



Article A New Species of Large Duck (Aves: Anatidae) from the Miocene of New Zealand ⁺

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Abstract: We describe a new species of extinct duck, *Miotadorna catrionae* sp. nov. (Anatidae, Tadornini, Tadorninae), based on a right humerus from the Miocene lacustrine deposits of St Bathans, Otago, New Zealand. Principal component analysis reveals that the new taxon is distinguished by its large size and relative proportions. This is the eighth and largest species of duck described from the St Bathans fossil assemblage and further underscores the global importance of this site for understanding anatid evolution.

Keywords: Tadornini; Miotadorna catrionae sp. nov.; fossil; shelduck; lacustrine; Bannockburn Formation

1. Introduction

In the St (Saint) Bathans area of Central Otago, New Zealand, outcrops of the Bannockburn Formation, a late early–earliest middle Miocene lacustrine sequence, include a rich fossil biota from the ancient Lake Manuherikia [1–3]. The deposits have yielded the most diverse terrestrial vertebrate assemblage described from pre-Pleistocene Zealandia: numerous fish [4] and water birds, as well as rarer land birds, bats, lizards, frogs, crocodilians, a rhynchocephalian, a turtle and other mammal remains of uncertain affinity [2].

St Bathans is one of the richest localities for Miocene anatids worldwide, with seven species described to date [2]. Two geese may also have been present but remains thus far have been too fragmentary to allow their formal description [5]. Here, we describe a large anatid humerus and demonstrate that it represents a new species of large duck.

2. Material and Methods

Until now, most of the large anatid fossils from the St Bathans area were referred to the extinct shelduck *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara and Douglas, 2007 [6], while a few bones were referred to undescribed forms of geese [5,6]. We tested the hypothesis that all the large anatid humeri from this fossil assemblage represent one species. This was conducted by assessing morphological variation, using both morphometrics and anatomy.

We measured all large anatid humeri (those about the size of *M. sanctibathansi*) from the St Bathans assemblage housed at the Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand; NMNZ) and one specimen at the Geology Museum, Department of Geology, University of Otago (Dunedin, New Zealand; OU) that preserve at least one of the following: total length, proximal width, proximal depth, shaft width, distal width



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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). and depth of dorsal condyle (Appendix A). We then compared these data to humeral measurements (taken at NMNZ) of the extant paradise shelduck (*Tadorna variegata*) to assess whether the St Bathans humeri fall into more than one size class.

All fossils were measured with callipers to the nearest 0.1 mm. We defined total length as the maximum length parallel to the main axis of the shaft; proximal, distal and shaft width as the maximum transverse widths perpendicular to the main axis of the shaft, with the proximal width measured to the dorsal tubercle (excluding the deltopectoral crest where the latter projected further dorsally) and the shaft width measured at the distal end of the deltopectoral crest; proximal depth as the maximum cranio-caudal diameter of the humeral head when viewed proximally; and distal depth as the maximum cranio-caudal diameter of the dorsal condyle when viewed distally.

To test for different humeral proportions between taxa, we performed a correlationbased principal component analysis in Past 4.08 [7] (Figure 1C,D). Only humeri with all 6 measurements were included (see Appendix A). Additionally, we used frequency histograms of proximal depth and distal width to visualise sexual dimorphism (bimodal distribution) or the lack thereof (unimodal distribution) for both the fossils and *Tadorna variegata* (Figure 2).

Classification of the St Bathans anatids follows Worthy et al. [2]. Osteological nomenclature is derived from Baumel and Witmer [8] and Livezey and Zusi [9].



Figure 1. Cont.



Figure 1. Right holotype humeri of *Miotadorna catrionae* sp. nov. (NMNZ S.47273, left) and *Miotadorna sanctibathansi* (NMNZ S.42794, right) in different views: (**A**) caudal, (**B**) cranial, showing features referred to in the text. Measurements (in mm) for individual bone sections in (**B**) are as follows: i, 33.0; ii, 31.8; iii, 23.0; iv, 21.4; v, 33.3; total = 142.5. (**C**) PCA plot showing the first two principal components. The amount of variance explained per component is shown in parentheses. (**D**) Loadings for the first two principal components.



Figure 2. Cont.



Figure 2. Frequency of humeral proximal depth (**A**) and distal width (**B**) in *Tadorna variegata* and large St Bathans anatids, indicating sexual dimorphism (bimodal distributions) in *T. variegata* and probably in the St Bathans anatids.

3. Results

Our PCA revealed a pattern in which the vast majority of anatomical variation was captured by the first two principal components (Figure 1C,D). PC1 explains most of the variance (82.9%) and correlates with an even increase in all measurements. PC2 explains only 5.6% of the variance and describes a relative shape change where total length, proximal depth and proximal width increased while shaft width, distal width and distal depth decreased (Figure 1D). PC1 clearly separates male from female *T. variegata* and furthermore sets apart one of the St Bathans humeri (NMNZ S.47273) from all other St Bathans anatids. Below, we describe and compare this specimen in more detail and argue that it is sufficiently distinct to warrant the recognition of a new species, despite probable sexual dimorphism in *Miotadorna* (see Comments section).

SYSTEMATICS

Class Aves Linnaeus, 1758 Order Anseriformes Wagler, 1831 Family Anatidae Leach, 1819 Subfamily Tadorninae Reichenbach, 1849: Shelducks Tribe Tadornini Reichenbach, 1849 Genus Miotadorna Worthy, Tennyson, Jones, McNamara and Douglas, 2007 Miotadorna catrionae sp. nov. Tennyson, Greer, Lubbe, Marx, Richards, Giovanardi and Rawlence (Figure 1)

ZooBank reg. nr.: urn:lsid:zoobank.org:act:50C7E51F-9E4D-42E7-8D6D-950DB070BBC4 Holotype: NMNZ S.47273, right humerus.

Type locality: Mata Creek Site 9, St Bathans, Central Otago, 44° 52.8288' S, 169° 50.4162' E. NZ Fossil Record File Number H41/f0122. Bannockburn Formation, late early–earliest middle Miocene (Burdigalian–Langhian global stage, Altonian local stage), 18.7–15.9 Ma [1–4,10].

Etymology: After N.J.R.'s mother Catriona Drummond (1954–2020) who inspired his love of natural history.

Suggested English vernacular name: Catriona's shelduck.

Diagnosis: Shelduck characterized by a robust humerus (142.5 mm long) with a wide proximal and a narrow distal end. Differs from all other anatid humeri from St Bathans in its larger size, which is comparable to that of a small goose, such as the Egyptian goose (*Alopochen aegyptiaca*) (e.g., NMNZ OR.29470: humerus length 142.2 mm). It specifically differs from *Miotadorna sanctibathansi*—the largest previously described anatid from St Bathans—in having a longer, more tapered humerus with a wider proximal end but a similar-sized distal end (Figure 2B, Appendix A). Resembles *M. sanctibathansi* in having an elongate shaft, a prominent capital shaft ridge directed towards the ventral side of a markedly elevated dorsal tubercle, a relatively narrow dorsal pneumotricipital fossa that does not undercut the humeral head, an elongate deltoid crest that extends well distal of the bicipital crest, and in having the attachment of the superficial pronator muscle located cranial of centre on the ventral face.

Differs from anserines, which have also been reported at St Bathans [5], in lacking a prominent capital shaft ridge directed towards the humeral head and in having a capital shaft groove that undercuts the humeral head [11]; from Johnstones' duck Dunstanetta johnstoneorum Worthy, Tennyson, Jones, McNamara and Douglas, 2007 [6] in having a deeper brachial fossa that does not extend as close to the ventral margin of the bone and a shallower pit for the attachment of the superficial pronator muscle; from Enright's duck Matanas enrighti Worthy, Tennyson, Jones, McNamara and Douglas, 2007 [6] in having a narrower dorsal extension of the pneumotricipital fossa, a shaft that tapers distally, a larger and more excavated brachial fossa, a more cranially located pit for the attachment of the superficial pronator muscle on the ventral face, and a dorsal condyle that does not ventrally overlap the ventral condyle in cranial view [6]; and from *Manuherikia* spp. in having a narrower dorsal pneumotricipital fossa that does not undercut the humeral head, a broader medial ridge bounding the brachial fossa, the pit for the attachment of the superficial pronator muscle is more proximal relative to the ventral supracondylar tubercle, a distinct dorsal epicondyle and a dorsal condyle that is shorter distally than both the flexor process and the ventral condyle [2,6]. Use of 'medial ridge' (=shaft between brachial depression and ventral margin) follows Worthy et al. [6].

Description: The humerus is largely complete but distorted post-mortem (as indicated by the lack of any sign of healed fractures), with the proximal end twisted caudally relative to the shaft and the middle of the shaft displaced dorso-ventrally by about 10 mm. Its total length was calculated by adding together measurements of each fractured section (see Figure 1B). Note that some of this bone's distortion is in the cranio-caudal plane and, therefore, is not obvious in the figure. The head is prominent and excavated by a welldeveloped pneumotricipital fossa. The shaft is long and bears a prominent captial shaft ridge. The distal end is robust but notably narrower than the proximal end. The dorsal and ventral condyles are prominent, with the former being separated from the flexor process by a deep caudal depression.

Comments: Given that *M. catrionae* sp. nov. and *M. sanctibathansi* are phenotypically very similar, their differing sizes could plausibly reflect sexual dimorphism instead of two species. As *T. variegata* is characterized by having larger males [12], sexual dimorphism could also explain the size range observed in *Miotadorna*, as previously suggested [6]. Frequency histograms of proximal depth and distal width suggest bimodal (i.e., dimorphic) patterns in both the extant and extinct tadornines, however NMNZ S.47273 does not consistently follow this pattern (Figure 2). NMNZ S.47273 matches the larger, putatively male fossil subset in its distal width, but it is deeper than all fossils proximally. This change in relative position suggests that size differences related to sexual dimorphism alone are insufficient to explain its distinct anatomy. We consider that all the other fossil humeri we inspected (including three other humeri from Mata Creek Site 9) most likely belong to *M. sanctibathansi*.

4. Discussion

Miotadorna catrionae sp. nov. is the eighth anatid named from St Bathans, underscoring the global importance of this area for understanding the evolution of the family. Anatomically, *M. catrionae* sp. nov. closely resembles the previously described St Bathans shelduck *M. sanctibathansi*, to the extent that all the characters distinguishing the latter from other tadornines are also shared (where preserved) by *M. catrionae* sp. nov.: capital shaft ridge very well developed, separated from dorsal tubercle by a deep, distally-flaring groove; ventral pneumotricipital fossa relatively smaller, shallower, and more occluded internally by pneumatic bone; brachial fossa deepest in ventro-distal portion; shaft between brachial fossa and ventral margin rounded [13]. Only its larger size and proportional differences distinguish NMNZ S.47273 from the humeri of *M. sanctibathansi*, leading us to include both in the same genus.

The functional reasons for the distinctive shape of the humerus of *Miotadorna catrionae* sp. nov. remain to be investigated but a relatively narrow distal humeral end is found in a diverse group of Anatidae, including swans and *Manuherikia* ducks [6,11].

Our results show that *Miotadorna catrionae* sp. nov. co-occurs with a smaller form of tadornine at Mata Creek Site 9, that is probably *M. sanctibathansi* or possibly the female of the new species, though none of the smaller Mata Creek Site 9 humeri possess definitive features characteristic of the new species. Other, much smaller, anatids also occur in this layer: the minute Manuherikia duck *Manuherikia minuta* Worthy, Tennyson, Jones, McNamara and Douglas, 2007 [6] and *Manuherikia primadividua* Worthy, Scofield, Salisbury, Hand, De Pietri, Blokland and Archer [2]. A previous study suggested that two geese, approximately the size of *M. catrionae* sp. nov., also occurred within the wider St Bathans area [5]. No humeri have yet been identified that may belong to these species, thus we remain unable to resolve their status.

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Appendix A

Table A1. Measurements (in mm) of humeri of modern *Tadorna variegata* and large fossil St Bathans anatids. The acronym NMNZ is omitted from OR. and S. registration numbers for brevity. See Worthy et al. [2] and Schwarzhans et al. [4] for fossil location details. Abbreviations: ad: adult; F: female; M: male: juv: juvenile; Hum TL: Humerus total length; pHum wid: humerus proximal width; pHum dep: depth of humeral head; shaft wid: width of shaft; dHum wid: humerus distal width; dHum dep: depth of dorsal condyle.

Taxon	Age/Sex	Reg. No.	Location	Hum TL	pHum Wid	pHum Dep	Shaft Wid	dHum Wid	dHum Dep
St Bathans anatid **	-	S.42234	Croc L1	125.7	24.7	8.2	10.8	19.9	10.9
St Bathans anatid **	-	S.42272	Croc L1	114	-	8.4	9.5	-	-
St Bathans anatid **	-	S.42273	Croc L1	119.4	-	7.2	9.9	16.5	-
St Bathans anatid **	-	S.42274	Croc L1	-	23.8	8.3	-	-	-
St Bathans anatid **	-	S.42275	Croc L1	-	-	-	-	18.1	10.2
St Bathans anatid **	-	S.42313	HH1a	-	-	-	-	15.9	9.1
St Bathans anatid **	-	S.42497	Jim's Mata	-	-	-	-	17.1	10.5
St Bathans anatid **	-	S.42558	HH1a	-	-	-	-	16.4	9.1
St Bathans anatid *	-	S.42794	HH1a	122.8	25.3	8.3	10.1	17.3	10.3
St Bathans anatid **	-	S.42796	HH1a	-	-	-	-	18.1	10.8
St Bathans anatid **	-	S.42810	Croc L1	-	-	-	-	18.7	10.6
St Bathans anatid **	-	S.42931	Croc L3	-	-	-	-	17.9	10.9
St Bathans anatid **	-	S.42932	Croc L3	-	-	-	-	16.6	-
St Bathans anatid **	-	S.43069	HH1a	-	-	-	-	-	-
St Bathans anatid **	-	S.43131	HH1a	-	-	9.0	-	-	-
St Bathans anatid **	-	S.43974	HH1a	-	-	-	-	15.8	8.6
St Bathans anatid **	-	S.44162	HH1a	122.4	24.8	9.1	9.9	18.4	9.8
St Bathans anatid **	-	S.44221	HH1a	-	25.7	8.6	9.9	-	-
St Bathans anatid **	-	S.44352	Below HH1d	-	24.3	9.3	-	-	-
St Bathans anatid ***	-	S.47273	Mata 9	142.5	28.8	10.2	11.1	18.4	11.3
St Bathans anatid	-	S.49406	Mata 9	-	-	-	-	17.7	-
St Bathans anatid	-	S.49415	Mata 9	-	25.0	8.9	9.5	-	-
St Bathans anatid		S.49448	Croc L1	-	-	7.6	-	-	-
St Bathans anatid	-	S.50045	HH1a	-	-	-	-	15.6	8.6
St Bathans anatid	-	S.50082	HH1a	-	-	-	-	17.0	9.7
St Bathans anatid	-	S.50106	HH1a	-	-	-	-	17.5	10.1
St Bathans anatid	-	S.50117	HH1a	-	-	-	-	16.4	9.4
St Bathans anatid	-	S.50122	HH1a	-	-	7.6	-	17.7	-
St Bathans anatid	-	S.50189	Trench (HH1b)	-	-	8.2	-	-	-
St Bathans anatid	-	S.50957	Trench (HH1b)	-	-	-	-	15.6	-
St Bathans anatid	-	S.50959	Trench (HH1b)	-	-	-	-	16.0	9.6
St Bathans anatid	-	S.51151	Trench (HH1b)	-	-	-	-	16.2	9.1
St Bathans anatid	-	S.51220	Trench (HH1b)	-	-	-	-	18.0	-
St Bathans anatid	-	S.51284	Trench (HH1b)	-	-	-	-	15.1	8.4
St Bathans anatid	-	S.51411	HH1a	-	-	-	-	18.2	10.5
St Bathans anatid	-	S.51592	HH1a	-	-	8.0	-	-	-
St Bathans anatid	-	S.51728	Trench (HH1b)	-	-	-	-	18.9	11.0
St Bathans anatid	-	S.52562	HH1a	-	-	-	-	16.1	9.4
St Bathans anatid	-	S.52934	Trench (HH1b)	-	-	-	-	18.0	10.0
St Bathans anatid	-	S.53148	Trench (HH1b)	-	24.7	8.0	-	-	-
St Bathans anatid	-	S.53038	Trench (HH1b)	-	-	9.0	11.0	-	-
St Bathans anatid	-	S.53569	Mata 9	121.4	27.2	8.4	10.0	17.8	9.7

Taxon	Age/Sex	Reg. No.	Location	Hum TL	pHum Wid	pHum Dep	Shaft Wid	dHum Wid	dHum Dep
St Bathans anatid	-	OU.21957	Vinegar Hill	-	26.3	8.6	-	18.6	10.1
Tadorna variegata	ad F	OR.16471	Gisborne	120.7	23.3	8.1	9.9	17.3	9.1
Tadorna variegata	ad M	OR.16472	Gisborne	130.8	26.5	10.3	11.2	19.1	10.4
Tadorna variegata	ad M	OR.16473	Gisborne	128.7	25.3	9.5	10.5	18.7	10.2
Tadorna variegata	ad F	OR.16501	Gisborne	119.4	24.1	8.0	9.8	17.3	10.0
Tadorna variegata	ad F	OR.16590	Gisborne	120.0	24.1	8.8	10.0	17.7	9.8
Tadorna variegata	ad F	OR.24559	Wellington	118.5	24.0	8.8	9.4	16.8	9.8
Tadorna variegata	ad M	OR.25139	Wellington	130.2	25.8	9.5	10.5	19.5	10.7
Tadorna variegata	ad M	OR.25669	Wairarapa	130.1	25.9	9.2	11.5	19.0	10.6
Tadorna variegata	ad M	OR.26562	Bay of Plenty	132.0	26.7	9.5	11.0	19.4	10.8
Tadorna variegata	ad F	OR.26563	Bay of Plenty	122.2	24.1	8.2	10.1	17.3	9.3
Tadorna variegata	ad F	OR.29041	Wellington	119.3	23.8	8.3	9.2	17.2	9.9
Tadorna variegata	ad F	OR.29042	Wellington	122.8	23.5	8.2	10.0	17.1	9.6
Tadorna variegata	ad M	OR.29052	Canterbury	131.7	25.9	9.2	10.5	18.8	10.2
Tadorna variegata	ad F	OR.29053	Wellington	119.4	24.4	8.4	10.3	17.4	9.7
Tadorna variegata	ad F	OR.29054	Wellington	118.8	23.4	7.7	9.4	17.2	-
Tadorna variegata	ad F	OR.29061	Wellington	117.2	22.3	8.7	8.9	16.8	9.3
Tadorna variegata	imm F	OR.29133	Canterbury	117.5	23.5	8.2	9.9	17.0	9.5
Tadorna variegata	F	OR.30054	Otago	117.2	24.1	8.3	10.4	18.0	10.2
Tadorna variegata	F	OR.30205	Wellington	119.2	23.5	8.9	10.1	17.0	9.5
Tadorna variegata	juv F	OR.30312	Northland	120.4	23.6	7.9	9.7	17.1	9.4
Tadorna variegata	juv M	OR.30349	Northland	130.2	25.3	8.8	10.0	18.3	10.4
Tadorna variegata	juv F	OR.30350	Northland	118.2	22.7	7.7	9.0	16.5	8.9
Tadorna variegata	ad M	OR.30365	Northland	132.2	26.2	9.6	10.8	18.8	10.2
Tadorna variegata	juv F	OR.30366	Northland	116.0	22.2	7.7	8.8	15.8	9.2
Tadorna variegata	juv F	OR.30367	Northland	115.6	22.0	7.7	8.9	16.1	9.0
Tadorna variegata	juv M	OR.30368	Northland	131.7	24.7	9.1	10.0	18.7	9.9
Tadorna variegata	ad F	OR.30376	Northland	117.6	22.6	8.1	9.0	16.5	9.0
Tadorna variegata	ad F	OR.30377	Northland	116.1	23.1	8.1	9.4	17.1	9.8
Tadorna variegata	juv M	OR.30378	Northland	131.0	25.4	9.3	10.5	18.6	10.3
Tadorna variegata	juv M	OR.30379	Northland	128.8	26.0	8.6	10.6	18.8	10.2
Tadorna variegata	juv M	OR.30380	Northland	129.6	26.4	9.4	10.6	19.2	10.4
Tadorna variegata	ad M	OR.30427	Northland	128.9	24.7	8.8	9.8	18.3	10.5
Tadorna variegata	juv M	OR.30428	Northland	130.4	25.5	9.0	10.3	18.3	10.5
Tadorna variegata	ad M	OR.30429	Northland	130.5	25.4	9.7	10.8	18.9	10.4
Tadorna variegata	juv F	OR.30436	Northland	118.0	23.0	7.4	10.0	17.0	9.6
Tadorna variegata	ad M	OR.30437	Northland	128.9	25.1	9.5	10.3	18.8	10.3
Tadorna variegata	ad F	OR.30438	Northland	121.6	23.8	8.4	9.4	17.4	9.7
Tadorna variegata	ad M	OR.30444	Northland	134.5	25.6	9.1	10.5	19.0	10.3
Tadorna variegata	juv M	OR.30445	Northland	132.8	25.5	8.8	10.5	18.8	10.8
Tadorna variegata	juv F	OR.30448	Northland	122.8	24.1	8.4	9.7	17.3	9.6
Tadorna variegata	ad F	OR.30449	Northland	120.9	24.4	8.9	10.0	17.4	9.7
Tadorna variegata	juv M	OR.30450	Northland	128.4	25.7	9.0	10.0	18.6	10.2
Tadorna variegata	juv M	OR.30451	Northland	130.4	26.3	8.9	10.6	19.2	10.0
Tadorna variegata	ad M	OR.30456	Northland	127.3	25.9	9.5	10.7	19.0	10.6
Tadorna variegata	ad M	OR.30457	Northland	131.6	25.5	9.2	10.5	18.7	10.6
Tadorna variegata	ad F	OR.30458	Northland	117.9	24.0	8.3	9.6	17.4	9.8
Tadorna variegata	juv F	OR.30460	Northland	117.1	22.7	8.2	8.9	16.9	9.7
Tadorna variegata	juv M	OR.30461	Northland	127.2	25.0	8.5	9.7	18.2	10.5
Tadorna variegata	juv F	OR.30462	Northland	120.2	23.8	8.5	9.9	17.4	9.7
Tadorna variegata	ad M	OR.30463	Northland	133.8	25.4	9.3	10.5	19.1	10.5

Taxon	Age/Sex	Reg. No.	Location	Hum TL	pHum Wid	pHum Dep	Shaft Wid	dHum Wid	dHum Dep
Tadorna variegata	juv F	OR.30464	Northland	119.9	23.4	8.0	10.0	17.7	9.6
Tadorna variegata	juv F	OR.30465	Northland	117.6	23.7	7.8	9.8	16.9	9.6
Tadorna variegata	ad F	OR.30466	Northland	118.3	23.7	8.5	9.6	17.5	10.1
Tadorna variegata	juv F	OR.30467	Northland	118.9	23.7	8.7	9.7	17.1	9.5
Tadorna variegata	juv F	OR.30468	Northland	115.3	23.4	8.5	9.3	17.1	9.6
Tadorna variegata	juv F	OR.30521	Northland	118.9	23.5	8.2	8.9	16.9	9.7
Tadorna variegata	ad M	OR.30709	Wellington	129.2	25.2	9.1	10.4	18.4	10.5
Tadorna variegata	ad M	OR.30742	Wairarapa	129.3	25.1	9.1	10.3	18.4	10.2
Tadorna variegata	ad M	OR.30746	Wairarapa	130.3	25.5	9.6	10.2	18.5	10.0

Table A1. Cont.

* Holotype of *Miotadorna sanctibathansi*. ** Specimens referred to *Miotadorna sanctibathansi* by Worthy and Lee [13]. *** Holotype of *Miotadorna catrionae* sp. nov.

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