Emuarius*, dromornithids and passerines. Bitesantennary Site is a cave deposit in the Verdon Creek Sequence, on the northern section of the D-Site Plateau, where it intrudes into the widespread D-Site layer. It is possibly a System B site (Cooke, 1997a).

Specimens of five skeletal elements were obtained at Bitesanntennary Site in close proximity and are assumed to have been associated. Proximal tarsometatarsal fragments from White Hunter Site and Wayne's Wok Site allow direct comparison with each other but not with a distal tarsometatarsal fragment from Bitesantennary Site. Because the tarsometatarsal fragments all come from storks of comparable size and morphology, they are referred to the same taxon. A cervical vertebra from Neville's Garden Site (Early Miocene) is tentatively referred to this species because of its size and morphological similarity to that of living storks.

Ciconia louisebolesae n.sp.

Fig. 2

Holotype. QM F30290, right distal humeral fragment with surface damage to the anterior face of the condylus dorsalis, tuberculum supracondylare ventrale and dorsal border of sulcus humerotricipitalis.

Type locality. Bitesantennary Site, Riversleigh, northwestern Queensland, currently considered to be Early Miocene; Bitesantennary Local Fauna.

Paratypes. All from Bitesantennary Site. *Cranium*—QM F20910, neurocranium, lacking skull roof; *quadrate*—QM F20893, complete right element; *humerus*—QM F20911, proximal right element broken through distal to the midpoint of the crista bicipitalis and to the fossa pneumotricipitalis, and missing the tuberculum dorsalis and processus deltopectoralis; *tibiotarsus*—QM F31350, extreme proximal left element broken through the shaft through proximal end of the foramen interosseum proximale; damage to most projecting features, including both the cristae cnemialis, particularly the crista cnemialis caudalis, the medial edge of the facies articularis medialis, and extensively on the posterior edge along the area of contact between the facies articularis medialis and lateralis; *Tarsometatarsus*—QM F36446, right distal fragment broken through the shaft proximal to the fossa metatarsi I.

Etymology. Dedicated with love and respect to my mother, Louise Boles, for her guidance in my development as a person and her tolerance of my many transgressions.

Diagnosis. Similar in size to *C. ciconia* and *C. nigra*, but sufficiently different to recognize as a new species. It differs by the following suite of characters of the distal humerus: the condylus ventralis humeri is proportionally smaller, not extending as far ventrally; the epicondylus ventralis is closer to the distal end; the muscle scars distal to the epicondylus ventralis are more extensive (in ventral view) and more excavated (in anterior view), although less than in genera such as *Ephippiorhynchus*; and the posterodorsal corner is

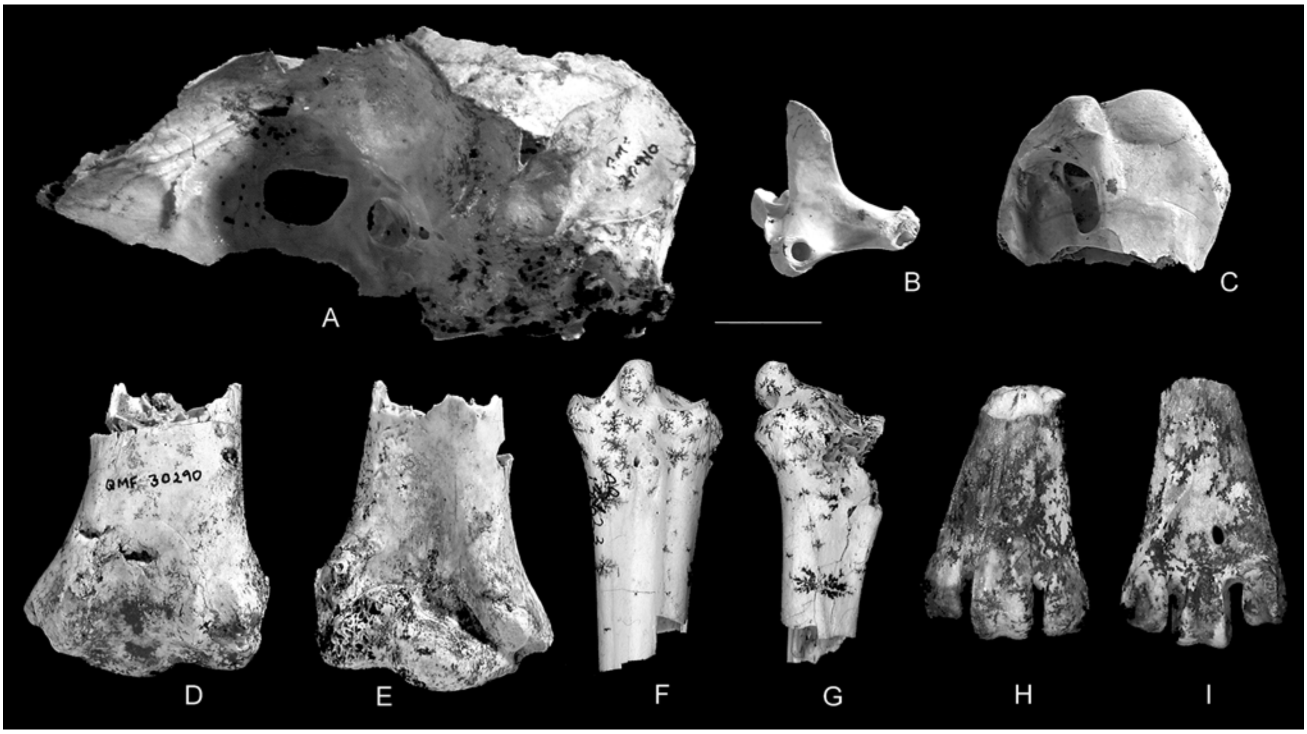

Fig. 2. Specimens of the fossil stork *Ciconia louisebolesae*. (*A*) partial skull (QM F20910, Bitesantennary Site), lateral view; (*B*) right quadrate (QM F20893, Bitesantennary Site), lateral view; (*C*) proximal right humerus (QM F20911, Bitesantennary Site), posterior view; (*D–E*) distal right humerus (holotype: QM F30290, Bitesantennary Site), (*D*) anterior view, (*E*) posterior view; (*F–G*) proximal left tarsometatarsus (QM F36447, Wayne's Wok Site), (*F*) anterior view, (*G*) lateral view; (*H–I*) distal right tarsometatarsus (QM F36446, Bitesantennary Site), (*H*) dorsal view, (*I*) plantar view. Scale = 10 mm.

more rounded (in dorsal view). The crista bicipitalis is not short (as in *C. maguari*) and is prominently extended. In its size and comparative narrowness of the incisura tibialis, the tibiotarsus more closely resembles that of the small species of *Ciconia* (e.g., *episcopus* and *abdimii*) rather than *C. ciconia* or the larger taxa.

Referred material. QM F50428 (Neville's Garden Site) cervical vertebra with only minor damage; QM F36445 (Wayne's Wok Site) left proximal tarsometatarsus with damage to the crista hypotarsi medialis and plantar face of cotyla lateralis; QM F36447 (White Hunter Site) proximal left tarsometatarsus missing most of hypotarsus.

Measurements. Tables 2–4.

Description

Cranium. Measurements as preserved: 31.7 mm width of parietal; 40.1 mm width at midline of orbits (front of specimen as preserved); 40.7 mm width at processes temporalis. The specimen comprises the rear of the skull missing the dome of skull dorsal to the fossa temporalis and in a line just across top of the orbitae, retaining most of the parietal and frontal on a level with the orbital rims; the lamina parasphenoidalis is present but palatal elements are missing; the interorbital septum is present to in front of the fontaculi interorbitales and about half way through the orbits. Many of the external structures are damaged, with the processus postorbitalis lost and the posteroventral border of the processus paraoccipitalis and edges of the lamina parasphenoidalis slightly to strongly abraded; a large opening in the centre of the septum interosseus is a post-mortem artefact. The orbitae are broad and rounded. The fossa temporalis is broad, with the crista temporalis nuchalis strongly developed. The processus zygomaticus is short and blunt. The foramen magnum is squarish oval, with the dorsal border broken. The condylus occipitalis is hemispherical, with the dorsal border abraded. The recessus tympanicus dorsalis is moderately small and round; the fenestra vestibule, foramen pneumaticum caudale and fenestra cochleae are tightly grouped in a small recess. The cotylae quadratica otici and squamosi are of similar circular shape and size. The interior of the cranial cavity is largely intact. The fossa cranii caudalis and fossa tecti mesencephale are broad and circular, with the crista tentorialis prominent.

Quadrate. Viewed anterodorsally, the element is very transversely expanded across the processus mandibularis and less so across the processus oticus; the midbody is comparatively thin between these processes, with the lateral side markedly concave. The crista tympanicum is low. The processus orbitalis is straight on its anterior border; its posterior border is straight until dorsal end, which curves to meet the anterior border at the apex. The capitula squamosum and oticum are elliptical, their long axes converging anteriorly (in posterodorsal view). The incisura intercapitularis is broad but shallow; it extends to a large round foramen pneumaticum located centrally on the posterodorsal surface. The region from the base of the capitulum squamosum, through this foramen, diagonally towards the base of the condylus lateralis is anteroposteriorly compressed compared to the rest of the element. The posterior surface between the processus mandibularis and processus oticus is very slightly concave (in lateral view).

Table 2. Measurements (mm) of the quadrate of *Ciconia louisebolesae* and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). *QM*, Queensland Museum, Brisbane.

	greatest length, processus oticus through processus mandibularis	greatest depth, processus orbitalis through processus mandibularis
Ciconia louisebolesae		
QM F20893	20.2	20.2
Ciconia ciconia	22.3; 0.8	20.5; 1.0
	21.7–23.2 (3)	19.3–21.7 (4)
Ciconia niger	20.6; 0.2	19.3; 0.1
	20.4–20.7 (2)	19.2–19.4 (2)
Ciconia maguari	24.2; 0.5	23.7; 2.7
	23.7–24.6 (3)	21.8–26.8 (3)
Ciconia episcopus	19.2; 1.0	17.4; 1.0
	18.8–20.8 (5)	15.8–18.6 (6)
Ciconia abdimii	17.5; 0.5	15.1; 0.6
	17.0–18.0 (4)	14.5–15.8 (4)
Anastomus lamelligerus	20.1 (1)	17.5; 0.4
	17.2–17.8 (2)	
Mycteria ibis	23.5; 0.3	24.7; 0.7
	23.3–23.9 (3)	24.5–25.3 (4)
Mycteria leucocephala	23.8; 0.7	24.9; 0.6
	23.3–24.3 (2)	24.5–25.3 (2)
Mycteria americana	23.4; 1.3	25.2; 2.0
	22.5–24.3 (2)	23.8–26.8 (2)
Leptoptilos crumeniferus	35.1 (1)	34.0 (1)
Jabiru mycteria	35.6; 0.1	39.1; 0.2
	36.5–36.6 (3)	38.9–39.3 (3)
Ephippiorhynchus	29.6; 1.9	28.6; 2.1
senegalensis	28.2–30.9 (2)	26.7–31.1 (4)
Ephippiorhynchus	29.2; 2.1	2.3; 1.5
asiaticus	26.9–31.5 (4)	25.8–29.1 (4)

The condylus medialis is the most medially projecting part of the element, while the projection of the condylus lateralis is the greatest laterally, exceeding that of the processus oticus. The condyli lateralis/caudalis lie perpendicular to the processus orbitalis. The small, oval condylus pterygoideus stands discrete from the condylus medialis, separated by a small sulcus.

Cervical vertebra. This is very elongate (greatest length 39.7 mm, proximal width 26.2 mm, proximal depth 19.8 mm, distal width 18.6 mm, distal depth 19.5) and agrees with modern *Ciconia ciconia* in morphology. It is not diagnosed further.

Humerus. In anterior view, the caput humeri is rounded, sloping dorsally from the apex more steeply than on the ventral side; it is moderately broad, becoming expanded at its anteroposterior midpoint. Its distal border on the posterior surface is obscure. The sulcus lig. transversus is broad and deep but short, confined to the ventral third of the anterior face, barely reaching the ventral border of the caput; it ends abruptly at the edge of the anterior face of the element. Its depth is augmented by a bordering ridge on its proximal side and the intumescentia humeri on the distal. The proximal surface of the intumescentia is flat and smooth and (in proximal view) is little inflated; it is tilted dorsally to join smoothly with the shallow, indistinct impressio coracobrachialis.

On the posterior surface, the broad incisura capitis separates the caput humeri from a long, deep and thickened area along the proximoventral border of the element, proximal to the fossa pneumotricipitalis, before merging with the proximal end of the posterior shaft surface without an obvious demarcation. Ventrally the prominent proximal section attenuates towards the crista bicipitalis, but protrudes substantially more posteriorly than the crista. On its ventral end, it supports the elongate scar for M. biceps brachii.

The tuberculum ventrale is relatively large, triangular-trapezoidal in shape and oriented proximodorsally. In proximal view, it sits at the apex of a triangular block bounded along its dorsal base by the sulcus lig. transversus. This triangular block protrudes posteriorly well beyond the rest of the proximal end of the element. The deep but moderately thin crus dorsale fossae runs distally from this, forming the dorsal border of the fossa pneumotricipitalis. The fossa is elliptical and highly pneumatic. The area between it and the crus ventrale fossae is excavated as a broad concave basin. The thick crus has a well marked, elongate scar for the attachment of M. scapulohumeralis caudalis. The crista bicipitalis is not well-developed ventrally.

The ridges bordering the sulcus scapulotricipitalis are short but moderately pronounced; they do not extend to the distal border. The ridge on the ventral side of the sulcus humerotricipitalis is broader and longer but about the same height as those defining the sulcus scapulotricipitalis. The sulcus humerotricipitalis is broad and shallow, with no obvious separation from the flat posterior surface of the shaft proximal to it; it is apparent only because of the bordering ridges. The fossa m. brachialis becomes confluent with the shaft on its dorsal and proximal sides and is poorly demarcated on its ventral side. The ridge along the ventral border supporting the tuberculum supracondylare ventrale is strongly developed and rather broad. In distal view, the condylus dorsalis humeri extends further anteriorly than does this ridge, which is turn projects only slightly more than the condylus ventralis humeri. The distal border of the condylus dorsalis humeri just reaches the dorsodistal corner. The condylus ventralis humeri is a rounded oval without obvious inflation. The incisura intercondylaris is moderately broad but shallow. The scars for M. flexor carpi ulnaris and M. pronator profundus face distally; they are adjacent, separated by only a thin ridge. The scars for M. ectepicondylo-ulnaris and M. extensor digitorum communis are shallower and less extensive.

Tibiotarsus. The specimen is too damaged to permit standard measurements for comparison with other taxa. The following measurements, taken from the specimen as preserved, give an indication of the general size: proximal width 15.5 mm; proximal depth (measured from the facies articularis medialis to the crista cnemialis lateralis in a direct anteroposterior line) 20.2 mm; in both cases, the actual value would be considerably greater, particularly for the latter measurement.

The crista cnemialis cranialis is broken; the remaining base is straight and does not extend far distally, although some distance further than the crista cnemialis lateralis. Their junction, at about a right angle, is marked by a shallow sulcus intercnemialis. The crista patellaris is straight, in both proximal and lateral views. The incisura tibialis is deeply incised, concave and moderately narrow; at its proximal

Table 3. Measurements (mm) of the humerus of *Ciconia louisebolesae* and other fossil and living species of storks, giving mean, standard deviation, range and sample size within parentheses. † indicates fossil taxa; values for *Ciconia maltha* from Howard (1942). *QM*, Queensland Museum, Brisbane.

	proximal width	**distal width**	**depth, condylus dorsalis humeri**
Ciconia louisebolesae			
QM F20911	32.9	—	—
QM F30290	—	28.2	14.9
Ciconia ciconia	39.6; 1.7	30.6; 0.8	16.1; 1.0
	37.2–40.9 (6)	28.8–31.5 (10)	15.2–17.3 (10)
Ciconia boyciana	—	33.8 (1)	18.9 (1)
Ciconia nigra	40.1;1.1	30.6; 0.6	16.4; 0.8
	38.9–40.9 (3)	30.0–31.2 (2)	15.6–17.2 (2)
Ciconia maguari	43.7; 1.0	33.5; 1.8	17.9; 0.8
	42.7–44.7 (4)	31.6–36.1 (5)	16.6–18.5 (5)
Ciconia episcopus	32.2; 2.8	23.9; 1.2	12.8; 0.8
	28.2–35.6 (6)	22.1–24.6 (4)	11.7–13.6 (4)
Ciconia stormi	—	21.9 (1)	11.4 (1)
Ciconia abdimii	28.3; 1.4	22.9; 0.5	12.3; 0.1
	26.5–30.0 (5)	22.4–23.2 (3)	12.2–12.4 (3)
Ciconia maltha †	46.2–53.3	38.7–40.7	—
Anastomus lamelligerus	26.5; 0.0	21.6; 0.9	11.5; 0.2
	26.3–26.6 (2)	20.6–22.3 (3)	11.3–11.7 (3)
Anastomus oscitans	—	20.0; 1.3	11.4; 0.6
		18.6–21.1 (3)	10.9–12.0 (3)
Mycteria ibis	34.6; 2.1	26.3; 1.2	14.3; 0.7
	33.1–38.2 (5)	24.5–27.5 (4)	13.8–15.3 (4)
Mycteria cinerea	—	27.2; 2.2	15.0; 1.1
		25.6–28.7 (2)	14.2–15.8 (2)
Mycteria leucocephala	31.9; 2.1	28.9; 0.9	14.9; 0.7
	31.7–32.0 (2)	28.2–29.5 (2)	15.4–16.4 (2)
Mycteria americana	34.1; 2.9	27.6; 1.6	14.9; 0.8
	31.0–36.7 (3)	25.9–29.7 (18)	13.0–16.5 (18)
Leptoptilos dubius	53.0 (1)	46.8 (1)	24.7 (1)
Leptoptilos crumeniferus	48.8; 0.7	47.7; 3.3	25.4; 1.6
	48.4–49.6 (3)	43.5–51.9 (7)	23.5–28.1 (7)
Leptoptilos javanicus	45.0; 3.9	36.1; 2.3	19.7; 0.9
	42.6–49.5 (3)	34.4–38.7 (3)	19.0–20.8 (3)
Jabiru mycteria	54.1; 1.4	40.8; 3.2	22.4; 1.9
	52.9–55.7 (3)	34.6–45.7 (10)	18.2–25.5 (10)
Ephippiorhynchus senegalensis	46.6; 2.2	36.1; 1.3	18.7; 0.5
	44.0–48.9 (4)	35.1–37.0 (2)	18.3–19.0 (2)
Ephippiorhynchus asiaticus	44.1; 1.8	35.9; 2.7	19.2; 1.6
	42.7–47.0 (9)	32.9–37.6 (9)	18.0–20.8 (9)

end, it merges with a shallow excavation on the proximal surface. Its posterior border flares abruptly medially as the anterior side of the rather narrow and strongly rounded facies articularis lateralis. Much of the proximal surface of the facies is missing but what remains indicates that this was markedly raised. The circular fossa retropatellaris is deeper and smaller than the flattened and shallowly concave facies articular medialis. The circular attachment for M. femorotibialis medialis is on the end of the crista medialis, facing posteromedially. The facies gastrocnemialis is relatively flat from the medial side of the crista cnemialis cranialis along the medial side of the shaft, before curving smoothly into the posterior face.

General agreement in morphology and the association of the Riversleigh tibiotarsal fragment with other stork material from Bitesantennary Site are used as the basis for allocating it to this taxon.

Tarsometatarsus. The eminentia intercotylaris is directed anteroproximally at about 50° from the horizontal, projecting further anteriorly than the cotylae. The rounded anterior side is elliptical (in anterior view) with its long axis directed proximodistally; from the apex, it slopes posterodistally on its posterior side. The lateral side drops directly to the cotyla lateralis; the medial side extends as a long sloping ridge, confluent with the anterior rim of the cotyla medialis to past its mediolateral midpoint. The apex is slightly broader than the base (in medial view).

The cotylae are roughly equal in both their anterior and posterior extents and thus in overall depth. In proximal view, the cotyla medialis is roughly circular over most of its border, with the anterior side flattened. Posterior to the anterior rim, the cotyla meets medial side of the eminentia intercotylaris in a smooth, gradual slope. The medial rim projects strongly proximally to a narrow edge. In anterior

Table 4. Measurements (mm) of the tarsometatarsus of *Ciconia louisebolesae* and other fossil and living species of storks, giving mean, standard deviation, range and sample size (in parentheses). † indicates fossil taxa; values for *Ciconia maltha* from Howard (1942). *QM*, Queensland Museum, Brisbane.

	proximal width across cotylae	**depth, cotyla lateralis**	**depth, cotyla medialis**	**distal width**	**medial depth, trochlea**			**greatest distal depth**
					metatarsi II	**metatarsi III**	**metatarsi IV**	
Ciconia louisebolesae								
QM F36445	c. 18.2	—	9.2	—	—	—	—	—
QM F36447	16.3	7.9	9.4	—	—	—	—	—
QM F36446	—	—	—	19.6	9.6	9.0	8.5	14.3
Ciconia ciconia	17.4; 1.5	9.0; 0.9	9.1; 0.6	19.9; 1.3	8.8; 0.4	9.3; 0.6	8.5; 0.5	15.3; 1.0
	14.2–19.3 (9)	7.4–10.1 (9)	8.4–9.8 (9)	17.7–21.7 (9)	8.3–9.6 (9)	8.3–10.2 (9)	7.8–9.3 (9)	13.5–16.6 (9)
Ciconia nigra	16.2; 0.4	8.6; 0.4	8.4; 0	18.9; 0.5	7.0; 0.3	8.9; 0.3	7.6; 0.2	15.1; 0.2
	15.9–16.7 (3)	8.2–8.9 (3)	8.4 (3)	18.4–19.3 (3)	6.6–7.3 (3)	8.5–9.1 (3)	7.5–7.8 (3)	14.9–15.2 (3)
Ciconia maguari	21.3; 0.4	11.2; 0.5	10.1; 0.7	23.2; 0.9	10.0; 0.8	10.9; 0.3	10.0; 0.3	18.0; 1.2
	20.7–21.6 (4)	10.7–11.7 (4)	9.3–10.8 (4)	22.2–24.2 (4)	9.4–11.2 (3)	10.5–11.2 (3)	9.5–10.3 (3)	17.0–19.7 (3)
Ciconia episcopus	14.4; 1.3	7.8; 0.8	7.8; 0.7	16.7; 1.1	7.2; 0.3	8.0; 0.6	7.2; 0.6	12.2; 0.7
	12.8–16.2 (6)	7.1–8.9 (6)	6.7–8.9 (6)	15.7–18.5 (6)	6.4–7.5 (6)	7.3–8.9 (6)	6.5–8.0 (6)	11.5–13.0 (6)
Ciconia abdimii	12.5; 0.9	7.0; 0.4	6.6; 0.4	14.9; 1.1	6.8; 0.6	7.3; 0.4	6.3; 0.4	10.7; 0.8
	11.1–13.5 (5)	6.6–7.4 (5)	6.2–7.1 (5)	13.9–15.6 (5)	6.2–7.7 (5)	6.7–7.5 (5)	5.9–7.0 (5)	9.6–11.8 (5)
†*Ciconia maltha*	20–24.5	—	—	23–28	—	—	—	—
Anastomus	13.4; 0.2	7.0; 0.6	7.4; 0.1	14.9; 0.6	7.1; 1.3	7.0; 0.5	5.7; 1.3	10.6; 1.3
lamelligerus	13.2–13.5 (2)	6.5–7.4 (2)	7.3–7.5 (2)	14.4–15.3 (2)	6.2–8.0 (2)	6.6–7.3 (2)	4.8–6.6 (2)	9.7–11.5 (2)
Mycteria ibis	15.4; 0.8	8.8; 0.9	8.9; 1.0	18.9; 0.8	8.4; 0.9	9.1; 0.6	7.8; 0.5	16.1; 1.5
	14.6–16.2 (4)	7.7–9.6 (4)	7.8–9.9 (4)	18.2–19.9 (4)	7.4–9.3 (4)	8.4–9.7 (4)	7.1–8.4 (4)	14.1–17.4 (4)
Mycteria	14.8; 0.7	9.3; 0.8	9.3; 0.3	17.8; 0	7.8; 1.3	8.8; 0	8.0; 0.2	15.4; 0.4
leucocephala	14.3–15.3 (2)	8.7–9.9 (2)	9.1–9.5 (2)	17.8 (2)	6.9–8.7 (2)	8.8 (2)	7.8–8.1 (2)	15.1–15.7 (2)
Mycteria	15.5; 0.3	9.3; 0.2	9.2; 0.1	18.7; 1.5	8.4; 0.7	8.8; 0.9	8.1; 0.4	16.4; 0.8
americana	15.2–15.9 (2)	9.1–9.4 (2)	8.7–9.2 (2)	17.4–19.7 (2)	7.2–8.9 (2)	7.9–9.1 (2)	7.6–8.8 (2)	14.5–18.2 (2)
Leptoptilos dubius	23.8 (1)	12.8 (1)	12.9 (1)	28.1 (1)	12.4 (1)	14.0 (1)	11.7 (1)	22.9 (1)
Leptoptilos	22.0; 0.9	13.1; 0.3	12.1; 0.9	26.6; 1.0	12.1; 1.0	13.5; 0.4	11.3; 0.9	20.7; 1.4
crumeniferus	20.8–23.2 (5)	12.8–13.6 (5)	11.1–13.0 (5)	25.0–27.6 (5)	10.9–13.2 (5)	13.1–14.0 (5)	10.3–12.2 (5)	18.2–21.4 (5)
Jabiru mycteria	24.8; 0.1	13.3; 0.5	13.5; 0.4	30.0; 0.1	12.2; 0.1	13.2; 1.3	12.6; 0.1	21.9; 0.9
	24.7–24.8 (3)	12.8–13.7 (3)	13.1–13.8 (3)	29.5–29.6 (3)	10.7–13.1 (3)	13.1–13.3 (3)	11.8–13.5 (3)	20.7–23.0 (3)
Ephippiorhynchus	21.1; 1.6	12.4; 1.6	11.4; 0.7	23.6; 1.6	10.3; 1.1	11.4; 0.1	10.5; 1.1	18.1; 1.6
senegalensis	19.6–23.3 (4)	11.0–14.6 (4)	10.9–12.4 (4)	22.3–22.6 (4)	9.8–11.8 (4)	10.5–12.7 (4)	9.8–12.0 (4)	17.0–20.5 (4)
Ephippiorhynchus	19.4; 1.3	11.5; 1.0	10.7; 0.7	22.4; 1.1	10.5; 1.1	10.8; 0.6	10.2; 0.6	19.4; 1.4
asiaticus	18.1–21.6 (9)	10.4–12.8 (9)	10.0–12.0 (9)	21.3–24.0 (9)	9.3–11.2 (8)	9.7–11.4 (9)	9.1–10.7 (9)	17.3–21.7 (9)

view, the cotyla medialis is situated more proximally than the cotyla lateralis.

The area intercotylaris immediately posterior to the eminentia intercotylaris has a shallow depression between the eminentia intercotylaris and the borders of the cotylae. It then slopes posteriorly to another, much more extensive depression just anterior to the hypotarsus. The medial side of this section is higher than the lateral side.

The hypotarsus has two cristae hypotarsi separated by a broad, open, moderately deep sulcus hypotarsi. There is a very thin, low ridge running through the sulcus parallel to the crista lateralis hypotarsi. On the lateral side of this low ridge, the sulcus slightly excavates the base of the crista lateralis hypotarsi such that this is narrower than the posterior margin. The configuration of the crista medialis hypotarsi cannot be assessed. The main axis of the hypotarsus runs through the eminentia intercotylaris about 20° medial to the anteroposterior midline. The hypotarsus is separated from the ridge of the lateral shaft surface by a moderately deep furrow and from the medial shaft surface by broader and shallower furrow; both furrows contain a small nutrient foramen.

The anterior face is excavated at the proximal end by a deep fossa infracotylaris dorsalis, which continues distally as a wide sulcus extensorius. The deepest part of this basin contains two foramina vasculare proximale at the same level, immediately proximal to the round tuberositas m. tibialis cranialis. On their medial side, the sulcus extensorius is prominent, bordered both medially and laterally by narrow ridges.

Viewed anteriorly, the lateral and medial margins of the proximal fragment of shaft converge distally. Distal to the rim on the medial side, the shaft curves medially to a projection level with the cotyla, before angling proximally into the medial rim of the cotyla. The lateral side also swings outwards to meet the rim of cotyla lateralis, but not as strongly. The curvature of the anterior shaft face to the eminentia intercotylaris is greater on the lateral side because of an anterior projection distal to the cotyla lateralis. A rounded projection lateral to the cotyla lateralis originates just distal to the rim, then collapses to a low, flat, broad ridge forming the lateral shaft surface. There is a thin, low ridge on the lateral shaft surface that starts near the midpoint of the cotyla, trending posterodistally towards the midline of the shaft, then more distally. On the medial side, the projection on the proximal end of the medial shaft face continues distally as the broad, rounded shaft margin.

On the distal end, the small portion of shaft that is retained is narrow before flaring to meet the trochleae. Its lateral margin is straight, the medial more curved to join trochlea metatarsi II (in dorsal view). There is a deep groove running proximodistally proximal to, and level with, the lateral border of the trochlea metatarsi III. It meets the foramen vasculare distale, which is obscured on the dorsal surface. The medial side of the dorsal face slopes to join the medial surface; the junction of the dorsal and lateral faces is rather abrupt.

On the plantar surface, the sulcus supratrochlearis plantaris is moderately shallow. It is not strongly demarcated laterally, but medially is confined by a moderately high, narrow ridge connecting the base of the trochlea metatarsi II and the fossa metatarsi I. This long, elliptical fossa is situated on the proximal end of the ridge. There is a low, very thin ridge running lateral to the midline and meeting the foramen vasculare distale, which is prominent on this side.

This fragment is markedly compressed dorsoplantarly. The dorsal surface is more or less straight (in medial view), with the dorsal side of the trochlea metatarsi III projecting beyond it. The ridge supporting the fossa metatarsi I protrudes further plantarly than does the rest of the plantar shaft surface. The sulcus intertrochlearis lateralis is broader and deeper than the sulcus intertrochlearis medialis.

The trochleae are arranged in a curve, viewed distally. The trochlea metatarsi II lies at an angle of about 10° medial to the dorsoplantar midline; the trochleae metatarsi III and IV are tilted laterally about 10° and 20° from this midline, respectively. The trochlea metatarsi IV projects further dorsally and distally than does the trochlea metatarsi II, but neither projects as far as the trochlea metatarsi III. The trochlea metatarsi II extends further plantarly than the trochlea metatarsi IV. The trochlea metatarsi II is rounded dorsally and distally; its plantar border comprises a triangular projection, with a wide fovea lig. collateralis occupying much of the medial surface. The trochlea metatarsi III is grooved on its dorsal surface, with the lateral side projecting slightly further distally. The other trochleae lack grooves on their dorsal surfaces, although the trochlea metatarsi IV has a shallow groove on its distal surface. The dorsal surface of the trochlea metatarsi IV is tilted laterally. The distoplantar corner forms a triangular projection, projecting beyond the rest of the trochlea, but it and the fovea lig. collateralis are less prominent than on the trochlea metatarsi II.

The two proximal fragments differ in size, but share the same morphology. The magnitude of the morphometric differences are within that exhibited by modern taxa (Table 4; see also Hancock *et al*., 1992 for measurements of living species).

Taphonomy

The occurrence of a stork in Wayne's Wok and White Hunter Sites is not surprising. Both support rich local faunas comprising species of a range of vertebrate groups, including many indicative of aquatic environments. In contrast, Bitesanntennary Site is an initially unlikely source of such a bird. It has also yielded many species (almost all bats with 11 species recorded; Hand, 1997), but on both faunistic and geological bases it is considered to be a cave-fill deposit. The other somewhat anomalous occurrence found here is that of the bulungamayine kangaroo *Ganguroo bilamina* (Cooke, 1997b).

There are several explanations for the presence of the non-bats *Ciconia louisebolesae* and *G. bilamina* in this cave deposit (see Baird, 1991b). It is possible that they used the cave as a shelter (*Ganguroo*) or there may have been a pool or other suitable foraging habitat within its immediate entrance. Otherwise the cave may have served as a predator's lair and these species represent prey items, or their carcasses may have been washed into the cave from outside after death. An entrance of the cave may have opened upward through the roof rather than to the side and thus served as a pitfall trap for unwary animals. The skeleton of a Yellow-billed Spoonbill *Platalea flavipes*, a bird of roughly similar size, shape and habits as *Ciconia* storks, has been recovered from Weekes Cave, South Australia; van Tets (1974) considered that it "may have become trapped in the sink hole after blundering into it" in search of residual water after a wet period in the usually dry environment.

Discussion

Despite the number of putative palaeospecies assigned to *Ciconia*, it is difficult to interpret the fossil history of this genus. The fragmentary nature of many of the remains makes comparisons troublesome; these do not lend themselves to clarifying any trends. The only species that are well represented are the large *C. maltha* and unnamed *Ciconia* of North America.

As currently construed, the genus *Ephippiorhynchus* occurs in equatorial Africa, represented by *E. senegalensis*, and in southern and southeastern Asia (but not Malaysia or Indonesia), southern New Guinea and northern and eastern Australia, represented by *E. asiaticus*. Its entry into Australasia from the north is unlikely to have been possible until Australia approached Asia and the New Guinean landmass was formed during the Late Miocene. Its current fossil record in Australia is compatible with this timetable and suggests that congeneric storks should not be recovered from earlier deposits. The Australasian and Asian populations are considered only subspecifically different and are separated by a substantial distributional gap. It seems unlikely that *E. asiaticus* was preceded into Australia by an earlier and now extinct congener. As there is no evidence of other large storks, such as marabous, all ephippiorhynchine-like storks in Australia should be expected to belong to this species.

The distribution of neospecies of *Ciconia* is throughout Eurasia, Africa and South America. During the Pleistocene, this extended to North America (*C. maltha*) and Australia (*C. nana*). It is not clear why the latter landmasses lost their representatives of this genus. In Australia, *Ciconia* had a rather long history (late Oligocene-Pleistocene). Species of *Ciconia* and *Ephippiorhynchus* are sympatric across much of their ranges in Africa and Asia, so there is no reason to believe that the arrival of *E. asiaticus* in Australia was a contributing factor to the extinction of *C. nana*. There are also marked differences in size and presumably in ecology, which would have precluded any direct competition. Possible competition might be more likely between *C. nana* and ibises of the genera *Threskiornis* and *Plegadis*. *Threskiornis* cf. *T. molucca* has been recorded from the Early Pliocene Bluff Downs Local Fauna, so it and *C. nana* would have co-existed, at least in time, if not in space.

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