Worthy, T.H., J.P. Worthy, A.J.D. Tennyson, R.P. Scofield, 2013. A bittern (Aves: Ardeidae) from the Early Miocene of New Zealand. Paleontological Journal 47(11): 1331-1343.

“The final publication is available at Springer via
http://dx.doi.org/10.1134/S0031030113110154

A BOTAURINE HERON (AVES: ARDEIDAE) FROM THE EARLY MIOCENE OF NEW ZEALAND

TREVOR H. WORTHY[1], JENNIFER P. WORTHY[1], ALAN J. D. TENNYSON[2], AND R. PAUL SCOFIELD[3]

[1]School of Earth and Environmental Sciences, Darling Building, The University of Adelaide, Adelaide, SA 5005, Australia; e-mail: trevor.worthy@adelaide.edu.au;

[2]Museum of New Zealand Te Papa Tongarewa, P.O. Box 467, Wellington, New Zealand; and

[3]Canterbury Museum, Rolleston Ave, Christchurch 8013, New Zealand

We dedicate this contribution to Evgeny Kurochkin whose impact in palaeornithology extended worldwide.

Date of Submission: 18 July 2012

Date of Acceptance: **************

Running Head: Miocene bittern New Zealand

ABSTRACT. – Herons (Aves: Ardeidae) are rare in the fossil record globally. Fossil taxa referred to Ardeinae and Nycticoracini are known from as early as the early Oligocene and ardeids undetermined to subfamily include some as old as the early Eocene. In Australasia, the pre-Pliocene record is restricted to one species from the early Miocene of New Zealand. On the basis of a tarsometatarsus and a coracoid we describe a new species of bittern (Ardeidae: Botaurinae) from the St Bathans Fauna, of early Miocene age, from Otago, New Zealand. This is only the third and the oldest pre-Quaternary record for Botaurinae globally.

Key words: Fossil heron, bittern, Ardeidae, St Bathans Fauna, Early Miocene

INTRODUCTION

The Recent herons (Aves: Ardeidae) are considered to belong to five subfamilies (Kushlan & Hancock, 2005), but only two or three have a Tertiary Fossil record (Ardeinae, the Day Herons; Botaurinae, the bitterns; and perhaps Cochleariinae, boat-billed herons if *Zeltornis ginsburgi* Balouet, 1981 is correctly attributed (Zelenkov 2011)). The ardeid fossil record, most recently reviewed by Scofield et al. (2010) and Zelenkov (2011), extends back as far as the Eocene (see also Sallaberry et al., 2010), although no Eocene taxa have been confidentially assigned to any subfamily (Mayr, 2009). Tertiary botaurins are sparse with just two records: 1, *Botaurus hibbardi* Moseley & Feduccia, 1975, from the Pliocene of Kansas and an undescribed botaurin from the Middle Miocene Sharga locality in Mongolia (Zelenkov, 2011). Recent herons are a virtually cosmopolitan family, found on all continents except Antarctica, and Mayr (2009) has speculated an African origin for the group. The present authors recently described the first pre-Quaternary fossil heron from Australasia: *Matuku otagense*, inferred to be a basal heron of indeterminate affinities, derived from the early Miocene St Bathans Fauna of New Zealand. Here we describe a second ardeid from the St Bathans Fauna, this time a small fossil bittern (Botaurinae) based on two fossil bones, attesting to a diversity of herons in the early Miocene of New Zealand.

The St Bathans Fauna

The St Bathans Fauna, is currently considered to be of late early Miocene age (Altonian, 19–16 Ma) however as it is poorly dated there is a possibility it is actually contemporaneous with the early Miocene Foulden Maar flora (23.2±0.2 Ma; D. Lee pers comm.). The fossil bearing strata are found in the lower Bannockburn Formation of the Manuherikia Group, in Otago, South Island, New Zealand (Worthy et al., 2007). The sediments were deposited in a shallow freshwater lake, about 5600 km^2 in area. During this epoch Otago had a warm climate and a sub-tropical flora that included laurels (Lauraceae) casuarinas (Casuarinaceae), eucalypts (*Eucalyptus*: Myrtaceae) and palms (Arecaceae), in addition to all but one of the 10 conifer genera living in New Zealand today, *Nothofagus* and araucarias (Araucariaceae) (Pole & Douglas, 1998; Pole et al., 2003; Lee et al., 2012).

The St Bathans Fauna includes nearly 40 taxa of birds, several bats and an archaic terrestrial mammal, a crocodilian, a turtle, a sphenodontid and squamates (Molnar & Pole, 1997; Worthy et al., 2006; Hand et al., 2007; Worthy et al., 2007; Worthy & Lee, 2008; Worthy et al., 2008, 2011a; Jones et al., 2009; Lee et al., 2009). Terrestrial and freshwater molluscs are diverse (unpubl. data), and fish are abundant (Schwarzhans et al., 2012). The avifauna of the St Bathans Fauna is dominated by anseriforms, with a minimum of eight taxa in five genera, but the fauna also includes ratites, procellariiforms, accipitriforms, gruiforms, charadriiforms, columbiforms, psittaciforms, apodiforms, and passeriforms (Worthy et al., 2007; Worthy & Lee, 2008; Scofield et al., 2010; Tennyson et al., 2010;

Worthy et al., 2010a, 2010b, 2011b, 2011c). The St Bathans avifauna is known from exposures along the Manuherikia River and at several nearby sites (see Schwarzhans et al., 2012 for location data and stratigraphic context).

METHODS

Abbreviations: Ma, million years ago. Institutions: –**AM**, Australian Museum, Sydney, Australia; **ANWC**, Australian National Wildlife Collection, CSIRO, Canberra, Australia; **CM**, Canterbury Museum, Christchurch, New Zealand; **NHMW**, Naturhistorisches Museum Wien, Austria; **NMB**, Naturhistorisches Museum Basel, Switzerland; **NMNZ**, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; **MV**, Museum Victoria, Melbourne, Australia; **SAM**, South Australian Museum, Adelaide, Australia; **SMF**, Sektion Ornithologie, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; **UNSW**, University of New South Wales, Sydney, Australia.

Anatomical Nomenclature: –Names for specific bone landmarks follow Baumel & Witmer (1993). Some common terms are abbreviated as follows: artic., articularis; lig., ligamentum; m., musculus; proc., processus; tub., tuberculum.

Measurements were made with Tesa® dial callipers and rounded to 0.1 mm.

Comparative material: The generic and species level taxonomy of the ardeids is complex and many issues are unresolved - here we follow Kushlan & Hancock (2005). The fossil was compared to the following extant taxa and specimens.

ARDEINAE Leach, 1820: *Agamia agami* (Gmelin, 1789), Agami Heron, SMF 2538; *Ardea cinerea* Linnaeus, 1758, Grey Heron, SAM B.49222; *A. herodias* (Linnaeus, 1758), Great Blue Heron, CM Av19902, SMF 2108; *A. goliath* Cretzschmar, 1829, Goliath Heron, CM Av7120, SMF 1860; *A. modesta* J.E. Gray, 1831, Eastern Great Egret, CM Av 16554, CM Av 22663, CM Av 26515, CM Av36581, CM Av36585, CM Av36587, CM Av36590, SAM B7900, B10489, B28062; *A. ibis* Linnaeus, 1758, Cattle Egret CM Av 29417, SAM B.40176; *A. pacifica* Latham, 1802, White-necked Heron, SAM B.32418; *Ardeola idae* (Hautlaub, 1860), Malagasy Pond Heron, SMF 8865; *Butorides striata* (Linnaeus, 1758), Striated Heron, SMF 4289; *B. virescens* (Linnaeus, 1758), Green Heron, SAM B.47752; *Egretta novaehollandiae* (Latham, 1790), White-faced Heron, CM Av 5215, CM Av 14806, CM Av 25210, SAM B.45492; *E. picata* (Gould, 1845), Pied Heron, SAM B. 38753, B.38754; *E. garzetta* (Linnaeus, 1766), Little Egret, SAM B. 38756; *Pilherodius pileatus* (Boddaert, 1783), Capped Heron, NHMW 1064; *Nycticorax nycticorax* (Linnaeus, 1758), Black-crowned Night Heron, NMB 5553, SMF 2679, 9636; *N. caledonicus* (Gmelin, 1789), Nankeen Night Heron, NMNZ OR.19310; SAM B.48523, B.55409; *Nyctanassa violacea* (Linnaeus, 1758), Yellow-crowned Night Heron, SMF 2435, NHMW 1063; *Syrigma sibilatrix,* (Temminck, 1824), Whistling Heron, NHMW 7.218, SMF 4762.

TIGRISOMATINAE BOCK, 1956: *Tigrisoma mexicanum* Swainson, 1834, Fasciated Tiger Heron, MV B13558.

BOTAURINAE Reichenbach, 1850: *Botaurus lentiginosus* (Rackett, 1813), American Bittern, CM Av 19627, SMF 3148; *B. poiciloptilus* (Wagler, 1827), Australasian Bittern, CM Av 5085, CM Av 5085, CM Av 5502, SAM B.6971; *B. stellaris* (Linnaeus, 1758), Eurasian Bittern, NHMW 5111; *Ixobrychus sinensis* (Gmelin, 1789), Yellow Bittern, NMNH 291696; *I. cinnamomeus* (Gmelin, 1789), Cinnamon Bittern, MV B.24113; *I. dubius* Mathews, 1912, Australian Little Bittern, SAM B48804, MV B30216, MV B12685, MV B30215; *I. eurhythmus* (Swinhoe, 1873), Schrenk’s Bittern, NHMW 5953; *I.*

minutus minutus (Linnaeus, 1766), Little Bittern, NHMW 4.575, 6.938; *I. flavicollis* (Latham, 1790), Black Bittern, ANWC 22065; *I. novaezelandiae* (Purdie, 1871), New Zealand Little Bittern, NMNZ S.5453.

COCHLEARIINAE Chenu & Des Murs, 1854: *Cochlearius cochlearius* (Linnaeus 1766), Boat-billed Heron, CM Av 39999, AM A.4126.

SCOPIDAE Bonaparte 1849: *Scopus umbretta* Gmelin, 1789, Hamerkop, CM Av 39998, SMF 6331.

BALAENICIPITIDAE Bonaparte, 1853: *Balaeniceps rex* Gould, 1850, Shoebill, SMF2423, 6293.

CICONIIDAE Sundevall, 1836: *Ciconia ciconia* (Linnaeus, 1758), White Stork, CM Av 33450, SAM B.49223.

THRESKIORNITHIDAE Poche, 1904: *Threskiornis molucca* Cuvier, 1829, Australian White Ibis, CM Av 16219; *T. spinicollis* Jameson, 1835, Straw-necked Ibis, SAM B.48524; *Plegadis falcinellus* Linnaeus, 1766, Glossy Ibis, CM Av 20692, SAM B39428.

Phylogenetic analyses: In order to test the qualitative assignment of the fossils to Botaurinae we made a two-stage phylogenetic analysis of the fossils using morphological data. Because the two fossils attributed to the new taxon (tarsometatarsus, coracoid) were among the elements analysed by Scofield et al. (2010) we first based our analysis on the character set and matrix used therein. However, we modified some of the characters used by Scofield et al. (2010) to reflect new observations of the compared taxa and added several new ones for a total of 54 characters. We scored all compared taxa by direct observations of specimens, which resulted in some changes to those scored from the literature previously. We modified the analysed taxa by addition of several heron species and restricted the outgroup to *Ciconia*, *Plegadis* and *Threskiornis spinicollis*. However initial analyses resulted in poor resolution of relationships, in large part because of a low ratio of numbers of characters to numbers of taxa, and as the fossil always had affinity with botaurins we excluded various taxa including those with missing data from the analysis. Our final analysis of this 54 character matrix had 24 taxa in the ingroup: 3 *Botaurus*, 4 *Ixobrychus, Scopus*, *Balaeniceps*, *Cochlearius*, 1 *Butorides*, 1 *Nycticorax, Nyctanassa*, *Syrigma*, *Pilherodius*, 5 *Ardea*, 2 *Egretta*, the fossil *Matuku otagense* and the new taxon described here. The characters are given in Appendix 1 and data are provided in Appendices 2 and 3. This matrix was analysed using PAUP (Swofford, 2002).

In a second stage of the analysis, we added new characters based on other parts of the skeleton to try to better resolve the topology of extant taxa and therefore provide a better scaffold in which to examine the relationships of the fossil taxon. First we added four new characters (characters 55-58) then we added 30 non-overlapping characters from Payne & Risley's (1976) matrix as corrected by McCracken & Sheldon (1998). In our matrix (Appendix 3), characters 59-70 and 71-88 equate to Payne & Risley's 2-13 and 15-32, respectively. We excluded Payne & Risley's (1976) characters 1, 14 and 33 as they overlapped our characters 53, 41 and 4, respectively. In addition, we note that in Payne & Risley's (1976) matrix, character 31 was coded the inverse of the character description, so 0 as described was coded 1 in the matrix and 1 as described was coded 0 in the matrix. We did not alter the matrix as this is only relevant if interpreting the apomorphic changes of this character. Our observations of skeletons led to us making further two minor changes to the Payne & Risley's coding of taxa as follows: for character 30 we changed *Cochlearius* to 1 and for character 3 we changed *Agamia* to 0. We scored the included Payne & Risley (1976) characters from direct observation for *I. dubius*, *Plegadis*, and *Threskiornis* *spinicollis* and scored *Ciconia ciconia* to replace *C. alba* to match our existing taxon sampling.

Parsimony analyses used heuristic searches with tree-bisection-reconnection (TBR) branch swapping, and 1,000 random addition replicates per search. Trees were rooted with the outgroup forming a polytomy at the base of the tree. Gaps were treated as a separate state. When calculating tree lengths, multistate taxa were treated as polymorphisms rather than ambiguity. In some analyses, 16 characters that varied in a morphoclinal way (1 2 3 4 7 9 11 13 14 15 16 17 19 24 41 42) were treated as ordered. Strict consensus trees were computed and presented. Bootstrapping used heuristic searches and the same options, but because of extensive homoplasy in the tree and the relatively low ratio of numbers of characters to numbers of taxa, the searches were modified to only retain a limited number of MPTs on each tree island: Hsearch addseq=random nchuck=100 chuckscore=10 abortrep=no Nreps=1000. Trees were manipulated and labelled in MrEnt (Zuccon & Zuccon, 2006).

SYSTEMATIC PALEONTOLOGY

Order Ciconiiformes Bonaparte, 1854

Family Ardeidae Leach, 1820

The fossils are assigned to Ardeidae because they have the following combination of features found only in this family: tarsometatarsus elongate; eminentia intercotylaris large and bulbous, extends proximal of cotylae rims; hypotarsus triangular in plantar view with crista medianoplantaris largest and most prominent, canal for tendon of m. flexor digitorum longus (fdl) large and enclosed, tendinal canal for m. flexor hallicus longus much shorter than fdl, and an open sulcus plantar of fdl for the tendons for m. flexor perforatus digiti II & m. flexor perforans et perforatus digiti II; tuberositas m. tibialis cranialis a single tuberosity; fossa parahypotarsalis medialis large; fossa metatarsal I absent with flat facet for articulation of metatarsal 1 planar with shaft surface; foramen vasculare distale small; trochlea metatarsi III longest, trochlea metatarsi II extends distal of trochlea metatarsi IV.

Genus *Pikaihao* Worthy, Worthy, Tennyson & Scofield gen. nov.

Etymology: – Derived from Maori; 'Pi' a prefix used for small birds and chicks and 'kaihao', for fisherman; gender is masculine (Moorfield, 2011).

Type species: – *Pikaihao bartlei* sp. nov.

Diagnosis: –As for species.

Species composition: – *Pikaihao bartlei* sp. nov.

Comparison: – Within Ardeidae, *Pikaihao bartlei* can be assigned to Botaurinae because the tarsometatarsus shares the unique characteristic of this group (including *Botaurus*, *Ixobrychus*) of the trochlea metatarsi III being strongly directed distolaterally relative to the shaft alignment when viewed in dorsal aspect, although we note that in *Ixobrychus flavicollis*, the trochlea is less strongly aligned than in other botaurines. The relatively medial position of the tuberositas m. tibialis cranialis is additional support for a botaurin affinity (shared by all except *I. flavicollis*), as this feature is otherwise only seen in *Ardeola*, *Butorides* and *Cochlearius*, with all other genera having the tuberositas centrally located on the shaft. *Scopus* and *Balaeniceps* differ markedly from ardeids in that the tuberositas m. tibialis cranialis comprises a pair of tuberosities, rather than one. This tarsometatarsus is bigger than those of all *Ixobrychus* species except the historically extinct and poorly known *I. novaezelandiae* (Purdie) and *Ixobrychus flavicollis* (Linnaeus), but markedly smaller than all *Botaurus* species, so *Pikaihao bartlei* was of intermediate size yet was still a small bittern. In *Pikaihao*, the plantar surface of the tarsometatarsus at mid length is markedly convex with the medial side of the shaft compressed into a crest and so differs from smaller *Ixobrychus* taxa e.g. *I. dubius, I. sinensis, I. minutus,* and the larger *I. flavicollis* and *I. novaezelandiae* which have a distinctly flattened plantar surface bound by a well-developed crista plantaris medialis on the plantar side of a thick medial facies lacking a crest. Distally, *Pikaihao* has a markedly broad lateral intertrochlear notch opening plantarly as seen in some *Ixobrychus* species e.g. *I. dubius* and *I. novaezelandiae,* but differing from the narrow notch in *I. flavicollis*.

The coracoid also has two features that suggest a botaurin relationship: 1, the broad medioventral insertion of the lig. acrocoraco-claviculae superficiale is characteristic of *Ixobrychus* and *Botaurus,* with other ardeid genera with the exception of *Butorides, Cochlearius,* and *Agamia,* having the two impressions of similar width and the acrocoracoid appearing more compressed in ventral view; 2, the straight margin of the facies artic. clavicularis overhanging the sulcus supracoracoideus between the tub. brachiale and the point of insertion for the lig. acrocoraco-procoracoideum is seen in botaurins, but differs from other ardeids (excluding *Syrigma*, *Ardeola*, *Nyctanassa*) where the tub. brachiale is more prominent sternally contributing to a curved facies. A well-developed groove separates the facies artic. humeralis from the planar ventral surface as seen in all botaurines, creating a ridge mentioned by Zelenkov (2011), but we found this groove/ridge in a variety of ardeins as well, e.g. *Ardea novaehollandiae, Nycticorax nycticorax, Butorides striata* so it appears of limited phylogenetic significance.

Species *Pikaihao bartlei* Worthy, Worthy, Tennyson & Scofield sp. nov. (Fig. 1)

Etymology: –Named for J. A. (Sandy) Bartle, Curator of Birds at the National Museum of New Zealand and the Museum of New Zealand Te Papa Tongarewa from 1976 to 2009, whose enthusiasm and commitment saw the transformation of the incipient collection of fossil birds into a major resource and the subsequent establishment of a curatorial position for it.

Holotype: –NMNZ S.53345, immature left tarsometatarsus (Fig. 1A-C), collected 15 April 2011 by the joint UNSW/CM/NMNZ expedition from Bed HH4, true left side Manuherikia River, Home Hills Station, Otago, New Zealand. 44° 54.472’S, 169° 51.434’E. New Zealand Fossil Record File Number H41/f0095. Bed HH4, a 5-15 cm thick clay-silt lens notable for the large number of shell fragments of the gastropod *Glyptophysa*, in it, was 25.63-25.83 m above the base of the Bannockburn Formation, Manuherikia Group, early Miocene (Altonian), 19-16 Ma (Schwarzhans et al., 2012) and contributes to the St Bathans Fauna.

Paratype: –NMNZ S.53346. Cranial part left coracoid (Fig. 1D-G), collected with holotype.

Diagnosis: – An ardeid differing from all other herons by the following combination of characters: the foramen vasculare distale is located markedly proximal of the trochlea metatarsi IV (autapomorphy), the trochlea metatarsi III is strongly directed distolaterally relative to the shaft alignment when viewed in dorsal aspect, the tuberositas m. tibialis cranialis is located close to the medial margin, and plantarly the mid-section of the shaft is convex.

Measurements of Holotype: –Total length 50.15 mm, proximal width 6.7+ mm, proximal depth 7.4 mm, mid-shaft width 2.9 mm, mid-shaft depth 2.1 mm, width at metatarsal facet 3.4 mm, distal width 6.8 mm, depth trochlea metatarsi III 3.7 mm.

Measurements of Paratype: –Length of cotyla scapularis to tip of acrocoracoid 5.8 mm, dorsoventral depth of acrocoracoid 3.2 mm.

Description: –The tarsometatarsus NMNZ S.53345 is immature as indicated by the porous periosteal surface, especially of the proximal end, rather than a smooth dense surface as typifies adults. However, the complete fusion of the tarsal cap and formation of a plantar plate on the crista medianoplantaris suggests that the bone had reached adult size. It is stained black. The fossil is well preserved except for a small area of breakage resulting in the loss of the plantar side of cotyla lateralis and part of the lateral side of the hypotarsus. The three trochleae had broken off but have been reattached to the rest of the fossil. The fossil is bowed laterally but no significance is attached to this: rather it is likely a result of distortion during the fossilization process.

Apart from those noted above the fossil displays the following features. The cotyla lateralis is displaced distally relative to the cotyla medialis. The sulcus extensorius is relatively deep proximally but does not extend far down the shaft before opening to the medial side of the bone, as there is no ridge dorsally along the medial margin such as there is laterally. Within the sulcus extensorius, the foramen vascularia proximalis lateralis occupies a central point on the bone and its medial counterpart is at the same proximodistal level but lies relatively close to the medial margin. A single elongate tuberositas m. tibialis cranialis lies immediately distal to the medial foramen and is close to but not abutting the medial margin. The impressio retinaculi extensori form a pair of crests aligned transversely on the dorsal surface just distal to the cotyla medialis. The shaft medially adjacent to the tuberositas is relatively dorsoplantarly compressed forming a thin rounded ridge that develops into a sharp crest extending to the mid-length of the bone, contributing to a markedly triangular cross-section. The fossa parahypotarsalis medialis is large but not deeply excavated into the base of the hypotarsus as it is in some taxa, e.g. *Nycticorax*. On the hypotarsus, the sulcus for the tendons of m. flexor perforatus digiti II & M. flexor perforans et perforatus digiti II opens laterally. Damage to the bone resulting in loss of the plantar part of the cotyla lateralis and some of the lateral hypotarsus has resulted in loss of almost all of the sulcus for the tendon of m. flexor hallicus longus, however a small part of it remains and is filled with sediment, which in proximal view reveals it was less than half the diameter of fdl and at a similar dorsal-plantar level. However, damage precludes determining whether it was open plantarlaterally as in *Ixobrychus* or enclosed as in some other genera. The crista medianoplantaris adjacent to the canal for fdl is very thin, being only about a fifth of the diameter of that canal.

Distally, the trochleae splay with trochlea metatarsi II diverging quite strongly from the shaft and trochlea metatarsi IV to a lesser degree. Trochlea metatarsi III has a deep medial sulcus extending over the dorsal surface which highlights the distolateral alignment of this trochlea relative to the shaft. On trochlea metatarsi IV, the medial rim is not so developed distally as is the lateral rim, so in dorsal view the trochlea lacks the distinct notch distally seen in most herons. Plantarly, the lateral side of trochlea IV is developed as a laterally projecting triangular process as seen in botaurines and some other taxa. The plantar rim of trochlea metatarsi IV is strongly developed into a crest extending well plantar of the medial rim. The foramen vasculare distale is very small and separated from the trochlea metatarsi IV by a space approximating the length of that trochlea. Between trochleae metatarsi IV and III the sulcus for the tendon opening to the incisura intertrochlearis lateralis is not roofed over by bone as it is in some herons, but this may relate either to damage or osteological immaturity. On the plantar surface, the area distal to the flat articular facet for metatarsal I is excavated into a shallow sulcus opening medially as it is in *Butorides*, *Ixobrychus*, and the fossil *Matuku*. In other heron genera, this area is flat, that is, in medial view there is no ‘notch’ distal to the articular facet. Along the whole of the shaft between the distal end of the crista medianoplantaris and the facet for metatarsal I, the plantar facies is convex, so differing from the flattened shaft in *Ixobrychus*.

The coracoid NMNZ S.53346 has the general morphology of a heron with the cotyla scapularis deep and cup-like; the proc. acrocoracoideus is markedly compressed lateromedially so is much deeper dorsoventrally than wide; the sulcus supracoracoideus is not pneumatic; the impressio ligamenti acrocoracohumeralis is well-marked; the ventral margin of acrocoracoid where the lig. acrocoraco-procoracoideum inserts overhangs ventrally the ventral shaft margin but is not hooked; dorsally the tub. brachiale for the insertion of lig. acrocoraco-acromion and plica synovialis coracoidea is small and rounded; the proc. procoracoideus is robust and extends slightly cranial of cotyla scapularis (but the tip is worn); and a foramen nervi supracoracoidei is lacking. Ventrally on the tip of the acrocoracoid, there are two impressions for the insertions of the lig. acrocoraco-claviculae superficiale, as typical of ardeids. However, the impressio that is more medioventrally located, is about twice the width of the more laterodorsal impression, contributing to the acrocoracoid appearing rounded in ventral view rather than markedly compressed lateromedially. The ventral shaft facies is flattened and separated from the facies artic. humeralis by a distinct groove. In dorsomedial view, the facies artic. clavicularis from the tub. brachiale to the point of insertion for the lig. acrocoraco-procoracoideum has a straight margin overhanging the sulcus supracoracoideus.

Comparison: – The genus *Pikaihao* is monotypic.

Remarks: – Another ardeid, *Matuku otagense*, is also present in the St Bathans Fauna and co-occurred in bed HH4 with *Pikaihao bartlei*, indicating sympatry of these two species. *Matuku otagense* differs greatly from NMNZ S.53345 by its much larger size, the tarsometatarsus has the trochlea metatarsi III aligned parallel with the shaft and the foramen vasculare distale has a more distal location. The coracoid assigned to *Matuku* differs from NMNZ S.53346 by its much larger size and a relatively larger tub. brachiale contributing to a curved facies artic. clavicularis over the sulcus supracoracoideus.

Phylogenetic analysis

54-character matrix: Preliminary analyses revealed that the 54 characters used in combination with more than the 27 taxa used in the final analysis had too much homoplasy and too few characters to resolve the taxa into a robust topology. Nevertheless all analyses found the new taxon associated with botaurin taxa, so in order to obtain some resolution, taxa were pruned to 27. In an heuristic search with 1000 replicates, where all characters were treated as unordered, 12 Most Parsimonious Trees were retained, tree length = 216, Consistency index (CI) = 0.3426, Homoplasy index (HI) = 0.6574, Retention index (RI) = 0.5563. The strict consensus tree had *Pikaihao bartlei* sister to *Ixobrychus eurhythmus* within a monophyletic clade of botaurin taxa that was sister to *Butorides*. Together this clade formed a polytomy with *Ardea* and *Egretta* species.

In a second preferred analysis, where 16 characters were ordered, with other settings the same as for the unordered analysis, 9 MPTs were found (Tree length = 222, CI = 0.3378, HI = 0.6622, and RI = 0.5586). In the strict consensus tree, taxa did not differ in topological order from that of the unordered analysis, but were better resolved, notably with *Ardea* and *Egretta* species forming a clade (Figure 2). In this tree, ardeids were grouped as a clade to the exclusion of *Balaeniceps* and *Scopus* and the outgroup taxa (Bootstrap support 77%). Although significant bootstrap support for clades within ardeids was generally lacking, *Cochlearius* was the sister of remaining ardeids. The ardeins formed a grade of taxa, successively branching after *Cochlearius,* first *Nyctanassa*, then *Nycticorax*, then a clade with *Pilherodius* sister to the pairing of the fossil *Matuku* and *Syrigma*. *Ardea* and *Egretta* species formed a clade with the exception of *Ardea ibis*, which is often placed in *Bubulcus*. Most deeply nested in the tree, all botaurins formed a monophyletic clade supported by two unambiguous apomorphies (trochlea III aligned distolaterally, CI=1.000, char. 6; sulcus for shallow flexor tendons flexor perforans et perforatus digiti II and flexor perforates digiti II bound by a high ridge laterally, char. 20). In this clade, *I. flavicollis* was sister to remaining botaurins, reflecting differences which with others noted above support its previous distinction as *Dupetor*. *Pikaihao bartlei* formed a polytomy with *Ixobrychus eurhythmus* and a clade of other *Ixobrychus* species and a well-supported clade of *Botaurus* species (Bootstrap support 68%).

88-character matrix: The expanded character set enabled a larger taxon sample to be analysed, so in the final analyses 32 taxa were included (Appendix 3). In an heuristic search with 1000 replicates, where 16 characters were ordered as per the preferred analysis of the 54-character matrix, 4 MPTs were found (Tree length = 380, CI = 0.3368, HI = 0.6632, and RI = 0.5994) that resulted in a well-resolved strict consensus tree (Figure 3), although within ardeids, bootstrap support for clades was found only within botaurines. As for the above analysis, botaurines formed a strongly supported clade (Bootstrap support 89%), supported by 10 unambiguous apomorphies of which five are most compelling (trochlea III aligned distolaterally, CI=1.000, char. 6; deltoid crest abuts at near right angles the cranial facies, CI=1.000, char. 55; femur, insertion for major part of m. obturatorius medialis on caudolateral margin distal to insertion of m. obturatorius lateralis: greatly enlarged into caudally prominent ridge, CI=0.500, char. 58; coracoid, dorsal sternal facet, extends more cranially, CI=1.000, char. 76 (=Payne & Risley 1976: character 20); obturator foramen closed caudally, CI=1.000, char. 87 (Payne & Risley 1976: character 31)).

Within this clade *Ixobrychus* was not monophyletic. *Ixobrychus flavicollis* was sister to a clade of remaining botaurines (Bootstrap support 61%) supported by six unambiguous apomorphies, but none were particularly compelling (CIs all <0.4). *Pikaihao bartlei* was embedded in an unresolved position in a paraphyletic series of *Ixobrychus* taxa on the stem for *Botaurus*, in what is essentially a polytomy of *I. minutus*, *I. eurhythmus*, the pairing of *I. dubius* + *I. sinensis* (Bootstrap support 67%), and *Botaurus* sp. (Bootstrap support 89%). At best these data suggest that *Pikaihao bartlei* is more closely related to *Ixobrychus* species exclusive of *Ixobrychus flavicollis*. The sister clade to the botaurines, lacking significant bootstrap support, was a large group of taxa comprising 3 subclades, again all with no significant support. Among these, *Egretta* sp. and *Butorides* formed a clade that was sister to a clade of five *Ardea* species and the grouping of six monotypic taxa (*Ardea ibis*, *Pilherodius*, *Tigrisoma*, *Agamia*, *Syrigma* and *Matuku*). The association of *Matuku* thus remains as it was in the analysis of the 54 character matrix. As in the analysis of the 54 character matrix, *Nycticorax*, *Nyctinassa* and *Cochlearius* were successively basal taxa to the other ardeids.

DISCUSSION

This description of *Pikaihao bartlei* indicates that in the early Miocene in New Zealand, Ardeidae was represented by at least two sympatric herons: *Matuku otagense*, an ardeid of undetermined subfamilial affinity (Scofield et al., 2010), and *Pikaihao bartlei* a small bittern (Botaurinae). Our initial phylogenetic analyses suffered from a combination of too few characters for the number of taxa and extensive homoplasy across taxa (McCracken & Sheldon, 1998), to the extent that few clades within ardeids had significant bootstrap support. The addition of the characters from Payne & Risley's (1976) led to an improved topological resolution of ardeid taxa but did not lead to any improvement in the resolution of *Pikaihao* among botaurines. This is not unexpected given that *Pikaihao* could not be assessed for any of the extra characters and was only scored for 30 (34%) of the 88 characters. Nevertheless, the degree of resolution in the strict consensus tree with monophyly of botaurins, *Ardea* species exclusive of *Ardea ibis*, and *Egretta* species, suggest that with the addition of further characters this dataset will effectively resolve ardeids. Improved resolution of the relationships of the fossil taxa is dependent on the discovery of further material. Our analyses provide support for the use of *Bubulcus* for the Cattle Egret, as advocated by Sibley and Monroe (1993) and supported by Li et al. (2011), as it does not associate with *Ardea* species in our analyses. Similarly, *Ixobrychus flavicollis* was always found to be the sister to remaining botaurines, providing support for its previous distinction as *Dupetor*, e.g. Sibley and Monroe (1993), although analysis of molecular data by Chang et al. (2003) and Zhang et al. (2004) suggested that it belongs in *Ixobrychus*.

Our analyses above provide some support for *Matuku* being referred to Ardeinae with an affinity towards *Syrigma* found in most analyses. However, there are no unambiguous apomorphies supporting this relationship and no significant bootstrap for it, nor for the whole clade of neotropical taxa sister to *Ardea ibis*. Given the significant amount of missing data in *Matuku*, such a relationship should be seen as very tentative at best. These analyses however, provided strong support for *Pikaihao* being included among botaurines, despite significant missing data. Autapomorphies, such as the proximally located foramen vasculare distale do not help resolve the relationships of this taxon, but this feature, the convex mid shaft plantar facies of the tarsometatarsus and its more elongate form distinguish it from *Ixobrychus*. *Pikaihao bartlei* is just the third and, being of early Miocene age, the oldest pre-Quaternary record for Botaurinae globally. In contrast, taxa referred to Ardeinae, including Nycticoracini, are known from as early as the early

Oligocene and ardeids undetermined to subfamily include some as old as the early Eocene (see Scofield et al., 2010 and Zelenkov, 2011).

This new taxon adds to an already rich waterbird fauna that previously lived on and around the large subtropical palaeolake Manuherikia, which now minimally includes two herons, eight waterfowl, one palaelodid, and several undescribed rails and waders (Worthy et al., 2007; Worthy & Lee, 2008; Scofield et al., 2010; Worthy et al., 2010b). The lake was rich in fish with at least a dozen species known (Galaxiidae 6, Retropinnidae 2, Eleotridae 4; see Schwarzhans et al., 2012) providing plentiful prey for piscivores. It is interesting that to date there is no evidence for other piscivores such as Pelecanidae, Phalacrocoracidae, Anhingidae, and Phoenicopteridae in this lake, although all are present in lacustrine deposits of older and younger age in Australia across the Tasman Sea (Worthy, 2011, 2012, and references therein). Conversely, the Australian record lacks fossil herons older than the Pliocene (Boles & Mackness 1994). Given the rare occurrence of many of these groups in the respective fossil records of New Zealand and Australia, it is premature to infer that their apparent absence reflects reality or not.

ACKNOWLEDGEMENTS

We thank the land owners Ann and Euan Johnstone who not only graciously allowed us access to their land but actively contributed to the excavations by working a digger. This work has been supported by a University of New South Wales Goldstar award (2011) to T.H. Worthy and an Australian Research Council grant DP120100486. P. Scofield acknowledges the support of the Mason Science and Technical Fund Award, New Zealand. We thank the following people for access to comparative material: Walter Boles, AM; Philippa Horton, SAM; Robert Palmer, ANWC; Wayne Longmore, MV; Gerald Mayr, SMF; Anita Gaumauf and Hans-Martin Berg, NHMW; and Vanesa De Pietri and

Loic Costeur, NMB. We thank Antoine Louchart and Federico Agnolin for comments that improved the manuscript.

REFERENCES

Balouet, J.C., *Zeltornis ginsburgi* n. g., n. sp. (Ardeidae, Aves), héron géant du Miocène inférieur du Djebel Zelten (Libye) // *CR Acad. Sci. Paris*, 1981, vol. 293, pp. 235–239.

Baumel, J.J., Witmer, L.M., Osteologia // In: Baumel, J.J. King, A.S. Breazile, et al., (Eds) *Handbook of avian anatomy: Nomina Anatomica Avium*, 2nd edition, 1993, pp. 45–132. Cambridge, Massachusetts: Publ. Nuttall Ornithological Club 23.

Bock, W.J., A generic review of the family Ardeidae (Aves) // *Amer. Museum Novit.*, 1956, no. 1779, pp. 1–49.

Boddaert, P., *Table des planches enluminéez d'histoire naturelle de M. D'Aubenton: avec les denominations de m.m. de Buffon, Brisson, Edwards, Linnaeus et Latham, precéde d'une notice des principaux ouvrages zoologiques enluminés* // 1783, Utrecht.

Boles, W.E., Mackness, B., Birds from the Bluff Downs Local Fauna, Allingham Formation, Queensland // *Rec. S. Austral. Mus.*, 1994, vol. 27, no. 2, pp. 139–149.

Bonaparte, C.-L., *Conspectus systematis ornithologiae* // 1849, Amsterdam: Westerman et Fil.

Bonaparte, C.-L., Classification ornithologique par series // *CR Acad. Sci. Paris*, 1853, vol. 37, pp. 641–647.

Bonaparte, C.-L., *Conspectus systematis ornithologiae. Annales Des Sciences Naturelles comprenant la zoologie, la botanique, l'anatomie et la physiologie compare acutee des deux régravegnes et l'histoire des corps organisés fossiles. Rédigée pour la* *zoologie par Audouin et Milne-Edwards; pour la botanique par Ad. Brongniart et Guillemin, Paris* // 1854, series 4, vol. 1, pp. 105–152.

Chang, Q., Zhang, B-W., Jin, H., Zhu, L-F., Zhou, K-Y., Phylogenetic relationship among 13 species of herons inferred from mitochondrial 12S r RNA gene sequences // Acta Zoologica Sinica 2003, vol 49, pt. 2, pp. 205-210.

Chenu, J.C., Des Murs, O., *Encyclopedie d'histoire naturelle ou traite complet de cette science…, &c. Par le Dr. Chenu. Oiseaux, avec le collaboration de M. Des Murs, //* 1854. Paris: Marescq and Compagnie.

Cretzschmar, P.J., Vögel. In: Rüppel, E., (Ed.), *Atlas zu der Reise im nördlichen Afrika* // 1829, pp. Heft 14, 39, pl. 26. Frankfurt am Main: Gedruckt und in commission bei H.L. Brönner.

Cuvier, G., *Le regne animal distribue d'apres son organisation, pour servir de base a l'histoire naturelle des animaux et d'introduction a l'anatomie comparee. Par m. le baron Cuvier,… Avec figures dessinees d'apres nature. Nouvelle edition, revue et augmentee* // 1829, vol. 1. Paris: Deterville et Crochard.

Elzanowski, A., Stidham, T.A., A galloanserine quadrate from the Late Cretaceous Lance Formation of Wyoming // *The Auk*, 2011, vol. 128, pp 138-145.

Gmelin, J.F., *Caroli a Linné … Systema naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis* // 1788–1793 [1789], Editio decimo tertia, aucta, reformata, vol. 3, vols. in 9 parts, Lipsiae.

Gould, J., *The Athenaeum. Journal of English and Foreign Literature, Science, and the Fine Arts* // 1850, vol. 1207, p. 1315. London.

Gould, J., [Mr Gould exhibited to the meeting four new species of bird from Australia,…] // *Proc. Zool. Soc. London*. 1845, vol 8, pp. 62-63.

Gray, J.E., Description of three new species of heron (*Ardea*), discovered by General Hardwick, in India // *Zool. Misc.*, 1831, vol. 1, pp. 19–20.

Hand, S., Beck, R., Worthy, T., et al., Australian and New Zealand bats: the origin, evolution, and extinction of bat lineages in Australasia // *J. Vertebr. Paleontol.*, 2007, vol. 27 (Abstracts), p. 86A.

Hartlaud, G., Systematische Uebersicht der Vögel Madagascars // *J. Orn.* 1860, vol. 8, pp. 161-180.

Jameson, R. [New Species of *Ibis* and *Turnagra*] // *Edinburgh New Philosophical Journal* 1835, vol. 19, pp. 212-215.

Jones, M.E.H., Tennyson, A.J.D., Worthy, J.P., et al., A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*) // *Proc. Roy. Soc. Biol. Sci.*, 2009, vol. 276, pp. 1385–1390.

Kushlan, J.A., Hancock, J., *Herons: Ardeidae* // 2005, Oxford: Oxford University Press.

Latham, J., *Index ornithologicus, sive Systema Ornithologiae; complectens avium divisionem in classes, ordines, genera, species, ipsarumque varietates: adjectis synonymis, locis, descriptionibus, & c.* // 1790, vol. 2. London: Leigh and Sotheby.

Latham, J., *Supplementum Indicis Ornithologici, sive Systematis Ornithologiae.* // 1802 London: G. Leigh, J. & S. Sotheby.

Leach, W.E., Eleventh Room, Upper floor. In: *Synopsis of the Contents of the British Museum*, 17th edition // 1820, London: Cox and Baylis, pp. 65-70.

Lee, M.S.Y., Hutchinson, M.N., Worthy, T.H., et al., Miocene skinks and geckos reveal long-term conservatism of New Zealand's lizard fauna // *Biol. Letters*, 2009, vol. 5, pp. 833-837.

Lee, D.E., Conran, J.G., Lindqvist, J.K., et al., New Zealand Eocene, Oligocene and Miocene macrofossil and pollen records and modern plant distributions in the

Southern Hemisphere // *The Botanical Review*, 2012. DOI 10.1007/s12229-012-9102-7.

Li, L., Zhou, X., Chen, X., Characterization and evolution of MHC Class II B genes in ardeid birds // J. Mol. Evol., 2011, vol. 72, pp. 474-483.

Linnaeus, C., *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis //* 1758, vol. 1, 10th edition, Holmiae (Stockholme): Laurentii Salvii.

Linnaeus, C., *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis //* 1766, vol. 1, pt. 1, 12th edition. Holmiae (Stockholme): Laurentii Salvii.

McCracken, K.G., Sheldon, F.H., Molecular and osteological heron phylogenies: Sources of incongruence // *Auk,* 1998, vol. 115, pp. 127-141.

Mathews, G.M., A reference list to the birds of Australia. *Novitates Zoologicae* // 1912, vol. 18, pp. 171-455.

Mayr, G., *Paleogene fossil birds* // 2009, Heidelberg and New York: Springer-Verlag.

Molnar, R.E., Pole, M., A Miocene crocodilian from New Zealand // *Alcheringa*, 1997, vol. 21, pp. 65–70.

Moseley, C., Feduccia, A., Upper Pliocene herons and ibises from North America // *Univ. Michigan Papers on Paleontology* 1975, vol. 12, pp. 71-74.

Moorfield, J.C., *Te Aka Māori-English, English-Māori dictionary and index* // 2011, Wellington: Pearson.

Payne, R.B., Risley, C.J., Systematics and evolutionary relationships among the herons (Ardeidae) // *Museum of Zoology, University of Michigan, Miscellaneous Publications* 1976, vol. 150, pt. i-iv, pp. 1-115.

Poche, F., Ein bisher nicht bertícksichtigtes zoologisches Werk aus dem Jahre 1758, in dem die Grundsiitze der binaren. Nomenklatur befolgt sind // *Zoologische Anzeiger*, 1904, vol. 27, pp. 495–510.

Pole, M., Douglas, B., A quantitative palynostratigraphy of the Miocene Manuherikia Group, New Zealand // *J. Roy. Soc. New Zealand*, 1998, vol. 28, pp. 405–420.

Pole, M., Douglas, B., Mason, G., The terrestrial Miocene biota of southern New Zealand // *J. Roy. Soc. New Zealand*, 2003, vol. 33, pp. 415–426.

Purdie, A.C. On a (supposed) new species of bittern, from the Lake District // *Trans. Proc. N. Z. Institute* [for 1870], 1871, vol. 3, pp. 99-100.

Rackett, T., *Catalogues of the birds, shells, and some of the more rare plants of Dorsetshire. From the new and enlarged edition of Mr. Hutchins's history of that country, with additions and a brief memoir of the author*, ed. R. Pulteney // 1813, London: Nichols, Son and Bentley, pp. 14.

Reichenbach, L., *Avium systema naturale. Das natürliche system der vögel mit hundert tafeln grössentheils original-abbildungen der bis jetzt entdeckten fast zwölfhundert typischen formen* // 1850, Leipzig: F. Hofmeister.

Sallaberry, M.A., Yury–Yáñez, R.E., Otero, R.A., et al., Eocene birds from the western margin of southernmost South America // *J. Paleontol.* 2010, vol. 84, pp. 1061–1070.

Schwarzhans, W., Scofield, R.P., Tennyson, A.J.D., et al., Fish remains, mostly otoliths, from the non−marine early Miocene of Otago, New Zealand // *Acta Palaeontol. Pol.*, 2012, vol. 57, pp. 319–350.

Scofield, R.P., Worthy, T.H., Tennyson, A.J.D., A heron (Aves: Ardeidae) from the Early Miocene St Bathans fauna of southern New Zealand // *Rec. Austral. Mus.*, 2010, vol. 62, pp. 89–104.

Sibley, C.G., Monroe, B.L. Jr. *A supplement to distribution and taxonomy of birds of the world* // 1993, New Haven, Connecticut: Yale University Press.

Swinhoe, R. On a new species of Little Bittern from China // *Ibis*, 1873, series 3, vol. 3, pp. 73-74.

Sundevall, C., Ornithologiskt System. *Kongliga Svenska Vetenskaps-Akademiens Händlingar, Stockholm* (1835) // 1836, pp. 43–130.

Swainson, E., *An encyclopaedia of geography: comprising a complete description of the earth, physical, statistical, civil, and political; exhibiting… the natural history of each country*, ed. H. Murray, pp. 1383 // 1834, London: Longman, Ross, Orme, Brown, Green and Longman.

Swofford, D.L., *PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods*), 4.10a //* 2002, Sinauer and Associates, Sunderland, USA.

Temminck, C.J., *Nouveau recueil de planches coloriées d'oiseaux, pour servir de suite et de complément aux planches enluminées de Buffon*, Temminck C.J. and Laugier de Chartrouse, M. *//* 1824, vol. 3. Paris: G. Levrault.

Tennyson, A.J.D., Worthy, T.H., Jones, C.M., et al.., Moa's Ark: Miocene fossils reveal the great antiquity of moa (Aves: Dinornithiformes) in Zealandia // *Rec. Austral. Mus.*, 2010, vol. 62, pp. 105–114.

Wagler, J.G., *Systema Avium //* 1827, Pars prima, 14–190, II (unpaginated). Stuttgart and Tubingen: J.G. Cottae.

Worthy, T.H., Descriptions and phylogenetic relationships of a new genus and two new species of Oligo-Miocene cormorants (Aves: Phalacrocoracidae) from Australia // *Zool. J. Linn. Soc.*, 2011, vol. 163, pp. 277-314.

Worthy, T.H., A new species of Oligo-Miocene darter (Aves: Anhingidae) from Australia // *The Auk*, 2012, vol. 129, pp. 96-104.

Worthy, T.H., Hand, S.J., Nguyen, J.M.T., et al., An Early Miocene acanthisittid wren (Aves: Acanthisittidae) from the St Bathans Fauna, Otago, New Zealand // *J. Vertebr. Paleontol.*, 2010a, vol. 30, pp. 479–498.

Worthy, T.H., Lee, M.S.Y., Affinities of Miocene (19–16 Ma) waterfowl (Anatidae: *Manuherikia, Dunstanetta* and *Miotadorna*) from the St Bathans Fauna, New Zealand // *Palaeontology*, 2008, vol. 51, pp. 677–708.

Worthy, T.H., Tennyson, A.J.D., Archer, M., Scofield, R.P., First record of *Palaelodus* (Aves: Phoenicopteriformes) from New Zealand // *Rec. Austral. Mus.*, 2010b, vol. 62, pp. 77–88.

Worthy, T.H., Tennyson, A.J.D., Archer, M., et al., Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific // *Proc. Nat. Acad. Sci. U.S.A*, 2006, vol. 103. pp. 19419–19423.

Worthy, T.H., Tennyson, A.J.D., Hand, S.J., Scofield, R.P., A new species of the diving duck *Manuherikia* and evidence for geese (Aves: Anatidae: Anserinae) in the St Bathans Fauna (Early Miocene), New Zealand // *J. Roy. Soc. New Zealand*, 2008, vol. 38, pp. 97–114.

Worthy, T.H., Tennyson, A.J.D., Hand, S.J., et al., Terrestrial turtle fossils from New Zealand refloat Moa’s Ark // *Copeia*, 2011a, vol. 2011, part 1, pp. 72-76.

Worthy, T.H., Tennyson, A.J.D., Jones, C., et al., Miocene waterfowl and other birds from Central Otago, New Zealand // *J. Syst. Palaeontol.*, 2007, vol. 5, pp. 1–39.

Worthy, T.H., Tennyson, A.J.D., Scofield, R.P., Fossils reveal an early Miocene presence of the aberrant gruiform Aves: Aptornithidae in New Zealand // *J. Ornithology*, 2011b, vol. 152, pp. 669-680.

Worthy, T.H., Tennyson, A.J.D., Scofield, R.P., An Early Miocene diversity of parrots (Aves, Strigopidae, Nestorinae) from New Zealand // *J. Vertebr. Paleontol.*, 2011c, vol. 31, pp. 1102-1116.

Zelenkov, N.V. *Ardea sytchevskayae* sp. nov., a new heron species (Aves: Ardeidae) from the Middle Miocene of Mongolia // 2011, *Paleontol. J.*, vol. 45, No. 5, pp. 572–579.

Zhang, B-W., Chang, Q., Zhu, L-F., Wei, F-W., Phylogeny of Botaurinae and classification of Black Bittern based on analyses of mitochondrial cytochrome *b* gene. *Chinese Journal of Zoology*, 2004, vol. 39, pp. 105-108.

Zuccon, A., Zuccon, D. *MrEnt v.2* // 2008, Program distributed by the authors at http://www.mrent.org

Figure. 1. *Pikaihao bartlei* n. gen. et sp., left tarsometatarsus NMNZ S.53345 in dorsal (A), plantar (B), and proximal (C) views and cranial part left coracoid NMNZ S. 53346 in dorsal (D), lateral (E), medial (F), and ventral (G) views. Scale bars: A,B = 20 mm, C = 5 mm, and D-G = 5 mm. Abbreviations: cs, cotyla scapularis; fah, facies artic. humeralis; fdl, canal for tendon of m. flexor digitorum longus; fhl, tendinal canal for m. flexor hallicus longus; fpm, fossa parahypotarsalis medialis; fvd, foramen vasculare distale; ila, impressio lig. acrocoracohumeralis; lacs, impressions for insertions of the lig. acrocoraco-claviculae superficiale; pII/ppII, canal for tendons for M. flexor perforatus digiti II & M. flexor perforans et perforatus digiti II; mf, metatarsal facet; tb, tub. brachiale; tc, tuberositas m. tibialis cranialis; TIII, trochlea metatarsi III.

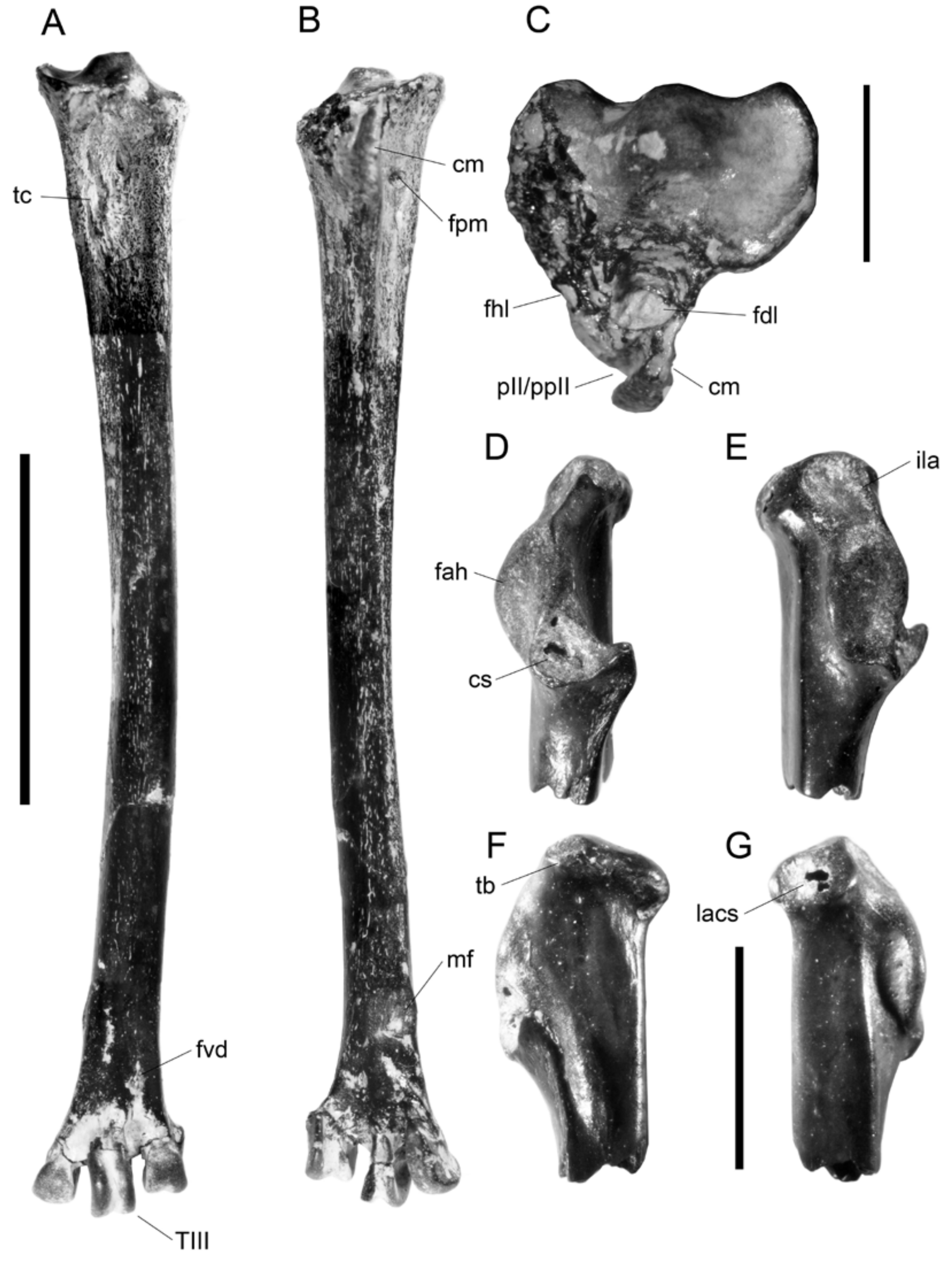

A
B
C
tc
cm
fpm
fhl
fdl
pII/ppII
cm
D
E
ila
fah
cs
F
G
tb
lacs
mf
fvd
TIII

Figure. 2. A strict consensus tree derived from 9 MPTs found in a heuristic search, 1000 replicates, of the 54-character dataset with 16 characters ordered, Tree length = 222, CI = 0.3378, HI = 0.6622, and RI = 0.5586. Bootstrap values >50% shown at nodes. Fossil taxa from St Bathans fauna highlighted in boxes.

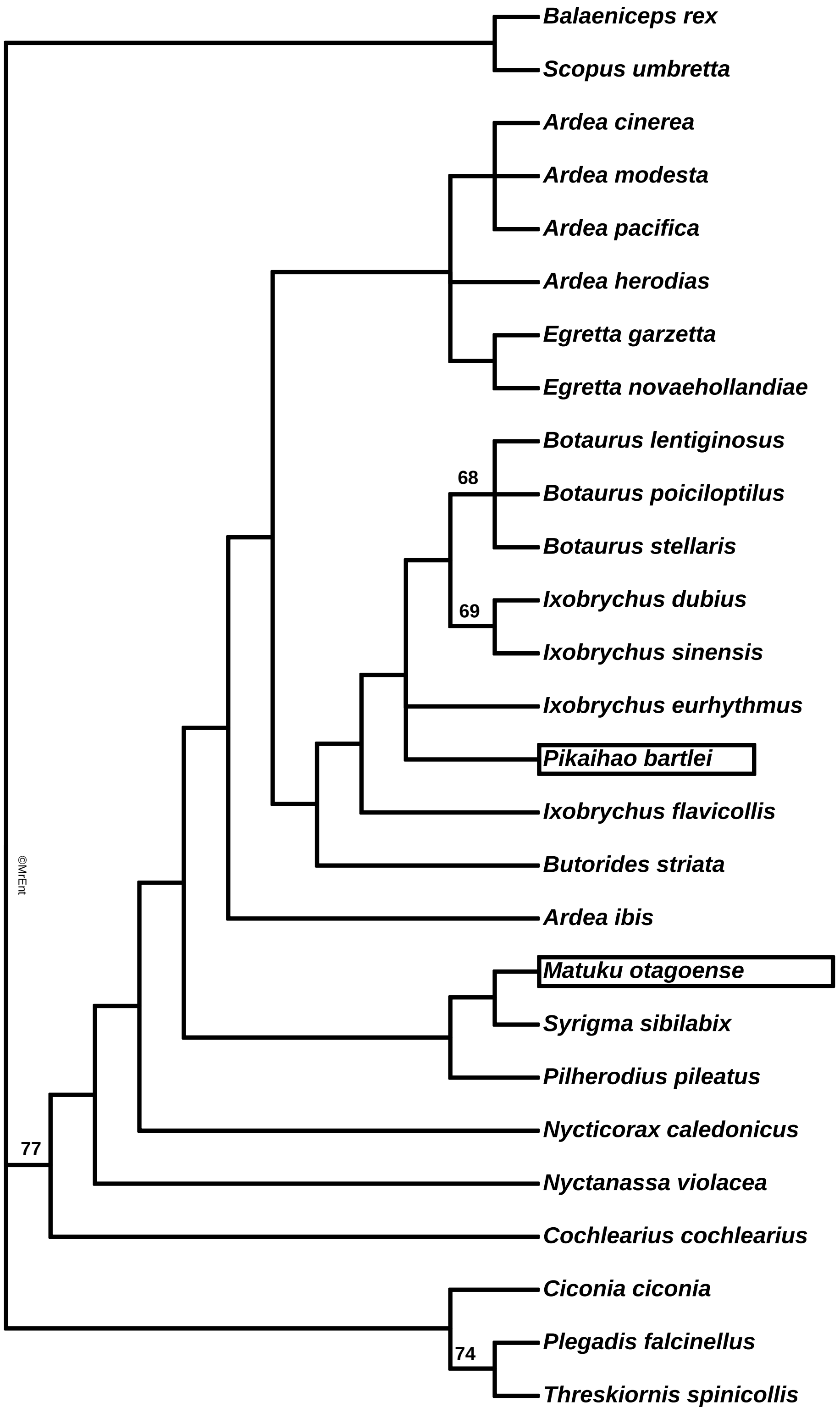
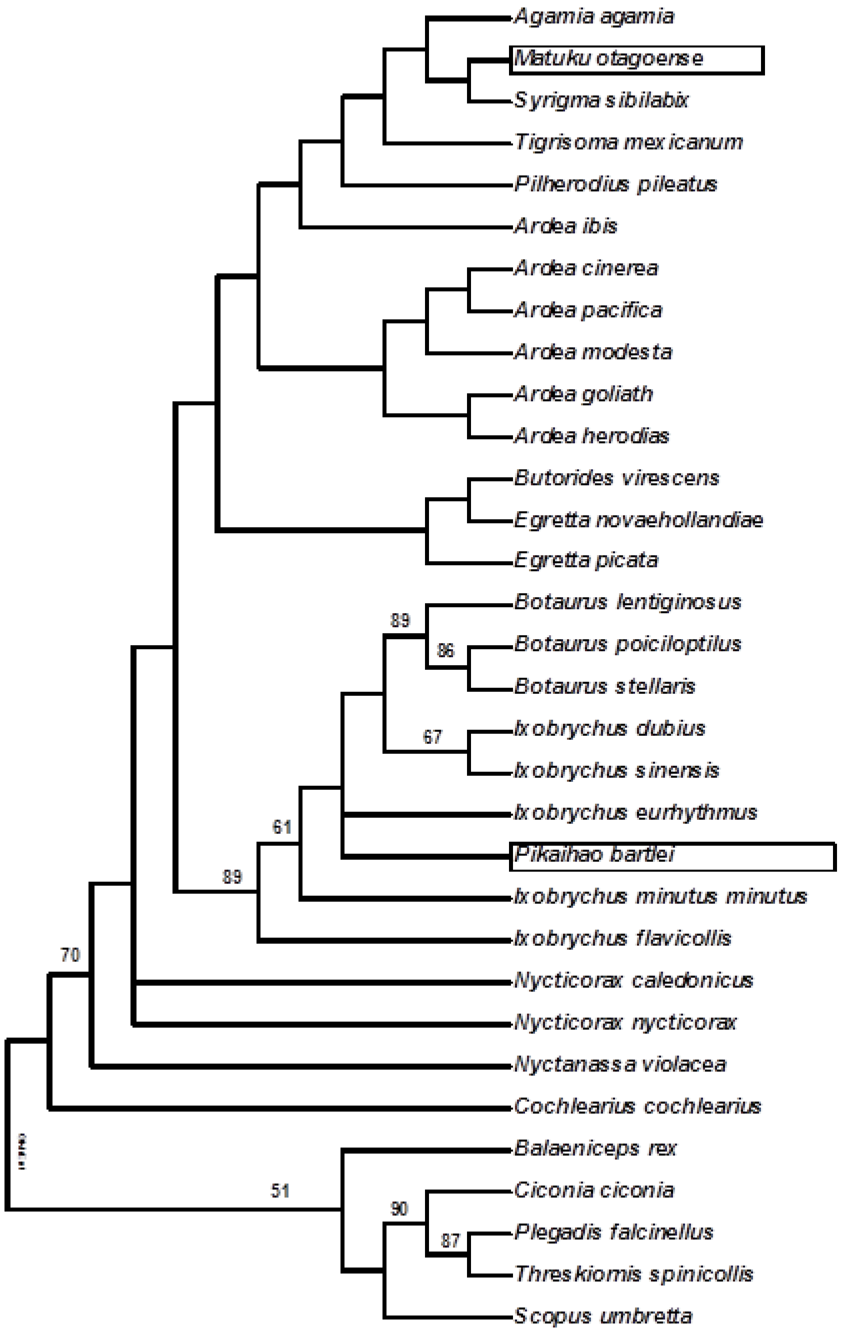


Figure 3. A strict consensus tree derived from 4 MPTs found in a heuristic search, 1000 replicates, with 16 characters ordered, of the 88-character dataset. Tree length = 380, CI = 0.3368, HI = 0.6632, and RI = 0.5994. Bootstrap values (1000 replicates) >50% shown at nodes. Fossil taxa from St Bathans fauna highlighted in boxes.



Appendix 1: List of characters used in phylogenetic analysis.

1. Tarsometatarsus, distal end, plantar aspect. Sulcus on trochlea metatarsi IV: 0. Absent; 1. Shallow; 2. Deep. Char. 1, Scofield et al. (2010).

2. Tarsometatarsus, distal end, plantar aspect. Sulcus on trochlea metatarsi III: 0. Absent; 1. Shallow; 2. Deep. Char. 2, Scofield et al. (2010).

3. Tarsometatarsus, distal end, dorsal aspect. Position of foramen vasculare distale on dorsal facies, specifically that part passing to the plantar surface, relative to the proximal end of trochlea metatarsi III: 0. Markedly proximal; 1. Subequal or just proximal to anterior margin trochlea; 2. Distinctly distal of anterior side trochlea. Note, state coded inapplicable (-) when distal foramen passing to plantar surface is absent. Modified from Char. 3, Scofield et al. (2010).

4. Tarsometatarsus, distal end, dorsal aspect. Size of distal foramen (restricted to part that passes to plantar surface): 0. Absent; 1. Small; 2. Large. Char. 4, Scofield et al. (2010).

5. Tarsometatarsus, distal end, dorsal aspect. Distal foramen, branching canal opening into inter-trochlear incision from main dorso-plantar canal: 0. Enclosed dorsally; 1. Open dorsally, thus forming a notch. Char. 5, Scofield et al. (2010).

6. Tarsometatarsus, distal end, dorsal aspect. Alignment of trochlea metatarsi III (or medial groove in it) relative to the axis of the shaft: 0. Parallel or slightly directed distolaterally; 1. Strongly directed distolaterally. Note: In *Ixobrychus flavicollis*, TIII is directed distolaterally not as strongly as in other *Ixobrychus* or *Botaurus*. Char. 6, Scofield et al. (2010).

7. Tarsometatarsus, distal end, dorsal aspect. Alignment of the medial margin of trochlea metatarsi II relative to the medial margin of the shaft: 0. Does not project; 1. Deviates at shallow angle; 2. Deviates at abrupt angle. Modified from Char. 7, Scofield et al. (2010).

8. Tarsometatarsus, distal end, dorsal aspect. Projection of plantar rim of trochlea metatarsi IV laterally to form distinct projection laterally: 0. No; 1. Yes.

9. Tarsometatarsus, distal end, dorsal aspect. Alignment of the lateral margin of trochlea metatarsi IV relative to the lateral margin of the shaft: 0. Parallel; 1. Protrudes at shallow angle; 2. Protrudes abruptly. Modified from Char. 8, Scofield et al. (2010).

10. Tarsometatarsus, distal end, dorsal aspect. Length and width of trochlea metatarsi IV distal of intertrochlear incision: 0. Short, length less than or equal to trochlear width; 1. Long, trochlea longer than wide.

11. Tarsometatarsus, distal end, plantar aspect. Fossa metatarsal I, specifically the articular facet for metatarsal I: 0. Absent; 1. Shallow or flat on facies; 2. Deep. Modified from Char. 9, Scofield et al. (2010).

12. Tarsometatarsus, distal end, plantar aspect. Area between facet for metatarsal I and base of trochlea metatarsi II: 0. Flat, coplanar with fossa; 1. Excavated to form distinct sulcus passing over medial facies.

13. Tarsometatarsus, shaft, dorsal aspect. Dorso-plantar compression of the proximal medial side of the shaft adjacent to the tuberositas m. tibialis cranialis: 0. None, shaft thick; 1. Weak, i.e. *Botaurus*; 2. Strong such that the medial margin is essentially a crest. Char. 10, Scofield et al. (2010).

14. Tarsometatarsus, shaft, dorsal aspect. Location of the tuberositas m. tibialis cranialis relative to medial side of the shaft: 0, Abuts medial margin, adjacent facies directed medially; 1, Close to medial side (about 2/3 shaft width laterad of tuberosity); 2, Distinctly towards centre (about ½ shaft laterad of tuberosity).

15. Tarsometatarsus, shaft, dorsal aspect. Sulcus extensorius: 0. Absent; 1. Shallow; 2. Deep. Char. 11, Scofield et al. (2010).

16. Tarsometatarsus, shaft, plantar aspect. Plantar metatarsal groove (sulcus flexorius): 0. Absent; 1. Shallow; 2. Deep. Char. 12, Scofield et al. (2010).

17. Tarsometatarsus, shaft, plantar aspect. Crista plantaris lateralis in proximal half: 0. Absent; 1. Weakly developed; 2. Strongly developed. Char. 13, Scofield et al. (2010).

18. Tarsometatarsus, proximal end, plantar aspect. Hypotarsus, length from cotylar margin to distal end of plantar surface of medial crista relative to width across cristae hypotarsi. 0. Length markedly greater than width; 1. Length subequal-slightly greater than width; 2. Length significantly less than width. Char. 14, Scofield et al. (2010).

19. Tarsometatarsus, proximal end, proximal aspect. Hypotarsus, depth relative to corpus depth. 0. Distinctly less than that of corpus; 1. Approximating corpus; 2. Greater than corpus. Char. 15, Scofield et al. (2010).

20. Tarsometatarsus, proximal end, plantar aspect. Hypotarsus, sulcus for shallow flexor tendons fpp2/fp2 (flexor perforans et perforatus digiti II, flexor perforatus digiti II) that are plantar of fdl: 0. Absent; 1. Shallow sulcus, barely enclosed laterally; 2. Deep sulcus bound by high lateral ridge, partly or wholly enclosed plantarly. Modified from Char. 16, Scofield et al. (2010).

21. Tarsometatarsus, proximal end, plantar aspect. Hypotarsus, sulcus for shallow flexor tendons fp3/fp4 (flexor perforatus digiti III et IV): 0. Absent or conjoined with fhl; 1, Present as shallow groove, separated from fhl by osseus bridge.

22. Coracoid, extremitas omalis, medial aspect. Sulcus m. supracoracoideus, pneumatic foramina penetrating acrocoracoid: 0. No; 1. Yes. Char. 17, Scofield et al. (2010).

23. Coracoid, extremitas omalis, ventral aspect. Where lig. acrocoraco-claviculae superficiale has two insertions, their arrangement, in ventral view: 0. Insertions of similar size, craniosternally elongate narrow sulci, medial one markedly offset sternally so overlaps less than half length lateral insertion, results in compressed acrocoracoid craniosternally longer than wide; 1. Medial insertion twice width of lateral one, overlaps lateral insertion by more than half its length, lateral one is a scar on lateral margin of acrocoracoid, results in relatively broad acrocoracoid; 2. Insertions of similar size, medial one offset cranially of lateral one. Note: In some outgroup taxa, the pattern of insertion scars differed markedly from these states, and were coded as (-).

24. Coracoid, extremitas omalis, dorsal aspect. Acrocoracoid - impressio ligamenti acrocoracohumeralis: 0. Flat; 1. Shallow; 2. Deep. Char. 19, Scofield et al. (2010).

25. Coracoid, extremitas omalis, dorsal aspect. Distance from omal end of facies artic. humeralis to tip of proc. acrocoracoideus: 0. Equal to dorso-ventral depth of facies artic. clavicularis; 1. Less than half of depth of clavicle facet; 2. Intermediate between 0 and 1. Char. 20, Scofield et al. (2010).

26. Coracoid, extremitas omalis, medial aspect. Relative positions of tub. brachiale dorsally, the articular facet for the clavicle, and the protuberance for the insertion of lig. acrocoraco-procoracoideum ventrally): 0. All three form a straight line, with brachial tuberosity lacking sternal prominence; 1. Brachial tuberculum with sternal projection, so sternal margin facies artic. clavicularis curved.

27. Coracoid, extremitas omalis, procoracoidal process. Extends significantly craniomedially of the scapular cotyla forming a flattened tub. apicalis procoracoidei: 0. Absent; 1. Present. Char. 22, Scofield et al. (2010).

28. Coracoid, extremitas omalis, dorsomedial aspect. Sulcus m. supracoracoideus, secondarily deepened dorsally adjacent to the facies artic. humeralis bound ventrally by rounded ridge extending sternally from under dorsal side of facies artic. clavicularis: 0. No; 1. Yes.

29. Coracoid, shaft, dorsal aspect. Foramen nervi supracoracoidei: 0. Absent; 1. Present. Char. 24, Scofield et al. (2010).

30. Coracoid, shaft, dorsal aspect. Extent of procoracoid sternally along shaft: 0. No extension, very short; 1. Elongate, extends for less than half the length of shaft. Char. 25, Scofield et al. (2010).

31. Coracoid, shaft, ventral aspect. Ventral shaft facies adjacent to facies artic. humeralis: 0. Planar; 1. Distinct groove separated planar facies of shaft from facies artic. humeralis; 2. Not like previous with facies artic. humeralis distinctly dorsal of ventral shaft facies.

32. Os quadratum, rostral aspect. Caput squamosum: 0. Rounded; 1. Triangular, broader at top, draws to point laterally/ventrally. Char. 26, Scofield et al. (2010).

33. Os quadratum, lateral aspect. Tubercle at dorsal end of crista tympanica: 0. Absent; 1. Immediately ventral of caput squamosum. Char. 27, Scofield et al. (2010).

34. Os quadratum, medial aspect. Foramen pneumaticum mediale: 0. Situated between crista tympanica and crista medialis (=foramen pneumaticum caudomediale of Elzanowski & Stidham 2011); 1. Situated rostrally of crista medialis(=foramen pneumaticum rostromediale of Elzanowski & Stidham 2011). Char. 28, Scofield et al. (2010).

35. Os quadratum, medial aspect. Foramen pneumaticum mediale when situated at intersection of crista tympanica and crista medialis: 0. Very small; 1. Large; 2. Not so placed. Char. 29, Scofield et al. (2010).

36. Os quadratum, medial aspect. Tubercle at dorsal end of crista medialis immediately ventral of caput oticum: 0. Absent; 1. Present. Char. 30, Scofield et al. (2010).

37. Os quadratum, ventral aspect. Articulation for pterygoid forms a raised tubercle in depressio praecondylaris on the lateral side of the medial condyle: 0. Absent, articular surface flush with floor of depression or side of condyle; 1. Present. Char. 31, Scofield et al. (2010).

38. Os quadratum, ventral aspect. Vallecula intercondylaris: 0. Area simply a shallow sulcus; 1. Forms fossa bounded on rostral edge by raised crista; 2. Deep U-shaped fossa opening via a broad, sometimes slightly constricted, sulcus onto rostral surface. Char. 32, Scofield et al. (2010).

39. Os quadratum, caudal aspect. Marked sulcus between condylus lateralis and condylus caudalis extending up to edge of crista lateralis: 0. Absent; 1. Present. Char. 33, Scofield et al. (2010).

40. Axis, cranial aspect. Dens, width relative to facies artic. atlantica: 0. Subequal; 1. Much narrower.

41. Axis, ventral aspect. Ratio of width of facies artic. atlantica to distance from facies artic. atlantica to caudalmost edge of facies artic. caudalis: 0. ≥ 35% (i.e. centrum fat and wide); 1. < 35% but > 25% (i.e. relatively long and narrow); 2. < 25% (i.e. very long and narrow). Char. 35, Scofield et al. (2010).

42. Axis, ventral aspect. Zygapophyses caudalis, shape: ratio of width to length: 0. Circular (ratio > 100%); 1. Oval (ratio > 70% but < 100%); 2. Teardrop or elongate (ratio < 70%). Char. 36, Scofield et al. (2010).

43. Axis, dorsal aspect. Zygapophyses cranialis shape (ratio of width to length): 0. Tending circular (ratio > 70%); 1. Elongate (ratio < 70%). Char. 37, Scofield et al. (2010).

44. Axis, dorsal aspect. Zygapophyses caudalis entirely prominent laterally relative to facies at mid length: 0. Not so; 1. Yes. Char. 39, Scofield et al. (2010).

45. Axis, ventral (or dorsal) aspect. Zygapophyses cranialis extend wholly laterally of lateral profile as distinct processes: 0. No; 1. Yes. Char. 40, Scofield et al. (2010).

46. Axis, lateral aspect. Processus spinosus (anapophysis), profile in anterior to mid part of length: 0. Markedly convex; 1. Flat to low convexity. Char. 41, Scofield et al. (2010).

47. Axis, lateral aspect. Processus spinosus (anapophysis): 0. Starts immediately posteriad of zygapophyses cranialis; 1. Starts farther posteriad, as initially flat. Char. 42, Scofield et al. (2010).

48. Axis, lateral aspect. Facies artic. cranialis: 0. Roughly at right angles to axis of bone; 1. Sloped anteroventrally. Char. 43, Scofield et al. (2010).

49. Axis, lateral and dorsal aspects. Length dens: 0. > length zygapophyses cranialis; 1. < length zygapophyses cranialis. Char. 44, Scofield et al. (2010).

50. Axis, lateral aspect. Corpus ventralis, foramen transversarium: 0. Complete, enclosed laterally; 1. Incomplete, open laterally, forming sulci. Note: in taxa scored 0, there was variation in the length of the bridge closing the foramen. Char. 45, Scofield et al. (2010).

51. Axis, lateral aspect. Corpus ventralis, pneumatic fossa: 0. Absent; 1. Present laterally. Note: we did not differentiate those taxa where pneumatic foramina are only in the anterior part of the corpus from those where foramina extend over mid to posterior parts of corpus. Char. 46, Scofield et al. (2010).

52. Rostrum mandibulae, dorsal aspect. Pars symphysialis, length of zone of fusion: 0. Very elongate (length >5 times width); 1. Elongate, greater than transverse width (length <5 times width); 2. Approximately equal to transverse width; 3. Transverse width considerably greater. Modified from Char. 47, Scofield et al. (2010).

53. Rostrum mandibulae, dorsal aspect. Shape: 0. Narrow and thin; 1. Broad and shallow; 2. Wide and deep, extremely modified. Char. 48, Scofield et al. (2010).

54. Rostrum mandibulae, lateral aspect. Os dentale: 0. Foramina densely cover whole lateral surface, e.g. *Threskiornis*; 1. Prominent foramina scattered, often concentrated in line towards cutting edge. Char. 49, Scofield et al. (2010).

Extra newly defined characters added in 88 character analysis.

55. Humerus, deltoid crest, relationship to cranial surface: 0, forms broad angle as oriented dorsally; 1, raised at near right angles to cranial facies.

56. Humerus, intumescentia humeralis: 0, not swollen towards dorsal side, grades evenly into area adjacent crista deltopectoralis for insertion of coracobrachialis; 1, swollen dorsally, distinctly cranially elevated above area of insertion of coracobrachialis forming distinct shallow sulcus between intumescentia and crista deltopectoralis .

57. Femur, fossa politea: 0, deep, extending distodorsally of proximal rim of condylus medialis; 1, shallower, nor deepened distodorsally of rim.

58. Femur, proximal end, caudal facies, insertion for major part of m. obturatorius medialis on caudo lateral margin distal to insertion of m. obturatorius lateralis: 0, low and rounded; 1, greatly enlarged into caudally prominent ridge.

Appendix 2: List of the 27 taxa used in Figure 2.

Ardea cinerea, Ardea herodias, Ardea ibis, Ardea modesta, Ardea pacifica, Balaeniceps rex, Botaurus lentiginosus, Botaurus poiciloptilus, Botaurus stellaris, Butorides striata, Ciconia ciconia, Cochlearius cochlearius, Egretta novaehollandiae, Egretta garzetta, Ixobrychus dubius, Ixobrychus eurhythmus, Ixobrychus flavicollis, Ixobrychus sinensis, Matuku otagoense, Nyctanassa violacea, Nycticorax caledonicus, Pilherodius pileatus, Plegadis falcinellus, Scopus umbretta, Syrigma sibilabix, Threskiornis spinicollis, Pikaihao bartlei.

Characters 1-54 for these taxa as listed in Appendix 3 are those used in the phylogenetic analyses of the taxa used in Figure 2. The data for *B. striata* and *E. garzetta* are given below as these species were not used in the 88 character analysis.

Butorides_striata 2 1 1 1 0 0 2 1 1 1 1 1 2 0 1 1 2 0 1 1 0 0 1 1 0 1 0 1 0 0 1 1 1 0 0 0 1 2 0 0 1 1 1 1 0 1 1 1 1 1 1 0 0 1
Egretta_garzetta 2 2 1 1 1 0 2 0 1 0 1 0 1 2 1 0 2 0 1 2 0 0 0 2 0 0 0 1 0 0 1 1 1 0 1 0 1 2 0 0 1 2 1 1 0 1 1 1 0 0 1 0 0 1

Appendix 3: Extended matrix, 32 taxa and 88 characters, includes Payne and Risley (1976) characters.

Agamia_agamia 1 2 2 1 0 0 2 0 1 0 1 0 1 2 1 0 1 1 2 1 0 0 1 2 0 1 1 1 0 0 0 0 1 0 1 1 1 2 0 1 2 1 1 1 0 1 0 0 0 0 1 0 0 ? ? ? ? ? 0 0 1 0 0 1 1 1 1 0 0 1 1 1 0 2 0 0 2 1 0 0 0 0 0 0 0 0 0 1
Ardea_cinerea 2 2 2 1 0 0 2 1 1 0 1 0 0 2 1 0 2 0 1 1 1 0 0 2 0 1 0 1 0 0 1 1 1 0 1 0 1 2 0 0 2 2 1 1 0 1 1 1 0 0 1 0 0 1 0 1 1 0 0 0 1 0 0 1 1 1 1 1 0 1 1 1 0 1 0 0 1 2 0 0 0 0 0 0 0 1 0 1
Ardea_goliath 2 2 1 1 0 0 2 0 1 0 1 0 1 2 1 0 2 0 1 1 0 0 0 1 0 1 0 ? 0 0 1 1 1 0 1 0 1 2 0 0 2 2 1 1 0 1 1 1 1 0 1 0 0 1 ? ? ? ? 0 0 1 0 1 1 1 1 1 0 0 1 1 1 0 1 0 0 1 2 0 0 0 0 0 0 0 1 0 1
Ardea_herodias 2 2 1 1 0 0 2 0 1 0 1 0 1 2 1 0 2 0 1 1 0 0 0 2 0 1 0 1 0 0 0 1 1 0 1 0 1 2 0 0 2 2 1 1 0 1 1 1 1 0 1 0 0 1 ? ? ? ? 0 0 1 0 0 1 1 1 1 1 0 1 1 1 0 1 0 0 1 2 0 0 0 0 0 0 0 1 0 1
Ardea_ibis 1 2 2 1 1 0 2 1 0 1 1 0 2 2 1 0 2 0 1 1 0 0 0 2 0 1 0 1 0 0 0 1 1 0 1 0 0 2 0 1 1 2 1 1 0 1 1 1 0 0 1 0 0 1 0 1 0 0 0 0 0 0 0 1 2 0 1 0 0 1 1 1 0 2 0 0 1 1 0 0 0 0 0 0 0 1 0 1
Ardea_modesta 1 2 2 1 0 0 2 1 1 0 1 0 1 2 1 0 2 0 1 1 0 (01) 0 (12) 0 1 0 1 0 0 1 1 1 0 1 0 1 2 0 0 2 2 1 1 0 1 1 1 0 0 1 0 0 1 0 1 1 0 0 2 1 0 0 1 1 1 1 0 0 1 1 1 0 1 0 0 1 2 0 0 0 0 0 0 0 1 0 1
Ardea_pacifica 2 2 2 1 0 0 2 1 1 0 1 0 0 2 1 0 2 0 1 1 0 1 0 2 0 1 0 0 0 0 1 1 1 0 1 0 1 2 0 0 1 1 1 1 0 1 1 1 0 0 1 0 0 1 0 1 1 0 0 0 1 0 0 1 1 1 1 0 0 1 1 1 0 1 0 0 1 2 0 0 0 0 0 0 0 1 0 1
Balaeniceps_rex 1 1 1 2 0 0 2 0 2 1 2 0 1 2 2 1 2 1 1 1 1 1 2 0 2 0 1 0 1 0 0 0 0 1 2 0 1 0 0 1 0 1 1 1 0 0 0 0 0 0 1 2 1 1 ? ? ? ? 1 3 1 - 2 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 1 0 0 - 0 1 1 0 1
Botaurus_lentiginosus 2 2 - 1 0 1 0 0 0 0 1 0 1 0 1 0 2 1 2 2 1 0 1 1 0 0 1 0 0 0 1 1 1 0 1 0 1 2 0 0 2 1 0 1 0 1 1 1 0 0 1 0 0 1 ? ? ? ? 0 0 1 1 0 1 1 0 1 1 0 1 1 1 0 1 1 1 3 1 1 1 0 0 1 0 0 0 1 0
Botaurus_poiciloptilus 2 2 - 0 (01) 1 2 0 0 0 1 0 1 1 1 0 2 1 1 2 1 0 1 2 0 0 1 0 0 0 1 1 1 0 1 0 1 2 0 0 2 2 1 1 0 1 1 1 0 0 1 1 0 1 1 1 ? ? 0 0 1 1 0 1 1 0 1 0 1 1 1 1 0 1 1 1 1 0 1 1 0 0 1 2 0 0 1 0
Botaurus_stellaris 2 2 - 0 1 1 2 0 0 0 1 0 1 1 2 0 2 1 2 2 1 0 1 2 0 0 0 0 0 0 1 1 1 0 1 0 1 2 0 0 1 1 1 1 0 1 1 1 0 0 (01) 1 0 1 ? ? ? ? 0 0 1 1 0 1 1 0 1 0 1 1 1 1 0 1 1 1 1 1 1 1 0 0 1 2 0 0 1 0
Butorides_striata 2 1 1 1 0 0 2 1 1 1 1 1 2 0 1 1 2 0 1 1 0 0 1 1 0 1 0 1 0 0 1 1 1 0 0 0 1 2 0 0 1 1 1 1 0 1 1 1 1 1 1 0 0 1 ? ? ? ? 0 1 1 0 0 1 1 1 1 1 0 1 1 1 0 2 0 0 3 1 0 0 0 0 0 0 0 0 0 1
Butorides_virescens 1 2 1 1 0 0 2 0 1 1 1 1 2 1 1 0 1 0 2 2 0 0 1 1 0 1 0 1 0 0 1 1 1 0 1 0 1 2 0 0 2 2 0 1 0 1 1 1 0 0 1 0 0 1 0 1 1 1 0 1 1 0 0 1 1 1 1 1 0 1 1 1 0 2 0 0 3 1 0 0 0 0 0 0 0 0 0 1
Ciconia_ciconia 2 2 1 2 0 0 1 0 1 1 1 0 1 2 2 1 1 0 1 0 - 0 - 0 0 1 1 0 0 1 2 0 1 1 2 0 0 0 0 1 0 2 0 1 0 0 0 1 1 0 1 1 0 1 0 0 1 0 0 2 0 3 2 ? ? ? 1 1 0 1 - 0 0 0 0 0 1 0 1 0 0 1 1 0 0 1 0 0
Cochlearius_cochlearius 2 2 2 1 0 0 1 0 0 1 1 0 (12) 1 2 0 1 1 2 1 1 0 1 2 0 0 1 0 0 0 1 0 1 0 0 0 0 2 0 1 0 1 1 1 0 0 0 1 1 0 1 3 1 1 0 0 0 0 1 3 1 2 2 0 2 0 0 0 1 0 0 0 0 2 1 0 0 1 0 0 2 0 1 0 0 1 0 1
Egretta_novaehollandiae 1 2 1 1 0 0 2 0 1 0 1 0 (12) 2 1 0 2 0 1 2 1 0 0 1 0 1 0 1 0 0 1 1 0 0 1 0 0 2 0 0 1 2 1 1 0 1 1 1 0 1 1 0 0 1 0 1 1 1 0 1 0 0 0 1 2 0 1 1 0 1 1 1 0 1 0 0 1 3 0 0 0 0 0 0 0 0 0 1
Egretta_picata 2 2 1 1 0 0 2 1 2 0 1 0 2 2 1 0 1 0 1 2 1 0 0 2 0 1 0 1 0 0 0 1 1 0 1 0 1 2 0 0 1 2 1 1 0 1 1 1 0 0 1 0 0 1 0 1 1 0 0 1 0 0 0 1 1 1 1 1 0 1 1 1 0 2 0 0 1 2 0 0 0 0 0 0 0 0 0 1
Ixobrychus_dubius 2 2 1 1 (01) 1 2 1 0 0 1 1 1 0 1 0 2 1 2 2 0 0 1 2 0 0 1 1 0 0 1 1 1 0 1 1 0 2 0 0 1 2 1 1 0 1 1 1 1 0 1 1 0 1 1 1 1 1 0 1 1 1 0 1 0 0 1 0 1 1 1 1 0 2 1 1 3 1 1 1 0 0 1 0 0 0 1 1

Ixobrychus_eurhythmus 2 2 0 1 1 1 1 1 1 0 1 1 2 0 1 0 2 1 2 2 0 0 1 2 0 0 1 0 0 0 1 1 0 0 0 0 1 2 0 0 2 2 1 1 0 1 0 1 0 0 1 0 0 1 ? ? ? ? 0 1 1 1 0 1 0 0 1 0 1 1 1 1 0 2 1 1 3 3 1 1 0 0 1 0 0 0 1 0

Ixobrychus_minutus_minutus 2 2 (-1) (-1) 0 1 1 1 0 0 1 1 2 1 1 0 2 1 1 2 0 0 1 2 0 0 0 1 0 0 1 1 1 0 1 0 0 2 0 0 1 1 1 1 0 1 0 1 0 0 1 0 0 1 ? ? ? ? 0 1 1 1 0 1 0 0 1 0 1 1 1 1 0 2 1 1 3 0 1 1 0 0 1 0 0 0 1 0

Ixobrychus_sinensis 2 2 1 1 1 1 1 1 0 0 1 1 1 1 1 0 2 1 2 2 0 0 1 2 0 0 1 1 0 0 1 1 1 0 1 1 0 2 0 0 2 1 1 1 0 1 1 1 1 0 1 1 0 1 ? ? ? ? 0 1 1 1 0 1 0 0 1 0 1 1 1 1 0 2 1 1 3 2 1 1 0 0 1 0 0 0 1 0

Matuku_otagoense 2 2 1 1 0 0 1 0 0 0 1 1 ? ? 1 0 2 ? ? ? ? 0 ? 1 1 1 0 1 0 0 0 0 1 0 0 1 1 2 0 1 1 1 0 1 0 0 1 1 0 1 1 1 0 1 ?

Nyctanassa_violacea 2 2 1 1 1 0 2 1 0 0 1 0 1 2 1 0 1 0 1 1 1 0 0 (12) 0 0 0 1 0 0 1 1 1 0 1 0 1 2 0 0 0 1 0 1 0 0 1 1 1 1 1 1 0 1 ? ? ? ? 0 0 1 3 2 1 1 0 1 1 0 0 0 0 0 1 1 0 1 2 0 0 0 0 1 0 0 0 0 1

Nycticorax_caledonicus 2 2 2 1 0 0 2 1 1 0 1 0 2 2 1 0 1 1 1 1 1 0 0 2 0 1 0 1 0 0 0 1 1 0 1 1 1 2 0 0 0 1 1 1 0 0 1 1 0 0 1 1 0 1 0 1 1 0 0 0 1 2 1 1 1 0 1 0 1 0 0 0 0 1 1 0 0 2 0 1 0 0 1 0 0 0 0 1

Nycticorax_nycticorax 2 2 1 1 0 0 2 1 1 0 1 0 2 2 1 0 1 1 2 1 0 0 0 2 0 1 0 1 0 0 1 1 1 0 1 0 1 2 0 0 0 1 1 1 0 0 1 1 1 1 1 0 0 1 ? ? ? ? 0 0 1 2 1 1 1 0 1 0 1 0 0 0 0 1 1 0 0 2 0 1 0 0 1 0 0 0 0 1

Pilherodius_pileatus 2 2 1 1 1 0 2 0 0 0 1 0 2 2 1 1 2 0 1 1 0 0 0 1 0 1 0 0 0 0 0 1 1 0 1 0 1 2 0 0 1 2 1 1 0 0 0 1 1 0 1 1 0 1 ? ? ? ? 0 1 1 0 0 1 1 1 1 0 0 1 1 1 0 1 0 0 3 2 0 0 0 0 0 0 0 0 0 1

Plegadis_falcinellus 1 1 0 2 0 0 1 0 1 0 1 1 1 2 1 1 2 0 1 0 - 1 0 1 0 1 1 1 1 1 0 0 1 0 1 0 0 0 0 1 0 2 1 1 1 1 1 1 0 0 1 0 0 0 0 1 1 0 0 2 1 3 0 1 2 0 1 2 0 1 - - 0 0 0 0 0 0 1 0 0 1 1 0 - 1 0 ?

Scopus_umbretta 1 2 1 2 0 0 1 0 1 0 (12) 0 (01) 2 0 1 2 0 1 1 1 1 2 1 2 - 0 1 0 0 0 0 0 1 2 0 0 2 0 1 0 0 1 1 0 0 0 1 1 0 1 0 0 1 ? ? ? ? 0 2 0 - 2 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1

Syrigma_sibilabix 2 2 1 1 0 0 2 0 2 0 1 0 2 2 1 0 2 1 2 1 0 0 0 1 0 0 1 1 0 0 0 1 1 0 1 1 0 2 0 1 1 1 0 1 0 1 1 1 0 0 1 1 0 1 ? ? ? ? 0 1 1 3 0 1 1 0 1 0 0 1 0 1 0 2 0 0 3 0 0 0 0 0 0 0 0 1 0 1

Threskiornis_spinicollis 1 1 0 2 0 0 1 0 1 0 1 0 1 2 2 1 2 0 0 0 - 1 - 1 0 1 1 0 1 1 0 0 1 0 1 0 1 0 0 1 0 2 1 1 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 2 0 3 0 1 2 0 1 2 0 1 - - 0 0 0 0 0 0 1 0 0 1 1 0 0 1 0 0

Tigrisoma_mexicanum 2 2 1 1 1 0 2 0 1 1 1 1 2 2 1 0 2 1 1 1 1 0 0 1 0 1 1 1 0 0 0 1 1 0 1 0 1 2 0 1 1 1 1 0 0 1 0 1 0 0 1 0 0 1 0 0 0 0 0 2 1 0 2 2 3 1 0 1 0 1 1 1 0 1 1 0 0 0 0 0 0 1 1 0 1 1 0 1

Pikaihao_bartlei 2 2 2 0 1 1 1 1 1 1 0 1 1 2 1 1 0 1 0 2 2 ? 0 1 2 0 0 0 1 0 0 1 ?

Ixobrychus_flavicollis 2 2 1 1 0 1 2 1 1 0 1 1 2 2 1 0 1 1 1 2 0 0 1 2 0 1 0 1 0 0 1 1 1 0 1 0 1 2 0 0 1 2 1 1 0 1 0 1 0 0 1 1 0 1 1 1 1 1 0 0 1 1 0 1 2 0 1 0 1 1 1 1 0 1 1 1 3 2 1 1 0 0 1 0 0 0 1 0