



## Paleornithological Research 2013

Proceed. 8<sup>th</sup> Internat. Meeting Society of  
Avian Paleontology and Evolution

Ursula B. Göhlich & Andreas Kroh (Eds)



ZooBank LSID: urn:lsid:zoobank.org:pub:2BE243F0-2119-4F59-9F1F-0CF16A8D00EC

# A fossil stone-curlew (Aves: Burhinidae) from the Late Oligocene/Early Miocene of South Australia

WALTER E. BOLES<sup>1</sup>, MELANIE A. FINCH<sup>2</sup>, RENE H. HOFHEINS<sup>2</sup>, PATRICIA VICKERS-RICH<sup>2</sup>, MARY WALTERS<sup>2</sup> & THOMAS H. RICH<sup>3</sup>

<sup>1</sup> Ornithology Section, Australian Museum, Sydney, N.S.W., Australia; E-mail: walter.boles@austmus.gov.au

<sup>2</sup> School of Geosciences, Monash University, Clayton, Victoria, Australia,

<sup>3</sup> Museum Victoria, Melbourne, Victoria, Australia

**Abstract** — *Wilaru tedfordi* nov. gen. et nov. spec. is a fossil burhinid from Upper Oligocene/Lower Miocene sites in northern South Australia. Almost all specimens come from Lake Pinpa, with a few recovered from Lake Palankarina and Billeroo Creek. Numerous specimens have been recovered, representing most elements of the pectoral girdle, forelimb and hindlimb. This is the oldest known burhinid. It shares several morphological character states with the genus *Esacus* and, like that taxon, had a proportionally long humerus and short tarsometatarsus, although the difference is much more pronounced. Also like species of *Esacus*, and in contrast to those of *Burhinus*, *Wilaru* may have frequented the shorelines of lakes and rivers.

**Key words:** Burhinidae, stone-curlew, *Wilaru tedfordi*, Late Oligocene/Early Miocene, Australia

## Introduction

The Burhinidae is a distinct but low diversity group in the order Charadriiformes. Currently, it includes nine extant species, two named fossil species and one fossil subspecies, found globally in a variety of habitats. These fossil and extant species are placed in two genera, *Burhinus* ILLIGER, 1811 (containing nine species and the fossil subspecies) and *Esacus* LESSON, 1831 (two species). Colloquially, burhinids are known as thick-knees owing to their prominent ankle joints.

Burhinids are long-legged, terrestrially foraging and breeding birds. They are good fliers, but prefer to spend most of their time on the ground. Most species of *Burhinus* are similar in structure, with moderately long wings and legs (body length 320–480 mm, wing length measured from

bend of wrist to longest primary 200–248 mm, mass 290–535 g). The considerably larger *B. grallarius* (LATHAM, 1802) (body length 540–590 mm, wing length 270–288 mm, mass 580–860 g) has similar proportions except for its markedly elongated tarsometatarsus. The two species of *Esacus* are more stocky birds than those of *Burhinus*. *Esacus magnirostris* (VIEILLOT, 1818) is of similar general size to *B. grallarius* (body length 530–570 mm, wing length 270–300 mm), but it has proportionally shorter legs and a larger bill and is notably heavier (870–1130 g). *Burhinus* and *Esacus* species also differ in habitat preferences. Modern burhinids occur in temperate and warm zones of the Americas, Africa, Middle East and Indo-Australasia. The species of *Esacus* are found on the shorelines of oceans and rivers, while those of *Burhinus* “tend to frequent a variety of exposed, largely low-lying, flat or

rolling landscapes” (HUME 1996) from temperate open woodland to semi-arid to arid country with little vegetation and avoiding forest and heavily vegetated areas.

Two extant species, one from each genus, occur in Australia. *Burhinus grallarius*, the Bush Thick-knee, commonly inhabits grassy woodlands and rarely associates with water bodies (GEERING *et al.* 2007). *Esacus magnirostris*, the Beach Thick-knee, is strictly coastal, inhabiting a variety of types of beaches (GEERING *et al.* 2007).

There has been limited osteological work on burhinids. SHUFELDT (1915) described the skeleton of *E. magnirostris* but did not compare this taxon to other species. STRAUCH (1978) and LIVEZEY (2010) incorporated all species in larger studies of the Charadriiformes, but detected very little variation in the post-cranial skeletons. Differences were largely confined to the skull, with members of *Esacus* having more massive bills than those of *Burhinus* (GEERING *et al.* 2007).

The fossil record of the Burhinidae is sparse. Of reliably identified fossil burhinids, there are two named palaeospecies, *Burhinus lucorum* BICKART, 1981 (Lower Miocene Sheep Creek Formation, late Hemingfordian, Nebraska, United States) and the Late Pleistocene *B. aquilonaris* FEDUCCIA, 1980 (Sanborn Formation, Kansas). Quaternary-aged burhinid fossils (living neospecies and undetermined species *Burhinus* sp.) are known from several continents (BRODKORB 1967; HOWARD 1971), and a palaeosubspecies of the living *B. bistriatus* (*B. bistriatus nanus* BRODKORB, 1959) has been described from the Bahamas. BAIRD (1991) noted the presence of *B. grallarius* in Quaternary cave deposits in Australia.

A supposed burhinid from Upper Cretaceous sediments in Antarctica was reported by CORDES (2002) in a conference abstract, but no formal paper on this material has been published. Burhinid-like post-cranials from Eocene of Australia (BOLES 1999) were referred to the Graculavidae, a form-family created to accommodate various taxa with similar post-cranial skeletons and for which the cranial material was unknown. The possibility has been raised that these may be anseriform (ELZANOWSKI & BOLES 2012). HARRISON & WALKER (1976) reported a burhinid from the Late Eocene of England, but this was dismissed by MAYR (2006) as not being even

assigned to the Charadriiformes with certainty.

VICKERS-RICH (1991) cited a large collection of burhinid fossils recovered from several Late Oligocene/Early Miocene-aged sites in the Lake Eyre region of northern South Australia, with most elements of the skeleton represented. This taxon was regarded as “clearly a form distinct from the Australian forms of today, at least rating a new specific recognition” (VICKERS-RICH 1991, p. 760). Here, on the basis of this material, the most extensive for any paleospecies in this family, we describe the first burhinid fossil genus and species from Australia.

### Study Area

The fossils discussed in this paper were recovered from fluvio-lacustrine sites in two depositional regions of the Lake Eyre Basin in South Australia (Fig. 1). A small number of fossils came from Lake Palankarinna (28°46–47' S, 138° 24' E) in the western Tirari Sub-basin (= Lake Eyre Sub-basin) from localities in the Etadunna Formation. Burhinids from the Ngapakaldi Fauna were collected from several sites on the western side of Lake Palankarinna, while a single burhinid bone from the Ngama Local Fauna was recovered from Mammalon Hill at the northern end of the lake.

Lake Pinpa (= Pine Lake) (31°8' S, 140° 13' E) and the neighbouring Billeroo Creek (31° 6' S, 140° 14' E) in the eastern Callabonna Sub-basin (= Tarkarooloo Sub-basin) contain the Pinpa Fauna, which occurs in sediments that lie near the top of the Namba Formation in the green dolomitic claystones cropping out on the west side of Lake Pinpa. Three bones came from Billeroo Creek, while the vast majority of all specimens were found at Lake Pinpa, in particular, Site C (“an area on the western shore of the lake that extends north from the E-W cross lake track to about the location of the base of my measured section of 1971, *e.g.*, grid coord. 317148, Curnamona [1:250.000] sheet, (R. Tedford, pers. comm., 30 August 2006)”, cited by WORTHY (2009). Within Site C, almost all were found at a single location, QMAM 47, by two of us (P. VICKERS-RICH and T. RICH), who participated in the 1971 joint Queensland Museum–American Museum of Natural History Museum expedition

led by R. (Dick) H. TEDFORD.

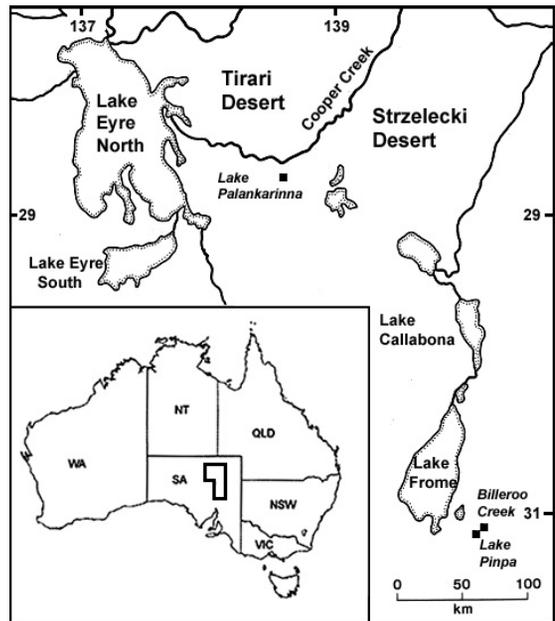
A review of the available evidence by WOODBURN *et al.* (1994, p.485) concluded “that all of the isotopic, foraminifera and magnetostratigraphic data are consistent with an approximate age of 24–26 my for the Etadunna Formation in the Lake Eyre Basin”. WOODBURN *et al.* (1994) are followed regarding correlation between the Etadunna and Ngama Formations and nomenclature of local faunas and mammal zones. They correlated Zone A of the Etadunna Formation, the oldest mammal zone, containing the Minkina LF, with the Pinpa Fauna in the Namba Formation and Zone B, containing the Ditjimanka Local Fauna at Lake Palankarinna, with the Ericmas Fauna in the upper part of the Namba Formation. WOODBURN (1986) and WOODBURN *et al.* (1994) identified the black and brown claystone beds at Mammalon Hill as the youngest part of the Etadunna Formation cropping out at Lake Palankarinna. In sum, the oldest is the Pinpa Fauna, followed by the Ngapakaldi Fauna, with the Ngama Local Fauna youngest. The setting is dominantly lacustrine and partly fluvial and outcrop sporadic.

The collections have been made through several field visits by various institutions and these often have locality site codes. Most of the specimens were collected during joint Queensland Museum–American Museum expeditions in 1971 and 1973; these have site localities with prefix QMAM (1971: 41, 47, 59; 1973: 125, 133, 151, 199, 243, 264). A few fossils were obtained during fieldwork by the University of California, Museum of Paleontology (site codes V-5375, V-5762, V-5764).

### Material and Methods

Anatomical terminology follows that of BAUMEL & WITMER (1993). Measurements (mm) were generally taken following STEADMAN (1980) except where explained below. All measurements were taken with electronic digital callipers and rounded to 0.1 mm.

All major elements of the limbs and pectoral girdle are represented in the fossil collection. The material studied here is housed in several institutions, but the vast majority is in the Ameri-



**FIGURE 1.** Locations in northeastern South Australia, central Australia, at which *Wilaru tedfordi* nov. spec. material was found: Lake Pinpa, Lake Palankarinna and Billeroo Creek.

can Museum of Natural History, New York (specimen registration number prefix AMNH); a few are in the collections of the University of California Museum of Paleontology, Berkeley (UCMP), Museum Victoria, Melbourne (MV) and South Australian Museum, Adelaide (SAM). Representative specimens of the elements were transferred to the South Australian Museum from the American Museum holdings.

Comparative skeletons were made available from the collections of Museum Victoria, Melbourne (MV), Australian Museum, Sydney (AM) and Australian National Wildlife Collection, Canberra (ANWC): *Burhinus grallarius* (MV B20430, B25090, AM O.43444, O.44452, O.63417, O.66366, ANWC B30772, B30774, B30775), *B. oedincnemus* (LINNEAUS, 1758) (AM O.69165), *B. bistratus* (WAGLER, 1829) (MV B13715), *B. capensis* (LICHTENSTEIN, 1823) (MV B13648, ANWC B23045), *Esacus magnirostris* (MV W6587, B13191, B14255, AM O.65024, ANWC B23052). These were supplemented by images of material of additional species provided by the United States Museum National Museum, Washington (USNM), Los Angeles County Museum of Natural History, Los Angeles (LACM), and Natural History Museum

(British Museum), Tring (BM): *B. senegalensis* (SWAINSON, 1837) (USNM 553053, 322589), *B. vermiculatus* (CABANIS, 1868) (USNM 291425, 430630), *B. superciliaris* (TSCHUDI, 1843) (LACM Ecuador 1–6, 9–12) and *B. oedicnemus* (BM A5582). These were used to assist in assessing characters but not for measurements. The extant *Esacus recurvirostris* (CUVIER, 1829) was not represented, but it is similar to *E. magnirostris*. The fossil burhinid species *Burhinus lucorum* and *B. aquilonaris* were represented by a cast (AMNH 10215) and by an image from the University of Kansas Natural History Museum, Lawrence (KNHM 6822), respectively.

Abbreviations: art., articularis; d, distal; L, left; o, omal; lig., ligamentum/ligamentum/ligamentosa; m, musculus/musculi; p, proximal; R, right; s, shaft; tub., tuberculum/tuberculi. For institutional acronyms, see above.

## Systematic Palaeontology

### Order Charadriiformes HUXLEY, 1867

#### Family Burhinidae MATHEWS, 1912

The characters on which the skeletal elements are referred to the Burhinidae are given in the descriptions below. For those elements for which diagnostic characters could not be identified on the material available assignment to this family was made for those most comparable to modern burhinid morphology.

#### Genus *Wilaru* nov. gen.

**Type and only species:** *Wilaru tedfordi* nov. spec.

**Diagnosis:** *Wilaru* differs from *Burhinus* and *Esacus* by having a unique combination of characters, including the following. Humerus: caput humeri merges with tuberculum dorsale without being separated by a notch; fossa pneumotricipitalis larger and deeper and extends to margo caudalis; fossa m. brachialis extends across proximal sides of condyli to dorsal and ventral borders of cranial face. Scapula: acromion much longer; tub. coracoideum larger and more bulbous. Coracoid: omal half deflected further medially; sulcus m. supracoracoidei with flatter dorsal border; processus procoracoideus short and triangular,

lacking cranially-directed strap-like projection; projection on the sternal end of the medial margin more distally located. Carpometacarpus: dorsal and ventral rims of the trochlea carpalis extend caudally to about the same extent; sulcus tendineus deeper. Femur: collum femoris more constricted; facies art. antitrochanterica with more prominent caudally protruding lip. Tarsometatarsus: much shorter in proportion to humerus; proximal and distal ends proportionally wider; apex of the eminentia intercotylaris broader and more rounded; crista lateralis hypotarsi longer and thinner; sulcus extensorius much shallower on distal half of shaft; trochlea metatarsi II with greater medial inflection; trochlea metatarsi II with greater plantar extent. Additional characters are given below.

**Etymology:** ‘Wilaru’ for ‘stone curlew’ in the language of the Australian Dieri tribe of the Lake Eyre region of South Australia (BLAKE 1981).

#### *Wilaru tedfordi*, nov. spec.

(Figs 2–4, 5A–B)

**Holotype** (Fig. 3D, E): Left humerus SAM P48925 (formerly AMNH 11442) missing proximodorsal corner of processus deltopectoralis, ventral border of processus bicipitalis, with the shaft fractured and repaired. Collected by T.H. RICH and P. VICKERS-RICH in 1971 on joint Queensland Museum–American Museum of Natural History expedition led by R.H. TEDFORD.

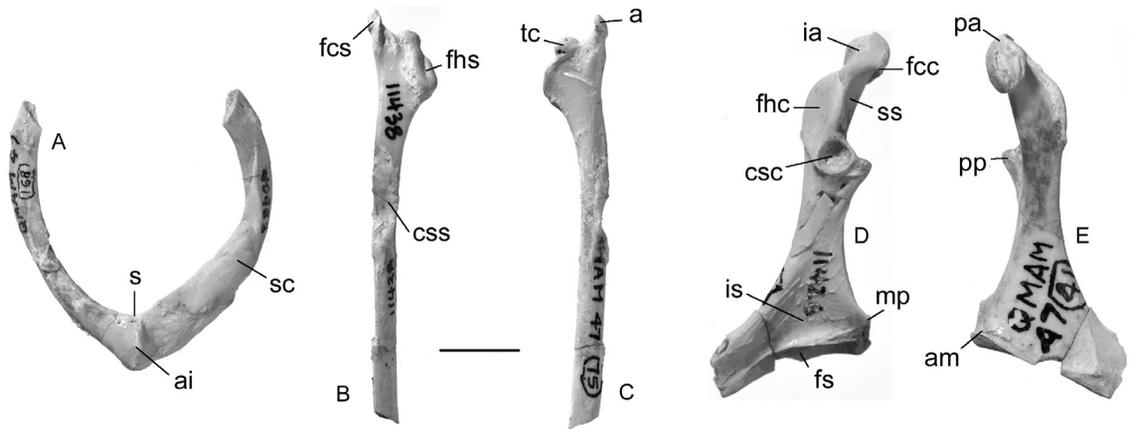
**Diagnosis:** As for genus.

**Etymology:** After Richard H. TEDFORD (1929–2011) of the American Museum of Natural History, who led the 1971 expedition during which these fossils were collected and, who along with R.A. STIRTON (University of California, Berkeley), spent many field seasons in South Australia, the first comprehensive surveys of the region for fossil vertebrates.

**Type locality:** Lake Pinpa, Site C, collection code QMAM 47 (31° 07' S, 140° 13' E), South Australia.

**Horizon and age:** Namba Formation, late Oligocene–early Miocene (24–26 my) (WOODBURN *et al.* 1994), Pinpa LF.

**Distribution:** Late Oligocene (24–26 my), South Australia, Australia: Lake Pinpa and Billeeroo Creek, Namba Formation, Pinpa LF; Lake



**FIGURE 2.** Pectoral girdle elements of *Wilaru tedfordi* nov. spec.: **A**, furcula AMNH 11983 (caudal view); **B**, **C**, proximal right scapula SAM P48923 (formerly AMNH 11438) (lateral and medial views); **D**, **E**, left coracoid AMNH 11426 (dorsal and ventral views). a, acromion; am, angulus medialis; ai, apophysis interclavicularis; csc, cotyla scapularis; css, corpus scapulae; fcc, facies art. clavicularis; fcs, facies art. clavicularis; fhc, facies art. humeralis; fhs, facies art. humeralis; fs, facies art. sternalis; ia, impressio lig. acrocoracohumeralis; is, impressio m. sternocoracoidei; mp, medial projection on sternal end of coracoid; pa, processus acrocoracoideus; pp, processus procoracoideus; s, symphysis; sc, scapus clavicularum; ss, sulcus m. supracoracoidei; tc, tub. coracoideum. Scale bar equals 10 mm.

Palankarina, Etadunna Formation, Ditjimanka LF, Zone B.

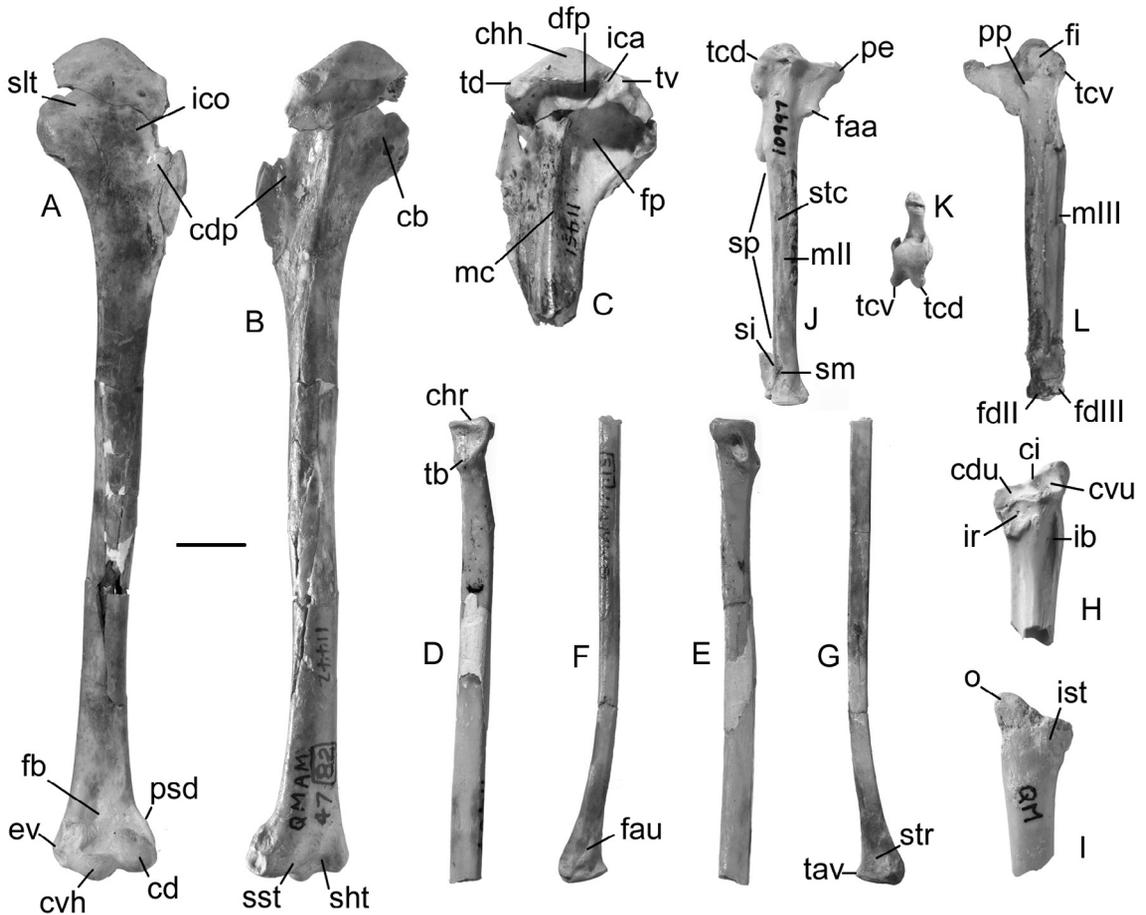
**Measurements of holotype:** Length=123.3 mm, depth of caput humeri=6.2 mm, distal width=15.1 mm, distal depth=8.8 mm.

**Paratypes:** Humeri (Fig. 3C), Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11402 pR, AMNH 11403 pR, AMNH 11404 pR and AMNH 11405 pL, each retaining only caput humeri and tuberculum dorsale; AMNH 11406 pR retaining caput humeri and proximal section of crista deltopectoralis; AMNH 11407 pR lacking caput humeri and proximal edges of cristae deltopectoralis and bicipitalis; AMNH 11409 dL lacking fragment of shaft; AMNH 11441 dR retaining about half the shaft; AMNH 11451 L in two parts with the proximal end retaining some shaft and missing the edge of the crista deltopectoralis; AMNH 11452 dL retaining about half the shaft; AMNH 11454 pR with crista deltopectoralis and crista bicipitalis damaged; AMNH 11470 dR in good condition; AMNH 11476 dR lacking shaft with damage to surface of condylus lateralis. Lake Pinpa, Site C, collection code QMAM133, Namba Formation, Pinpa Fauna: AMNH 10836 dR with condyli heavily abraded. Lake Pinpa, Site C, collection code QMAM243, Namba Formation, Pinpa Fauna: AMNH 10859 dL missing

condylus ventralis. Lake Pinpa, Site C, Namba Formation, Pinpa Fauna: AMNH 10723 dL quite abraded. Lake Palankarina, Site 5 (V5765), RHT#455, Etadunna Formation, Ditjimanka LF: UCMP 57005 dL with about 50% of shaft.

**Description:** Humeri: Assignment of the humeral fossils to the Burhinidae is based on the following suite of characters. The non-pneumatic fossa pneumotricipitalis is broad, relatively deep, rather rectangular and has its major axis directed about 145° to shaft. The impressio coracobrachialis is wide and shallow, poorly defined ventrally and distally (in cranial view). The processus supracondylaris dorsalis, strongly developed in most charadriiforms, is small and relatively close to the distal end, roughly level with proximal border of the condylus dorsalis.

*Wilaru* differs from living burhinids in the following features: The caput humeri merges more smoothly with the tuberculum dorsale, rather than being separated by a depression or notch (cranial view). The proximal third of the shaft on both the dorsal and ventral sides slopes sharply away from the margo caudalis. On the ventral side, this results because the fossa pneumotricipitalis is large and deep and extends to the margo caudalis, rather than being separated by a gap c. 30% of the fossa width as in other burhinids. A crus dorsale fossae does not appear to be present;



**FIGURE 3.** Forelimb elements of *Wilaru tedfordi* nov. spec.: **A, B**, left humerus SAM P48925 (formerly AMNH 11442; holotype) (cranial and caudal views); **C**, proximal left humerus AMNH 11451 (caudal view); **D, E**, proximal left radius AMNH 11464 (ventral and dorsal views); **F, G**, distal left radius AMNH 11464 (ventral and dorsal views); **H, I**, proximal right ulna unnumbered; **J, K**, right carpometacarpus SAM P48928 (formerly AMNH 10997) (dorsal and proximal views); **L**, right carpometacarpus AMNH 11448 (ventral view). cb, crista bicipitalis; cd, condylus dorsalis; cdp, crista deltopectoralis; cdu, cotyla dorsalis; chh, caput humeri; chr, cotyla humeralis; ci, crista intercotylaris; cvh, condylus ventralis; cvu, cotyla ventralis; dfp, dorsal fossa pneumotricipitalis; ev, epicondylus ventralis; faa, facies art. alularis; fau, facies art. ulnaris; fb, fossa m. brachialis; fdII, facies art. digitalis major; fdIII, facies art. digitalis minor; fi, fossa infratrochlearis; fp, fossa pneumotricipitalis; ib, impressio brachialis; ica, incisura capitis; ico, impressio coracobrachialis; ir, incisura radialis; ist, impressio m. scapulotricipitalis; mc, margo caudalis; mII, os metacarpale majus; mIII, os metacarpale minus; o, olecranon; pe, processus extensorius; pp, processus pisiformis; psd, processus supracondylaris dorsalis; sht, sulcus humerotricipitalis; si, sulcus interosseus; sm, symphysis metacarpalis distalis; sp, spatium intermetacarpale; sst, sulcus scapulotricipitalis; slt, sulcus lig. transversus; stc, sulcus tendineus; str, sulcus tendineus; tav, tub. aponeurosis ventralis; tb, tub. bicipitale radii; tcd, dorsal rim of trochlea carpale; tcv, ventral rim of trochlea carpale; td, tub. dorsale; tv, tub. ventrale. Scale bar equals 10 mm.

this absence, whether natural or owing to breakage, might overemphasise the medial extension of fossa deltopectoralis.

The shaft appears to be more or less straight; this may be an artefact of how damage to this area was reconstructed, but specimens retaining smaller sections of shaft are similar in this regard; the distal quarter of the shaft is only

slightly curved (ventral view) with less curvature on the ventral margin where it merges with the epicondylus ventralis (cranial view); in other burhinds, the shaft is more sigmoid and has a more ventrally directed curve (cranial view). The fossa m. brachialis is pronounced, extending across the proximal sides of condyli to the dorsal and ventral borders of the cranial face. The proc.

supracondylaris dorsalis is flatter and even less developed than in modern burhinids. The condylus ventralis is more prominent both cranially (distal view) and distally, protruding further, and being spherical rather than oblong (cranial view).

Overall the humerus in *Wilaru* is large and similar in robustness to that of *Esacus* (distal width slightly less than *Esacus* and similar to that of *B. grallarius*) but substantially more so than in other burhinids. The caput humeri is fairly large and hemielliptical. The sulcus lig. transversus is broad but occupies only the ventral side of the caput humeri (cranial view). The proximal end of the fossa pneumotricipitalis undercuts the prominently developed tuberculum ventrale and produces a triangular indentation in the border.

MAYR (2011) scored burhinids as having a single fossa pneumotricipitalis and STRAUCH (1978) scored *Esacus* as having a single fossa. T.H. WORTHY (pers. comm.), however, noted that, in some specimens of *Esacus* at least, there is a narrow but distinct second fossa located dorsally. The area immediately distal to the caput humeri on the caudal face is excavated in such a manner to create a second fossa in both *Esacus* and *Wilaru*, but not in *Burhinus*.

The tuberculum dorsale is extensive and flat (but clearly elevated off the shaft facies). The crista deltopectoralis is moderately extensive distally, joining the shaft rather smoothly; in no specimen is the crista sufficiently undamaged to provide further description. The crista bicipitalis follows the curve of the fossa pneumotricipitalis. The epicondylus ventralis does not protrude far from the ventral corner of the distal end (cranial view). The sulcus humerotricipitalis is wide and shallow and the ridge between this and the sulcus scapulo-tricipitalis is low.

**Referred specimens:** None of the specimens were associated, although several were in close proximity and most were found in the same small area at one site at Lake Pinpa (Site C, QMAM47). It was assumed that, given the number of burhinid remains at the site, these represented most skeletal elements. Ongoing examination indicates that some specimens initially assigned to the Burhinidae more likely represent one or more other taxa. These are omitted here. Likewise, among the remaining putative burhinid speci-

mens, some are too fragmentary or damaged to assign to this family with any confidence and so are not considered further. Of those that are here referred to the new taxon, some are done so more tentatively than others. When diagnostic characters cannot be identified on the material available, assignment is made for those most comparable to modern burhinid morphology. Measurements are given in Table 1 (Appendix).

*Furcula* (Fig. 2A) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10983, furcula missing articular ends to both scapus clavicularae; SAM P48922 (formerly AMNH 11479), symphyseal fragment retaining part of the left scapus clavicular. For the material, there are no readily distinguishable characteristics except for size, which seems more massive than in most other burhinids (but similar in size to that of *Esacus*), with thicker scapus clavicularae, especially near the apophysis interclavicularis. The symphysis is longer than the adjacent scapus clavicularae and the apophysis interclavicularis projects caudally as a low but prominent ridge.

*Scapula* (Fig. 2B, C) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10989 pR retaining a third of shaft; AMNH 10990 pL end missing acromion; AMNH 11434 pL; AMNH 11435 pL; SAM P48923 (formerly AMNH 11438) pR and about half the shaft; AMNH 11463 pR, retaining about half of shaft with tip of acromion missing; AMNH 11477 pR with tip of the acromion damaged.

These specimens are referred to *Wilaru* because of their relative abundance in the site with the other burhinid fossils and the absence of any other potential scapular specimens. This is while recognising that there are some major morphological differences between them and the scapulae of modern burhinids: The acromion is much longer and more pointed overall and the bulbous tuberculum coracoideum is much larger than in any other burhinid.

The facies art. clavicularis is folded laterally, also seen in *Esacus*. The facies art. humeralis is more rounded and less elongate proximodistally than in modern burhinids and it has a distinct indentation running through its proximodistal

midline (lateral view). The facies art. humeralis is separated from the tuberculum coracoideum by a low but distinct notch, rather than being confluent with it. The portion of the corpus scapulae that is preserved is straight and rather thin. The extremitas caudalis are missing; preserved lengths are 52.1 mm (SAM P48923) and 43.4 mm (AMNH 11463).

*Coracoid* (Fig. 2D, E) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48924 (formerly AMNH 11412) R missing processus lateralis and tip of angulus medialis; AMNH 11414 oR; AMNH 11426 L missing processus lateralis and tip of angulus medialis; AMNH 11428 R in two non-joining pieces retaining sections of shaft, a proximal fragment with abrasion to processus procoracoideus and a distal end with abraded sternal end and missing tips of processus lateralis and angulus medialis; AMNH 11433 R missing distal border, processus lateralis and angulus medialis; AMNH 11458 L abraded and missing processus lateralis; AMNH 11473 oL with general abrasion to edges; AMNH 11478 oR broken through about midshaft. Lake Palankarina, Mammalon Hill, Etadunna Formation, Ngama LF: SAM P23625 R without processus lateralis.

These fossils are referred to the Burhinidae because there is a well developed projection on the sternal end of the medial margin, identified by MAYR (2011) as characteristic of the burhinid coracoid. The omal end is large, rather bulbous and more massive than in many families with similarly sized coracoids. The facies art. clavicularis overhangs, and is deeply undercut by the sulcus m. supracoracoidei; the distal border of the facies is more or less straight across most of its length (slight protrusion at midpoint), not sloping sternomedially as in some taxa (e.g., *Haematopus*).

The coracoid is a stout and strong bone. The facies art. clavicularis is expanded dorsoventrally and extends beyond the proximal shaft on the dorsal and ventral sides (lateral view). The processus procoracoideus is rather short and triangular at base. The sulcus m. sternocoracoidei is deep, strongly bordered dorsally and ventrally. The facies art. humeralis is large, slightly longer than the impressio lig. acrocoracohumeralis. The

cotyla scapularis is deep and distinct. The impressio m. sternocoracoidei is shallow, very broad mediolaterally and extends omally along shaft. The facies art. sternalis is deep with a prominent ridge separating it from the impressio m. sternocoracoidei (dorsal view). The sternomedial corner is squared off between the project on the medial border and the angulus medialis. The processus lateralis is missing in all specimens.

*Wilaru* differs from modern burhinids in having the omal half deflected further medially (30–40°) in relation to the main shaft (ventral view), with the medial border of the shaft more curved (ventral view). The sulcus m. supracoracoidei has a flatter dorsal border. The processus acrocoracoideus extends dorsally and ventrally beyond the fossa art. humeralis, rather than being slightly narrower than, or subequal to the width of the fossa (lateral view). The cranially-directed strap-like projection on the end of the processus procoracoideus, seen in modern taxa, is not present. The projection on the sternal end of the medial margin is placed more distally than in modern burhinids.

*Radius* (Fig. 3D, E, F, G) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11410 pR with abrasion to edges of cotyla humeralis; AMNH 11411 dL damaged on distal end, particularly tub. aponeurosis ventralis and ventral face; AMNH 11453 R most of the shaft missing the proximal and distal ends; AMNH 11464 L in two pieces comprising both ends and almost complete shaft; AMNH 11468 dR slightly abraded particularly on distocaudal corner; AMNH 11469 dL retaining about third of shaft; AMNH 11471 dR; and SAM P48927 (formerly AMNH 11431) pR including distal half of shaft with slight abrasion to cotyla humeralis. Lake Pinpa, Site C, collection code QMAM125, Namba Formation, Pinpa Fauna: AMNH 10800 dL abraded on surface of dorsal face. Lake Pinpa, Site C, collection code QMAM151, Namba Formation, Pinpa Fauna: AMNH 10943 dL abraded on distal surface. Lake Pinpa, Site C, collection code QMAM243, Namba Formation, Pinpa Fauna: AMNH 10744 pL with abrasion on edges of cotyla humeralis and tub. bicipitale radialis; and AMNH 10813 dR with detailed features lost to abrasion. Billeroo Creek,

Site 3, collection code QMAM 199, Namba Formation, Pinpa Fauna: AMNH 10777 dL with abraded end; AMNH 11060 pR with abraded edges to cotyla humeralis. Lake Palankarinna, White Sands Basin, Etadunna Formation, Zone B, Ditjiminka LF: MV P.199593 dL.

The fossil fragments of the radius referred to this family agree with the morphology of modern burhinids in overall shape. The radius of *Wilaru* is slightly less robust than that of *Esacus*, comparable in size with that of *B. grallarius*, and larger than that of other extant species.

*Wilaru* has a more prominent facies art. ulnaris produced as a ridge running proximodistally on the ventral surface of the distal end. The cotyla humeralis is rather rectangular (deeper than wide) in (proximal view), agreeing with the modern configuration, although abrasion to the edges of this structure in most specimens adds some uncertainty to ascertaining the shape. The tuberculum bicipitale radii is a pronounced ridge. The shaft is smooth and slender; the degree of curvature cannot be assessed owing to breakage and repair of the specimen. The distal end is relatively flat and compressed (cranial view), with the distomedial corner rounded. The sulcus tendineus is shallow. The tuberculum aponeurosis ventralis is short and triangular, protruding cranially.

*Ulna* (Fig. 3H, I) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 10992 pL with abraded edges and missing olecranon; AMNH 10994 pL retaining about a quarter of shaft; SAM P48926 (formerly AMNH 11422) pL retaining about a quarter of shaft; AMNH 11456 pL includes an associated section of mid-shaft although pieces do not match neatly; AMNH 11457 pR retaining about a quarter of shaft; unnumbered pR in good condition.

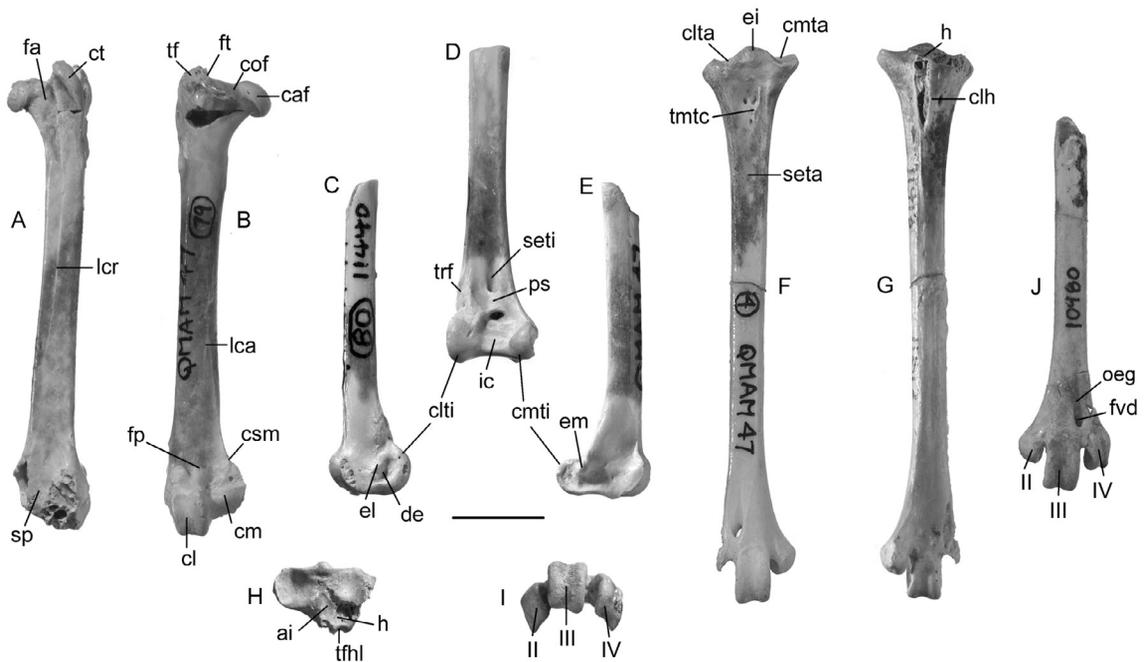
There are no complete specimens of this element, all of which are proximal fragments. The specimens provide a good match in structure with modern burhinid species, having the incisura radialis prominently developed and moderately deep and the tuberculum lig. collateralis ventralis obsolete. The ulnae are slightly smaller than in *Esacus*, comparable in size with *B. grallarius* and larger than in other burhinids, and are tentatively referred to *Wilaru*.

The olecranon is prominent with a bluntly rounded point. The incisura radialis bounded distally by a well developed and rugose ridge. The impressio m. scapulotricipitalis is a very shallow circular depression, separated from the shaft surface by low ridge, although like other burhinids, features of the dorsal face of the distal end are not strongly expressed. The crista intercotylaris is low (dorsal view). The cotyla ventralis is circular with moderately high borders. The impressio m. brachialis is long and narrow with parallel sides (ventral view). The shaft, where represented on the proximal fragment, is cylindrical, smooth and straight.

*Carpometacarpus* (Fig. 3J, K, L) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48928 (formerly AMNH 10997) R missing os metacarpale minus; AMNH 10998 pL proximal end with a third of os metacarpale minus; AMNH 11401 pL lacking os metacarpale majus and minus with facies artic. digitalis major damaged; AMNH 11432 R missing os metacarpale minus; AMNH 11448 R near complete but os metacarpale minus broken and embedded in plasticine and distal end damaged; AMNH 11460 L complete but os metacarpale minus broken and embedded in plasticine; AMNH 11462 pL missing distal third of os metacarpale major and all of os metacarpale minus; AMNH 11467 R complete but os metacarpale minus repaired and reattached in approximate position; AMNH 11474 dL symphysis metacarpalis distalis and distal half of os metacarpale majus. Lake Pinpa, Site C, collection code QMAM 243, Namba Formation, Pinpa Fauna: AMNH 10962 pR missing distal third of os metacarpale majus and all of os metacarpale minus.

The carpometacarpi are referred to the Burhinidae because the processus extensorius is elongated (proximal view), the dorsal surface of the os metacarpale majus is angular at mid length (but rectangular in cross section) and the facies art. digitalis minus projects distally about same extent as the facies art. digitalis majus, rather than further.

This element in *Wilaru* differs from that of modern burhinids in several aspects. The dorsal rim of the trochlea carpalis is roughly circular with its proximodistal length roughly equal to its



**FIGURE 4.** Hindlimb elements of *Wilaru tedfordi* nov. spec.: **A, B**, left femur SAM P48929 (formerly AMNH 11439) (cranial and caudal views); **C, D, E**, distal right tibiotarsus SAM P48930 (formerly AMNH 11440) (lateral, cranial and medial views); **F, G, H, I**, right tarsometatarsus AMNH 11413 (dorsal, plantar, proximal and distal views); **J**, distal left tarsometatarsus SAM P48931 (formerly AMNH 10980) (dorsal view). ai, area intercotylaris; caf, caput femoris; cof, collum femoris; cl, condylus lateralis; clh, crista lateralis hypotarsi; clta, cotyla lateralis; ckti, condylus lateralis; cm, condylus medialis; cmta, cotyla medialis; cmti, condylus medialis; csm, crista supracondylaris medialis; ct, crista trochanteris; de, depressio epicondylaris lateralis; ei, eminentia intercotylaris; el, epicondylus lateralis; em, epicondylus medialis; fa, facies art. antitrochanterica; fp, fossa poplitea; ft, fossa trochanteris; fvd, foramen vasculare distale; h, hypotarsus; ic, incisura intercondylaris; II, trochlea metatarsi II; III, trochlea metatarsi III; IV, trochlea metatarsi IV; lca, linea intermuscularis caudalis; lcr, linea intermuscularis cranialis; oeg, outer extensor groove; ps, pons supratendens; sp, sulcus patellaris; seta, sulcus extensorius; seti, sulcus extensorius; tf, trochanter femoris; tfhl, tendon for m. flexor hallucis longus; tmtc, tuberculum m. tibialis cranialis; trf, tub. retinaculi m. fibularis. Scale bar equals 10 mm.

craniocaudal width (in other burhinids it is more oblong and longer than wide) and extends further caudally, to roughly the same extent or slightly further as the caudal edge of the os metacarpale minus (dorsal view). The ventral rim of the trochlea carpalis extends to about the same extent. In *Esacus* and *Burhinus*, the dorsal rim only slightly exceeds caudally the caudal face of os metacarpale majus, while the ventral rim has a markedly greater extent compared to the dorsal rim and to the ventral rim in *Wilaru*. The sulcus tendineus, on the distal half of the dorsal face adjacent to the spatium intermetacarpale, is deeper (shallow to obsolete in extant burhinids).

The processus extensorius is bluntly pointed (proximal view). The borders of the facies articularis are well defined. The fossa infratrochlearis is entirely proximocaudal of the processus

pisiformis (the cranial and distal borders are level with the processus extensorius); it is more proximocranially-distocaudally oblong than the round shape in *Burhinus*, agreeing more closely with the condition in *Esacus*. The processus pisiformis is pronounced, with little excavation around its base. The os metacarpale majus and os metacarpale minus are straight and roughly parallel. The symphysis metacarpalis distalis is long, about 22–24% of the length of the spatium intermetacarpale. The sulcus interosseus spans the length of the symphysis metacarpalis distalis from the distal end of the spatium intermetacarpale (dorsal view).

*Femur* (Fig. 4A, B) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48929 (formerly AMNH 11439) L

with damage to caput femoris, both condyli and parts of proximal shaft; AMNH 11444 dR, fragment with damage to condyli.

The specimens are referred to the Burhinidae because of their overall similarity in size and morphology, and because of the suite of characters identified by HOWARD (1973): the trochanter femoris bends medially, the caput femoris projects abruptly, the shaft is straight and stocky, the sulcus intercondylaris is wide, the fossa poplitea is deep and the crista supracondylaris medialis is high and sharp.

Compared to living burhinids, the collum femoris in *Wilaru* is more constricted (proximal view) and the facies art. antitrochanterica has a more prominent lip protruding caudally over the shaft with the area immediately distal to this more excavated.

This is a sturdy, robust element, larger than in most burhinids, but noticeably smaller than in *Esacus*. The caput femoris is round and bulbous with a shallow but extensive fovea lig. capituli. The trochanter femoris is distinctly rounded on its cranial border (medial view), curving over the facies art. antitrochanterica (proximal view) and projecting proximally beyond the caput femoris (by about same distance as dorsoventral diameter of caput). The crista trochanteris recurves slightly over the facies art. antitrochanterica, with the mediocranially directed apex forming the fossa trochanteris. The ridge extending distally from the base of the trochanter femoris on the cranial face is sharply delineated, creating a deep and distinct depression between the caput and trochanter. The fossa on the pretrochanteric facies is moderately excavated between the strong linea intermuscularis cranialis and the cranial border of facies art. antitrochanterica. The shaft is straight in lateral, cranial and caudal views, lacking any pronounced curvature, is parallel-sided, and subcylindrical in cross-section. The fossa poplitea is extensive and bounded medially by the crista supracondylaris medialis, which links to the linea intermuscularis caudalis running proximally along the shaft's midline (caudal view). The sulcus patellaris is deep and broad. The condyli lateralis and medialis merge smoothly, almost confluent, with the shaft on the cranial side (lateral and medial views).

*Tibiotarsus* (Fig. 4C, D, E) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: AMNH 11417 dR with caudal side of condylus medialis missing; AMNH 11423 dL with damage to caudal surface; AMNH 11424 dR damaged on cranial side of condylus medialis; AMNH 11427 dL retaining section of shaft; AMNH 11430 dL with repaired damage to condyli and shaft; SAM P48930 (formerly AMNH 11440) dR; AMNH 11445 dR missing caudal face with shaft crushed and repaired; AMNH 11455 dL with condyli abraded. Billeroo Creek, Site 3, collection code QMAM199, Namba Formation, Pinpa Fauna: AMNH 10885 dR with heavy abrasion to condyli lateralis and medialis and damage to attached shaft. Lake Palankarina, Tedford Locality Site 3, (V5762), RHT#465, Etadunna Formation, Ditjiminka LF, collected R. H. Tedford 1957: UCMP 57152 dL with condylus lateralis damaged on caudal surface and missing distal edge. Lake Palankarina, SAM North, Etadunna Formation, Zone B, Ditjiminka LF: MV P.199595 dR with a portion of the adjoining shaft.

The distal fragments are referred to Burhinidae on the basis of agreement in size and morphology. They are intermediate in size between *Esacus* and *B. grallarius*. The sulcus extensorius is shallow and situated between the midline and medial border (cranial view). The degree of curvature of the shaft to meet the condylus medialis (cranial view) shows some variability among individuals from rather minimal (condylus more or less in line with shaft's medial border) to more pronounced (condylus medial to shaft border). The tuberculum retinaculi m. fibularis is large and flat, extending proximally well beyond the pons supratendineus. The condyli are of roughly equal widths (cranial view) and are parallel to each other and to the midline of the shaft. Both have raised borders and meet the shaft abruptly on their caudally and cranially sides. The condylus lateralis is a rounded oval in profile, the epicondylus lateralis is a low peak and the depressio epicondylaris lateralis is moderately deep. The condylus medialis is a more elongate oval and has a notch in the midpoint of its distal border (medial view). The caudal half of the condylus medialis slopes sharply medially from the epicondylus medialis

(expressed as a strong ridge) and has a strongly raised border. The incisura intercondylaris is wide, much more so than width of either condyli.

A single proximal fragment (AMNH 10986) lacks the end (cotylae and cristae), but the remaining sections agree in overall size and in the configuration of the crista fibularis. Despite these few similarities, it is too damaged to be referred to this taxon.

*Tarsometatarsus* (Fig. 4F, G, H, I, J) — Lake Pinpa, Site C, collection code QMAM47, Namba Formation, Pinpa Fauna: SAM P48931 (formerly AMNH 10980) dL with damage to trochlea metatarsi IV (this is accompanied in its box by an unnumbered pL fragment that has been repaired and is missing the hypotarsus; the two pieces do not fit comfortably together); AMNH 10981 dR; AMNH 11413 R with hypotarsus damaged and trochlea metatarsi IV missing.

The fossils agree with that of Burhinidae by being long, straight and slender and having both cotylae lateralis and medialis rounded (not oval) and deep. The trochlea metatarsi II is not recessed far plantarly relative to trochlea metatarsi III; its dorsal border is level with the midline of the trochlea metatarsi III, while its distal border is only slightly more proximal than that for trochlea metatarsi IV (STRAUCH 1978); it is not recurved dorsally. The angle formed between the trochleae metatarsi II and IV about 40° (distal view). Although only a dorsal fragment of the hypotarsus is preserved, the remaining section shows that it was rather deep on the lateral side, caudal to the cotyla lateralis, and retains a groove for the tendon of *m. flexor hallucis longus*. *Esacus* is also deeper in this section of the hypotarsus; *Burhinus* is less so, as are some other charadriiform groups, such as *Haematopus*, in which this lateral side of the hypotarsus is shallower. Unfortunately, the relative positions of the canalis for the tendon of *m. flexor digitorum longus* and the sulcus for the tendon of *musculi perforans et perforatus digiti 2*, identified by MAYR (2011) as important feature characterising some charadriiform groups, cannot be ascertained. He also reported that in burhinids the tendon of *musculus flexor digitorum longus* is enclosed in a bony canal (this is not so in some specimens of *B. grallarius*).

The area intercotylaris is round, smaller, more

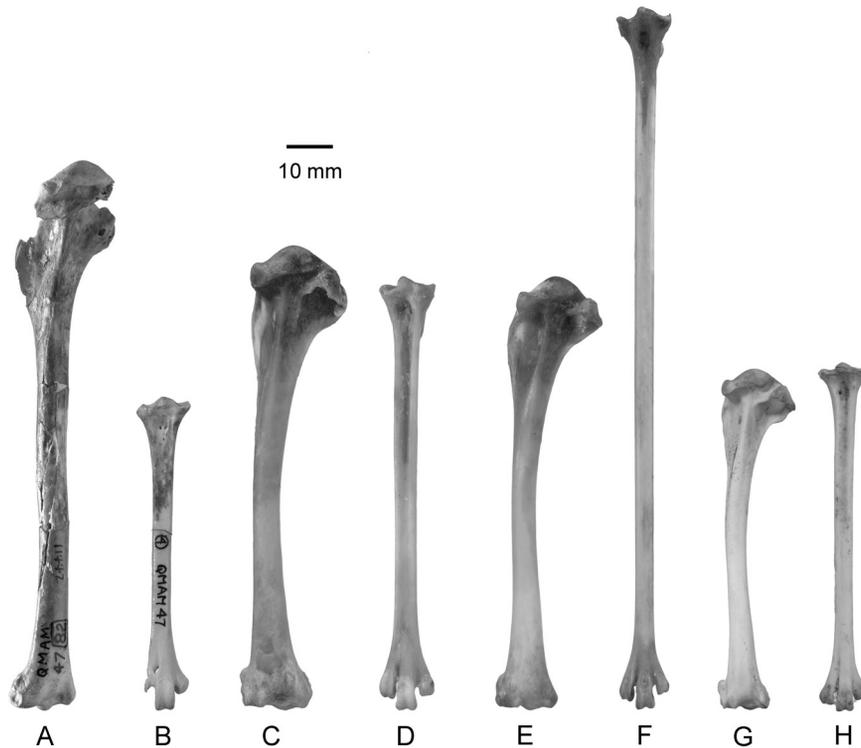
excavated than in *Haematopus*. The plantar rim of the cotyla lateralis is lower than in taxa such as *Haematopus* and is not visible in dorsal view. The tuberculum *m. tibialis cranialis* is broad and low, not projecting as far as in many charadriiform groups.

*Wilaru* differs from living burhinids in several features of the tarsometatarsus. In the fossil taxon, the proximal and distal ends are proportionally wider, both roughly 16–17% of the element length (compared to roughly 7.5–8% in other burhinids). The apex of the eminentia intercotylaris is broader and more rounded (dorsal view). The crista lateralis hypotarsi (as preserved) is longer and thinner than the short, broad condition in other burhinids (plantar view). The sulcus extensorius is much shallower distally from about midpoint of shaft. The foramen vasculare distale is larger and more obvious and the outer extensor groove (HOWARD 1929) leading into the foramen longer, wider and more excavated into shaft surface (dorsal view). The trochlea metatarsi II has greater medial inflection, particularly on the dorsal side (dorsal view), and its plantar extent is greater than 50% of that of the trochlea metatarsi III (<50% in other burhinids) (medial view).

The eminentia intercotylaris protrudes noticeably proximally. The sulcus extensorius is elongate and deep dorsally. The cotyla medialis is slightly larger than the cotyla lateralis. The lateral and medial borders of the shaft are straight and parallel until they converge slightly distally towards the trochleae, with the cross-section of the distal half roughly rectangular (wider than deep). The trochlea metatarsi II is not grooved. The widths of trochleae metatarsi II and IV are subequal. The rims of trochlea metatarsi III are parallel (plantar view). The trochleae metatarsi III and IV have a marked groove along the midline of the dorsal surface.

## Discussion

Most *Burhinus* species have more or less similar proportions (tarsus length:wing length 0.30–0.42). *Burhinus grallarius* is similar except for its markedly elongated tarsometatarsus (tarsus length:wing length 0.49). *Esacus magnirostris* has proportionally shorter legs (tarsus



**FIGURE 5.** Size comparisons of humeri (caudal view) and tarsometatarsi (dorsal view) of fossil and extant burhinids: **A**, *Wilaru tedfordi* nov. spec. SAM P48925 (formerly AMNH 11442). **B**, *Wilaru tedfordi* nov. spec. (AMNH 11413), **C**, **D**, *Esacus magnirostris*, **E**, **F**, *Burhinus grillarius* and **G**, **H**, *B. oediconemus*.

length:wing length 0.30), comparable to the lower end of the *Burhinus* range. This difference between the fore and hind limbs is expressed in most skeletal elements of *Esacus*. Its humerus and carpometacarpus are larger, but its tarsometatarsus is actually and proportionally shorter, than those of *B. grillarius* and several of the smaller species of *Burhinus* (Fig. 5, Appendix: Tab. 2). *Esacus* is also more robust in most of its skeletal elements than is *B. grillarius*.

The evidence suggests that *Wilaru* had a forearm length markedly greater than that of the hindlimb (Fig. 5). Demonstrating this is confounded by the fact that the available elements likely come from several individuals, which might have shown the same intraspecific size variation as seen in living taxa. Among living species of *Burhinus*, the ratio of humeral length to tarsometatarsal length varies from 0.72 to 0.86. Except for *B. grillarius*, however, the comparative samples are too small to give an indication of intraspecific variation. In this species, the range of hum:tmt ratios is 0.77–0.83. Comparing the longest humerus in the sample with the short-

est tarsometatarsus gives a value of 0.86. The reverse (shortest humerus versus longest tarsometatarsus) yields a ratio of 0.69. A comparative figure for the single humerus and tarsometatarsus of *Wilaru*, regardless of being from different individuals of possible different sizes, is 1.89. A similar finding comes from comparing the carpometacarpus and tarsometatarsus: in modern taxa, the ratio is 0.37–0.39, whereas in *Wilaru* (again with the same caveats) it is 0.80. For *Esacus magnirostris*, values for hum:tmt and cmc:tmt are 0.57 and 1.13, respectively, again outside the range of *Wilaru*. The values for *Wilaru* are well outside the range of modern taxa and thus likely valid indications that the fossil taxa had a much longer forelimb relative to the hindlimb than occurs in modern burhinid species.

Do these limb proportions suggest that *Wilaru* may have been less cursorially adapted than extant burhinids? The relatively short-legged *Esacus magnirostris* is not obviously less cursorial than the much longer-legged *B. grillarius*. The longer wings of *Wilaru* might be indicative of a greater reliance on flight than modern forms,

but there is no obvious evidence to support this. Alternatively, the limb proportions of *Wilaru* may reflect the ancestral condition in this lineage. Recent molecular studies (e.g., ERICSON *et al.* 2003) have placed the Burhinidae in a clade with the sheathbills (Chionidae) and the Magellanic Plover *Pluvianellus socialis* GRAY, 1846. Both are southern groups, suggesting that they and burhinds may have had southern origins. Morphological comparisons by MAYR (2011) identified cranial synapomorphies in the Burhinidae and Egyptian Plover *Pluvianus aegyptius* (LINNEAUS, 1758), a taxon not included in the molecular analyses. All these putatively related taxa have comparatively short tarsi compared to wing length. In living burhinids, the ratio of tarsal length to wing length is 0.30–0.49. *Pluvianus aegyptius*, with a tarsus:wing ratio of 0.25, may be most similar to the proportions and appearance of *Wilaru*.

When *W. tedfordi* lived in northern South Australia, fluvio-lacustrine conditions with inland seas existed where today open desert occurs (ALLEY 1998; MARTIN 2006). The marine regression that occurred during the Miocene and the northward drift of Australia into drier latitudes saw the development of more open landscape by the end of the Miocene (ALLEY 1998; MARTIN 2006), likely opening new niches and making flight less important in more open grassland conditions. As such, more cursorial burhinids took advantage of new ecospace.

FEDUCCIA (1980) considered that “species of *Burhinus* are . . . good indicators of tropical, dry savannah”. BICKART (1981), citing habitat preferences across the living species of burhinids, disagreed, noting that “such inferences . . . cannot be safely based merely being a burhinid”. It is suggested here that that *Wilaru* likely occupied shorelines of water bodies, much like species of *Esacus* do today.

Attempts to reconstruct the evolution and biogeography of the burhinids are hampered by the sparse fossil record and limited systematic attention to the family. The presence of *Burhinus lucorum* in North America in the early Miocene demonstrates that burhinids were widespread

by this time, and the living genus *Burhinus* was contemporaneous with *Wilaru*. The latter was thus unlikely to be directly ancestral to extant taxa. MEINERTZHAGEN (1924) published a revision of the family, recognising only a single genus, *Burhinus*. The traditional practice of most classifications has been to accept *Burhinus* and *Esacus*. LIVEZEY (2010), however, segregated *B. grallarius* from *Burhinus* and created two subfamilies, placing *grallarius* with *Esacus* in one and the remaining species of *Burhinus* in the other. Many of the diagnostic characters that LIVEZEY (2010) used were from the skull, not available in the material of *Wilaru*. Thus, the fossil taxon cannot be incorporated within Livezey’s classification.

In terms of limb proportions, *Wilaru* most closely resembles *Esacus*. These taxa also share several character states to the exclusion of *Burhinus*, including a small second dorsal fossa pneumotripicitalis, laterally folded facies art. clavicularis, more oblong fossa infratrochlearis and laterally deeper hypotarsus. Whether these similarities are phylogenetically important is uncertain. Determination of this and the placement of *Wilaru* in the classification of Burhinidae await further clarification of modern intrarelationships in the family (including molecular studies) and analysis using a greater coverage of the skeletal elements and incorporating *Wilaru*.

## Acknowledgments

We thank the staff of Museum Victoria, American Museum of Natural History, United States National Museum, Los Angeles County Museum of Natural History, Kansas University Natural History Museum, University of California Museum of Paleontology, South Australian Museum and Australian National Wildlife Collection who provided fossil and Recent specimens and images for this study. Trevor WORTHY (Flinders University, Adelaide) and an anonymous referee made valuable criticisms and suggestions. Carl BENTO, Australian Museum Photography Section, took the photographs.

## References

- ALLEY, N.F. (1998): Cainozoic stratigraphy, palaeoenvironments and geological evolution of the Lake Eyre Basin. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **144**: 239–263.
- BAIRD, R.F. (1991): Avian fossils from the Quaternary of Australia. – In: VICKERS-RICH, P., MONAGHAN, J.M., BAIRD, R.F. & RICH, T.H. (eds): Vertebrate palaeontology of Australasia. – pp. 809–870, Melbourne (Pioneer Design Studio).
- BAUMEL, J.J. & WITMER, L.M. (1993): Osteologia. – In: BAUMEL, J.J., KING, A.S., BREAZILE, J.E., EVANS, H.E. & VANDEN BERGE, C. (eds): Handbook of avian anatomy: Nomina anatomica avium. 2<sup>nd</sup> Edition. – *Publications of the Nuttall Ornithological Club*, **23**: 45–132.
- BICKART, K.J. (1981): A new thick-knee, *Burhinus*, from the Miocene of Nebraska, with comments on the habitat requirements of the Burhinidae (Aves: Charadriiformes). – *Journal of Vertebrate Paleontology*, **1/3-4**: 273–277.
- BLAKE, B.J. (1981): Australian Aboriginal languages. – 137 pp. Sydney (Angus & Robertson).
- BOLES, W.E. (1999): Early Eocene shorebirds (Aves: Charadriiformes) from the Tingamarra Local Fauna, Murgon, Queensland, Australia. – In: BAYNES, A. & LONG, J.A. (eds): Papers in Vertebrate Palaeontology. – *Records of the Western Australian Museum*, Supplement **57**: 229–238.
- BRODKORB, P. (1959): Pleistocene birds from New Providence Island, Bahamas. – *Bulletin of the Florida State Museum, Biological Sciences*, **4**: 349–371.
- BRODKORB, P. (1967): Catalogue of fossil birds: Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). – *Bulletin of the Florida State Museum, Biological Sciences*, **11**: 99–220.
- CABANIS, J.L. (1868): [Untitled]. – *Journal für Ornithologie*, **16**: 408–415.
- CORDES, A.H. (2002): A new charadriiform avian specimen from the early Maastrichtian of Cape Lamb, Vega Island, Antarctic Peninsula. Abstracts of papers; 62<sup>nd</sup> annual meeting, Society of Vertebrate Paleontology. – *Journal of Vertebrate Paleontology*, **22/Supplement**: 46A.
- CUVIER, G.L. (1829): Le Règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Edition 2, Volume 1. – 584 pp. Paris (Deterville et Crochard).
- ELZANOWSKI, A. & BOLES, W.E. (2012): Australia's oldest anseriform fossil: A quadrate from the Early Eocene Tingamarra Fauna. – *Palaeontology*, **55**: 903–911.
- FEDUCCIA, A. (1980): A thick-knee (Aves: Burhinidae) from the Pleistocene of North America, and its bearing on ice age climates. – *Natural History Museum of Los Angeles County Contributions in Science*, **330**: 115–118.
- GEERING, A., AGNEW, L. & HARDING, S. (2007): Shorebirds of Australia. – 256 pp. Collingwood, Victoria (CSIRO Publishing).
- GRAY, G.R. (1846): The genera of birds. Volume 3. – 185 pp. London (Longman, Brown, Green, and Longmans).
- HARRISON, C.J.O. & WALKER, C.A. (1976): Birds of the British Upper Eocene. – *Zoological Journal of the Linnean Society*, **59**: 323–351.
- HOWARD, H. (1929): The avifauna of Emeryville shell-mound. – *University of California Publications in Zoology*, **32**: 301–394.
- HOWARD, H. (1971): Quaternary avian remains from Dark Canyon Cave, New Mexico. – *Condor*, **73**: 237–240.
- HUME, R.A. (1996): Family Burhinidae (Thick-knees). – In: DEL HOYO, J., ELLIOT, A. & SARGATAL, J. (eds): Handbook of birds of the world. Volume 3. Hoatzin to Auks. – pp. 348–363, Barcelona (Lynx Edicions).
- ILLIGER, J.K.W. (1811): Prodomus systematis mammalium et avium additis terminis zoographicis utriusque classis. – I–XVIII+101–301pp. Berlin (Sumptibus C. Salfeld).
- LATHAM, J. (1802): Supplementum indicis ornithologici, sive systema ornithologiae. – 74 pp. London (Leigh & Sotheby).
- LESSON, R. (1831): Traité d'ornithologie, ou, Tableau méthodique des ordres, sous-ordres, familles, tribus, genres, sous-genres et races d'oiseaux. Livr 7. – 79 pp. Paris (F.G. Levrault).
- LICHTENSTEIN, M.H.K. (1823): Verzeichniss der Doubletten des Zoologischen Museums der Königl. Universität zu Berlin nebst Beschreibung vieler bisher unbekannter Arten von Säugethieren, Vögeln, Amphibien und Fischen. Volume X. – 118 pp. Berlin (J.F. Starcke).
- LINNAEUS, C. VON (1758): Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Vol. 1: Regnum animale Edition decima, reformata. – 823 pp. Stockholm (Laurentii Salvii).
- LIVEZEY, B.C. (2010): Phylogenetics of modern shorebirds (Charadriiformes) based on phenotypic evidence: Analysis and discussion. – *Zoological Journal of the Linnean Society*, **160**: 567–618.
- MARTIN, H.A. (2006): Cenozoic climatic change and the development of arid vegetation in Australia. – *Journal of Arid Environments*, **66**: 533–563.
- MAYR, G. (2009): Paleogene fossil birds. – 262 pp. Berlin, Heidelberg (Springer).
- MAYR, G. (2011): The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the

- conflict between morphology and molecules. – *Zoological Journal of the Linnean Society*, **161**: 916–934.
- MEINERTZHAGEN, A.C. (1924): XVI. – A review of the genus *Burhinus*. – *Ibis*, **66**: 329–356.
- SHUFELDT, R.W. (1915): On the comparative osteology of *Orthorhamphus magnirostris* (the Long-billed Stone-Plover). – *Emu*, **15**: 1–25.
- STRAUCH, J. (1978): The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. – *Transactions of the Zoological Society of London*, **34**: 263–345.
- STEADMAN, D.W. (1980). A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). – In: CAMPBELL, K.E. jr. (ed): Papers in Avian Paleontology Honoring Hildegard Howard. – *Contributions in Science, Natural History Museum of Los Angeles County*, **330**: 131–207.
- SWAINSON, W. (1837): The Natural History of the Birds of Western Africa. Vol. 2. – 263 pp. Edinburg (W.H. Lizars).
- TSCHUDI, J.J. (1843): Diagnosen einiger neuer Peruanischer Vögel. – *Archiv Naturgeschichte*, **9**: 385–390.
- VICKERS-RICH, P. (1991): The Mesozoic and Tertiary history of birds on the Australian plate. – In: VICKERS-RICH, P., MONAGHAN, J.M., BAIRD, R.F. & RICH, T.H. (eds): Vertebrate palaeontology of Australasia. – pp. 722–808, Lilydale (Pioneer Design Studio).
- VIEILLOT, L.J.P. (1818): Nouveau Dictionnaire d'histoire Naturelle, Appliquée aux Arts. Volume 23. – 612 pp. Paris (Deterville).
- WAGLER, J.G. (1829): Beiträge und Bemerkungen zu dem ersten Bande seines Systema Avium. – *Isis von Oken*, **22**: columns 505–519, 645–654, 736–762.
- WOODBURNE, M.O. (1986): Biostratigraphy and biochronology. – In: WOODBURNE, M.O. & CLEMENS, W.A. (eds): Revision of the Ektopodontidae (Mammalia: Marsupialia; Phalangeroidea) of the Australian Neogene. – *University of California Publications, Geological Sciences*, **131**: 87–93.
- WOODBURNE, M.O., MACFADDEN, B.J., CASE, J.A., SPRINGER, M.S., PLEDGE, N.S., POWER, J.D., WOODBURNE, J.M. & SPRINGER, K.B. (1994): Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. – *Journal of Vertebrate Paleontology*, **13**: 483–515.
- WORTHY, T.H. (2009): Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia. – *Zoological Journal of the Linnean Society*, **156**: 411–454.

## Appendix.

**TABLE 1.** Measurements of specimens of *Wilaru tedfordi* nov. spec. (mm). Scapula: *acro.-fac. art. hum.* measured from tip of the acromion to the distal edge of the facies art. humeralis. Coracoid: *proc. acro.-cot. scap.* measured from tip of the proc. acrocoracoideus to the sternal edge of the cotyla scapularis. Ulna: *olecranon-cot. dorsalis* measured from the tip of the olecranon to the cranial edge of the cotyla dorsalis. Tibiotarsus: *cond. lat.*, condylus lateralis; *cond. med.*, condylus medialis.

<b>FURCULA</b>	<b>length, symphysis</b>	<b>depth, symphysis</b>	<b>breadth, widest point</b>
AMNH 10983	7.7	6.0	33.0
SAM P48922 (= AMNH 11479)	6.4	5.1	

<b>SCAPULA</b>	<b>proximal width</b>	<b>depth, fac. art. hum.</b>	<b>acro.-fac. art. hum.</b>
AMNH 10989	10.1	3.3	12.5
AMNH 10990		3.5	
AMNH 11434	8.3	4.1	12.5
AMNH 1143	9.7	4.3	11.6
AMNH 11463		4.3	
AMNH 11477		4.2	12.0
SAM P48923 (= AMNH 11438)	8.4	4.0	13.6

<b>CORACOID</b>	<b>length</b>	<b>proximal width</b>	<b>width. fac. art. hum.</b>	<b>proc. acro.-cot. scap.</b>
AMNH 11414		4.1	5.1	15.5
AMNH 11426		4.9	6.0	17.4
AMNH 11428		5.4	5.7	15.9
AMNH 11433		4.4	5.3	15.9
AMNH 11458	36.9	4.9	6.1	17.0
AMNH 11473		<i>c.</i> 4.5	5.7	15.8
AMNH 11478			6.0	18.1
SAM P23625	38.9		6.9	19.6
SAM P48924 (= AMNH 11412)	35.9	4.7	6.1	17.0

<b>HUMERUS</b>	<b>length</b>	<b>prox. width</b>	<b>prox. depth</b>	<b>depth caput humeri</b>	<b>distal width</b>	<b>distal depth</b>
AMNH 10836					<i>c.</i> 13.9	
AMNH 10723					14.7	
AMNH 10859					15.9	
AMNH 11402				6.4		
AMNH 11403				5.8		
AMNH 11404				5.9		
AMNH 11405				5.9		
AMNH 11406				6.1		
AMNH 11409					13.3	
AMNH 11441					14.6	8.3
AMNH 11451		22.8	8.9	5.9	15.1	8.3
AMNH 11452					15.2	9.3
AMNH 11454		23.2		6.7		
AMNH 11470					14.0	7.9
AMNH 11476					15.1	
SAM P48925 (= AMNH 11442)	123.3			6.2	15.1	8.8
UCMP 57005					14.9	8.8

<b>RADIUS</b>	<b>length</b>	<b>prox. width</b>	<b>prox. depth</b>	<b>distal width</b>
AMNH 10744		4.5	4.7	
AMNH 10777				6.7
AMNH 10800				7.4
AMNH 10813				<i>c.</i> 6.8
AMNH 10943				6.9
AMNH 11060		<i>c.</i> 4.2	<i>c.</i> 5.3	
AMNH 11410		4.6	4.8	
AMNH 11411				7.9
AMNH 11464	<i>c.</i> 113.5	4.5	4.8	6.7
AMNH 11468				6.9
AMNH 11469				6.6
AMNH 11471				7.3
MV P.199593				7.3
SAM P48927 (= AMNH 11431)		4.4	4.7	

<b>ULNA</b>	<b>prox. width</b>	<b>olecranon-cot. dorsalis</b>
AMNH 10992	9.4	
AMNH 10994	10.8	8.8
SAM P48926 (= AMNH 11422)	11.3	8.6
AMNH 11456	11.0	7.6
AMNH 11457	9.6	7.7
unnumbered	9.2	7.8

<b>CARPOMETA-CARPUS</b>	<b>length</b>	<b>prox. width</b>	<b>prox. depth</b>	<b>distal depth</b>
AMNH 10962		13.6	4.6	
AMNH 10998		12.9	4.7	
AMNH 11401		12.0	4.7	
AMNH 11448	54.8	15.2	5.2	5.6
AMNH 11460	52.2	12.2	4.9	5.6
AMNH 11462		13.6	4.9	
AMNH 11467	53.5	13.3	5.6	4.6
AMNH 11474				5.0
SAM P48928 (= AMNH 10997)	50.7	13.3	4.7	6.0

<b>FEMUR</b>	<b>length as pre-served</b>	<b>prox. width</b>	<b>prox. depth</b>	<b>distal width</b>	<b>distal depth. medial side</b>
AMNH 11444				10.6	8.1
SAM P48929 (= AMNH 11439)	52.8	10.5	10.3	17.4	

<b>TIBIOTARSUS</b>	<b>distal width</b>	<b>distal depth. cond. lat.</b>	<b>distal depth. cond. med.</b>
AMNH 10885	9.9	7.7	9.8
AMNH 11417	10.6	8.8	
AMNH 11423	10.6	8.2	
AMNH 11424	9.6	7.2	
AMNH 11427	10	7.6	9.2
AMNH 11430	9.8	7.6	9.2
AMNH 11445	10.2	9.1	10
AMNH 11455	10.2	7.5	9.6
MV P.199595	9.8	7.9	9.3
SAM P48930 (= AMNH 11440)	10.1	7.6	9.6

TARSOMETA-TARSUS	length	prox. width	distal width	distal depth
AMNH 10981			10.6	8.0
AMNH 11413	66.0	11.5		7.7
SAM P48931 (= AMNH 10980)			11.5	8.1
unnumbered		10.6		

**TABLE 2.** Comparative measurements (mm) of the humerus, carpometacarpus and tarsometatarsus of *Wilaru tedfordi* nov. spec. and extant species of *Burhinus* and *Esacus*.

	<i>Burhinus oedicnemus</i>	<i>Burhinus capensis</i>	<i>Burhinus bistriatus</i>	<i>Burhinus grallarius</i>	<i>Esacus magnirostris</i>
Humerus	76.7	79.0–80.6	84.7	87.2–101.3	102.5–103.7
Carpometacarpus	39.2	41.4–41.6	40.5	46.0–50.9	51.1–52.4
Femur	47.2	47.5–50.9	51.9	53.1–61.2	62.2–65.9
Tarsometatarsus	73.4	97.4	98.1	118.3–147.5	91.0–91.1

