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A swan-sized fossil anatid (Aves: Anatidae) from the early Miocene St Bathans Fauna of New Zealand

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Abstract

A large fossil anserine-like anatid (Aves, Anatidae, *Notochen bannockburnensis* gen. et sp. nov.) is described based on a distal humerus from the lower Bannockburn Formation, early Miocene (19–16 Ma), St Bathans Fauna from New Zealand. Its morphology and size suggest that this taxon represents an early swan rather than a goose. Extant anserines are split into Northern and Southern Hemisphere clades. The St Bathans Fauna is known to have the oldest anserines in the Southern Hemisphere, unnamed cereopsines perhaps ancestral to species of *Cnemiornis* (New Zealand geese). The elongate and flat morphology of the tuberculum supracondylare ventrale of the new species, however, preclude affinities with cereopsines. It is a rare taxon and the eighth anatid represented in the fauna and is the largest known anseriform from the Oligo-Miocene of Australasia. We also reassess other large anatid specimens from the St Bathans Fauna and identify *Miotadorna catrionae* Tennyson, Greer, Lubbe, Marx, Richards, Giovanardi & Rawlence, 2022 as a junior synonym of *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara & Douglas, 2007.

Key words: early Miocene; fossil waterfowl; Anseriformes; Manuherikia Group; Central Otago

Introduction

The St Bathans Fauna derives from a series of early Miocene sites near St Bathans, Otago, New Zealand (Worthy *et al.* 2007). It provides a comprehensive window into the evolution of the New Zealand non-marine vertebrate fauna between the late Cretaceous and the late Pleistocene (Worthy *et al.* 2007, 2017; King *et al.* 2009; Thomsen 2021). New Zealand is renowned for its late Pleistocene–Holocene terrestrial vertebrate fauna being dominated by birds (Worthy & Holdaway 2002; Gibbs 2006). It included 217 indigenous breeding species, of which 145 (67%) were endemic in 27 (30.5%) endemic genera; 58 species (25%) are now extinct (Worthy *et al.* 2017). From where and when this unique fauna was assembled was poorly understood until recently, in part due to the absence of a pre-Pleistocene fossil record. Most commentary on this issue until the 1990s was necessarily largely subjective and based on morphologically derived relationships and the degree of differentiation of taxa, while assuming varying influences of vicariance and dispersal as assembly factors (e.g., Buller 1869; Hutton 1873; Fleming 1979; Millener 1990; Fordyce 1991). The widespread more recent use of molecular data has confirmed many assumptions but has also thrown up surprising new insights into some relationships and divergence timing (e.g., Goldberg *et al.* 2008; Boast *et al.* 2019; Rawlence *et al.* 2019, and references therein). The discovery of fossil bones in lower Miocene lacustrine deposits in Central Otago in 1978 (Douglas *et al.* 1981; Fordyce 1991) revealed the potential for the fossil

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record to provide insight into these questions, but the diversity of this fauna was not appreciated until the St Bathans Fauna was first reported and named in 2007 (Worthy *et al.* 2007). Following continuous investigations since 2001, the St Bathans Fauna is now recognised as one of the more diverse early Miocene faunas in the world (Worthy *et al.* 2017, 2022).

The sites producing the St Bathans Fauna occur in exposures of the Bannockburn Formation within a few kilometres of St Bathans in Central Otago, South Island; see Schwarzhans *et al.* (2012) and Worthy *et al.* (2022) for locality maps. The lacustrine Bannockburn Formation, deposited in the large palaeolake Manuherikia (~5600 km^2), overlies the fluvial and swamp-derived sediments of the Dunstan Formation, together comprising the Manuherikia Group (Douglas 1986; Mildenhall 1989). Palynological evidence suggests that the Bannockburn Formation and hence the St Bathans Fauna are late lower–middle Miocene (Burdigalian–Langhian global stage, Altonian local stage, 19–16 Ma) in age (Mildenhall 1989; Mildenhall & Pocknall 1989; Pole & Douglas 1998; Reichgelt *et al.* 2015).

The St Bathans Fauna includes a diverse suite of terrestrial taxa, including leiopelmatid frogs, skinks, geckos, sphenodontids, turtles, crocodilians, mammals (bats and non-volant forms), and more than 40 taxa of birds, as reviewed in Worthy *et al.* (2017, 2022). Waterfowl are the most important avifaunal component in the St Bathans Fauna in terms of both absolute numbers of fossils—several thousand—and taxonomic diversity. Seven species have been described in the genera *Manuherikia*, *Matanas*, *Dunstanetta*, and *Miotadorna* (Worthy *et al.* 2007, 2008, 2022). The four species of *Manuherikia* and one of *Dunstanetta* are interpreted as erismaturines (see Worthy & Nguyen 2020; Worthy *et al.* 2022), whereas *Miotadorna sanctibathansi* Worthy, Tennyson, Jones, McNamara & Douglas, 2007 was referred to Tadorninae, and *Matanas enrighti* Worthy, Tennyson, Jones, McNamara & Douglas, 2007 possibly to Anatinae (Worthy *et al.* 2007). Two larger taxa have been interpreted as anserines; one is similar to *Cereopsis* but both are represented by rare and fragmentary material (Worthy *et al.* 2008). Accurate assessment of the relationships of these putative anserines has not been possible with the available material, which until now did not include a humerus, one of the more diagnostically important elements for anatids. Therefore, the discovery of a distal humerus of a large anseriform in one of the key sites producing the St Bathans Fauna in 2020 is important and the subject of this contribution.

Material and methods

Nomenclature. We follow Dickinson & Remsen (2013) for modern taxa. Publication dates for modern taxa can be found in Dickinson & Remsen (2013), so herein both authors and publication dates are only given for fossil taxa. Names for specific bone landmarks follow Baumel & Witmer (1993).

Abbreviations. Institutions: CM, Canterbury Museum, Christchurch, New Zealand; FUR, Flinders University Palaeontology Laboratory, Adelaide, South Australia; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; SAM, South Australian Museum, Adelaide, South Australia. Other: F, female; M, male.

Comparative material. Anhimidae: *Anhima cornuta* (Linnaeus) CM 2015.175.6. Anseranatidae: *Anseranas semipalmata* (Latham): SAM B36790, B39824 F, B48035 M. Anatidae: *Cereopsis novaehollandiae* Latham: SAM B32829, B36209 M, B39638, B39767, B46631; *Cnemiornis calcitrans* Owen: CM 2013.2.8190; *Coscoroba coscoroba* (Molina), Carnegie Museum of Natural History, Section of Birds, A5212, CT scan available at https://creativecommons.org/licenses/by-nc/4.0/. *Cygnus olor* (Gmelin): SAM B46397 M, B45337; *Cygnus atratus* (Latham): SAM B46112 M, B46120 F, B46121 F, B46123 M, FUR 287; *Anser caerulescens* (Linnaeus): SAM B36868; *Anser anser* (Linnaeus): CM Av7127; *Branta canadensis* (Linnaeus): CM 2017.63.2, 2017.63.3; *Plectropterus gambensis* (Linnaeus): CM Av9772; *Tadorna tadornoides* (Jardine & Selby): SAM B39878. Accipitridae: *Haliaeetus leucogaster* (Gmelin): SAM B59157; *Aquila audax* (Latham): SAM B46613. Ciconiidae: *Ephippiorhynchus* (*Xenorhynchus) asiaticus* (Latham): SAM B5098; *Leptoptilos crumenifer* (Lesson): SAM B5060; *L. dubius* (Gmelin): SAM B5058. *Pelecanus conspicillatus* Temminck: SAM B46635, B46690. Otididae: *Ardeotis australis* (Gray): SAM B5096, B39070. Gruidae: *Antigone rubicunda* (Perry): SAM B32551. Phoenicopteridae: *Phoenicopterus ruber* Linnaeus: SAM B11552; *Phoenicopterus chilensis* Molina: SAM B25448; Palaelodidae: *Palaelodus ambiguus* Milne-Edwards, 1863, Oligo-Miocene: CM Av11396, St Gérand-le-Puy, France.

Results

Description and comparison

The fossil CM 2017.37.919 preserves the distal 140 mm of a right humerus similar in size to that of *Cygnus atratus* or *Cereopsis novaehollandiae*. It represents less than half of the total length of the complete humerus, as the nutrient foramen is not present in the preserved section (Figure 1). The specimen is broken and projecting eminences, such as the condylus dorsalis, were slightly worn prior to fossilisation. The cortical bone of the shaft is thin, less than 1 mm where assessable. This has contributed to the bone being somewhat shattered and, especially distally, partially crushed. The specimen is missing the condylus ventralis, the processus flexorius, and much of the caudal facies distally, and the tuberculum supracondylare dorsale has been broken. Despite this damage, the specimen preserves sufficient features to enable its identity to be assessed.

The specimen has the bone surface of the fossa musculi brachialis compressed inwards, but the margins of the fossa are discernible, forming an oval 7 mm long (proximodistally) by 6 mm wide (dorsoventrally) that is slightly offset dorsally of centre. The ventral margin of the fossa is widely separated from the ventral shaft margin; it lies 3 mm dorsal to the tuberculum supracondylare ventrale and 7 mm dorsal to the ventral side of this tuberculum. Similarly, the dorsal margin of the fossa is separated by 5 mm from the dorsal facies of the shaft. The fossa is overlapped proximodistally by minimally 20% (2 mm) of the length of the tuberculum supracondylare ventrale.

The tuberculum supracondylare dorsale is broken but its preserved base shows that it was formerly markedly prominent dorsally relative to the epicondylus dorsalis and that the maximum projection was proximodistally level with the proximal margin of the condylus dorsalis (see Figure 1).

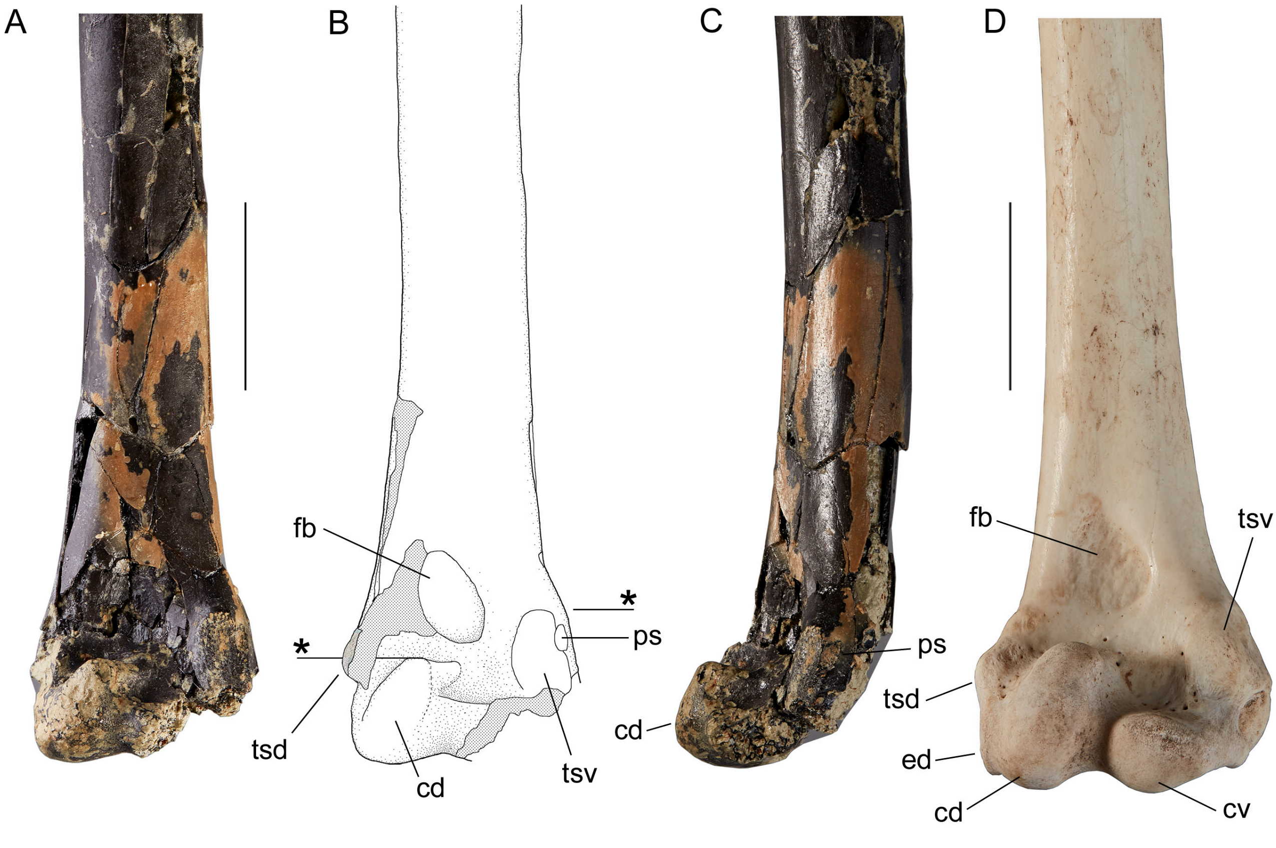

FIGURE 1. Distal right humerus, CM 2017.37.919, A–C. A, cranial view; B, interpretive drawing; C, cranioventral aspect to show lack of elevation of tuberculum supracondylare ventrale; D, *Cygnus atratus* FUR 287. Irregular areas with dense stippling are those where surface features of the bone are missing due to breakage. The probable former extent of tuberculum supracondylare dorsale is reconstructed (dark shading). The two horizontal lines marked with * show the relationships of the condylus dorsalis and tuberculum supracondylare dorsale and the proximal extent of tuberculum supracondylare ventrale. Note that shaft width in *Cygnus* (D) is similar to the fossil (A) whereas distal width is much greater. **Abbreviations**: cd, condylus dorsalis; cv, condylus ventralis; ed, epicondylus dorsalis; fb, fossa musculi brachialis; ps, insertion of musculus pronator superficialis; tsd, tuberculum supracondylare dorsale; tsv, tuberculum supracondylare ventrale. Scale bars are 20 mm.

A pair of well-defined scars on the caudodorsal facies of the epicondylus dorsalis for the origin of musculus flexor carpi ulnaris (most caudodistal) and the origin of musculus supinator (proximocranially adjacent the latter) (Matsuoka & Hasegawa 2007) have the usual anseriform form of two equal-sized oval pits aligned across the epicondyle at about 45 degrees to the shaft axis. The caudal-most pit is deepest and slightly craniocaudally narrower than the other. While erosion has lowered their rims exposing trabecular bone, and hence the dorsal prominence of the epicondylus dorsalis is eroded away, the length of each pit is less than twice its width.

The surface of the sulcus scapulotricipitalis is preserved caudally and it merges distally with the condylus dorsalis; the sulcus reveals that while the epicondylus dorsalis is worn, its rim cannot have been very prominent caudally or distally relative to the sulcus. However, exposure of trabecular bone dorsally adjacent to the condylus dorsalis shows that the epicondylus dorsalis was formerly more prominent dorsally than as preserved.

The condylus dorsalis is well-preserved distally where it is relatively flat as seen in cranial aspect; it differs markedly from that in *Cygnus atratus* in which the condyle is highly convex distally. While the proximocranial prominence of the condyle is worn overall, condylar shape can be assessed and reveals that overall proximodistal length slightly exceeds lateromedial width, but less so than for *C. atratus*, where length well exceeds width.

Only a small part of the dorsal margin of the condylus ventralis survives, and none of the processus flexorius or the epicondylus ventralis. However, the entire tuberculum supracondylare ventrale is well preserved. The facet on the tuberculum is proximodistally elongate—9.5 mm long by, maximally, 6 mm wide—flat and aligned parallel to the shaft axis; rather than proximally elevated and tilted distally, it faces cranially and is barely elevated from a rounded shaft facies proximal to it (see Figure 1C). The scar for the origin of the proximal head of musculus pronator superficialis is a discrete pit abutting the proximal half of the facet on the tuberculum.

The fossil is from a large bird, which immediately rules out many taxa. It is easily distinguished from large birds such as accipitriforms and ciconiids, wherein the distal humerus is markedly expanded ventrally, such that the facet on the tuberculum supracondylare ventrale is offset ventrally to the shaft in cranial aspect. Additionally, in these taxa, the tuberculum supracondylare ventrale is relatively smaller and aligned markedly distoventrally and the facet is tilted distodorsally (rather than being flat and directed cranially). Humeri of procellariiforms, such as diomedeids, differ markedly by having a very large and deep fossa musculi brachialis.

Humeri of phoenicopteriforms, e.g., *Phoenicopterus ruber* and *P. chilensis*, are also easily distinguished from the fossil by the fossa musculi brachialis being very proximally elongate and deep distally where it closely abuts the tuberculum supracondylare ventrale. Additionally, the tuberculum supracondylare ventrale is narrower and preceded proximally by a narrow, rounded ridge, and the ligamental attachment facet on it is more elevated and aligned more distoventrally. A second phoenicopteriform family, Palaelodidae, is a group represented in the St Bathans Fauna by *Palaelodus aotearoa* Worthy, Tennyson, Archer and Scofield, 2010 (Worthy *et al.* 2010). The mid-sized palaelodid, *Palaelodus ambiguus* Milne-Edwards, 1863, has a broad shaft relative to the distal width, as observed in the fossil, and a small oval fossa musculi brachialis. However, the palaelodid differs from the new fossil in several ways: it is smaller, the facet on the tuberculum supracondylare ventrale is aligned more distoventrally and is narrower, the fossa musculi brachialis is located proximal to this facet, and the condylus dorsalis has a more convex distal profile.

Humeri of pelecaniforms, such as *Pelecanus conspicillatus*, are similar to the fossil in lacking marked distoventral expansion of the humerus, but differ greatly: the fossa musculi brachialis is very elongate proximally and the impressio in it extends to the dorsal shaft margin; the fossa is secondarily deepened distoventrally; the fossa ends distally well proximal to the tuberculum supracondylare ventrale; the tuberculum supracondylare ventrale is undercut dorsally by a pneumatic fossa; the facet on this tuberculum is relatively much narrower; the epicondylus dorsalis projects dorsally and separates the condylus dorsalis from the dorsal margin to a much greater extent; and the proximodistal length of the condylus dorsalis is, in cranial aspect, about twice its dorsoventral width.

Otid humeri, such as for *Ardeotis australis*, are clearly distinguished by the fossa musculi brachialis being much larger and proximally elongate, narrowly separated from the medial margin, and extending close to the dorsal margin. The distalmost part of the epicondylus dorsalis does not project dorsally to the condylus dorsalis in cranial aspect. The tuberculum supracondylare dorsale has its maximal dorsal projection proximal to the condyle (not adjacent to it, as in the fossil). The sulcus scapulotricipitalis is narrower and deeper, being bound laterally by a robust ridge caudodistally. The condylus dorsalis, in cranial aspect, has a noticeably flattened distal profile, and distally is not separated from the condylus ventralis by a notch. The tuberculum supracondylare ventrale is proximodistally shorter, and while the scar for the origin of the proximal head of musculus pronator superficialis abuts the facet, it does so more distally. Moreover, the humerus of *A. australis* is smaller than the fossil and is dorsally arched and has a sigmoid shape in dorsal aspect, both lacking in the fossil.

Humeri of large gruids, such as *Antigone rubicunda*, differ notably from the fossil in having a very large and proximally elongate fossa musculi brachialis, and by the tuberculum supracondylare ventrale being relatively proximodistally shorter, such that it barely extends proximal to the condylus dorsalis, and it is tilted distodorsally.

TABLE 1. Measurements (mm) of the fossil humerus CM 2017.37.919 compared to those of selected anseriforms demonstrating that it is similar in size to those of *Anseranas* and the anserines but considerably larger than the shelduck. 'Depth dorsal condyle' is taken from the cranial margin of the condylus dorsalis to the sulcus scapulotricipitalis caudally; 'SWcran where parallel near distal end' is taken in cranial view where the sides first become parallel proximal of the fossa musculi brachialis; 'SWmin depth' was measured at the same point as the cranial width taken over the craniocaudal depth; 'Distal width pits-tsv' is measured from the distal rim of the scar on the caudodorsal facies of the epicondylus dorsalis for the origin of musculus flexor carpi ulnaris to the ventral side of the tuberculum supracondylare ventrale; * worn, so originally was likely to be 0.5 mm larger.

	Fossil CM 2017.37.919	*Anseranas semipalmata* SAM B36790	*Cereopsis novaehollandiae* SAM B39638	*Cygnus atratus* FUR287	*Anser caerulescens* SAM B36868	*Tadorna tadornoides* SAM B39878
Depth dorsal condyle	13.2*	13.1	14.6	16.8	12.3	9.7
SW at proximal side fossa musculi brachialis	17	15.1	14	17.2	12.3	9.8
SWcran where parallel near distal end	13.5	11.3	11.4	12.8	10.6	7.9
SWmin depth	11.7	10.2	10.0	11.8	8.6	7.1
Distal width pits-tsv	23.3	21.3	22.7	28.3	20.3	15.1

The fossil is similar to humeri of anseriforms in overall proportions, low tuberculum supracondylare dorsale and the shape of the tuberculum supracondylare ventrale, however, details allow its affinity to be further refined. The fossil differs from humeri of *Anhima cornuta* (state in brackets) by a flatter, wider, more parallel-sided tuberculum supracondylare ventrale (proximally pointed and elevated so faces distally), the scar for the origin of the proximal head of musculus pronator superficialis abuts the facet on the tuberculum supracondylare ventrale (well-separated, centred on the ventral facies), the fossa musculi brachialis is proximodistally short (elongate, extends two times height of the condylus dorsalis).

The fossil humerus is distinguished from those of *Anseranas semipalmata* (state in brackets) by: larger size, the tuberculum supracondylare ventrale being aligned with the shaft (directed markedly distoventrally) and distinctly separated from the fossa musculi brachialis (abutting on the proximodorsal margin), the pits for the origins of musculus flexor carpi ulnaris and musculus supinator are of equal size and depth (while the scar for musculus supinator forms a pit, that for musculus flexor carpi ulnaris is not excavated into a pit).

Its overall form is more similar to that of anatids, which have a broad shaft and relatively little ventral expansion of the distal end, a broad, cranially directed, flattened tuberculum supracondylare ventrale and the form of the epicondylus dorsalis with parallel, well-marked, oval pits for the origins of musculus flexor carpi ulnaris and musculus supinator.

While damage precludes ascertaining its original size, the tuberculum supracondylare dorsale clearly was dorsally prominent, which is a feature shared with *Cereopsis novaehollandiae* and species of *Cygnus*. However, the fossil is distinguished from humeri of *C. novaehollandiae* (state in brackets) by: slightly larger size, less distal width expansion (the tuberculum supracondylare ventrale lies ventral to shaft), the facet on the tuberculum supracondylare ventrale is elongate and parallel to the shaft (short, length and width of facet about equal, elevated distally), the fossa musculi brachialis is oval and centrally located (larger, more elongate, such that the impression extends farther proximally [1.5x the proximodistal length of the condylus dorsalis], dorsally the fossa extends close to the dorsal margin, and it is secondarily deepened both proximally and ventrodistally, and is deepest distally), and distal projection of the condylus dorsalis is weakly convex (markedly convex), and the pits for the origins of musculus flexor carpi ulnaris and musculus supinator are of equal size and depth (the more caudal scar for musculus flexor carpi ulnaris forms a very shallow pit, compared to that for musculus supinator).

Cnemiornis calcitrans (CM 2013.2.8190) is a large Quaternary relative of *C. novaehollandiae*, see Gill *et al.* (2010). It shares with *C. novaehollandiae* an elongate brachial fossa that is secondly deepened both proximodorsally and distoventrally, but further differs from the fossil in having a much smaller tuberculum supracondylaris ventrale relative to the condylus dorsalis.

The fossil shares with humeri of anserine species in *Cygnus*, *Coscoroba, Branta* and *Anser* a relatively small ovate fossa musculi brachialis. However, it is distinguished from *Cygnus olor*, *C. atratus* (similar size), and *Anser caerulescens*, *A. anser* and *Branta canadensis* (smaller), (their state in brackets) by: the shaft is stouter relative to the distal width (more ventrally expanded, tuberculum supracondylare ventrale positioned ventral to shaft); caudally it has a less robust and prominent rim to the sulcus scapulotricipitalis (robust and prominent); the condylus dorsalis is weakly convex distally (strongly convex); the facet on the tuberculum supracondylare ventrale is elongate (about as long as wide in *C. olor*, *B. canadensis* and *A. anser*, *A. caerulescens*, but the facet is more elongate in *C. atratus*, approaching that for the fossil); the facet on the tuberculum supracondylare ventrale extends well proximal to the condylus dorsalis and proximodistally overlaps the fossa musculi brachialis (does not, or only slightly extends, proximal to the condyle, and is distal to the fossa); the facet is parallel to the shaft (tilted distally in *A. anser, A. caerulescens* and *B. canadensis*); and origin of the proximal head of musculus pronator superficialis abuts the facet on the tuberculum supracondylare ventrale (distinctly separated caudally from the facet). The fossil seems to have a low to absent epicondylus dorsalis adjacent to the condylus dorsalis and so appears to differ from cygnines, which have a prominent epicondylus dorsalis; it is low in *A. caerulescens* and not prominent in *B. canadensis*. However, this is an artefact of erosion, as trabecular bone in the fossil is exposed on the dorsal facies adjacent to the condylus dorsalis indicating wear of the epicondyle.

Humeri of *Coscoroba coscoroba* differ from the fossil by: the scar for the origin of the proximal head of musculus pronator superficialis being distinctly separated caudally from the facet on the tuberculum supracondylare ventrale; a proximodistally elongate condylus dorsalis with a markedly convex distal profile; a short tuberculum supracondylare ventrale that barely surpasses proximally the condylus dorsalis.

The fossil differs from humeri of *Plectropterus gambensis* (state in brackets) by the prominent tuberculum supracondylare dorsale (lacking), the scar for the origin of the proximal head of musculus pronator superficialis abutting the facet on the tuberculum supracondylare ventrale (distinctly separated caudally from the facet), the tuberculum supracondylare ventrale projecting well proximad to the condylus dorsalis (only just surpassing it) and well overlapping the fossa musculi brachialis (not overlapping), and the incisura intercondylaris forming an apparently shallow notch in the distal profile (deep). Tadornines such as species of *Tadorna* share the same differences but are also rather smaller. *Miotadorna sanctibathansi*, for example NMNZ S42794 (holotype), CM2013.18.705, and CM2013.18.731, the hitherto largest anatid from the St Bathans Fauna, is interpreted as a tadornine (Worthy *et al.* 2007, 2022) and, apart from being rather smaller than CM 2017.37.919, differs in having the facet on the tuberculum supracondylare ventrale as wide as it is long and distinctly elevated proximally so that it faces distally. In addition, the scar for the origin of the proximal head of musculus pronator superficialis is proximal to the facet on the tuberculum supracondylare ventrale and is distinctly caudally separated from it and positioned at mid-depth on the ventral facies.

CM 2017.37.919 is larger than all other extant anatid humeri. Other large extinct anatids are all insular endemic taxa, such as the derived anatine Hawaiian moa-nalos (Olson & James 1991) and the Maltese swan *Cygnus falconeri* Parker, 1866 (Parker 1866; Northcote 1982), which were large flightless birds with relatively small humeri.

Reassessment of previously described indeterminate anserines from the St Bathans Fauna

Worthy *et al.* (2008) associated four specimens under the taxon ‘Anserinae, genus and species indeterminate A’. Two cranial fragments of left coracoids NMNZ S.50823 (length humeral facet 16.7 mm, width 10.9 mm) and NMNZ S.50824 (length humeral facet 16.2 mm, width 10.8 mm) were postulated to have an undetermined anserine affinity. A proximal fragment of a left radius (NMNZ S.50020) and a right scapula (NMNZ S.50822, maximum proximal width from the humeral facet to the acromion 15.8 mm, length humeral facet 10.8 mm, width humeral facet 6.5 mm, shaft depth 6.8 mm) were described as most similar to *Cereopsis novaehollandiae*. Here, we report an additional coracoid fragment NMNZ S53149 (humeral facet length 17.4 mm and width 11.4 mm) that is morphologically similar to these other anserine coracoids (NMNZ S.50823, 50824).

Measurements (mm) of *Cereopsis novaehollandiae* SAM B.39638 (coracoid humeral facet length 16.5, width 10.3 mm) are very similar to values of these anserine coracoids, but those for the scapula (maximum proximal width from humeral facet to acromion 17.0 mm, length humeral facet 12.9 mm, width humeral facet 6.2 mm, and shaft depth 9.1 mm) are rather larger, suggesting that the coracoids and scapula attributed to the St Bathans anserine 'Genus and species indeterminate A' were from different-sized birds.

However, Worthy *et al.* (2008) also described evidence for a second, smaller anserine based on two coracoids that were best exemplified by NMNZ S.42797, a left coracoid from Bed HH1a, Manuherikia River, which was listed as 'Anserinae, genus and species indeterminate B'. This coracoid is more slender than those of *Cereopsis novaehollandiae* and smaller and more slender than the fragments attributed to 'Anserinae, genus and species indeterminate A'. However, NMNZ S.42797 shares with *C. novaehollandiae* a foramen nervi supracoracoidei, a feature not otherwise seen among anserines, suggesting that it could belong to a cereopsine (Livezey 1996; Worthy *et al.* 1997). Therefore, the coracoid NMNZ S.42797 is better associated with the scapula NMNZ S50822 and radius NMNZ S50020, for which a cereopsine affinity was proposed by Worthy *et al.* (2008).

As the fossil humerus described herein shows clear differences from cereopsines, only the coracoids attributed to 'Genus and species indeterminate A' among these previously described anserine fossils can parsimoniously be associated with this new humerus.

Comparisons can be made between measurements (mm) of the humerus of the same individual *C. novaehollandiae* used in the coracoid comparisons and those for the fossil humerus CM 2017.37.919 (Table 1). These reveal that the fossil CM 2017.37.919 is from a slightly larger bird, assuming similar proportions, than that represented by two of the coracoid fragments previously described as Genus and species indeterminate A, but that it is appropriate for the newly recorded anserine fragmentary coracoid NMNZ S53149. The range of variation observed in these three fossil coracoids is not great and would be encompassed by intraspecific variation. The fossil humerus CM 2017.37.919 can therefore be associated with these three coracoid fragments based on similar size and shared unknown anserine affinity. Given that the combination of features described above for the humerus is unique among anseriforms and reveals a large anatid probably related to anserines, it is described as a new taxon.

Aves Linnaeus, 1758

Anseriformes Wagler, 1831

Anatidae Leach, 1819

Notochen bannockburnensis gen. et sp. nov.

urn:lsid:zoobank.org:act:BC0E01B9-66A0-4D66-BA09-ECF52C529F9A
urn:lsid:zoobank.org:act:E5500207-D342-4AD2-8D9F-9302E5F2502C

Holotype: CM 2017.37.919 (figure 1), a distal right humerus

Diagnosis: A swan-sized anatid in which the distal humerus is little expanded ventrally, the tuberculum supracondylare ventrale is not distinctly ventral to the shaft, is flattened rather than elevated facing somewhat distally, elongate and extends well proximal to the condylus dorsalis, and is widely separated from but proximally surpasses the distal end of a small ovate fossa musculi brachialis.

Type Locality: Croc Site, Layer 1, c.10 cm thick sand and cobble layer, in a 3 m cliff on the north side of a small hill, west side Mata Creek, near St Bathans, Otago. 44° 53.370' S 169° 50.26998' E. NZ Fossil Record File Number H41/f84.

Stratigraphy and age: 3.5 m above base of the Bannockburn Formation, Manuherikia Group, 19–16 Ma, early Miocene (see Worthy *et al.* 2022).

Etymology: After *notios* southern, Gk, and *chen*, from *Chenopis*, the endemic subgenus of goose-like swans of Australasia, feminine, and *bannockburnensis* for 'of the Bannockburn, alluding to its source from the Bannockburn Formation'. Suggested common name Bannockburn swan.

Measurements (mm): Preserved length 114, depth dorsal condyle 13.2, shaft width just proximal to fossa brachialis 17.0, shaft where not crushed 27 mm proximal to fossa brachialis 13.5 wide by 11.7 deep, diameter from pits for the origin of musculus flexor carpi ulnaris and origin of musculus supinator to the ventral side of tuberculum supracondylare ventrale at its mid-length 23.3.

Referred specimens: NMNZ S50823, S50824, two omal parts left coracoid, Bed HH1b [not Bed HH1a, contra Worthy *et al.* 2008, wherein the bed was misidentified], Trench Excavation, Manuherikia River Section; NMNZ S53149, omal part R coracoid, Bed HH1b, Trench Excavation, Manuherikia River Section. All are from the basal 25 m of the Bannockburn Formation in the *Manuherikia lacustrina* biostratigraphic zone (Worthy *et al.* 2022) and part of the St Bathans Fauna (Worthy *et al.* 2008; Schwarzhans *et al.* 2012). As described in Worthy *et al.* (2008), these coracoids are very fragmentary: they feature a short broad facies articularis humeralis, a dorsoventrally broad base to the processus acrocoracoideus where it extends from the facies articularis humeralis, dorsal part sulcus supracoracoideus lacking pneumatic foramina, and a deep cup-like cotyla scapularis. Therefore, the structure of the processus procoracoideus and all parts more sternal are unknown and so these specimens do not afford any insights on relationships.

Tentatively referred is CM Av40461, a proximal part of the right shaft of a humerus, collected 9-Jan-08, from Bed HH1a, Manuherikia River. The width of the shaft at the distalmost edge is 12.4 mm and the width is 14.7 mm at the distal end of the crista deltopectoralis. Of appropriate size for CM 2017.37.919, it shows that the distal end of musculus latissimus dorsi abuts the crista deltopectoralis and that caudally the margo caudalis is compressed forming a rounded acute capital shaft ridge, as it does in species of *Cereopsis* and *Cygnus*.

Remarks: *Notochen bannockburnensis* cannot be certainly referred to one or other of Cygnini or Anserini, as separation of these taxa on the distal humerus is principally by the distal projection of processus flexorius; it extends past the condylus ventralis in the Anserini but it does not in the Cygnini (Louchart *et al.* 2005), and this part of the fossil is missing. However, the large size, with distal width similar to that of *Cygnus atratus*, but with a stouter shaft, suggests a referral to Cygnini is likely.

No Oligo-Miocene anatids of similar size are known from Australia (Worthy 2009). Given the age disparity and geographic separation it is not likely that *Notochen bannockburnensis* could relate to the few European Oligocene-early Miocene putative anserines, but where taxa are comparable, differences exist. *Guguschia nailiae* Aslanova & Burczak-Abramowicz, 1968 is a swan-sized anseriform of late Oligocene-early Miocene age that differs by an absence of a facet on the tuberculum supracondylare ventrale and a larger tuberculum supracondylare dorsale (Aslanova & Burczak-Abramowicz 1968). Both *Cygnopterus affinis* (van Beneden, 1883) of middle Oligocene age and *Cygnopterus neogradensis* Kessler & Hír, 2009 of middle Miocene age, have a proximodistally short facet for the attachment of the anterior articular ligament, see Lambrecht (1931, Taf. II, 1, 2) and Kessler & Hír (2009). The known material of *Cygnavus senckenbergi* Lambrecht, 1931, from the early Miocene, lectotype left femur and a distal tibiotarsus and phalanx, and *Cygnavus formosus* Kurochkin, 1968, early Oligocene, a tibiotarsus, are incomparable. *Cygnopterus alphonsi* Cheneval, 1984, synonymised with *Cygnavus senckenbergi* Lambrecht, 1931 by Mlíkovský (2002), has a worn humerus referred to it, however the details of the tuberculum supracondylare ventrale are not discernible in the publication (Cheneval 1984).

All similar-sized anserines of middle–late Miocene are placed in modern genera. The exception is the late Miocene-Pliocene *Afrocygnus chauvireae* Louchart, Vignaud, Likius, Mackaye & Brunet, 2005 from Africa, which has a similarly distally robust shaft and differs by the scar for the attachment anterior articular ligament being rather circular instead of proximodistally elongate as in the fossil (Louchart *et al.* 2005).

Discussion

Notochen bannockburnensis is the eighth anatid to be described and named from the St Bathans Fauna. It reveals that large swan or goose-like birds lived alongside the diversity of smaller forms dominated by erismaturines. However, *N. bannockburnensis* and *Miotadorna sanctibathansi* were likely to be, at least in part, terrestrial graziers, whereas the erismaturine anatids were probably mainly aquatic herbivores given their diving and swimming adaptations (see Worthy *et al.* 2022).

After this manuscript was submitted, *Miotadorna catrionae* Tennyson, Greer, Lubbe, Marx, Richards, Giovanardi & Rawlence, 2022 was described from the St Bathans Fauna (Tennyson *et al.* 2022) based on a specimen (NMNZ S.47273) excavated by THW in 2017. We agree with those authors that the fossil described is of a species of *Miotadorna*. Most of the remaining 41 specimens Tennyson *et al.* (2022) listed as 'large anatids' were either described as, or referred to, *Miotadorna sanctibathansi* by Worthy *et al.* (2007), or were subsequently identified and catalogued as such by THW before their deposition in NMNZ. As Tennyson *et al.*'s Figure 2B shows, *Miotadorna* has well-marked size dimorphism, which mirrors that of the sexual size dimorphism of *Tadorna variegata* and so is presumed to be sexual size dimorphism as seen in most large anatids. The distal width value of the holotype of *Miotadorna catrionae* (S.47273) lies within the grouping of larger specimens in Tennyson *et al.* (2022: figure 2B) that predictably would be male specimens of *M. sanctibathansi*. However, this value underestimates original distal width, as the bone is worn dorsally to expose trabecular bone and the entepicondylar region is slightly crushed. These authors carried out a Principal Component Analysis (Tennyson *et al.* 2022, figure 1), which showed, as expected, clear separation of male and female *Tadorna variegata*; the five complete specimens of *Miotadorna* used likewise fell into two groups, with similar separation on PC1 as for *Tadorna*, four smaller individuals and one larger specimen, S.47273. Tennyson *et al.* (2022) admitted that the holotype of *M. catrionae* S.47273 cannot be distinguished from *M. sanctibathansi* on any qualitative characters that were used to erect that taxon and that only proportional differences and size distinguish it. Additional important similarities with *M. sanctibathansi* concern the shape of the tuberculum supracondylare ventrale; the facet on this tuberculum is wider than high and tilted distally and the scar for the origin of the proximal head of musculus pronator superficialis, while on the ventral facies, is proximal to the facet. A sample of five is insufficient to assess intraspecific proportional variation, nevertheless, the 'narrow' distal end can be assessed by the ratio proximal width over distal width, which ranges 1.24–1.52 for the four *M. sanctibathansi* and is 1.56 for S.47273. Adding 1.0 mm to its given distal width to allow for wear, results in a ratio of 1.48, i.e., within the range of the other specimens. While S.47273 had the largest proximal width (28.8 mm) in the sample assessed by Tennyson *et al.* (2022), larger specimens of *M. sanctibathansi* exist: e.g., CM2013.18.33 has a proximal width of 30.9 mm, and CM2013.18.731 has proximal and distal widths, 27.1 and 17.5 mm, respectively, for a ratio of 1.55. Rather than interpreting the large, distorted S.47273 as a second species, we consider it a more parsimonious hypothesis to consider it as a large specimen of the larger sex of *Miotadorna sanctibathansi*: we, therefore, synonymise *Miotadorna catrionae* with *M. sanctibathansi*.

There remains one other undescribed anatid from the St Bathans fauna. As argued above, it is best represented by NMNZ S.42797, a left coracoid from Bed HH1a, Manuherikia River, that was listed as 'Anserinae, genus and species indeterminate B' by Worthy *et al.* (2008), and which is more slender than those of *Cereopsis novaehollandiae* and those referred to *Notochen bannockburnensis*. NMNZ S.42797 shares with *C. novaehollandiae*, a foramen nervi supracoracoidei, a feature not otherwise seen among anserines, suggesting that it could belong to a cereopsine. Cereopsines have a long history in New Zealand, as evidenced by the two highly derived species of *Cnemiornis* that are the sister species of *Cereopsis novaehollandiae* (see Worthy *et al.* 1997). With it, we now associate the two other specimens, NMNZ S.50822, a right scapula, from Bed HH4, Manuherikia River Section and NMNZ S.50020, a left radius, from Site 1, Vinegar Hill, that were described in detail by Worthy *et al.* (2008), who concluded they evidenced the presence in the St Bathans Fauna of an anserine more similar to *Cereopsis* than other anatids. Clarity on the relationships of this species, however, requires new material, preferably a humerus which could support these preliminary conclusions. However, both *Notochen bannockburnensis* and this possible cereopsine are markedly less common than *Miotadorna sanctibathansi*. Elements of the cereopsine are likely to overlap in size with specimens of the larger sex of *M. sanctibathansi*, which may make accurate referral of fragmentary specimens or less diagnostic elements difficult.

Notochen bannockburnensis and this possible cereopsine are the oldest anserines known from the Southern Hemisphere. Together they suggest that the sister relationship of Northern vs Southern Hemisphere anserines, as shown by the molecular-based sister-group relationship of *Cereopsis* and *Coscoroba* with northern anserines (Gonzalez *et al.* 2009; Sun *et al.* 2017), has a long history. The *Anser-Cereopsis* dichotomy was dated at 15.42 Ma by Kuhl *et al.* (2021), however the presence of identifiable cereopsines earlier than this in the St Bathans Fauna suggests an earlier divergence. Moreover, the comparatively recent divergence of all modern anserine genera (Ottenburghs *et al.* 2016; Sun *et al.* 2017; Kuhl *et al.* 2021) precludes any likely close similarity of them with the St Bathans fossils.

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Roles of the authors. THW conceived the project, identified the specimens, measured and compared the specimens, and drafted the manuscript. RPS and VDP provided additional comparisons and measurements. All authors partook in fieldwork, helped interpret the results presented herein, and edited the manuscript.

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