

A Heron (Aves: Ardeidae) from the Early Miocene St Bathans Fauna of Southern New Zealand

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ABSTRACT. We describe a fossil heron, based on seven fossil bones, from the Early Miocene Bannockburn Formation at Saint Bathans, Central Otago in the south of New Zealand. Based on a phylogenetic analysis of 50 morphological characters, we determine the new heron is a member of Ardeidae but, in an analysis where we retrieve three major lineages in Ardeidae: (1) bitterns, (2) egrets and true herons, and (3) night herons, there is no support for a sister group relationship with any of these clades. We discuss aspects of the higher taxonomy of the herons based on our phylogeny.

SCOFIELD, R. PAUL, TREVOR H. WORTHY & ALAN J.D. TENNYSON, 2010. A heron (Aves: Ardeidae) from the Early Miocene St Bathans Fauna of southern New Zealand. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 89–104.

The herons (Aves: Ardeidae) are a cosmopolitan group, found on all continents except Antarctica. The group's fossil record may extend back as far as the Eocene (Table 1 and references therein), however, analyses to date of the fossil taxa are not informative of their intrafamilial phylogenetic relationships. The Recent herons are currently divided into five subfamilies (Kushlan & Hancock, 2005; Table 2). Ardeinae and Botaurinae have a fossil record extending into the Miocene; the Tigrisomatinae's only fossil occurrence is in the Pleistocene of the West-Indies (see Table 1 and references therein); and there are no fossil records for Argaminae or Cochleariinae. Here we describe a fossil heron based on seven fossil bones, from the Early Miocene Saint Bathans Fauna of New Zealand.

Geological setting and St Bathans Fauna

The St Bathans Fauna, of late Early Miocene age, Altonian, 19–16 Ma, is derived from the lower Bannockburn Formation of the Manuhirikia Group, in Otago, South Island, New Zealand (Worthy *et al.*, 2007). The sediments were deposited in a shallow freshwater lake, about 5600 km² in area, in a warm climate, with a surrounding vegetation including casuarinas (Casuarinaceae), eucalypts (Eucalyptus: Myrtaceae) and palms (Arecaceae), in addition to the typical New Zealand podocarps (Podocarpaceae), *Nothofagus* and araucarias (Araucariaceae) (Pole & Douglas, 1998; Pole *et al.*, 2003). The diverse fauna provides the only data on the terrestrial vertebrates existing in New Zealand during the

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Table 1. The fossil record of the Ardeidae.

taxon ^a	age	location	reference	notes
Ardeid subfamily indeterminate [or undetermined]				
Ardeidae sp	Eocene	Washington State, USA	(Mustoe, 2002)	Based on fossil footprints
<i>Ardea piveteaui</i>	Upper Eocene	Montmartre, France	(Brunet, 1970; Cracraft, 1971)	Specimen considered too fragmentary—should simply be ardeid sp. (Cracraft, 1971)
<i>Calcardea junnei</i>	Lower Eocene	Wyoming, USA	(Gingerich, 1987)	
<i>Eoecornis ardetta</i>	Middle Eocene	Wyoming, USA	(Shufeldt, 1915)	
<i>Ardeagrands arborea</i>	Late Miocene	Golbočica, Moldova	(Kuročkin & Ganea, 1972)	
<i>?Ardea alba</i>	Miocene	Abu Dhabi	(Harrison, 1979)	Specimen considered too fragmentary—should simply be ardeid sp. (Stewart & Beech, 2006)
Ardeinae				
<i>Proardea amissa</i> (synonyms are <i>Proardeola walkeri</i> and <i>Ardea aurelianensis</i>)	?Late Eocene-Late Oligocene-Miocene	France	(Milne-Edwards, 1892; Lambrecht, 1933)	Synonymy <i>vide</i> C. Mourer-Chauviré (Olson, 1985: 167; Mlíkovský, 2002)
<i>Ardea basaltica</i> (synonym is <i>Anas basaltica</i>)	Lower Oligocene	Czech Republic	(Bayer, 1882)	Synonymy <i>vide</i> Mlíkovský & Švec (1989)
<i>Ardea</i> sp.	Mid-Miocene	Nebraska, USA	(Becker, 1986)	
<i>Egretta subfluvia</i>	Late Miocene or Early Pliocene	Florida, USA	(Becker, 1985)	
<i>Ardea polkensis</i>	Early Pliocene	Florida, USA	(Brodkorb, 1955)	
<i>Ardea howardae</i>	Plio / Pleistocene	Ethiopia	(Brodkorb, 1980)	
<i>Butorides validipes</i>	Late Pliocene	Florida, USA	(Campbell, 1976)	
Nycticoracinae [sensu Payne & Risley (1976)]				
<i>Nycticorax</i> sp.	Early Oligocene	Egypt	(Rasmussen <i>et al.</i> , 1987)	
<i>Zeltornis ginsburgi</i>	Miocene	Libya	(Balouet, 1981)	
<i>Nycticorax</i> sp.	Miocene	Kenya	(Dyke & Walker, 2008)	
Botaurinae				
<i>Palaeophoyx columbiana</i>	Upper Pleistocene	Florida, USA	(McCoy, 1963)	Originally referred to Ardeinae but synonymized with extant <i>Botaurus lentiginosus</i> by Olson (1974)
Tigrisomatinae				
<i>Tigrisoma mexicanum</i>	Pleistocene	Cuba	(Olson & Suarez 2008)	
taxa no longer considered herons				
<i>Proherodius oweni</i>			(Lydekker, 1891)	Now considered <i>Aves incertae sedis</i> , because of the lack of diagnostic characters in the existing material (Dyke, 2001)
<i>Botauroides parvus</i>			(Shufeldt, 1915)	Transferred to the Primobueconidae by Feduccia (1996) and to the Sandcoleidae by Houde & Olson (1992)
<i>Xenerodiops mycter</i>	Early Oligocene	Egypt	(Rasmussen <i>et al.</i> , 1987)	Originally placed in a new family Xenerodiopidae but this was synonymized into Nycticoracinae by Mlíkovský (Olson, 1985; Mlíkovský, 2002;
				Mlíkovský, 2003). G. Mayr (2009) considers this to differ from extant ardeids in a number of features and placed it as <i>incertae sedis</i>
<i>Calcardea junnei</i>	Lower Eocene	Wyoming, USA	(Gingerich, 1987)	G. Mayr (2009) considers this to differ from extant ardeids in a number of features and placed it as <i>incertae sedis</i> .

^a Nomenclature as originally described.

entire Tertiary and includes a crocodylian, a sphenodontid, squamates, at least 30 taxa of birds, several bats and an archaic terrestrial mammal (Molnar & Pole, 1997; Worthy *et al.*, 2006; Hand *et al.*, 2007; Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy *et al.*, 2008; Jones *et al.*, 2009). In addition, undescribed terrestrial and freshwater molluscs are diverse (unpubl. data), and fish are abundant (McDowall & Pole, 1997; McDowall *et al.*, 2006; Lee *et al.*, 2007).

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 procellariiforms, accipitriforms, gruiforms, charadriiforms, columbiforms, psittaciforms, apodiforms, and passeriforms (Worthy *et al.*, 2007; Worthy & Lee, 2008; Worthy *et al.*, 2010).

The St Bathans avifauna is known from exposures along the Manuherikia River and at several other nearby sites (see Worthy *et al.*, 2007 for location data). The fossils described here derive from three discrete layers (HH1a, HH1b and HH4) in the Manuherikia River Section. These layers are poorly aged but considered to be late Early Miocene age, 19–16 Ma. It is not known what temporal period they represent nor the interval between them. They have revealed thousands of avian fossils, but the seven fossils described here are the only heron remains identified to date.

The primary layer (HH1a; NZFRN H41/f0088) is 6.88–7.00 m above the base of the Bannockburn Formation. It is mostly greenish gray fine sand, sometimes intermixed with quartz granules/pebbles, and organic debris, incorporating carbonate-encrusted mud rip-up clasts and rare oncolite fragments derived from algal growth and abundant bone fragments. In the HH1a strata, most of the heron fossils come from an excavated pit extending approximately 20–40 m from the current riverbank. A single element (the mandible tip) comes from a trench 60 m inland from the riverbank in a layer (HH1b; NZFRN H41/f0103) which is 9.5–9.58 m above base of the Bannockburn Formation. The third stratum (HH4; NZFRN H41/f0096) was a discrete lens, up to 5–15 cm thick, in a clay layer exposed 20 m downstream from HH1a in the riverbank itself and is 25.63–25.83 m above the base of the Bannockburn Formation. This lens was completely quarried away in 2008 and was characterized by abundant fragments of the freshwater gastropod *Glyptophysa*, but it also contained terrestrial vertebrate remains.

Materials and methods

Institutional abbreviations. AM, Australian Museum, Sydney, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MV, Museum Victoria, Melbourne, Australia; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; SAM, South Australian Museum, Adelaide, South Australia, Australia; UMMZ, University of Michigan Museum of Zoology, Michigan, United States of America; NMNH, National Museum of Natural History, Washington, D.C., United States of America.

Anatomical nomenclature. Names for specific bone landmarks follow Baumel & Witmer (1993) with English translations of less specific areas on each element following Howard (1929). Here we use the terms plantar and dorsal rather posterior and anterior to describe positions on the tarsometatarsus following Baumel & Witmer (1993). For the nomenclature of the hypotarsal canals

Table 2. Recent and extant nomenclature of the family Ardeidae based on the nomenclature of Kushlan & Hancock (2005).

subfamilies	tribes	genera	common name
Tigrisomatinae		<i>Tigrisoma</i> <i>Tigriornis</i> <i>Zonerodius</i>	Tiger herons
Agaminae		<i>Agamia</i>	Agami heron
Cochleariinae		<i>Cochlearius</i>	Boat-billed heron
Ardeinae	Ardeini	<i>Ardeola</i> <i>Butorides</i> <i>Ardea</i>	Day herons
	Egrettini	<i>Egretta</i> <i>Nyctanassa</i> <i>Pilherodius</i> <i>Syrigma</i>	Egrets
	Nycticoracini	<i>Nycticorax</i> <i>Gorsachius</i>	Night herons
Botaurinae		<i>Zebrilus</i> <i>Ixobrychus</i> <i>Botaurus</i>	Bitterns

we follow Strauch (1978). Nomenclature of the avian quadrate follows Elzanowski *et al.* (2000). Some common terms are abbreviated as follows: *L*, left; *R*, right; *lig*, ligamentum; *tuber*, tuberculum; *Ma*, million years ago; *indet*, indeterminate. Other abbreviations follow Baumel & Witmer (1993). Anatomical landmarks are abbreviated in figure captions.

Comparative material (Some features were scored from illustrations in Payne & Risley [1976]. In these cases the registration numbers of the specimens used in these illustrations are given in square brackets). The generic and species level taxonomy of the ardeids is complex and many issues are unresolved—here we follow Kushlan & Hancock (2005).

Ciconiiformes Bonaparte, 1854

Ardeidae Leach, 1820: Ardeinae Leach, 1820: *Ardea herodias* (Linnaeus, 1758), Great Blue Heron, CM Av19902; *Ardea goliath* Cretzschmar, 1829, Goliath Heron, CM Av7120; *Ardea 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; *Ardea ibis* Linnaeus, 1758, Cattle Egret CM Av 29417 [NMNH 430524, NMNH 430525, UMMZ 209241]; *Egretta rufescens* (Gmelin, 1789), Reddish Heron [UMMZ 136370]; *Egretta novaehollandiae* (Latham, 1790), White-faced Heron, CM Av 5215, CM Av 14806, CM Av 25210; Whistling Heron, [UMMZ 158606, 158607]; *Nycticorax caledonicus* (Gmelin, 1789), Nankeen Night Heron, NMNZ OR.19310; SAM B.48523; *Nyctanassa violacea* (Linnaeus, 1758), Yellow-crowned Night Heron, [UMMZ 85046, UMMZ 130935, UMMZ 133607]; *Pilherodius pileatus* (Boddaert, 1783), Capped Heron, [UMMZ 156863].

Tigrisomatinae Bock, 1956: *Tigrisoma mexicanum* Swainson, 1834, Fasciated Tiger Heron, MV B13558; *Syrigma sibilatrix*, (Temminck, 1824).

Botaurinae Reichenbach, 1850: *Botaurus lentiginosus* (Rackett, 1813), American Bittern, CM Av 19627; *Botaurus poiciloptilus* (Wagler, 1827), Australasian Bittern, CM Av 5085, CM Av 5085, CM Av 5502; *Ixobrychus sinensis*

(Gmelin, 1789), Yellow Bittern, [NMNH 291696, 488913]; *Ixobrychus minutus* (Linnaeus, 1766), Little Bittern, CM Av 7122, [UMMZ 151097].

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

Scopidae Bonaparte, 1849: *Scopus umbretta* Gmelin, 1789, Hamerkop, CM Av 39998.

Balaenicipitidae Bonaparte, 1853: *Balaeniceps rex* Gould, 1850, Shoebill, [UMMZ 215884].

Ciconiidae Sundevall, 1836: *Ciconia ciconia* (Linnaeus, 1758), White Stork, CM Av 33450.

Threskiornithidae Poche, 1904: *Threskiornis molucca* Cuvier, 1829, Australian White Ibis, CM Av 16219; *Plegadis falcinellus* Linnaeus, 1766, Glossy Ibis, CM Av 20692.

Pelecaniformes Sharpe, 1891

Phalacrocoracidae Reichenbach, 1850: *Phalacrocorax carbo* (Linnaeus, 1758), Black Shag, CM Av 17299.

Phoenicopteriformes Fürbringer, 1888

Phoenicopteridae Bonaparte, 1831: *Phoenicopter ruber* Linnaeus, 1758, American Flamingo, CM Av 7113.

Determining if all bones are from the same species. In order to determine whether all the elements described here are from the same medium-sized heron an intra-element ratio comparison of elements was made using Simpson's ratio-diagrams (Simpson, 1941).

Phylogenetic analyses

The phylogenetic analyses were aimed principally at determining the relationships of the fossil heron bones from the St Bathans Fauna. They were thus mainly constrained to the use of characters derived from the available elements: the tarsometatarsus; the cranial end of a coracoid; a quadrate; an axis vertebra; and a tip of a mandible. In the present analyses, 24 terminal taxa were included. Six taxa were defined as the outgroup: five Ciconiiformes—*Balaeniceps rex*, *Ciconia ciconia*, *Threskiornis molucca*, *Plegadis falcinellus*, a flamingo *Phoenicopter ruber* and a pelecaniform *Phalacrocorax carbo*. The sister taxon to ardeids is unknown, but is usually considered to be a member of the Ciconiiformes. The details of this relationship, however, are poorly understood. For example, using a significant number of DNA loci, Hackett *et al.* (2008) found the Threskiornithidae to form a clade with the ardeids, with other Ciconiiformes as their sister group, but Livezey & Zusi (2007), using a large morphological dataset considered the Ardeidae to form their own order, the Ardeiformes, and to be the sister group to all other Ciconiiformes including

Threskiornithidae. To take into account this uncertainty, we sampled a wide variety of Ciconiiformes. We sampled all four extant resident Recent New Zealand species of ardeids: *Ardea novaehollandiae*; *Ardea modesta*; *Botaurus poiciloptilus* and *Nycticorax caledonicus* and species from two of the three extralimital ardeid subfamilies (see *Comparative material*).

By comparing the fossil elements with specimens of Recent ardeids we defined a set of characters (Appendix 1), which were scored for all taxa (Appendix 2). Many are new characters, although some derive from features described by others (e.g., Strauch, 1978; Livezey & Zusi, 2007). Missing data was identified as either: (1) Inapplicable characters (coded as “—”), which could not be objectively scored in a particular taxon due to extensive divergence obscuring homology, or (2) Unknown characters (coded as ?) which were not preserved in the specimens examined. We scored features of the proximal tarsometatarsus despite it not being represented in the fossil material, so as to increase the numbers of characters and improve resolution of compared taxa. The phylogenetic analyses used PAUP* 4.0b10 (Swofford, 2002). While distinguished in our matrix (Appendix 2), PAUP treats both types of missing data in the same fashion.

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. When calculating tree lengths, multistate taxa were treated as polymorphisms rather than ambiguity. Bootstrapping used heuristic searches and the same options. Strict consensus trees were computed and presented. Trees were manipulated and labelled in MrEnt (Zuccon & Zuccon, 2008).

Bayesian analyses

The program MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to determine posterior probabilities for clades in the tree. The analyses were performed with the same characters and ordering assumptions as above; however, the outgroup was restricted to *Phalacrocorax carbo* as multiple outgroups are not allowed.

The following priors were used. Characters were assumed to have rate variability distributed according to gamma parameter (rates = gamma) with flat prior distribution (0–200). In the morphological data set, only variable characters were assumed to have been included (coding = variable).

Two independent analyses were run simultaneously to check for adequacy of convergence, each for 5,000,000 generations, sampled every 1,000 generations. To improve exploration of tree topology space, the heating parameter was set to 0.20, six chains (one cold and five incrementally-heated) per analysis were used, and branch swapping was set at three times the default (nswaps = 3). The time to convergence for topology, stationarity, and all parameters was checked using Tracer v. 1.3 (Rambaut & Drummond, 2004); the first 1,000 sampled trees were discarded as burnin. A standard “all-compatible” consensus tree, where all clades are shown regardless of posterior probabilities values, was produced by combining the post-burnin 4001 samples from each run. Posterior probability values for a node are the percentage of sampled generations that have that node.

Systematic paleontology

Order Ciconiiformes Bonaparte, 1854

Family Ardeidae Leach, 1820

The fossils are referred to the Ardeidae using characteristics of the tarsometatarsus and coracoid.

The tarsometatarsi (NMNZ S.50003 and S.51264) can be distinguished from other Aves by the combination of the following characters (based on Brodkorb, 1980 and pers. obs.):

- 1 Shaft long, narrow, wider than deep, narrowest just proximal of base of trochlea metatarsi II;
- 2 Hypotarsal ridges (crista hypotarsus) extends considerably less than ½ the length of the shaft;
- 3 Trochlea metatarsi II and III extend about the same distance distally;
- 4 Absence of a sulcus flexorius;
- 5 A distinct raised facet for the articulation of metatarsal I rather than a sulcus;
- 6 Trochlea metatarsi II–IV roughly in the same dorso-plantar plane;
- 7 No medial inflection in trochlea metatarsi II or lateral deflection in trochlea metatarsi IV.

In addition, herons are typified by a single small closed tendinal canal (canalis hypotarsi) and a single distinct hypotarsal ridge (crista hypotarsi), both not preserved in the available material.

The cranial extremity of the coracoid (NMNZ S.50004) can be diagnosed as an ardeid by the combination of the following characters (based on Brodkorb, 1980; Gilbert *et al.*, 1981 and pers. obs.):

- 1 Brachial tuberosity (tuber. brachiale) present;
- 2 Raised oval humeral facet (facies artic. humeralis) faces dorsally;
- 3 Absence of a deep groove running along the medial face between the brachial tuberosity and the tip of the procoracoid (proc. procoracoideus);
- 4 Relatively small hook-shaped procoracoid bent slightly medially;
- 5 Distance between scapular facet (cotyla scapularis) and cranial most end of acrocoracoid (proc. acrocoracoideus) approximately equal to width of shaft at the procoracoid;
- 6 Scapular facet, raised and flattened but not cup-like.

Matuku n.gen.

Type species. *Matuku otagoense* n.sp.

Diagnosis. Tarsometatarsus shaft relatively short and robust: trochlea metatarsi II with slight medial deflection; trochlea metatarsi III in line with axis of shaft; trochlea metatarsi IV deeply grooved distally; foramen vasculare distalis with dorsal opening distinct from intertrochlear incision and large; and crista planataris medialis dorso plantarly thick. The coracoid is distinguished by three autapomorphies:

- 1 the extremely short distance from the cranial side of the clavicular facet (facies articularis clavicularis) to the omal tip of the facet;
- 2 a broad triangular (impressio ligamentum acrocoracohumeralis), rather than the rectilinear

impression normally seen in herons;

- 3 the clavicle facet (facies clavicularis) on the acrocoracoid (proc. acrocoracoideus) overhangs the supracoracoidal sulcus as a prominent lip, rather than the acrocoracoid being in line with the medial margin of the sulcus.

Etymology. *Matuku* is the New Zealand Māori word for a heron. As the name ends in a “u” it is treated as neuter as specified by Article 30.2.4 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999).

Matuku otagoense n.sp.

Holotype. NMNZ S.50003: Distal end, shaft and lateral proximal edge of left tarsometatarsus with fragmentary lateral cotyla and basal hypotarsus; the three trochlea are preserved but the distal foramen is obscured; the medial proximal end is missing. The bone was already fragmented *in situ* when discovered and has subsequently been repaired in the laboratory (Figs 1, 2). It was collected on 9 January 2007 during a University New South Wales, NSW, Australia/University of Adelaide, South Australia/Canterbury Museum, Christchurch, NZ/Museum of New Zealand Te Papa Tongarewa, Wellington, NZ, expedition.

Diagnosis. As for genus.

Etymology *otagoense*, Latin, after Otago province in southern New Zealand, where the excavations take place; gender neuter, conforming to the gender of the generic name.

Type locality. Home Hills Station, Site HH4, true left side Manuherikia River, Otago, New Zealand. 44° 54.472'S 169° 51.434'E. NZMS 260 H41/618843, New Zealand Fossil Record File Number H41/f0095. The site was first exposed by river erosion between February 2005 and March 2006. Bones were recovered from the site in March 2006 and January 2007.

Stratigraphy/Age/Fauna. Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna. HH4 is a 5–15 cm thick clay-silt layer notable for the large number of shell fragments of the gastropod *Glyptophysa*. It is located 2.15–2.35 m above the top of an obvious oncolite layer and 25.63–25.83 m above base of Bannockburn Formation.

Measurements of holotype. See Table 3.

Paratypes. NMNZ S.51264. Distal end of tarsometatarsus, missing distal end of all three trochlea (HH1b Trench excavation, 15 January 2008); NMNZ S.50004. Cranial end of right coracoid, broken approximately half way down shaft (HH1a, 8 January 2007); NMNZ S.50852. Left quadrate missing entire proc. orbitalis (HH4, 8–16 January 2008); NMNZ S.50854. Left quadrate missing entire proc. orbitalis (HH1a, 15 January 2008); NMNZ S.50853. Axis with damage to caudal end of proc. caudalis (HH4, 8–16 January 2008); NMNZ S.51174. Tip of mandible including most of mandibular symphysis, but with damage to tip (HH1b trench excavation, 14 January 2008).

Tarsometatarsus (NMNZ S.51264, not illustrated).

In its exterior appearance, this fragmentary element does not differ significantly in any way from NMNZ S.50003. The exceptional preservation of the distal foramen in this specimen, however, allows us to see a feature that can not be discerned in NMNZ S.50003. In NMNZ S.51264, the dorsal opening of the foramen does not open into the inter-

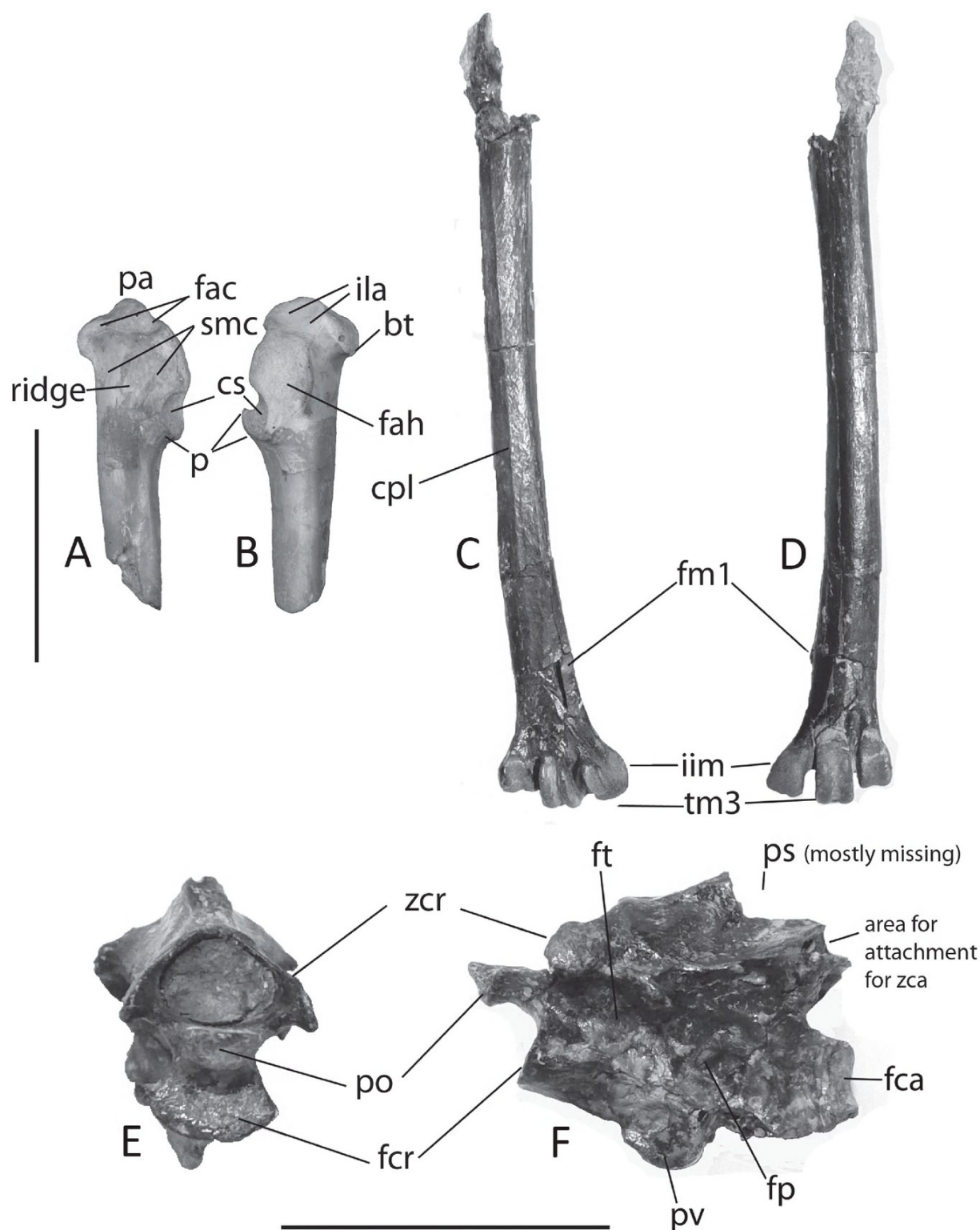


Figure 1. Specimens of the fossil heron *Matuku otagoense*. Scale bar is 1 cm. Right coracoid, extremitas omalis, paratype of *Matuku otagoense*, S.50004, HH1a, in medial (A) and lateral (B) aspects; left tarsometatarsus, holotype of *Matuku otagoense*, S.50003, HH4, in plantar (C) and dorsal (D) aspects; and referred axis vertebra S.50853, HH4, in cranial (E) and left lateral (F) aspects. Abbreviations: **fac**, clavicular facet, *facies articularis clavicularis*; **smc**, supracoracoidal sulcus, *sulcus musculi supracoracoidei*; **ridge**, character 23 “Slight ridge running sternally, barely dividing sulcus into two segments”; **pa**, acrocoracoid, *processus acrocoracoideus*; **fah**, humeral facet, *facies art. humeralis*; **ila**, impression for the acrocoracohumeral ligament, *impressio ligamentum acrocoracohumeralis*; **bt**, brachial tuberosity; **p**, procoracoid, *proc. procoracoideus*; **cpl**, crista plantaris lateralis; **fm1**, fossa metatarsal I; **iim**, Incisura intertrochlearis medialis; **tm3**, trochlea metatarsi III; **po**, dens, *processus odontoideus*; **fcr**, cranial facies of articulation, *facies articularis cranialis*; **zcr**, prezygapophysis, zygapophysis cranialis; **fca**, caudal facies of articulation, *facies art. caudalis*; **zca**, postzygapophysis, zygapophysis caudalis; **p**, hypapophysis, *proc. ventralis corporis*; **fp**, pneumatic foramen, *foramen pneumaticum*; **ps**, spinous process, *proc. spinosus*; **ft**, transverse foramen, *foramen transversarium*.

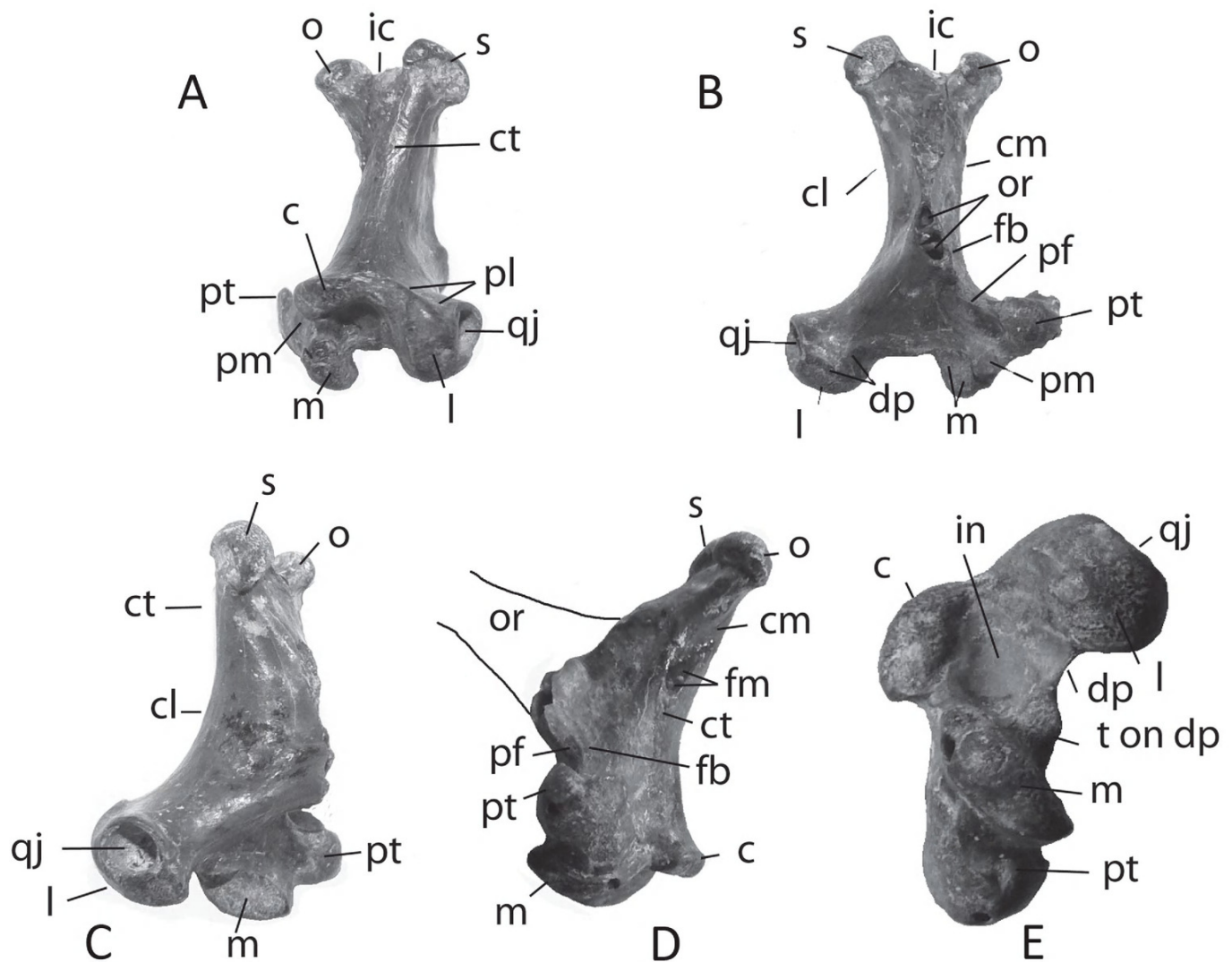


Figure 2. Referred specimens of the fossil heron *Matuku otagoense*. Scale bar is 1 cm. Left quadrate (S. 50852; HH4): (A) caudal aspect; (B) rostral aspect; (C) lateral aspect; (D) medial aspect; (E) ventral aspect. Abbreviations: **o**, capitulum oticum; **ic**, vallecule intercapitularis; **s**, capitulum squamosum; **ct**, crista tympanica; **c**, condylus caudalis; **pt**, condylus pterygoideus; **pm**, processus medialis; **m**, condylus medialis; **l**, condylus lateralis; **pl**, processus lateralis; **cm**, crista medialis; **cl**, crista lateralis; **or**, processus orbitalis; **fb**, fossa basiorbitalis; **pf**, facies pterygoidea; **dp**, depressio praecondylaris; **qj**, cotyla quadratojugalis; **fm**, foramen pneumaticum mediale; **in**, vallecule intercondylaris; **t on dp**, tubercle on depressio praecondylaris.

trochlear incision but is separated from it, by a thin lamella giving the foramen three openings, one dorsally, one opening to the incision and one plantarly. This feature appears to be a feature the fossil shares only with *Syrigma* and *Botaurus* amongst the ardeids examined.

Differential diagnosis of tarsometatarsi

Subfamily Ardeinae

(Day Herons, Egrets, Night Herons)

Support for the inclusion of *Matuku* in Ardeidae is provided by a single unambiguous apomorphy: the absence of a plantar metatarsal groove (*sulcus flexorius*) and coincident presence of metatarsal facet. The tarsometatarsi of night herons (tribe Nycticoracini) differ from those of other members of the Ardeidae, by the following combination of characters (Steadman *et al.*, 2000):

- 1 The trochlea metatarsi IV is slightly grooved distally, rather than deeply grooved or ungrooved.
- 2 The distal foramen (foramen vasculare distale) is small and placed more proximally than the proximal end of trochlea metatarsi III.

- 3 The trochlea metatarsi III is deflected laterally from the axis of the shaft (corpus tarsometatarsi) in night herons (this character is shared only with bitterns).
- 4 The trochlea metatarsi II has slight deflection from the shaft (corpus tarsometatarsi) so extends only slightly mesad of the shaft, not markedly.
- 5 The crista plantaris medialis is prominent proximally.
- 6 There is a lack of obvious dorsal metatarsal (sulcus extensorius) and plantar metatarsal grooves (sulcus flexorius) with the crista plantaris lateralis being indistinct.

Matuku otagoense differs from members of Nycticoracini in all these features and most noticeably in the lack of lateral deflection of trochlea metatarsi III and in having a large distal foramen. Additionally, members of this tribe have the medial margin of the shaft immediately distal to the cotyla medialis dorso-plantarly compressed forming a prominent thin crest, which *Matuku otagoense* lacks.

Tarsometatarsi of day herons and egrets (Tribes Ardeini and Egrettini respectively) have obvious dorsal metatarsal and plantar metatarsal grooves, with a distinct

Table 3. Measurements of *Matuku otagoense*. Alphabetical notation given is used in Fig. 4. NMNZ S.51264 and S.51174 were not measured due to their fragmentary nature.

abbreviation	description	mm
tarsometatarsus (holotype S.50003)		
A	maximum distal width	12.9
B	maximum distal depth	7.9
C	width of trochlea metatarsi III	3.8
	preserved length	92.6
D	estimated total length	ca. 98
right coracoid (S.50004)		
E	maximum cranial width (from humeral facet to brachial tuberosity)	8.0
F	maximum shaft width (below procoracoid)	5.4
G	length of humeral facet	8.3
H	depth of humeral facet	5.7
left quadrate (S.50852)		
I	depth from capital squamosum to cond. lateralis	16.9
J	depth from capital squamosum to cond. medialis	16.9
left quadrate (S.50854)		
I	depth from capital squamosum to cond. lateralis	16.8
J	depth from capital squamosum to cond. medialis	16.9
axis (S.50853)		
K	width of facies artic. cranialis	4.1
L	inter condyle distance	13.6
M	width single zygapophysis caudalis	3.6
N	depth single zygapophysis caudalis	3.6
O	greatest width (estimated across zygapophyses caudalis)	10.3

lateral intermuscular line (crista plantaris lateralis). The tarsometatarsi of *Egretta* and most *Ardea* are much longer with comparatively narrower shafts than *Matuku otagoense*, but those of *Butoroides* and *Ardea ibis* are shorter and more gracile than the fossil. We conclude therefore, that the St Bathans fossil is not an ardein heron.

Subfamily Cochleariinae (Boat-billed Herons)

The tarsometatarsus of *Cochlearius* (Cochlearinae) is very similar to that of *Nycticorax* but differs in the following characters: in *Cochlearius* the dorsal metatarsal groove is slightly deeper and usually more well defined; the intercortylar prominence usually projects less proximally; the trochlea metatarsi III is less elevated relative to the trochlea metatarsi IV; the trochlea metatarsi II is less wide. None of these features are found in *Matuku otagoense*.

Subfamily Botaurinae (Bitterns)

The tarsometatarsi of bitterns have a prominent plantar metatarsal groove (sulcus flexorius) with a prominent central intermuscular line (crista plantaris), quite unlike the flatter morphology of *Matuku otagoense*. Also, the trochlea metatarsi III is deflected laterally from the shaft axis and they have a very small or lack a distal foramen.

Subfamily Tigrisomatinae (Tiger herons)

The tarsometatarsi of tiger herons differs from *Matuku otagoense* in the more proximal position of dorsal opening of the distal foramen relative to the proximal end of trochlea metatarsi III (equal in *Matuku*), the significant medial protrusion of trochlea metatarsi II from the shaft (weak in *Matuku*), and

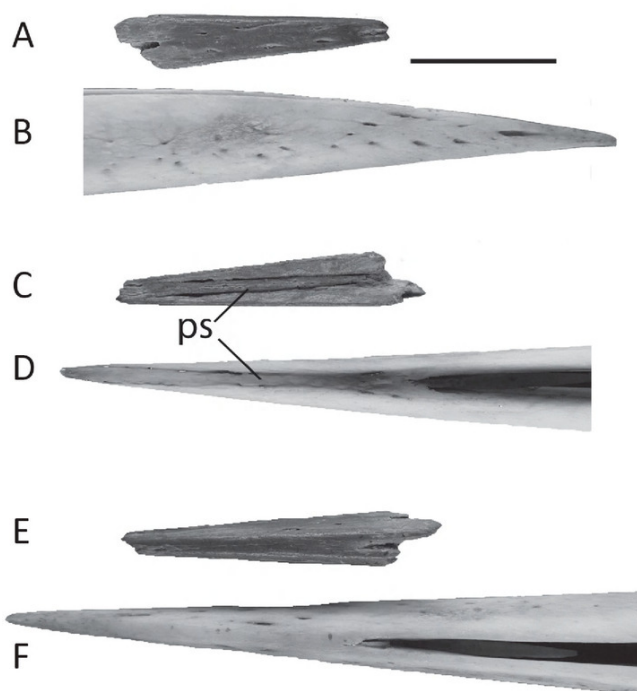


Figure 3. Mandible tips of referred specimen of the fossil heron *Matuku otagoense* n.sp., (S.51174, HH1a), (A, C, E) and Recent Nankeen Night Heron *Nycticorax caledonicus*, SAM B.48523, South Australia, (B, D, F). Scale bar is 1 cm. Rostrum mandibulae: in medial aspect (A, B); in dorsal aspect (C, D), and in ventral aspect (E, F) ventral aspect. Abbreviation: ps, pars symphysialis.

the weak crista plantaris lateralis (strong in *Matuku*).

Subfamily Agaminae (Agami Heron)

Although not examined by us, the skeleton of *Agamia* is said to differ little in morphology from the Ardeini and Egrettini (Payne & Risley, 1976).

Coracoid (Fig. 2). The fossil coracoid most closely matches that of *Cochlearius*. The three autapomorphies on the coracoid (see diagnosis of *Matuku* above) justify the placement of *Matuku otagoense* outside the five traditional subfamilies of Ardeidae.

Quadrates (S.50852, Fig. 2; S.50854, not illustrated)

The two quadrates are typical ardeid quadrates. In overall proportions and morphology they are most similar to *Cochlearius* but differ in lacking a large foramen pneumaticum mediale. These quadrates, that we refer to *Matuku*, are distinguished by one autapomorphy from all living species of the Ardeidae examined: in ventral aspect the vallecule intercondylaris is a deep “U” shaped fossa, opening into a wide sulcus on the rostral surface.

Axis (Fig. 1). The axis does not differ significantly from some extant members of the Egrettini and Ardeini, although the knob-like protruding hypapophysis (*processus ventralis corporis*) is more similar to *Cochlearius*. However, *Matuku* differs from *Cochlearius* in relative proportions. The axis of *Matuku* is not as elongate as it is in *Ardea* and *Egretta*, nor so short and robust as it is in *Nycticorax*.

Mandible tip (Fig. 3). The mandible tip referred to *Matuku* is most similar in proportions to that of *Nycticorax*, with the symphysis much shorter than it is in *Egretta* or *Ardea*. A mandible of this type suggests a bill designed for the stabbing capture of prey.

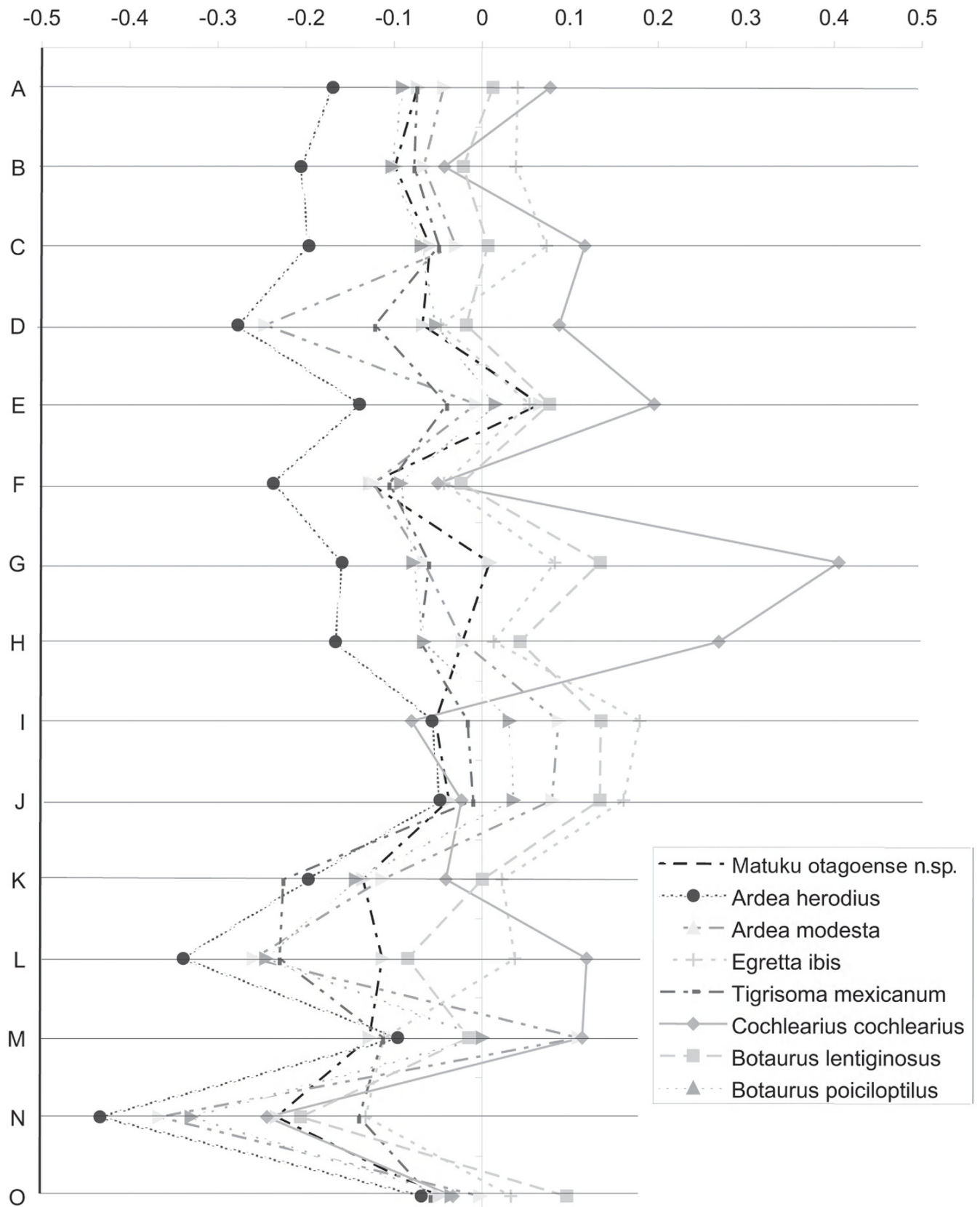


Figure 4. Ratio diagram (after Simpson, 1941) using measurements of *Nycticorax caledonicus* as the origin (i.e. log of measurement of *Nycticorax caledonicus* is equivalent to 0). This diagram indicates that the relative proportions of the fossil heron bones vary in a similar way to those of other herons and so it is likely that the fossil bones come from a single species. Abbreviations: (A), tarsometatarsus, maximum distal width; (B), tarsometatarsus, maximum distal depth; (C), tarsometatarsus, width of trochlea metatarsi III; (D), Tarsometatarsus, estimated total length; (E), coracoid, maximum cranial width (from hum. facet to brachial tub.); (F), coracoid, maximum shaft width (below procoracoid); (G), coracoid, length of humeral facet; (H), coracoid, depth of humeral facet; (I), quadrate, mean of 2 individuals, depth from capit. squam. to cond. lateralis; (J), quadrate, mean of 2 individuals, depth from capit. squam. to cond. medialis; (K), axis, width of facies articularis cranialis; (L), axis, inter-condyle distance; (M), axis, width of single zygapophyses caudalis; (N), axis, depth single zygapophyses caudalis; (O), axis, greatest width (across facies artic. caudalis).

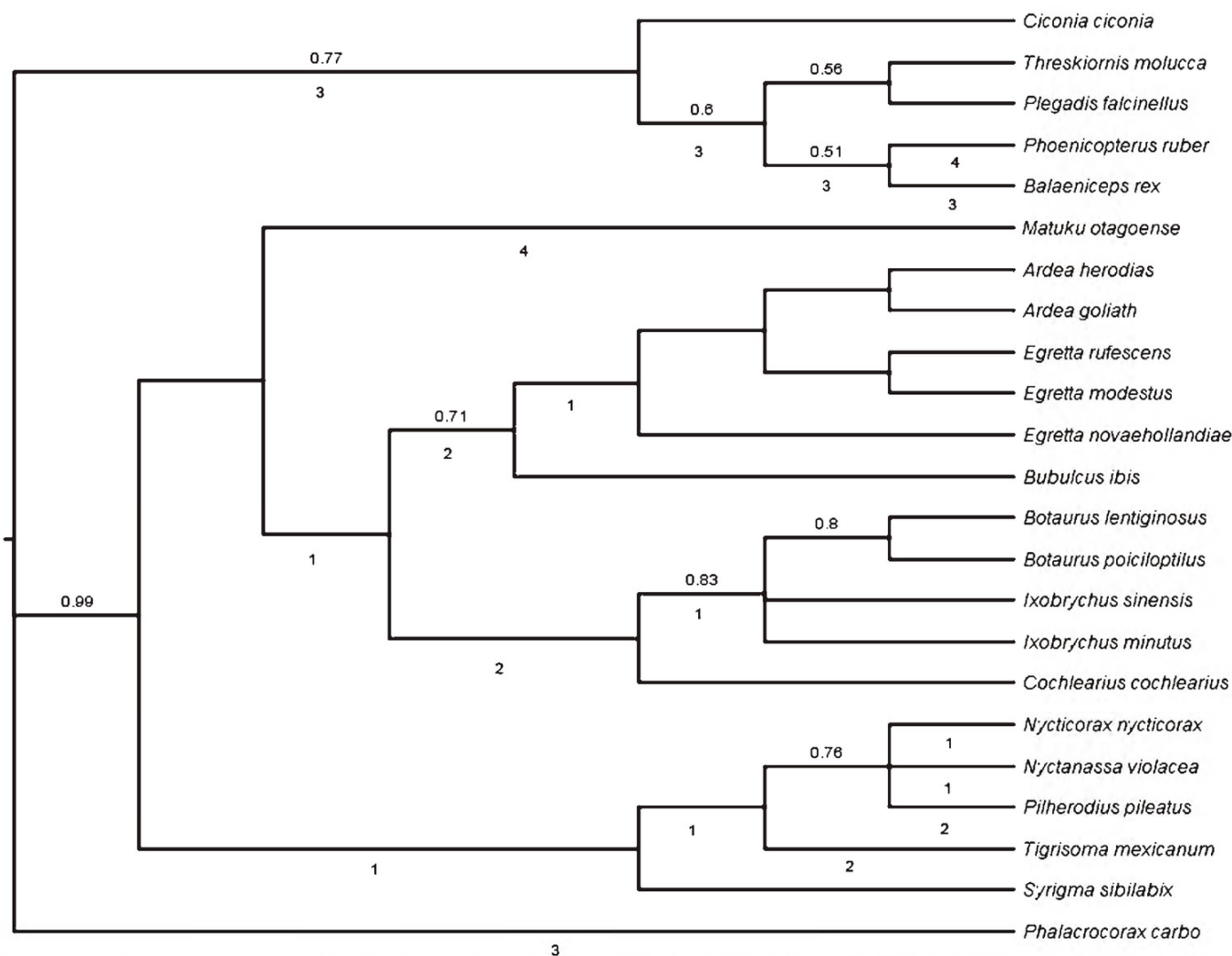


Figure 5. A strict consensus tree of the 12 shortest trees (length = 153, CI = 0.4444, HI = 0.5556, RI = 0.7222) in which the topology was constrained with Ardeidae as sister group to an outgroup comprised of the non ardeid Ciconiiformes and the pelecaniform—*Phalacrocorax carbo*. Bootstrap support values (> 0.50) are shown above and the number of significant (> 0.50) unambiguous apomorphies are shown below the corresponding node.

Are the elements from the same species?

Comparison of available measurements from *Matuku* (Fig. 4) with those of living species of heron using Simpson Ratio diagrams (Simpson, 1941), suggests that these elements are probably from the same species as they co-vary from the standard taxon in a fashion consistent to that seen in other taxa.

Phylogenetic analyses

We defined 50 multistate characters and coded these for 18 ingroup and six outgroup taxa. The non-ardeid Ciconiiformes, the pelecaniform and the phoenicopteriform were defined as the outgroup. The remaining 18 terminal taxa, including the four extant Recent New Zealand herons and the fossil taxon, were unconstrained.

We tried including *Scopus* in the data set and found that it tended to have a sister relationship to herons in preliminary analyses, but in the present dataset its inclusion introduced conflict in the data causing a polytomy of it and the main heron clades. For this reason we present the analyses with it excluded. Similarly, preliminary analyses with all characters unordered resulted in 562 shortest trees, length 146. But when 19 characters (characters 1, 2, 4, 6–14, 18, 19, 23, 25, 35, 36, 47) that clearly formed morphoclines, were treated as ordered, the analysis retrieved just 12 shortest trees, length 153, for which a strict consensus tree was completely resolved.

For this our preferred tree, we show bootstrap support (1000 bootstrap replicates of the Heuristic search) and the numbers of unambiguous apomorphies supporting each node (Fig. 5).

Our strict consensus tree of the 12 shortest trees retrieved three major clades of herons with significant bootstrap support: 1 a bittern clade (bootstrap 83%), egrets and day herons (bootstrap 71%), and a clade of night herons (bootstrap 76%) (Fig. 5). Although we used few elements and, in general, only scored characters that were present in our poorly preserved fossil specimens, our analysis does not support the monophyly of the true day herons (Tribe Ardeini; Kushlan & Hancock, 2005), despite this group being only represented by *Ardea* in our analyses, but does support the monophyly of the bittern subfamily Botaurinae. Like many other authors, we find the genera *Ardea* and *Egretta* to both be polyphyletic. The boat-billed heron was found to be sister to the bittern clade, but this relationship was weak (bootstrap < 50%; 4 unambiguous apomorphies).

Matuku otagoense is strongly supported as a member of the Ardeidae (Bootstrap 99%), but there is no support for it being a member of the *Ardea-Egretta* clade (Bootstrap = 71%, 2 unambiguous apomorphies), the bittern clade (Bootstrap = 83%, 3 unambiguous apomorphies), or the night herons *Nycticorax*, *Nyctinassa* and *Pilherodius* (Bootstrap = 76%, 3 unambiguous apomorphies). However, 4 unambiguous apomorphies support *Tigrisoma* joining the

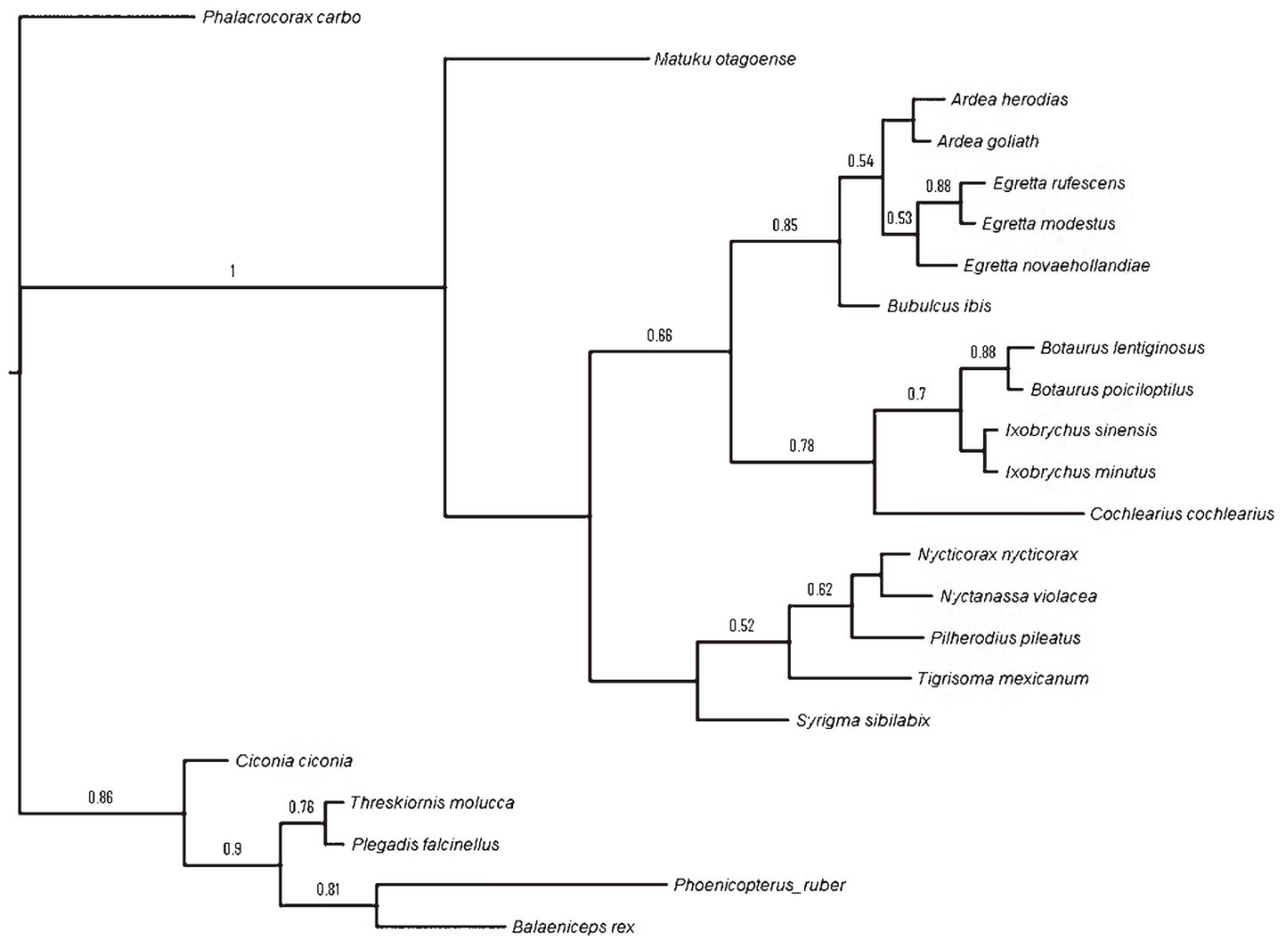


Figure 6. A Bayesian consensus tree derived from 4,001 trees sampled: Run 1 (mean = -546.302, s.d. = 0.099, Effective Sample Size = 3208.424); Run 2 (-546.223, 0.113, 2388.97). Support values are shown above the corresponding node.

night herons as a clade, and 2 unambiguous apomorphies support *Syrigma* joining this enlarged night heron clade to the exclusion of the St Bathans heron. There is no support (no unambiguous apomorphies, Bootstrap < 50%) for *Matuku otagoense* forming a clade with egrets and bitterns sister to night herons, and there is only limited support for a clade of egrets and bitterns to the exclusion of SB heron (1 unambiguous apomorphy, Bootstrap = 0.250).

A Bayesian consensus tree derived from 4,001 trees sampled after the burnin period has credibility values (percentage posterior probabilities) exceeding 0.50 as shown in Fig. 6. The probability plot in Tracer plateaued by 250,000 generations, so the burnin discard of 1,000,000 generations was more than adequate. The two runs achieved stationarity and convergence: log likelihood statistics (LnL) after Burnin = 4001 for Run 1 (mean = -546.302, s.d. = 0.099, Effective Sample Size = 3208.424); Run 2 (-546.223, 0.113, 2388.97), and after 5,000,000 generations the average standard deviation of split frequencies was 0.03750, well within the recommended cutoff value of < 0.1.

The Bayesian consensus tree (Fig. 6), retrieved the same three well supported clades as the parsimony analysis and differed in topology from the parsimony consensus tree (Fig. 5) only in the branching order of the three main clades and in which nodes all had weak Bootstrap support. This is

unlikely to be the result of missing data in *Matuku* as only four characters are missing thus we consider that this data set simply is not adequate to resolve these deeper relationships.

So in summary these analyses show that *Matuku otagoense* is a member of Ardeidae but there is no support for a sister group relationship with any of the main groups of herons.

Discussion

The finding of a heron in the St Bathans Fauna is not surprising given the lacustrine nature of the sediments, but highlights once again the significance of this, New Zealand's only tertiary terrestrial fossil assemblage (Worthy *et al.*, 2007). It is noteworthy however that these layers have revealed thousands of avian fossils, but the seven isolated bones of *Matuku otagoense* described here are the only heron remains identified to date.

This is the first fossil ardeid that we are aware of whose relationships have been determined by phylogenetic analysis. The majority of previous fossil specimens have been referred to either *Ardea* or *Nycticorax*, but most were not assigned to genera or subfamily by shared apomorphies and thus we consider their relationships to be uncertain. Our analyses reveal phylogenetic relationships (Figs 5, 6) that indicate no support for the inclusion of *Matuku otagoense* within

any extant genus or clade and that it was not closely related to any living taxon. We consider this more than adequate evidence for the erection of a new genus, *Matuku*.

The fossil record of ardeids older than the Early Pleistocene is sparse, although they have been recorded as far back as the Eocene and from several continents (North America, Europe—or Eurasia, Africa) (Table 1). The St Bathans fossil is the first ardeid identified in the Tertiary of Australasia and its basal placement may be significant in calibrating the molecular clock for the group.

Our Bayesian analysis found limited support for the novel result that the neotropical boat-bill heron *Cochlearius* may be sister to the Botaurinae. *Cochlearius* has generally been placed in a monotypic family, the Cochleariidae (Peters, 1931; Wetmore, 1951) until E. Mayr & Amadon (1951) reduced it to subfamily level in the Ardeidae. Bock (1956) then went further and included it within Nycticoracinae. Payne & Risley (1976) and Payne (1979) placed it in a tribe, Cochlearini, related to but separate from night-herons, based on a combination of morphological and plumage characters. Some osteological (Cracraft, 1967; Livezey & Zusi, 2007) and genetic work (Sheldon *et al.*, 2000) has shown that it may be separate from Nycticoracinae and perhaps has a closer relationship to Tigrisominae (Sheldon, 1987; Sheldon *et al.*, 1995; McCracken & Sheldon, 1998). Until now no one has suggested as far as we are aware any relationship between boat-bill herons and the bitterns.

ACKNOWLEDGMENTS. The authors are indebted to the generous efforts of many field assistants in the St Bathans Fauna project, particularly Jenny Worthy for field and laboratory assistance. We are particularly grateful for the support of the land owners Ann and Euan Johnstone. This research was made possible by the grant to Sue Hand and Mike Archer which is part of the project DP0770660 funded by the Australian Research Council, and is also supported by the Brian Mason Technical Fund of Canterbury Museum. We thank Paul Sweet of the AMNH and James Dean of the NMNH for arranging the loan of material for this study.

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Appendix 1

List of characters used in phylogenetic analysis.

- 1 **Tarsometatarsus, distal end, plantar aspect.** Sulcus on trochlea metatarsi IV:
 - 0 Absent
 - 1 Weak
 - 2 Strong
- 2 **Tarsometatarsus, distal end, plantar aspect.** Sulcus on trochlea metatarsi III:
 - 0 Absent
 - 1 Weak
 - 2 Strong
- 3 **Tarsometatarsus, distal end, dorsal aspect.** Position of distal foramen (foramen vasculare distale) relative to the proximal end of trochlea metatarsi III:
 - 0 Equal
 - 1 More proximal, with distal margin of foramen level with proximal margin of trochlea
 - 2 More distal
- 4 **Tarsometatarsus, distal end, dorsal aspect.** Size and shape of distal foramen:
 - 0 Absent
 - 1 Small and circular
 - 2 Large and slit shaped
- 5 **Tarsometatarsus, distal end, dorsal aspect.** Distal foramen, branching canal opening into inter-trochlear incision from main dorso-plantar canal:
 - 0 Closed dorsally
 - 1 Open dorsally, thus forming a notch
- 6 **Tarsometatarsus, distal end, dorsal aspect.** Orientation of trochlea metatarsi III relative to the axis of the shaft (corpus tarsometatarsi):
 - 0 Parallel
 - 1 Slightly bent laterally
 - 2 Strongly bent laterally
- 7 **Tarsometatarsus, distal end, dorsal aspect.** Protrusion of trochlea metatarsi II from the medial margin of the shaft (corpus tarsometatarsi):
 - 0 Does not protrude
 - 1 Gradually protrudes
 - 2 Abruptly protrudes

profile of trochlea on medial side meets shaft at distinct angle
- 8 **Tarsometatarsus, distal end, dorsal aspect.** Protrusion of trochlea metatarsi IV from the lateral margin of the shaft (corpus tarsometatarsi):
 - 0 Does not protrude
 - 1 Protrudes gradually
 - 2 Protrudes abruptly
- 9 **Tarsometatarsus, distal end, plantar aspect.** Fossa metatarsal I:
 - 0 Absent
 - 1 Shallow
 - 2 Deep

- 10 **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
- Note, this is related to the depth of the fossa parahy-potarsalis medialis
- 11 **Tarsometatarsus, shaft, dorsal aspect.** Dorsal metatarsal groove (sulcus extensorius):
- 0 Absent
 - 1 shallow
 - 2 Deep
- 12 **Tarsometatarsus, shaft, plantar aspect.** Plantar metatarsal groove (sulcus flexorius):
- 0 Absent
 - 1 Shallow
 - 2 Deep
- 13 **Tarsometatarsus, shaft, plantar aspect.** Crista plantaris lateralis:
- 0 Absent
 - 1 Weakly developed
 - 2 Strongly developed
- 14 **Tarsometatarsus, proximal end, plantar aspect.** Hypotarsus, length relative to width [Character 2269 of Livezey & Zusi (2007)]:
- 0 Length greater than width
 - 1 Length slightly less than width
 - 2 Length significantly less than width
- 15 **Tarsometatarsus, proximal end, proximal aspect.** Hypotarsus entirely plantar of corpus, and depth [Character 2270 of Livezey & Zusi (2007)]:
- 0 Distinctly less than that of corpus
 - 1 Approximating corpus
 - 2 Greater than that of corpus
- 16 **Tarsometatarsus, proximal end, plantar aspect.** Hypotarsus, sulcus for shallow flexor tendons fpp2/fp2 (flexor perforans et perforatus digiti II, flexor perforatus digiti II). [This is the tendinal passage 2 of Strauch (1978: fig. 29C). *Tigrisoma* has a single sulcus plantar of tc1 but which sulcus is slightly divided by a low ridge on the medial calcaneal ridge indicating 2 tendons in this sulcus, presumably 2 and 6 Character modified from character 2279 of Livezey & Zusi (2007)]:
- 0 Absent
 - 1 Distinct sulcus separated from sulcus for more lateral fp3/fp4 (flexor perforatus digiti III et IV)
 - 2 Enclosed or near enclosed canal
- 17 **Coracoid, extremitas omalis, medial aspect.** Sulcus musculi supracoracoideus:
- 0 No foramen below clavicular facet (facies articularis clavicularis)
 - 1 Foramen immediately below dorsal margin of the clavicular facet
 - 2 Foramen immediately below ventral margin of the clavicular facet
- 18 **Coracoid, extremitas omalis, medial aspect.** Proc. acrocoracoideus, and supracoracoidal sulcus—lateromedial compression across the transverse plain:
- 0 Absent
 - 1 Weakly or not compressed thus essentially circular
 - 2 Moderately compressed
- 19 **Coracoid, extremitas omalis, dorsal aspect.** Acrocoracoid—impressio ligamenti acrocoracohumeralis:
- 0 Absent
 - 1 Shallow
 - 2 Deep
- 20 **Coracoid, extremitas omalis, dorsal aspect.** Distance from omal end of facies artic. humeralis to tip of proc. acrocoracoideus:
- 0 Equal to dorsoventral depth of clavicle facet (facies artic. clavicularis)
 - 1 Less than half of depth of clavicle facet
- 21 **Coracoid, extremitas omalis, procoracoidal process.** Ventrally, a concave groove forming a caudal extension of supracoracoidal sulcus. [Character 1285 (in part) of Livezey & Zusi (2007)]:
- 0 Absent
 - 1 Present
- 22 **Coracoid, extremitas omalis, procoracoidal process.** Extends cranomedially of the scapular cotyla forming a flattened tuberculum apicalis procoracoidei. [Character 1289 of Livezey & Zusi (2007)]:
- 0 Absent
 - 1 Present
- 23 **Coracoid, extremitas omalis, medial aspect.** Sulcus musculi supracoracoideus:
- 0 Smooth
 - 1 Slight ridge running sternally, barely dividing sulcus into dorsal and ventral segments
 - 2 Strong ridge bisecting sulcus
- 24 **Coracoid, shaft, dorsal aspect.** Foramen nervi supracoracoidei:
- 0 Absent
 - 1 Present
- 25 **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
 - 2 Elongate, extends for greater than half length of shaft
- 26 **Os quadratum, rostral aspect.** Caput squamosum:
- 0 Rounded
 - 1 Triangular, broader at top, draws to point laterally/ventrally
- 27 **Os quadratum, lateral aspect.** Tubercle at dorsal end of crista tympanica:
- 0 Absent
 - 1 Immediately ventral of caput squamosum
 - 2 Present, separated from caput squamosum
- 28 **Os quadratum, medial aspect.** Foramen pneumaticum mediale:
- 0 Situated between crista tympanica and crista medialis
 - 1 Situated rostrally of crista medialis
- 29 **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
- 30 **Os quadratum, medial aspect.** Tubercle at dorsal end of crista medialis immediately ventral of caput oticum:
- 0 Absent
 - 1 Present
- 31 **Os quadratum, ventral aspect.** Tubercle on depressio praecondylaris immediately caudad to medial condyle:
- 0 Absent
 - 1 Present
- 32 **Os quadratum, ventral aspect.** Vallecule intercondylaris:
- 0 Area simply a shallow sulcus
 - 1 Forms fossa bounded on rostral edge by raised crista
 - 2 Shallow fossa with narrow sulcus onto rostral surface
 - 3 Deep and U shaped fossa, opening with wide sulcus onto rostral surface
- 33 **Os quadratum, caudal aspect.** Prominent sulcus between condylus lateralis and condylus caudalis running up to edge of crista lateralis:
- 0 Absent
 - 1 Present
- 34 **Axis, cranial aspect.** Dens:
- 0 Wider than facies articularis atlantica
 - 1 Not so
- 35 **Axis, ventral aspect.** Ratio of width of facies artic. cranialis to distance from facies artic. cranialis to caudalmost edge of facies artic. caudalis:
- 0 Greater than or equal to 35% (i.e. centrum fat and wide)
 - 1 Less than 35% but greater than 25% (i.e. relatively long and narrow)
 - 2 Less than 25% (i.e. very long and narrow)

- 36 **Axis, ventral aspect.** Zygapophyses caudalis (postzygapophysis) shape: ratio of width to length:
 0 Circular (ratio greater than 100%)
 1 Oval (ratio greater than 70% but less than 100%)
 2 Teardrop or elongate (ratio less than 70%)
- 37 **Axis, dorsal aspect.** Zygapophyses cranialis (prezygapophysis) shape (ratio of width to length):
 0 Tending circular (ratio greater than 70%)
 1 Elongate (ratio less than 70%)
- 38 **Axis, dorsal aspect.** Proximal (or cranial edge) of arcus atlantis (neural arch):
 0 Concave
 1 Straight
- 39 **Axis, dorsal aspect.** Zygapophyses caudalis prominent laterally relative to facies at mid length:
 0 Not so
 1 Yes
- 40 **Axis, ventral (or dorsal) aspect.** Zygapophyses cranialis extend laterally of lateral profile as distinct processes:
 0 No
 1 Yes
- 41 **Axis, lateral aspect.** Processus spinosus (anapophysis), dorsal profile between zygapophyses:
 0 With distinct convex profile (markedly raised anteriorly, not flat)
 1 Lacking convex profile
- 42 **Axis, lateral aspect.** Processus spinosus (anapophysis):
 0 Starts immediately posteriad of zygapophyses cranialis
 1 Starts farther posteriad, so initially flat
- 43 **Axis, lateral aspect.** Facies artic. cranialis:
 0 Roughly at right angles to axis of bone
 1 Sloped anteroventrally
- 44 **Axis, lateral and dorsal aspects.** Dens:
 0 Greater than length of zygapophyses cranialis
 1 Less than length of zygapophyses cranialis
- 45 **Axis, lateral aspect.** Corpus ventralis, foramen transversarium:
 0 Complete, enclosed laterally
 1 Incomplete, open laterally, forming sulci
- 46 **Axis, lateral aspect.** Corpus ventralis, pneumatic fossa:
 0 Absent
 1 Present laterally, secondary sulci are present posteriorly
- 47 **Rostrum mandibulae, dorsal aspect.** Pars symphysialis, length of zone of fusion:
 0 Considerably greater than transverse width
 1 Approximately equal to transverse width
 2 Transverse width considerably greater
- 48 **Rostrum mandibulae, dorsal aspect.** Shape:
 0 Narrow and thin
 1 Broad and bulbous
 2 Wide and deep, extremely modified
- 49 **Rostrum mandibulae, lateral aspect.** Os dentale:
 0 Foramina densely cover whole lateral surface
 1 Prominent foramina mainly along cutting edge
 2 Foramina indistinct
- 50 **Rostrum mandibulae, dorsal aspect.** Pars symphysialis, relative width of symphysis:
 0 Narrow (ratio of width to length < 5)
 1 Broad (ratio of width to length > 5)

Appendix 2

Character matrix of 50 morphological characters used for phylogenetic analyses. Symbols used in matrix: * = (01); + = (12).

	1	1111111112	222222223	3333333334	4444444445
	1234567890	1234567890	1234567890	1234567890	1234567890
<i>Matuku otagoense</i> n.sp.	220100101?	102???0101	1000001001	13011111110	0100000011
<i>Ardea herodias</i>	1102111112	1020110110	1000010000	12012211110	1111010010
<i>Ardea goliath</i>	1101111212	1020110110	1000010000	12012211110	1111010010
<i>Egretta rufescens</i>	1121111211	1020110210	1000010000	02012211110	1111110010
<i>Ardea modestus</i>	1121111211	10201102*0	1000010000	02012211110	1111010010
<i>Egretta novaehollandiae</i>	110111121*	1020110110	1000010000	02011211110	1011010010
<i>Ardea ibis</i>	1101111012	1020110110	1000010000	02011111110	1111010010
<i>Nycticorax nycticorax</i>	2211102012	*01011021*	0000001010	12010+1010	011001001*
<i>Nyctanassa violacea</i>	2211102012	0010110111	0000001010	1201010010	0111010011
<i>Ptilerodius pileatus</i>	2201102022	0011110211	0000001010	1201021010	0111110011
<i>Tigrisoma mexicanum</i>	2221102112	1010210210	1100011010	1201121010	0011010011
<i>Botaurus lentiginosus</i>	2221020011	1021220110	0100010000	12012211110	1111110011
<i>Botaurus poiciloptilus</i>	2221020011	1021220120	0100010000	12012211110	1111110011
<i>Ixobrychus sinensis</i>	2221121011	1021220120	0100010000	12012211110	1111010011
<i>Ixobrychus minutus</i>	2221121011	1021220120	0100010000	12012211110	1111010011
<i>Cochlearius cochlearius</i>	2101120011	2021210020	0100001021	02010111110	1111010111
<i>Syrigma sibilabix</i>	2221022010	1010110211	1000000000	0201021010	0111010011
<i>Scopus umbretta</i>	2211101011	1020201010	1000000000	1201020110	1111102111
<i>Ciconia ciconia</i>	2212001101	2110100220	*110101121	0000021001	1111100011
<i>Threskiornis molucca</i>	1111002111	2120102220	1111101121	0000021001	1111100011
<i>Plegadis falcinellus</i>	1111002111	2120102120	1111101121	0000021001	1111100011
<i>Phoenicopterus ruber</i>	1122102201	0120100020	1121101121	0010001000	1111102201
<i>Phalacrocorax carbo</i>	2212010110	2020100200	0000001121	0110001001	1111100010
<i>Balaeniceps rex</i>	1111010110	1020100120	1111101121	10000200*1	1111102111



Scofield, R Paul, Worthy, T. H., and Tennyson, Alan J D. 2010. "A heron (Aves: Ardeidae) from the Early Miocene St Bathans fauna of southern New Zealand. In Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution, ed. W.E. Boles and T.H. Worthy." *Records of the Australian Museum* 62(1), 89–104.
<https://doi.org/10.3853/j.0067-1975.62.2010.1542>.

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