

MIOCENE WATERFOWL AND OTHER BIRDS FROM CENTRAL OTAGO, NEW ZEALAND

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SYNOPSIS Abundant fossil bird bones from the lower Bannockburn Formation, Manuherikia Group, an Early-Middle Miocene lacustrine deposit, 16–19 Ma, from Otago in New Zealand, reveal the “St Bathans Fauna” (new name), a first Tertiary avifauna of land and freshwater birds from New Zealand. At least 23 species of birds are represented by bones, and probable moa, Aves: Dinornithiformes, by eggshell. Anatids dominate the fauna with four genera and five species described as new: a sixth and largest anatid species is represented by just one bone. This is the most diverse Early-Middle Miocene duck fauna known worldwide. Among ducks, two species of dendrochenines are most numerous in the fauna, but a tadornine is common as well. A diving petrel (Pelecanoididae: *Pelecanoides*) is described, so extending the geological range of this genus worldwide from the Pliocene to the Middle Miocene, at least. The remaining 16 taxa are left undescribed but include: a large species of gull (Laridae); two small waders (Charadriiformes, genus indet.), the size of *Charadrius bicinctus* and *Calidris ruficollis*, respectively; a gruiform represented by one specimen similar to *Aptornis*; abundant rail (Rallidae) bones, including a common flightless rail and a rarer slightly larger taxon, about the size of *Gallirallus philippensis*; an ?eagle (Accipitridae); a pigeon (Columbidae); three parrots (Psittacidae); an owl nightjar (Aegothelidae: *Aegotheles* sp.); a swiftlet (Apodidae: *Collocalia* sp.); and three passerine taxa, of which the largest is a member of the Cracticidae. The absence of some waterbirds, such as anserines (including swans), grebes (Podicipedidae) and shags (Phalacrocoracidae), among the abundant bones, indicates their probable absence from New Zealand in the Early-Middle Miocene.

KEY WORDS Avifauna, fossils, new taxa, Anatidae, lacustrine, Early-Middle Miocene, New Zealand

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INTRODUCTION

The main islands of New Zealand lie between 34 and 47°S, some 1400 km east of Australia, in the South Pacific Ocean. Most of the original continental fragment is now submerged beneath the ocean and New Zealand now comprises an archipelago of over 660 islands greater than 1 ha in area, with North Island (114 740 km²), South Island (151 120 km²) and Stewart Island (966 km²) accounting for 98.8% of the land. New Zealand was once part of Gondwana, but has been an archipelago since its separation from Australia and Antarctica around 82 million years ago (Ma; Cooper & Millener 1993; Sutherland 1999).

The Recent indigenous terrestrial flora and fauna is highly distinctive and attests to a Gondwanan influence with *Nothofagus* (beech) and *Podocarpus* forests; arthropods such as velvet worms (Onychophora) and giant weta (Stenopelmatidae, Orthoptera); and vertebrates such as primitive frogs (Anura, Leiopelmatidae), tuatara (Rhynchocephalia, Sphenodontidae) and moa (Aves, Dinornithiformes). Some 245 breeding species of bird and approximately 64 lizards (Scincidae, *c.* 35 sp.; Gekkonidae, *c.* 29 sp.) dominate the Recent fauna, with land mammals represented by only three species of bats (Worthy & Holdaway 2002).

New Zealand has a relatively rich Cenozoic record of marine birds, especially penguins, but there are few other described species (Fordyce & Jones 1990; Turbott 1990; Fordyce 1991). In contrast, the terrestrial fossil vertebrate record, while very rich in the late Quaternary (Worthy & Holdaway 2002), is one of the world's poorest for the pre-Quaternary period. Except for fragmentary Late Cretaceous (80–71 Ma) dinosaur material (Molnar & Wiffen 1994) and isolated moa bones from marine sediments up to 2.5 Ma (Worthy *et al.* 1991; Worthy & Holdaway 2002), the terrestrial record older than 1 Ma is very limited. A small avifauna from 1 Ma shoreline deposits near Marton, in the lower North Island, includes several species that are unknown from late Quaternary faunas and at least two Recent moa species (Worthy 1997).

The entire Cenozoic is represented by a single undescribed fauna from the Early–Middle Miocene Manuherikia Group, in Central Otago, South Island, known to contain two anatids and undetermined fish, discovered in 1978 (Douglas *et al.* 1981; Douglas 1986; Fordyce 1991). This fauna was extended by the discovery of a single crocodylian angular from the same formation in 1989 (Molnar & Pole 1997).

The Manuherikia Group sediments have been the focus of much palaeobotanical work investigating both mac-

rofloras and palynofloras (Mildenhall 1989; Mildenhall & Pocknall 1989; Pole 1989, 1992a–c, 1993a–g, 1997; Pole & Douglas 1998), culminating in the summary of vegetation and environment by Pole *et al.* (2003). Between the collection made by Ewan Fordyce *et al.* in 1980–1981, from the Vinegar Hill site (Fordyce 1991: 1234), and 2001, the only vertebrate specimen reported was a crocodylian angular, which was fortuitously exposed in a low cliff at an undisclosed locality (Molnar & Pole 1997). Fordyce (1991: 1235) figured a carpometacarpus, a tarsometatarsus and a coracoid, identified as anatids, from his Vinegar Hill collections. Pole *et al.* (2003) have figured another anatid carpometacarpus and avian eggshell from the basal Bannockburn Formation in Mata Creek, which is also the source of the crocodylian angular (B. Douglas pers. obs.). Fordyce (2003) figured some of the bones from Vinegar Hill, which were presumed to represent a duck and a small goose.

In view of the obvious potential for vertebrates, we began our main investigation of the Manuherikia Group sediments specifically to find vertebrate faunas in November–December 2001 (Worthy *et al.* 2002a, b) after initial forays to the region in January 2000 (A.J.D.T.) and April 2001 (C.J.). We targeted strata where vertebrates might be concentrated and began by visiting the sites described by Douglas (1986) as having bird bones, as well as other Lower Bannockburn Formation exposures where similar bone deposits might be expected and whose palynology was described in Pole & Douglas (1998). J.A.M., with guidance from Mike Pole (Pole *et al.* 2003: 420), began the investigation of the Mata Creek exposures. C.J., A.J.D.T. and T.H.W. worked at the sections on the Manuherikia River and Mata Creek. Our investigations of the Vinegar Hill exposures in 2001 suggested that they would be comparatively unfruitful and difficult to work, as they lacked running water for sieving operations, so we have since concentrated efforts on sites in the Mata Creek and Manuherikia River where the lower Bannockburn Formation is exposed.

Employing wet sieving techniques in the field and later sorting of the concentrate under laboratory conditions, we have recovered a rich and diverse vertebrate fauna, which we hereafter call the St Bathans Fauna. Mollusc remains are preserved in the beds, reflecting the alkaline nature of the sediments with fragments of the bivalves *Hyridella* sp. being most common, but rare freshwater and land gastropods are also present (site HH1a). Fish bones dominate all assemblages and represent two main taxa (numerous ?Gobiidae and rare Galaxiidae) and are not discussed further here. There are hundreds of fossils from other vertebrates that are identifiable at some taxon-level. The purpose of this paper is

to place on record the diversity of the avifauna from the lower Bannockburn Formation in the Manuherikia Group. The remains of other terrestrial vertebrates, including sphenodontids, skinks and geckos, crocodylians and bats and other mammals alluded to in Worthy *et al.* (2002a, b) will be described elsewhere.

Geological and palaeoenvironmental setting

Terrestrial vertebrate bones are locally concentrated in late Early–Middle Miocene (Altonian Stage, 16–19 Ma) Manuherikia Group strata, identified at several outcrop sites near St Bathans, Central Otago, New Zealand (Fig. 1; Douglas *et al.* 1981; Douglas 1986; Molnar & Pole 1997; Worthy *et al.* 2002a, b; Pole *et al.* 2003). A detailed stratigraphy and palaeogeographical reconstruction of the Manuherikia Group fluvial Dunstan Formation and overlying lacustrine Bannockburn Formation has been described by Douglas (1986). The ages of these strata are known from palynological evidence (Mildenhall & Pocknall 1989) and from more recent detailed palynostratigraphical zonation of the terrestrial bone bearing outcrops (Pole & Douglas 1998). The terrestrial bone-bearing beds in the Manuherikia River section are assigned to the Casuarinaceae biozone (Pole & Douglas 1998; fig. 6) and correlated with late Early Miocene–earliest Middle Miocene. This period approximately corresponds with a profound environment change identified in the Manuherikia Group strata from warm ever-wet rainforest to cooler temperatures and pronounced seasons, also seen elsewhere in the world at about this time (Flower & Kennett 1994).

The terrestrial bones typically occur in the lowest 30 m of the Bannockburn Formation (Fig. 2), mostly within discontinuous sandy or muddy sand layers of lacustrine shallow sublittoral–littoral (near shore) sediments. They are deposits of a large freshwater lake (Lake Manuherikia) that extended in excess of 5600 km² (Douglas 1986). The lake was surrounded by a broad (extensive) fluvial plain with major channels and interchannel flood-basins. Shallow wetland habitats were vegetated by grasslands, herbfields and peat-forming swamp–woodland. Relatively dry Casuarinaceae woodland occurred nearby (Douglas 1986; Pole *et al.* 2003) and it can be inferred that deltas formed at major points of sediment entry to the lake.

METHODS

We collected bones during fieldwork in the following periods: 21–26 April 2001 (C.J.); 27 November–7 December 2001 (J.A.M.); 8–13 December 2001 A.J.D.T./T.H.W./C.J. *et al.*; 1–6 October 2002 (A.J.D.T./T.H.W. *et al.*); 16–19 March 2003 (A.J.D.T./T.H.W. *et al.*); 18–25 February, 2004 (A.J.D.T./T.H.W. *et al.*).

Excavations were carried out at three main locations near St Bathans in Central Otago, South Island: 1, Manuherikia River 44° 54' 29''S; 169° 51' 30''E in sites (= layers) we have termed HH1a–e, HH2 and HH3 after Home Hills Station where the site is situated (see Fig. 1); 2, Mata Creek, particularly the 'Croc Site', 44° 53' 22''S; 169° 50' 16''E; 3, Vinegar Hill, 44° 52' 37''S; 169° 44' 57''E.

The vertebrate fossils were mainly recovered from sandstone beds. The sediment was excavated by hand and gently

washed over 1 mm to a maximum of 4 mm mesh sieves with as little mechanical disruption as possible. All material from HH1a during and after October 2003 was washed only on 1 mm mesh. Larger bones were collected in the field and all material that was retained on the sieves was bagged in bulk and later sorted under laboratory conditions a few grains at a time on trays. All vertebrate bone fragments, with the exception of shapeless slivers of fish bone, fish otoliths and land and freshwater gastropod fragments were recovered. T.H.W. and A.J.D.T. identified and catalogued the material into the fossil vertebrate collection, Museum of New Zealand Te Papa Tongarewa (MNZ). Mollusc remains were deposited in the mollusc collection, MNZ.

Abbreviations

Institutions

AM, Australian Museum, Sydney, Australia; ANWC, Australian National Wildlife Collection, CSIRO, Canberra, Australia; AU, Geology Department, University of Auckland, Auckland, New Zealand; BMNH, The Natural History Museum, London, United Kingdom; CM, Canterbury Museum, Christchurch, New Zealand; MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington (formerly National Museum of New Zealand, Dominion Museum and Colonial Museum), New Zealand; UCBL, Université Claude Bernard-Lyon 1, St. Gérand-le-Puy, France.

Skeletal elements and descriptive terms used

The following abbreviations apply to single and plural usage of the elements. **Ant**, anterior; **cmc**, carpometacarpus; **cor**, coracoids; **cran**, cranium; **fem**, femora; **fur**, furculae; **hum**, humeri; **pel**, pelves; **pt**, part; **rad**, radii; **scap**, scapulae; **stern**, sternum; **tib**, tibiotarsi; **tmt**, tarsometatarsi.

Anatomical nomenclature for specific bone landmarks follows Baumel & Witmer (1993) with English translations, or names following Howard (1929), thereafter. Some common terms are abbreviated as follows: **artic.**, *articularis*; **cond.**, *condylus*; **m.**, *musculi*; **proc.**, *processus*; **tub.**, *tuberculum*. L is left and R is right elements. L or R elements are sometimes prefixed with either 'p' or 'd', to indicate that either the proximal or distal parts, respectively, of the element is represented.

Measurements

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

TL, greatest length, except for the coracoid (which was measured down the medial side) and femora (which were measured from the proximal end of the *crista trochanteris* to the *cond. lateralis*).

PW, proximal width in the lateromedial plane; femora were measured from the *caput femoris* through the mid-depth point of the neck to the lateral side.

SW, shaft width at mid-length (except for tibiotarsi where it was the minimum value) in a lateromedial plane.

DW, distal width.

Tibiotarsi AL, length measured from the proximal articular surfaces to the *cond. lateralis*.

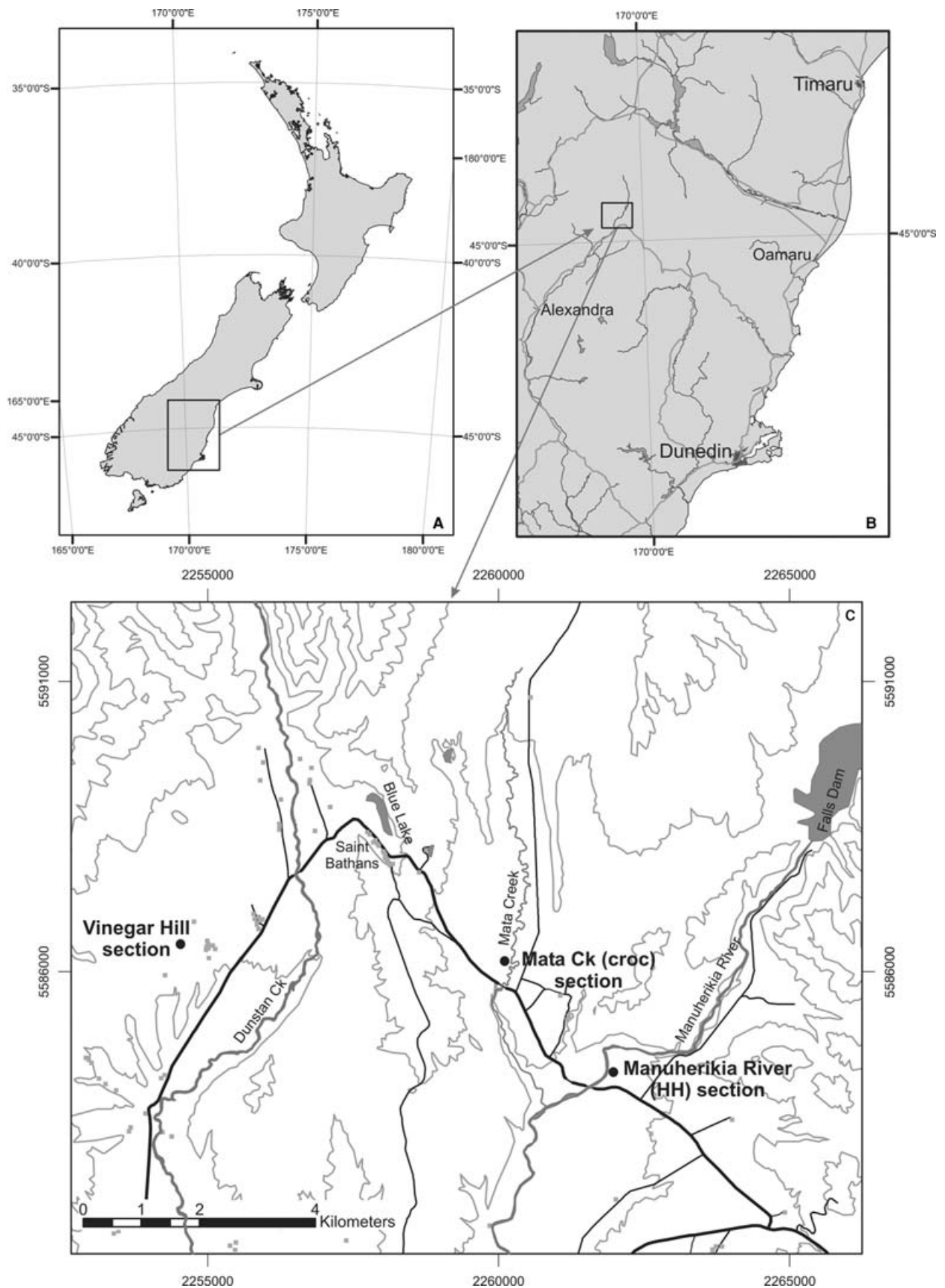


Figure 1 Location of the fossil sites within New Zealand. In C, roads (bold lines) and contours (light irregular lines) are shown as well as the Manuherikia River and its tributaries. Ck, Creek.

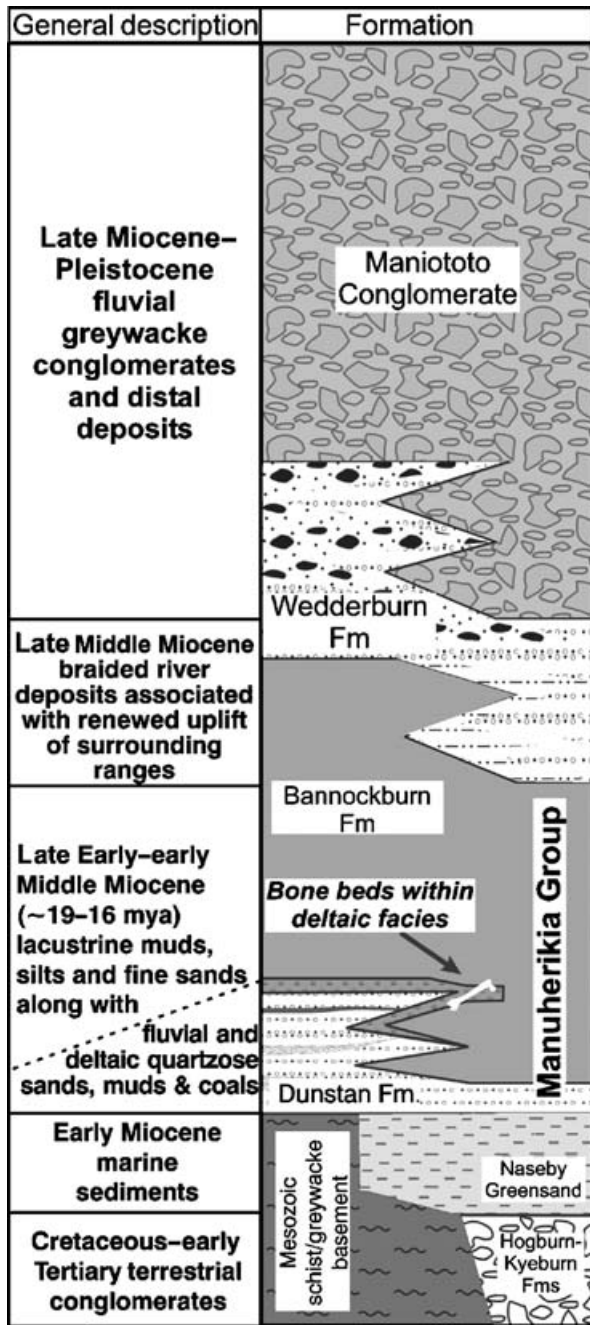


Figure 2 A generalised lithostratigraphy showing the relationship of the Manuherikia Group strata to bounding units, as well as the position of the fossil beds in the strata. Fm(s) formation(s).

Tibiotarsi PW, measured across the articular surface.
Tarsometatarsus DW, this was measured at right angles to the shaft.

Comparative material

The following comparative material was consulted during studies of the anatid material. All are modern unless stated otherwise. Reference specimens of non-anatid taxa specific-

ally referred to are embedded in the text concerning the relevant families.

Anseranas semipalmata Latham, magpie goose: AM O59362; *Dendrocygna arcuata* (Horsfield), wandering whistling duck: AM O64697 male; *Dendrocygna eytoni* (Eyton), plumed whistling duck: MNZ 27024; *Cereopsis novaehollandiae* Latham, Cape Barren goose: MNZ 25217, 25143; *Cnemiornis gracilis* Forbes, North Island goose: fossil, notably MNZ S35683-706; *Cnemiornis calcitrans* Owen, South Island goose: fossil, notably MNZ S35266; *Cygnus atratus* (Latham), black swan: MNZ 15266, 15267, 17250; *Cygnus olor* (Gmelin), mute swan: MNZ 16454; *Anser anser* (Linnaeus), greylag goose: MNZ 20812, 24519; *Branta canadensis* (Linnaeus), Canada goose: MNZ 23745, 26738, 26739, 26740, 26741; *Stictonetta naevosa* (Gould), freckled duck: MNZ 25141; *Thalassornis leuconotus* Eyton, white-backed duck: BMNH 1901.10.20.156; *Mionetta blanchardi* (Milne-Edwards), fossil, Université Claude Bernard – Lyon 1 (UCBL) from St. Gérard-le-Puy, France, all prefixed with FSL: L hum 332.274, R hum 332.277, R ulna 331.783, R ulna 331.788, L cmc 331.497, R cmc 331.492, L cor 331.364, R cor 331.381, L fem 331.176, R fem 331.185, L tib 331.104, R tib 331.109, L tmt 331.005, R tmt 331.007, CM Av11394, 2 ant stern, pt cran, fur, LR scap, pt 2 pel, LR MII.1, 2L1R cmc, R rad, LdR ulna, 1L2R cor, 1L2R hum, LR tmt, 1L3R tib, 1L2R fem, CM Av13902, 2L6R cor, 1R3L hum, 2L1R cmc, pt fur (both lots from St. Gérard-le-Puy); *Oxyura australis* Gould, blue-billed duck: CM Av31408; AM O65518; *Oxyura jamaicensis* (Gmelin), ruddy duck: ANWC 22640 (ANSS 386), ANWC 22641 (ANSS 391), MNZ 27335; *Oxyura vantetsi* Worthy, New Zealand blue-billed duck: specimens (fossil) listed in Worthy (2004a, 2005); *Biziura lobata* (Shaw), musk duck: MNZ 26190, 26191, CM Av71116; *Malacorhynchus membranaceus* (Latham), Australian pink-eared duck: MNZ 23880, 23881; *Malacorhynchus scarletti* Olson, Scarlett's duck: fossil humeri – MNZ S1276, 1823, 2379, 5145, 5492, 7584, 5714, 5736, 7599, 10080, 10477, 10478, 10966, 11447, 12190, 13119, 14153, 17097, 17226, 17655, 19400, 19505, 19506, 19531, 20758, 21656, 22402; fossil coracoids – MNZ S1939, 16632, 21082, 21541; *Tadorna variegata* (Gmelin), paradise shelduck: MNZ 15146, 16471, 16472, 16473, 16501, 16590, 24559, 25139, 25669, 26562, 26563; *Tadorna radjah* (Lesson), radjah shelduck: MNZ 26206, 26207; *Tadorna tadornoides* (Jardine & Selby), Australian shelduck: MNZ 22921, 23888a, 27367, ANWC 22240; *Tadorna tadorna* (Linnaeus) common shelduck: MNZ 12280; *Alopochen aegyptiaca* (Linnaeus), Egyptian goose: ANWC 22239 (ANSS 753), male, BMNH 1930.3.24.217, unsexed; *Chloephaga picta* (Gmelin), upland goose: BMNH 1860.11.4.15; *Cairina moschata* (Linnaeus), muscovy duck: MNZ 19842; *Stictonetta naevosa* Gould, freckled duck: MNZ 25141; *Hymenolaimus malacorhynchus* (Gmelin), blue duck: MNZ 16699, 23924, 24586, 24587; *Somateria mollissima* (Linnaeus), common eider: MNZ 12277, 12278, 12279; *Bucephala albeola* (Linnaeus), bufflehead: MNZ 12708, 12709; *Lophodytes cucullatus* (Linnaeus), hooded merganser: MNZ 12706; *Mergus australis* Hombron & Jacquinot, Auckland Island merganser: MNZ S30046, S31777, collections of fossils from Chatham Island; *Mergus serrator* Linnaeus, red-breasted merganser: MNZ 12707; *Chenonetta finschi* (Van Beneden), Finsch's duck: fossil, MNZ specimens, notably S35885; *Chenonetta jubata* (Latham), maned duck: MNZ

1487, 23188a, 25142, 25400, 25194a; *Nettapus pulchellus* (Gould), green pygmy-geese: MNZ 27025, 27026; *Anas chlorotis* G. R. Gray, brown teal: MNZ 14978, 15628, 15935 (= CM Av31828), 18898, 21544, 22086, 22802, 22806, 24535, 24536, 24537, 25105, 25106, 26630, 26631, 26940a, 26941a, 26942a, 26943a, 26944a, 26945a, 26946, 26947, 26949, 26950a, 26951a, 26952a; *Anas aucklandica* (Gray), Auckland Island teal: MNZ 24367, 24052; *Anas nesiotis* (Fleming), Campbell Island teal: MNZ 25727, 26742; *Anas gracilis* Buller, grey teal: MNZ 19351, 19348, 19301, 19322, 13688, 19323, 26815 (ex 24545), 18099, 19324, CM Av36764; *Anas superciliosa* Gmelin, grey duck: MNZ 13686, 15030, 16586, 18132, 16476, 17341, 17261, 16698, 16584, 24607; *Anas rhynchos variegata* (Gould), Australasian shoveler: MNZ 17000, 18971, 16591, 24588, 24589, CM Av36112, CM Av19237, CM Av19117, CM Av19238; *Aix galericulata* (Linnaeus), Mandarin duck: MNZ 27368; *Aythya novaeseelandiae* (Gmelin), New Zealand scaup: CM Av22382, CM Av22413, MNZ 8726, 13685, 16588, 16589, 17001, 17002, 17003, 23144, 24245; *Aythya australis* (Eyton), Australian white-eyed duck: AM O65772; *Aythya affinis* (Eyton), lesser scaup: MNZ 24041.

Extinct taxa were identified using the characters previously described as follows: *Biziura* (Worthy 2002), *Oxyura vantetsi* (Worthy 2004a, 2005), *Malacorhynchus scarletti* (Worthy 1995; Worthy & Gill 2002) and *Chenonetta finschi* (Worthy & Olson 2002). Most of the characters used are described in detail in the anatid comparisons given by Worthy (2004a).

TAXONOMIC ISSUES

In this work, specimens are identified to lowest taxonomic level using character suites. New taxa are defined by unique combinations of characters and differential diagnoses. In some cases preserved characters do not enable generic determination and, as the material is 16–19 Ma, we assume attribution to modern genera is possible but unlikely. For example, a distal half of a rail femur is similar in all the modern genera *Gallirallus*, *Rallus*, *Dryolimnas* or *Gallinula*, so is unlikely to be correctly referred even if these genera were extant in the early Miocene. In many cases, specimens can only be identified at the family level at present.

We use the term ‘*cf*’ (Latin *confer* = to compare) to denote similarity and the term ‘*magn*’ (Latin *magnitudo*) to indicate similar size without implying a possible relationship, following Olson & Rasmussen (2001). So, for example, ‘*cf Pelecanoides* sp., *magn P. urinatrix*’ should be interpreted to mean that the specimen is similar to *Pelecanoides* and similar in size to *P. urinatrix*.

TAPHONOMY

Bed HH1a, in the Manuherikia River Section, from which many of the bones described here were recovered, is 6.88–7.00 m above the base of the Bannockburn Formation. It dips at 40° to the southwest with a strike of 80° North. HH1a comprises a greenish grey silt or fine sand locally intermixed with quartz granules/pebbles and organic debris, incorporating algae encrusted rip-up clasts of mud, rare oncolite fragments and abundant bone fragments. This material was probably

reworked and concentrated by wave or current action in the littoral lake environment.

The clay layer underlying HH1a is slightly humped and hollowed (± 5 cm) over its lateral extent. The fossiliferous sands deposited on this surface contain ripples, about 10–12 cm between crests that indicate a current direction essentially down dip or parallel to the adjacent Manuherikia River. A result of this is that coarser material was deposited as lenses down-current of the humps on the lower clay layer.

In HH1a the fossil bones include many which are black in colour and usually have rounded edges. Others are brown in colour and generally have less wear. A few specimens of both brown and black fossils have algae-derived calcareous coatings. None of the vertebrate material is articulated and most bones are broken. Rounding may indicate wear due to fluvial transport, but the influence of biotic taphonomic agents such as crocodylians cannot be excluded and is known to be significant in, for example, Miocene lacustrine sites in Australia (J.A.M., unpubl. data). The fragmented nature of much of the material could be explained by its origin as predated remains left by either crocodylians or raptors. The predominance of distal wing elements and the relative scarcity of trunk elements such as pelves, sterna and vertebrae, could be explained by predation, but equally, these scarcely represented elements have a higher surface area–weight ratio enabling their selective removal by current from the depositional area. These observations indicate that in both sites, few specimens are in primary deposition sites, with most transported to some degree and some having been reworked from an earlier deposition event. There is, however, no significant time interval between these initial deposits as both preservation types contain the same species mix.

Layers HH1b–e in the Manuherikia River Section have similar sedimentary features to that of HH1a and so are presumed to have been deposited within similar near-shore conditions. HH2 in the Manuherikia River Section is stratigraphically about 14.3 m above HH1a. HH3 was a 2–3 cm thick lens of calcified reed and oncolite fragments, sandwiched between massive green clay layers about 300 mm thick and 1140 mm below the base of the sand layer HH2c. The HH2 sequence begins with a 160 mm thick green clay layer (HH2a), with abundant calcified reed and oncolite fragments in the lower 30 mm. The primary bone-bearing horizon (HH2b) is a 30 mm thick clay/silt zone rich in calcareous fragments that underlies HH2c, a 170 mm thick layer of homogenous fine sands with rare bones throughout.

The ‘Croc Site’ beside Mata Creek was the other significant site we worked. It is so named as the main fossil-bearing layer, which we term Layer 1, is the source of the crocodylian angular described by Molnar & Pole (1997). This layer has similar depositional features to HH1a: a 5–10 cm thick bed of silty medium–coarse pale sand, with silt rip-up clasts laid down on a similar thickness of clean pale sands. Layer 1 is about 10 cm below a >1 m thick shale bed (that presently caps the exposure) and *c.* 3.5 m above the Dunstan/Bannockburn contact. The sand below Layer 1 rests on an irregular erosion surface and in places infills desiccation cracks; it varies in thickness along the exposure. The boundary between Layer 1 and the lower sand is marked by rust-coloured iron/gypsum concretions in the better drained parts of the exposure, which incorporate fossils in their upper half.

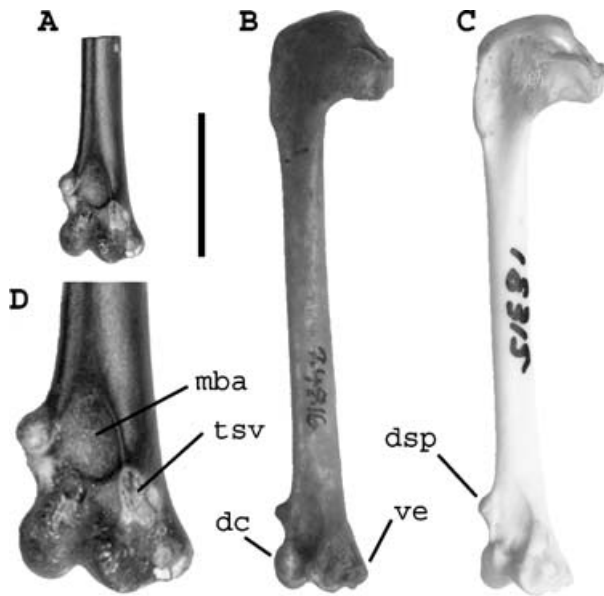


Figure 3 Comparison of *Pelecanoides* right humeri in cranial view. **A**, *P. miokuaka* sp. nov., MNZ S42431; **B**, *P. georgicus*, extant, MNZ 24816; **C**, *P. urinatrix chathamensis*, extant, MNZ 18315; **D**, *P. miokuaka* sp. nov., MNZ S42431 at 2x scale. Abbreviations: dc, dorsal condyle; dsp, dorsal supracondylar process; mba, *musculus brachialis anticus*; tsv, *tuberculum supracondylare ventrale*; ve, ventral epicondyle. Scale bar = 10 mm.

SYSTEMATIC PALAEOLOGY

Order PROCELLARIIFORMES Fürbringer, 1888

Family PELECANOIDIDAE Gray, 1871

Genus PELECANOIDES Lacépède, 1799

This bone (humerus) is identified as a diving petrel *Pelecanoides* sp. distinct from other procellariids because of the combination of the following features: the shaft is distinctly flattened, in cranial view the proximal origin of the *cond. dorsalis* is close to the dorsal margin rather than mid way between the dorsal margin and the *tub. supracondylare ventrale* as is the case in *Puffinus*, the *proc. supracondylaris dorsalis* is short, blunt and not rotated cranially, the *fossa m. brachialis* is relatively shallow and the *epicondylaris ventralis* is relatively elongate.

Pelecanoides miokuaka sp. nov. (Figs 3A, D)

HOLOTYPE. MNZ S42431, distal right humerus.

LOCALITY AND HORIZON. Croc Site L1, in 3 m cliff north side of small hill left side Mata Creek, Otago, New Zealand, (44° 53' 22''S; 169° 50' 16''E). Layer 1, c. 10 cm thick silty-sand layer, c. 3.5 m above the Dunstan/Bannockburn contact, Manuherikia Group, Early-Middle Miocene, 19–16 Ma.

MEASUREMENTS. Maximum distal width through condyles = 6.4 mm, shaft width at proximal side of the dorsal supracondylar process = 3.6 mm.

ETYMOLOGY. From the Miocene age and the Maori name for diving petrels 'kuaka'.

DIAGNOSIS. A *Pelecanoides* species of similar size to *P. georgicus* Murphy & Harper, 1916 that differs from all known species by the following combination of features: the impression of *musculus brachialis anticus* within the brachial fossa being deeper and deepest distoventrally and extending dorsally to the base of the dorsal supracondylar process, the *cond. ventralis* is not linked to the ventral supracondylar tubercle by a ridge, resulting in the facies between the ventral supracondylar tubercle and the ventral condyle being flat rather than housing a broad fossa and the ventral epicondyle has smaller ligamental attachment points and is smaller.

REMARKS. The fossil is similar in size to humeri of *P. georgicus* and slightly smaller than those of *P. urinatrix* Gmelin, 1789 (Table 1). In modern taxa (specimens listed, Table 1), e.g. *P. u. chathamensis* Murphy & Harper, 1916 (Fig. 3C), *P. u. exsul* Salvin, 1896, *P. u. urinatrix* Gmelin, 1789, *P. georgicus* (Fig. 3B) and *P. garnotii* (Lesson, 1828), the humerus has a shallow impression of *musculus brachialis anticus* (see Howard 1929: fig 21) which is not noticeably deeper distoventrally and which, only in some *P. georgicus*, extends to the base of the dorsal supracondylar process. As in all of these taxa, the fossil has a pneumatic foramen in the brachial fossa adjacent to the dorsal condyle. In modern taxa there is a prominent ridge linking the ventral condyle and the ventral supracondylar tubercle, which results in the facies between the supracondylar tubercle and the ventral condyle housing a broad fossa. In these taxa, the ligamental attachment points on the cranio-ventral facies of the ventral epicondyle, otherwise called the entepicondylar prominence (Howard 1929), are larger than those in the fossil and more distally directed. Humeri of *P. magellani* (Mathews, 1912–1913) were not examined, but as this taxon is considered close to *P. georgicus* and as *P. garnotii* is the most divergent of modern forms (Penhallurick & Wink 2004), yet still has identical distal humerus morphology to the others, it is unlikely that *P. magellani* differs from other modern taxa in this respect.

Pelecanoides miokuaka was not compared directly with *P. cymatotrypetes* Olson, 1985a of Early Pliocene age from South Africa, which was diagnosed on features of the proximal humerus and coracoid. *Pelecanoides cymatotrypetes* did not differ in any other way from the modern taxa (S. Olson, pers. comm., 26 June 2004) and it is of similar size to *P. u. exsul* and so slightly bigger than MNZ S42431. Therefore *P. miokuaka* is not only geologically very much older than any other known specimen, but is qualitatively distinct from all known *Pelecanoides* species.

Order ANSERIFORMES Wagler, 1831

Family ANATIDAE Leach, 1820

There are a great number of anseriform bones in the St Bathans Fauna, but as there is no association of bones of individuals, with one exception, and as some taxa overlap in size, only sufficient fossils to characterise the taxa represented are presented below. In Anseriformes, the most useful post-cranial element for determining phylogenetic relationships is the

Table 1 Dimensions (mm) of humeri for *Pelecanoides* species compared to the fossil MNZ S.42431.

Maximum DW	<i>georgicus</i>	<i>exsul</i>	<i>chathamensis</i>	<i>urinatrix</i>	<i>garnotii</i>	S.42431
Mean	6.5	6.9	6.9	7.2	8.0	6.4
Standard error	0.12	0.04	0.06	0.09		
Standard deviation	0.34	0.24	0.21	0.35		
Minimum	6.0	6.5	6.7	6.5		
Maximum	7.1	7.4	7.3	7.8		
Count	8	33	11	15	1	
SW above brachial fossa	<i>georgicus</i>	<i>exsul</i>	<i>chathamensis</i>	<i>urinatrix</i>	<i>garnotii</i>	S.42431
Mean	3.6	3.7	3.8	4.0	4.4	3.6
Standard error	0.06	0.03	0.06	0.05		
Standard deviation	0.17	0.20	0.20	0.19		
Minimum	3.4	3.2	3.5	3.7		
Maximum	3.9	4.1	4.1	4.3		
Count	8	33	11	15	1	

Shaft width above the brachial fossa was taken immediately proximad of the dorsal supracondylar process. Specimens used: *P. urinatrix chathamensis* (MNZ 26821, 27178, 27223, 807, 18097, 18098, 18277, 18315, 18316, 18341, 27232); *P. urinatrix urinatrix* (MNZ 25644, 25645, 25646, 25647, 25648, 25649, 25724, 26370, 27150, S.35324); *P. urinatrix exsul* (MNZ 893, 908, 17623, 17624, 17625, 18096, 24785, 24786, 25848, 26371, 26372, 26564, 26565, 26883 (left), 27013, 27014); *P. georgicus* (MNZ 24790, 24816, 24817, 24818, 24819, 24820, 24821, 24822); *P. garnotii* (USNM 614776). DW, distal width; SW, shaft width at mid-length.

humerus (Woolfenden 1961; Worthy 2004a). The coracoid is often found complete in fossil faunas and is also an important taxonomic element (Woolfenden 1961). Pelvic elements, while specifically very diagnostic, tend to have morphologies dominated by functional adaptations. For example, the diving anatids *Aythya*, *Mergus* and *Oxyura* have grossly similar leg bones but are not considered to be very closely related (Donne-Goussé *et al.* 2002; Sraml *et al.* 1996). As humeri and coracoids dominate the St Bathans Fauna, while crania, sterna and pelves are only represented by fragments, we define anatid taxa on humeri with some comment on referred coracoids. More complete skeletal descriptions and a detailed phylogenetic assessment of taxa awaits correct attribution of other skeletal elements to taxa following future analyses and fossil finds.

Subfamily DENDROCHENINAE Livezey & Martin, 1988

The following taxon is referred to Dendrocheninae as the humerus has the unique combination of characters, in part listed by Livezey & Martin (1988): (1) it is not elongate being proportioned as in *Anas*; (2) a prominent capital shaft ridge is directed towards an elevated *tub. dorsale* (dorsal tubercle); (3) presence of a broad flattened dorsal part of the *fossa pneumotricipitalis* with plane sub-parallel to shaft; (4) the *crista deltopectoralis* (deltoid crest) is dorsally concave; (5) the ventral part of the *fossa pneumotricipitalis* is closed or not pneumatic; (6) the space between the *tub. supracondylare ventrale* (facet for the anterior articular ligament) and the *cond. dorsalis* (dorsal condyle) is wider than the facet, unlike members of the more primitive Dendrocygninae where the space is narrower (Woolfenden 1961: 6); (7) absence of a distinct *proc. supracondylaris dorsalis* (dorsal supracondylar process). At least the characters (1), (2), (3), (5), (6) and (7) are derived with respect to Anseranatidae and Anhimidae, the sister taxon of Anatidae, and are derived with respect to *Dendrocygna*, e.g. *D. eytoni* (Eyton, 1838). Char-

acters (1), (2) and (3) are derived with respect to *Thalassornis* within Anatidae.

Other than members of the Dendrocheninae, a closed ventral pneumotricipital fossa (character 5) is shared by *Thalassornis*, *Oxyura*, *Biziura*, *Malacorhynchus* and tribe Aythyini. However, humeri of *Thalassornis* are more elongate with the capital shaft ridge directed towards the head and they lack a distinct dorsal part to the pneumotricipital fossa. In *Thalassornis*, *Oxyura* and *Biziura*, the attachment point of the superficial pronator muscle has merged with the ventral edge of the attachment for the anterior articular ligament and *Thalassornis* and *Biziura* have a much more elongated deltoid crest. Aythyini lack a capital shaft ridge, do not have an elevated dorsal tubercle and have a convex dorsal surface to the deltoid crest.

Genus MANUHERIKIA gen. nov.

TYPE SPECIES. *Manuherikia lacustrina* gen. et sp. nov., by monotypy.

ETYMOLOGY. After the region in Central Otago and the name of the geological formation from which the fossils are derived. The gender is feminine.

DIAGNOSIS. Small dendrochenines characterised by the following combination of humeral characters: (1) the dorsal tubercle is ovate with the long axis aligned with the shaft; (2) the dorsal part of the ventral pneumotricipital fossa is deeply excavated under the head caudally between the capital shaft ridge and the *incisura capitis* (capital groove); (3) the *crus dorsale fossae* is large and prominent, extending distally to a point level with where the *crista bicipitalis* joins the shaft; (4) the *fossa m. brachialis* is deep and bound by a sharp ridge medially; (5) the facet for the attachment for the anterior articular ligament is elevated and tilted distally; (6) the attachment point for the *m. pronator superficialis* (superficial pronator muscle) on the ventral facies is level with

the tip of the facet for the attachment for the anterior articular ligament.

REMARKS. Livezey & Martin (1988) reported that, in *Mionetta blanchardi* (Milne-Edwards, 1863), the muscle scar of the external head of the triceps (dorsal pneumotricipital fossa herein) does not undercut the head as it does in *Dendrochen robusta* Miller, 1944. In the specimens of *blanchardi* available to us, the dorsal pneumotricipital fossa does undercut the head, as it does in *Manuherikia*, so we assume that it does so to a greater extent in *Dendrochen*. Livezey & Martin (1988) also reported that, in *Mionetta*, the attachment facet for the anterior articular ligament is not elevated and parallels the palmar surface of the shaft rather than being rotated distally. However, in the specimens available to us, we note that while the facet is relatively smaller than in *Manuherikia*, it is elevated and rotated distally when examined from the medial perspective. *Mionetta* differs further from *Manuherikia* by a relatively deeper brachial depression that is separated from the medial margin by a broader and rounded ridge.

Livezey & Martin (1988) stated that Dendrocheninae was characterised by caudal (anconal) prominence of the *epicondylus dorsalis* (ectepicondyle) relative to the *processus flexorius* (entepicondyle) when the humerus is resting on its cranial surface. However, this is constrained by the development and size of the deltoid crest that prohibits rotation of the distal end when the bone rests on its cranial surface. Thus, for example, the unrelated *Tadorna variegata* (Gmelin, 1789) has the 'dendrochenine' condition depicted in Livezey & Martin (1988: figs 4A, B). That *Manuherikia* humeri, when lying on their cranial surface, have both dorsal and ventral condyles touching the resting surface and therefore the entepicondyle and ectepicondyle on a plane parallel to that surface does not preclude their membership in Dendrocheninae.

Humeri of *Manuherikia* are most similar to those of either *Mionetta blanchardi* or *Malacorhynchus*. They differ from *Mionetta* in that the shape of the dorsal tubercle is ovate with its long axis parallel to the shaft rather than semi-triangular with its short axis along the shaft as in *Mionetta*. A major difference is in the deep brachial depression bounded by a sharp ridge medially, whereas *Mionetta* has a well rounded ridge medially. *Malacorhynchus* differs from

Manuherikia in that the humerus has a more sigmoid shaft that does not narrow distally, the capital groove opens into the dorsal part of the pneumotricipital fossa at the same depth as the fossa even though the fossa is excavated under the head. The capital shaft ridge is less well developed only in the smaller *M. membranaceus* (Latham, 1802), it being well developed in *M. scarletti* Olson, 1977a. The *crus dorsale fossae* does not extend so far distally in *Malacorhynchus* as in *Manuherikia* and *Mionetta*.

Oxyura shares with *Manuherikia* an elongate and prominent *crus dorsale fossae*, but it differs markedly as the deep fossa extending under the head is greatly expanded dorsally so that its flat floor occupies the area where the capital shaft ridge lies in *Manuherikia*.

***Manuherikia lacustrina* gen. et sp. nov.** (Figs 4G, H, 5D, H, I, 6D)

HOLOTYPE. MNZ S42307 complete L humerus with part of the distal margin of the bicipital crest missing (Figs 4H, 5H).

TYPE LOCALITY. Home Hills Station, Site 1a (HH1a), true left side Manuherikia River, Otago, New Zealand, 44° 54' 29"S; 169° 51' 30"E.

HORIZON. Bed HH1a, a sand layer 6.88–7.0 m above the base of the Bannockburn Formation, Manuherikia Gp, Early–Middle Miocene, 16–19 Ma.

DISTRIBUTION. Layers HH1a, HH1b, HH2b, all on Manuherikia River section, Croc Site L1, Mata Creek, Otago, New Zealand.

MEASUREMENTS OF HOLOTYPE. See Table 2.

PARATYPES. MNZ S40094 pL humerus, HH1a; MNZ S42306 complete R humerus, HH1a (Figs 4G, 5D, 5I); MNZ S42308 worn R humerus, HH1a.

ETYMOLOGY. To reflect the fact that this bird lived in a lake.

DIAGNOSIS. A species of *Manuherikia* about the size of *Anas rhynchotis* Latham, 1802, in which the humerus shaft narrows distally and the dorsal part of the pneumotricipital fossa is

Table 2 Measurements (mm) of humeri (hum) and coracoids (cor) of *Manuherikia lacustrina* sp. nov.

Site	Cat No. MNZ S	Element	TL	PW dt-bc	Depth ch	SW max	SW min	DW	Depth dc
HH1a Holotype	42307	L hum	76.1	15.7	5.6	5.9	4.9	–	5.7
HH1a	42306	R hum	73.9	13.3	5.6	5.2	4.5	9.7	5.8
HH1a	40094	pL hum	–	16.3	5.7	5.9	–	–	–
HH1a	42308	R hum	70.3	–	4.9	5.5	4.1	–	5.4
			ML	L p-ma	L hf		SW	DW	
HH1a	40455	L cor	39.8	30.5	8.2		4.2	16.2	
HH1a	42310	L cor	–	32.1	9.6		4.2	–	
HH1a	42309	L cor	40.6	30.8	8.7		4.2	17.0	
HH1a	42311	L cor	40.5	30.8	8.9		4.5	–	
HH1a	40095	pR cor	–	–	8.5		3.9	–	
HH1a	40454	R cor	45.3	35.7	9.7		4.2	–	

Humeri: TL, total length; PW dt-bc, proximal width from dorsal tubercle to bicipital crest; Depth ch, depth caput humeri; SWmax, maximum shaft width at mid-length; SWmin, minimum shaft width in caudal view; DW, greatest distal width; Depth dc, depth dorsal condyle.

Coracoids: ML, length down medial side; L p-ma, length from procoracoid to medial angle; L hf, length of humeral facet; DW, width sternal articulation.

Element: L, left; R, right; P, proximal.

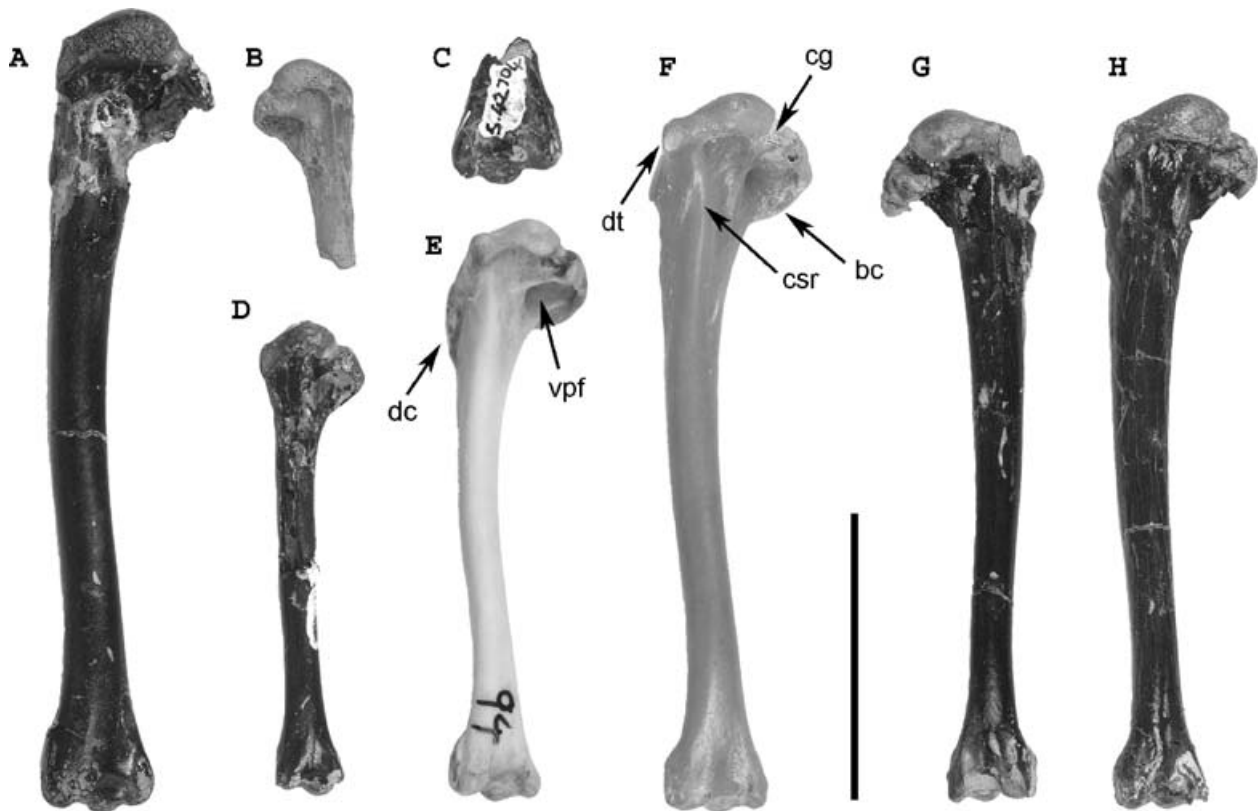


Figure 4 Comparison of fossil and recent humeri in caudal view. **A**, *Matanas enrighti* gen. et sp. nov., holotype MNZ S42281; **B**, *Manuherikia minuta* gen. et sp. nov., paratype MNZ S41067; **C**, *Matanas enrighti* gen. et sp. nov., paratype MNZ S42704; **D**, *Manuherikia minuta* gen. et sp. nov., holotype MNZ S42317; **E**, *Malacorhynchus membranaceus*, Recent, MNZ 23881; **F**, *Mionetta blanchardi*, from St Gérard-le-Puy, FSL 332.274; **G**, *Manuherikia lacustrina* gen. et sp. nov., paratype MNZ S42306; **H**, *Manuherikia lacustrina* gen. et sp. nov., holotype MNZ S42307. Abbreviations: bc, bicipital crest; cg, capital groove; csr, capital shaft ridge; dc, deltoid crest; dt, dorsal tubercle; vpf, ventral pneumotricipital fossa (closed – not pneumatic). Scale bar = 30 mm.

very deeply excavated, forming an abrupt drop from the capital groove into the fossa.

REFERRED MATERIAL. HH1a – MNZ S40438, dR hum; S40474, dR hum; S40476, dL hum; S42326, dL hum; S42624, pL hum; S42625, dL hum; S42626, dR hum; S42627, pL hum; S42628, dR hum; S42701, dL hum; S42702, dR hum; S42703, pL hum; S42739, dR hum; S42745, R hum; S42746, dL hum; S42747, dL hum; S42748, dR hum; S42749, pR hum; HH1b – S40961, dL hum; Croc Site L1 – S42222, dL hum; S42223, dR hum; S42237, pR hum; S42238, pR hum; S42239, dR hum; S42240, pR hum; S42243, dL hum; S42367, pR hum; S42368, dL hum; S42393, pLpR hum; S42394, pL hum; S42417, pL hum; S42418, pL hum; S42508, pL hum; S42509, pR hum; S42510, dL hum; S42529, dR hum.

MNZ S40454, R cor; S40455, L cor; S42311, L cor; S42309, L cor; S42310, L cor (Fig. 6D); S40095, pR cor; S40087, L cor; S41056, pR tib with most of shaft; S42722, L tib; S42241, R fem; S42242, L fem; S42798, L tmt; S42565, L tmt. There are many other 'medium-sized' anatid bones that probably belong to this taxon, but we refrain from referring them to species at this stage pending better knowledge of the sympatric similar-sized taxa described below.

MEASUREMENTS. See Table 2.

REMARKS. Humeri of *Manuherikia lacustrina* are most similar to those of either *Mionetta blanchardi* (Figs 4F & 5J) or *Malacorhynchus scarletti*. They differ from both *Mionetta* and *Malacorhynchus*, in addition to the generic difference listed above, most notably in that the shaft narrows distally and the distal end is narrower, similar to the condition in *Oxyura*.

While no associated bones of single skeletons are known, the size and relative frequency of taxa among element types allows probable referral of other skeletal elements. Humeri of *Manuherikia lacustrina* are common and only the sympatric *Matanas* (described herein) has a similar length humerus, but it is known from few specimens. Associated femora, tibiotarsi and tarsometatarsi of appropriate size each have one abundant morphotype for which the femur has the shaft bent ventrally over its distal third of length and a deep *fossa poplitea*, the tibiotarsus has enlarged cnemial crests and a flattened anterior surface, while the tarsometatarsus is relatively short, with a broader than deep shaft and *trochlea metatarsi II* strongly deflected towards the plantar surface and set proximally relative to trochlea IV such that it does not extend distally as far as the inter-trochlear notch between trochlea II and IV. These features are typical of diving ducks, which, along with the tapering shaft of the humerus (seen in *Mergus*, *Aythya* and *Oxyura*) suggests this taxon was a specialist diver. Although Livezey & Martin (1988)

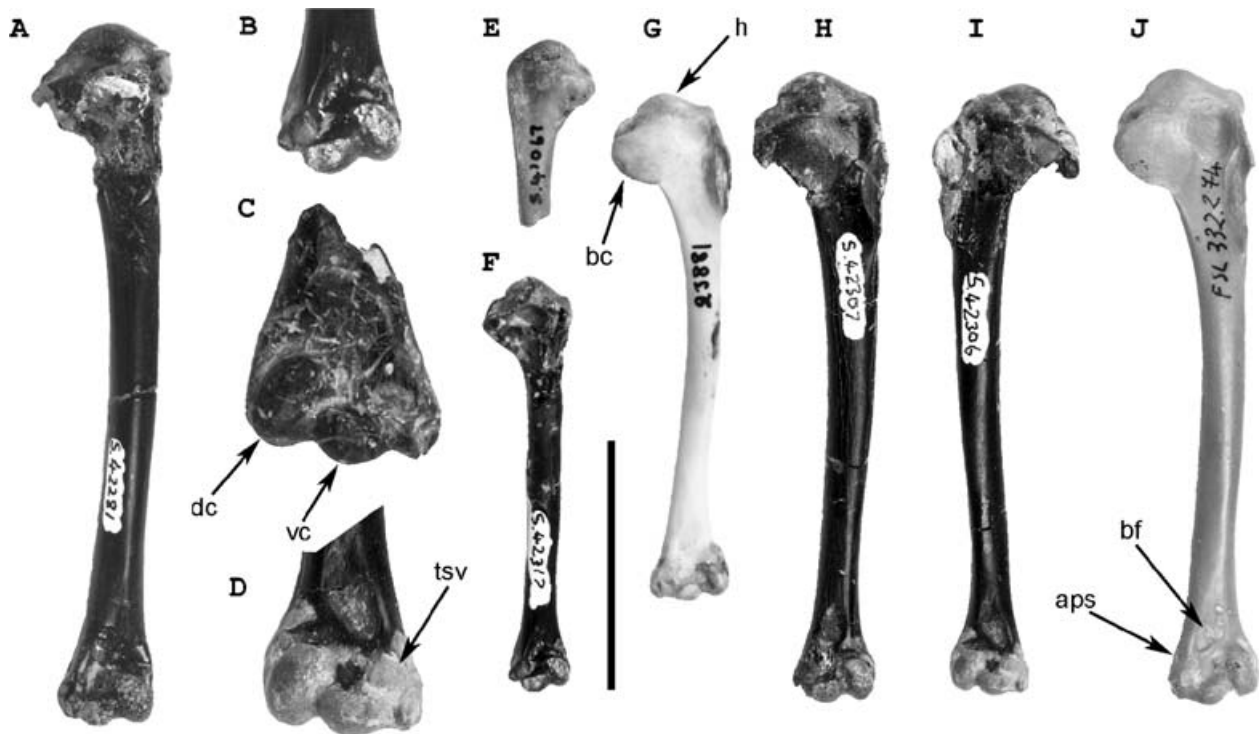


Figure 5 Comparison of fossil and Recent humeri in cranial view. **A**, *Matanas enrighti* gen. et sp. nov., holotype MNZ S42281; **B, F**, *Manuherikia minuta* gen. et sp. nov., holotype MNZ S42317; **C**, *Matanas enrighti* gen. et sp. nov., paratype MNZ S42704; **D, I**, *Manuherikia lacustrina* gen. et sp. nov., paratype MNZ S42306; **E**, *Manuherikia minuta* gen. et sp. nov., paratype MNZ S41067; **G**, *Malacorhynchus membranaceus*, Recent, MNZ 23881; **H**, *Manuherikia lacustrina* gen. et sp. nov., holotype MNZ S42307; **J**, *Mionetta blanchardi*, from St-G erand-le-Puy, FSL 332.274. Abbreviations: aps, fossa for attachment of superficial pronator muscle; bc, bicipital crest; bf, brachial fossa; dc, dorsal condyle; h, head; tsv, tubercle for attachment of anterior articular ligament; vc, ventral condyle. Scale bar = 30 mm, but **B, C, D** are at 2x scale.

suggested *Mionetta* was moderately specialised for diving on the basis of a closed ventral pneumotricipital fossa, a sternal pneumatic foramen and compression of the distal tarsometatarsus, we note that diving taxa such as *Mergus* have an open or highly pneumatic ventral pneumotricipital fossa and that *Mionetta* femora lack strong dorso-ventral shaft curvature and have a shallow popliteal fossa, the tibiotarsi lack anterior flattening of the shaft and elevated cnemial crests, while the tarsometatarsus lacks a dorsoplantarily flattened shaft and the trochlea for digit II is not strongly recurved distally, as in the manner of all specialised diving ducks.

Fossil anatid coracoids of appropriate size have two morphotypes, of which the common sort is taken to be *Manuherikia lacustrina* (Fig. 6D). In these, the *proc. acroracoides* (acroracoid) lacks any pneumatic foramina and overhangs the shaft medially, the *facies artic. clavicu-laris* (facet for articulation of clavicle or brachial tuberosity) is notched between the dorsal and ventral lobes, the dorsal lobe of the clavicle facet overhangs the *sulcus m. supracoracoidei*, the supracoracoidal sulcus is not excavated under the *facies artic. humeralis* (humeral facet), the *proc. procoracoideus* (procoracoidal process) lacks a foramen, the ventral surface of the blade has a shallow hollow or *impressio m. supracoracoideus*, immediately anterior of the *facies externa* of the *crista artic. sternalis*, and the ventral sternal facet is not prominent (Fig. 6D).

Mionetta (Fig. 6E) and *Malacorhynchus* (Fig. 6B) coracoids share all these features, except in both the hollow on

the ventral blade surface is deeper than in *Manuherikia*, as noted for *Mionetta*, but not *Malacorhynchus*, by Livezey & Martin (1988). Furthermore, *Malacorhynchus* has a prominent ventral sternal facet and the acroracoid overhangs the shaft to a greater extent. Lack of pneumatic foramina in the acroracoid is a plesiomorphic feature shared with *Anseranas*, *Thalassornis* and *Dendrocygna* (Livezey 1996a). Its presence in anserines and tadornines (although secondarily lost in many of the latter) appears to be an apomorphic state. At least two apomorphic characters distinguish *Anseranas* coracoids from those of all other anatids: the presence of a large pneumatic fossa dorsally and cranial of the sternal facet and a procoracoidal foramen that opens into the shaft. *Dendrocygna* and *Thalassornis* differ from Dendrochenines in that the *impressio m. supracoracoideus* forms a very distinct and deep depression on the ventral blade surface (Livezey 1986, 1996a), a feature shared with *Stictonetta*.

Manuherikia lacustrina is the most abundant bird species in the Manuherikia Group deposits.

***Manuherikia minuta* gen. et sp. nov.** (Figs 4B, D, 5B, E, F, 6A)

HOLOTYPE. MNZ S42317 complete L humerus with shaft crushed caudally (Fig. 4D, 5B, 5F).

LOCALITY AND HORIZON. Home Hills Station, Site 1a (HH1a), true left side Manuherikia River, Otago, New

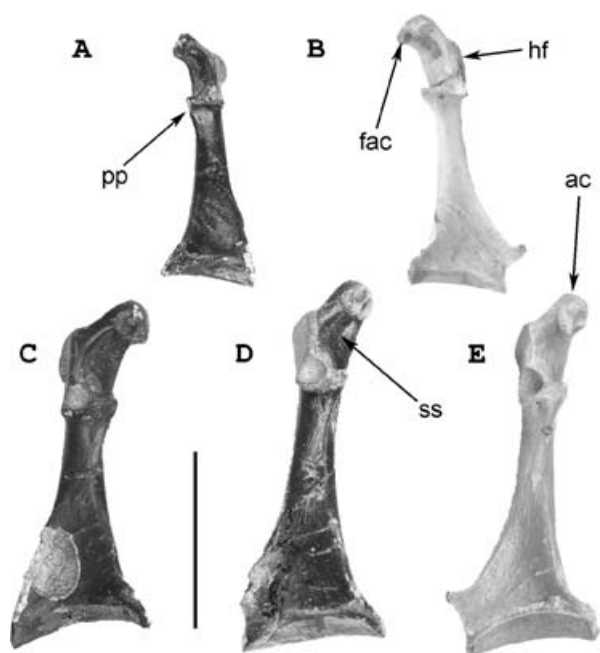


Figure 6 Comparison of fossil and Recent coracoids referred to as follows: **A**, *Manuherikia minuta* gen. et sp. nov. MNZ S42804; **B**, *Malacorhynchus membranaceus*, recent, MNZ 23881 (reversed); **C**, *Matanas enrighti* gen. et sp. nov., MNZ S42312; **D**, *Manuherikia lacustrina* gen. et sp. nov., MNZ S42309; **E**, *Mionetta blanchardi*, from St-G erand-le-Puy, FSL 331.364. Abbreviations: ac, acrocoracoid; fac, facies articularis clavicularis; hf, humeral facet; pp, procoracoidal process; ss, supracoracoidal sulcus. Scale bar = 20 mm.

Zealand, 44° 54' 29" S; 169° 51' 30" E. Bed HH1a, a sand layer 6.88–7.0 m above the base of the Bannockburn Formation, *Manuherikia* Gp, Early–Middle Miocene, 16–19 Ma.

DISTRIBUTION. Beds HH1a and HH2 on *Manuherikia* River section, Croc Site L1, Mata Creek, Otago, New Zealand.

MEASUREMENTS OF HOLOTYPE. See Table 3.

PARATYPES. MNZ S41067, pR hum, Croc Site L1 (Figs 4B, 5E); MNZ S42809, R hum, Croc Site L1; S40472, dL hum, HH1a; S42318, pR hum, HH1a; S42276, pR hum, Croc Site L1.

ETYMOLOGY. Named for its extremely small size.

DIAGNOSIS. A very small species of *Manuherikia* in which the humerus shaft does not narrow distally.

REFERRED MATERIAL. Several coracoids are referred to *M. minuta* on the basis of size and form. They are a small version of those referred to *M. lacustrina*, which unlike those of all other anatids in the fauna lack pneumatic foramina in the acrocoracoid. The referred bones, MNZ S42320, S42803 and S42804 (Fig. 6A), from HH1a, are small (Table 3), have the acrocoracoid slightly overhanging the medial margin, lack pneumatic foramina in the supracoracoidal sulcus or under the acrocoracoid, lack a fossa within the supracoracoidal sulcus adjacent to or extending under the humeral facet, have the dorsal lobe of the clavicle facet slightly overhanging the supracoracoidal sulcus and the ventral surface of the blade is slightly concave.

Other specimens referred principally by size include: MNZ S42345, R ulna, Croc Site L1, length 49.87 mm; MNZ S42319, dR ulna, HH1a; MNZ S42280, pR ulna, Croc Site L1; MNZ S42278, R cmc, length 32.4 mm, Croc Site L1; MNZ S42279, R scap, Croc Site L1; MNZ S42277, dL fem, Croc Site L1;

MEASUREMENTS. See Table 3.

REMARKS. *Manuherikia minuta* is slightly smaller and has the same postcranial skeletal proportions as the pink-eared duck *Malacorhynchus membranaceus*, but it differs in that the humerus has a more prominent capital shaft ridge and a deeper brachial fossa, while on the coracoid the clavicle facet is not as well developed as it is in *Malacorhynchus*. *Manuherikia minuta* differs most significantly from *M. lacustrina*, which was interpreted as a diver, in smaller size and that the shaft has parallel sides rather than narrowing distally. Other fossil postcranial elements of a small anatid presumably belong to *M. minuta*. These include ulnae (MNZ S42345, S42319) and carpometacarpi (MNZ S42278), which show no signs of their being from a flightless bird or one of reduced flight ability, as well as leg bones (e.g. distal femur MNZ S42277, distal tibiotarsi MNZ S42757, 42805, tarsometatarsus MNZ S42636), that are of appropriate size for a tiny duck. So we interpret the type series of *M. minuta* as being from a tiny volant duck rather than the reduced elements of a larger flightless form. Apart from the femur having a relatively deep popliteal fossa, available specimens

Table 3 Measurements (mm) of humeri (hum) and coracoids (cor) of *Manuherikia minuta* sp. nov.

Site	Cat No. MNZ S	Element	TL	PW	Depth ch	SW max	SW min	DW
HH1a Holotype	42317	L hum	50.4	11.1	3.7	3.9	3.3	7.7
HH1a	42318	pR hum	–	11.6	4.0	–	–	–
Croc Site L1	41067	pR hum	–	10.8*	3.6	–	–	–
Croc Site L1	42276	pR hum	–	11.4*	3.7	–	–	–
HH1a	40472	dL hum	–	–	–	–	–	8.2
Croc Site L1	42809	R hum	~53	–	3.4+	4.1	3.7	–
	MNZ S	Element	ML	L hf	SW			
HH1a	42803	L cor	28.3	6.2	3.3			
HH1a	42804	R cor	27.7	6.3	3.3			
HH1a	42320	pR cor	–	6.2	3.0			

d, distal. For all other abbreviations, see Table 2.

do not permit knowledge of whether this small duck had other morphological features associated with diving forms, e.g. dorsoventrally bent shaft of femur, anteriorly flattened tibiotarsus with elevated cnemial crests.

Subfamily TADORNINAE Reichenbach, 1849–1850

Tribe TADORNINI (Reichenbach, 1849–1850)

The following taxon is referred to Tadornini as the humerus has the unique combination of characters, in part listed by Woolfenden (1961): (1) humerus elongate, being only more so in *Biziura*, *Dendrocygna*, *Thalassornis*, anserines and more primitive anatids; (2) capital shaft ridge prominent and directed towards ventral side of a markedly elevated external tuberosity; (3) relatively narrow dorsal pneumotricipital fossa that does not undercut the head; (4) deltoid crest flaring and dorsally concave, elongate, extending well distad of bicipital crest; (5) ventral pneumotricipital fossa highly pneumatic, opening to bone interior; (6) the attachment point for the superficial pronator muscle is located, centrally to slightly cranial of centre, on the ventral facies level with the top of the facet for the attachment of the anterior articular ligament. Character (2) is here considered to be derived in Tadornini, with the plesiomorphic condition of the capital ridge directed towards the head in Anhimidae and Anseranatidae, the sister taxa of Anatidae, and only in *Dendrocygna* and *Thalassornis* within Anatidae. Character (3) is also derived in Tadornini, with the plesiomorphic condition (absence of a flattened dorsal pneumotricipital fossa) in Anhimidae, Anseranatidae, *Dendrocygna* and *Thalassornis*. Character (5) is considered to be a retained plesiomorphic character as seen in Anhimidae, Anseranatidae and *Dendrocygna*, however, the size of the fossa is much enlarged compared with these taxa. Characters (1), (4) and (6) are retained plesiomorphic features.

Genus MIOTADORNA gen. nov.

TYPE SPECIES. *Miotadorna sanctibathansi* gen. et sp. nov., by monotypy.

ETYMOLOGY. To reflect our view that this anatid is a Miocene shelduck similar to *Tadorna*.

DIAGNOSIS. A tadornine the size of *Tadorna variegata* in which the humerus has a relatively smaller and much shallower ventral pneumotricipital fossa that is more occluded internally, by pneumatic bone, than in other tadornines – pneumatic bone extends from the interior to the level of the *crus dorsale fossae*; *crus dorsale fossa* short, ending well proximad of level that bicipital crest joins to shaft, unlike *Tadorna* where both ridges end level with each other on the shaft; capital shaft ridge very well developed and separated from the dorsal tubercle by a deep distally-flaring groove; the brachial depression is deepest in the ventro-distal portion; the shaft between the brachial depression and the ventral margin is rounded and wider than the facet for the attachment of the anterior *articularis* ligament.

REMARKS. The modern tadornines *Tadorna variegata*, *T. tadornoides* (Jardine & Selby, 1828), *T. radjah* (Lesson, 1828) and *T. tadorna* (Linnaeus, 1758) all differ substantially from *Miotadorna* in that their humeri have a much more pneumatic ventral pneumotricipital fossa, with bone

struts no closer to the opening than below the capital shaft ridge. The capital shaft ridge is sharper proximally in the fossil taxon so that there is a distinct groove between it and the dorsal tubercle that is not present in modern tadornines. In *Tadorna*, the brachial fossa is shallow and flat, separated from the medial margin by a narrow ridge. The three tadornines in the Australasian region were separated generically by Livezey (1997a, b), with the two larger taxa, *T. tadornoides* and *T. variegata*, being placed in the unbanded shelduck subgenus *Casarca* Bonaparte, 1838 and *T. radjah* being left in *Tadorna*. We leave all in *Tadorna* following Dickinson (2003).

The African sheldgoose *Alopochen aegyptiacus* (Linnaeus, 1766) has humeri with a more marked concavity of the dorsal surface of the deltoid crest and a weaker capital shaft ridge than in *Tadorna* and *Miotadorna*. As in other modern tadornines it has a highly pneumatic ventral pneumotricipital fossa. *Alopochen* differs from *Tadorna* and is similar to *Miotadorna* in that the brachial depression is relatively small, centrally placed and is separated from the ventral facies by a broad rounded surface wider than the facet for the attachment of the anterior articular ligament, however not markedly deeper in its distomedial part as it is in *Miotadorna*.

Of the South American sheldgeese, only bones of *Chloephaga picta* (Gmelin, 1789) were examined. Livezey (1997a, b) found that *Chloephaga* and *Alopochen* formed the sister group to the shelducks in *Tadorna* inclusive of *Casarca*, but the relationship of the three genera was not resolved by Donne-Goussé et al. (2002). Humeri of *Chloephaga* have a very weak capital shaft ridge, with the shaft slightly compressed adjacent to the angle of the deltoid crest but well-rounded from there proximally, and so differ markedly from those of *Tadorna* and *Alopochen aegyptiacus*. Otherwise, they are similar to other tadornines.

Miotadorna sanctibathansi gen. et sp. nov.

(Figs 7A, D, 8A, D, 9A, B)

HOLOTYPE. MNZ S42794, R humerus, complete but for slight erosion of bicipital crest and, distally, the articular facet for the anterior ligament is broken and the *proc. flexorius* is lacking its caudal margin (Figs 7A, 8A).

TYPE LOCALITY AND HORIZON. Home Hills Station, Site 1a (HH1a), true left side Manuherikia River, Otago, New Zealand, 44° 54' 29" S; 169° 51' 30" E. Bed HH1a, a sand layer 6.88–7.0 m above the base of the Bannockburn Formation, Manuherikia Gp, Early–Middle Miocene, 16–19 Ma.

DISTRIBUTION. Layer HH1a; Croc Site L1, Mata Creek, Otago, New Zealand.

MEASUREMENTS OF HOLOTYPE. Length = 122.9 mm, proximal width = 25.2 mm, depth of caput humeri = 8.42 mm, mid-shaft widths = 9.58 × 8.03 mm, distal width = 17.48 mm, depth of dorsal condyle = 10.14 mm.

PARATYPES. MNZ S42272, R hum, Croc Site L1; MNZ S42273, R hum, Croc Site L1; MNZ S42274, pR hum, Croc Site L1; MNZ S42275, dL hum, Croc Site L1.

ETYMOLOGY. From the fact that this bird used to live in the environs of the old gold mining centre of St Bathans near which the fossil sites are located.

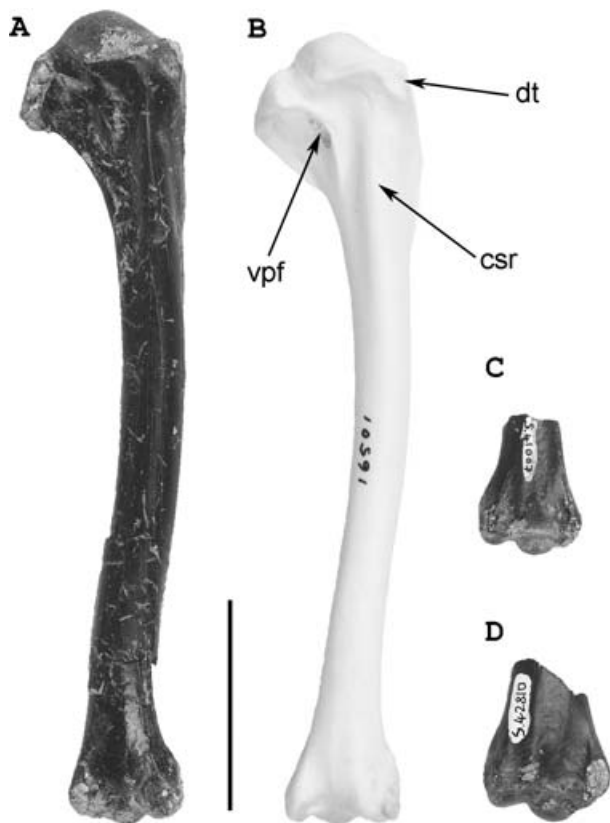


Figure 7 Comparison of fossil and Recent anatid humeri in caudal view: **A**, *Miotadorna sanctibathansi* gen. et sp. nov., holotype MNZ S42794; **B**, *Tadorna variegata* MNZ 16501, Recent; **C**, *Dunstanetta johnstoneorum* gen. et sp. nov., holotype MNZ S41007; **D**, *M. sanctibathansi* gen. et sp. nov., MNZ S42810. Abbreviations: csr, capital shaft ridge; dt, dorsal tubercle; vpf, ventral pneumatic foramen (open, pneumatic). Scale bar = 30 mm.

DIAGNOSIS. As for the genus.

REFERRED MATERIAL. MNZ S42313 dR hum, HH1a; MNZ S42234, L hum, Croc Site L1; MNZ S42810, dL hum, Croc Site L1 (Figs 7D, 8D); MNZ S42796, dR hum, HH1a.

MNZ S40093, R cor, HH1a; MNZ S42271, L cor, Croc Site L1; MNZ S42217, R cor, Croc Site L1; MNZ S42235, R cor, Croc Site L1; MNZ S42808, R cor, Croc Site L1 (Fig. 9A); MNZ S42795, R cor, HH1a (Fig. 9B).

MEASUREMENTS. See Tables 4 and 5.

REMARKS. The range in size of the fossil humeri indicates that *Miotadorna* had marked sexual size dimorphism as seen in modern tadornines.

A series of coracoids is referred to *Miotadorna* on the basis of expected size relative to the humeri and form. Assuming the fossil taxon had coracoids proportioned as in *Tadorna variegata*, the length of the four fossil humeri for which estimation of total length is possible indicates a coracoid medial length range of 48.7–53.7 mm (conversion ratio is 0.4269; for *T. variegata* data, see Table 6), or length from the procoracoid to the sternal facet with a range of 34.7–38.1 mm (conversion ratio is 0.3027; for *T. variegata* data, see Table 6).

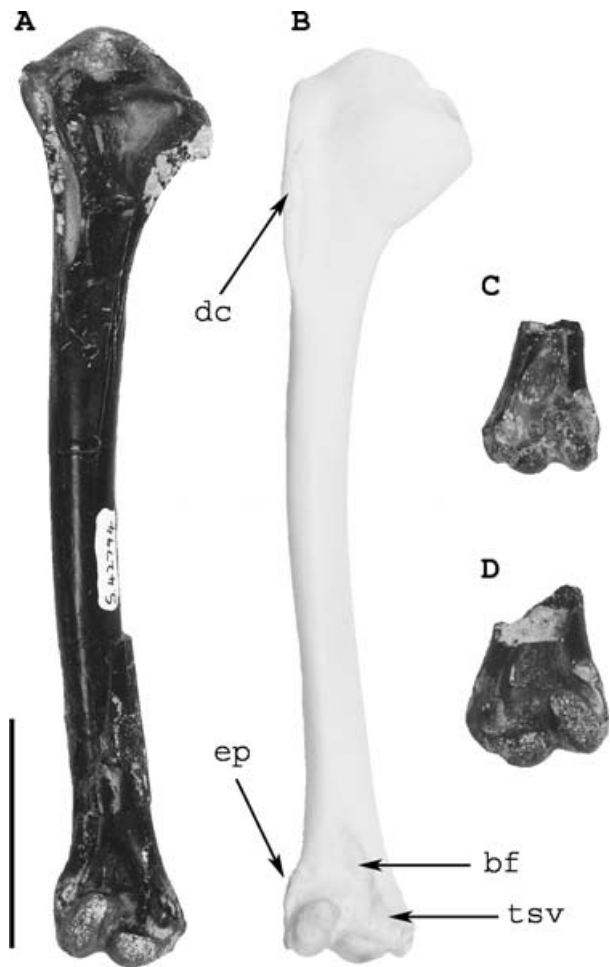


Figure 8 Comparison of fossil and Recent anatid humeri in cranial view: **A**, *Miotadorna sanctibathansi* gen. et sp. nov., holotype MNZ S42794; **B**, *Tadorna variegata* MNZ 16501, Recent; **C**, *Dunstanetta johnstoneorum* gen. et sp. nov., holotype MNZ S41007; **D**, *M. sanctibathansi* gen. et sp. nov., MNZ S42810. Abbreviations: bf, brachial fossa; dc, deltoid crest; ep, ectepicondylar process; tsv, tubercle for attachment of anterior articular ligament. Scale bar = 30 mm.

Smaller and larger distal humeri (Table 4) indicate a probable greater range in coracoid size. We suspect that fossil coracoids with medial lengths of 46.4, 47.4 and ~53 mm and lengths from the procoracoid to the sternal facet of 33.6–38.6 mm (Table 5) are also *Miotadorna*. A worn specimen (MNZ S40456) has a medial length of about 58 mm and may represent a maximum size for *Miotadorna*. Like tadornines, in these fossil coracoids the procoracoid process is robust and short without a foramen and is not rotated ventrally, the acrocoracoid slightly overhangs the shaft medially and the least shaft width is towards the humeral end of the mid point. They differ from all modern tadornines, except *Alopochen*, in that they have an open pneumatic foramen penetrating the *proc. acrocoracoideus* between the dorsal and ventral lobes of the *facies artic. clavicularis*. Other features include: (1) a prominent dorsal lobe of the clavicle facet that forms the anterior boundary to the supra-coracoid sulcus; (2) a supra-coracoid sulcus not excavated under the humeral facet;

Table 4 Measurements (mm) for humeri (hum) of *Miotadorna sanctibathansi* gen. et sp. nov.

Site	Cat No. MNZ S	Element	TL	PW max	PW dt-bc	Depth ch	SW max	SW min	DW	Depth dc
Croc L1	42234	L hum	125.8	–	19.1	8.3	10.2	8.8	19.6	–
Croc L1	42272	R hum	114.0	–	18.4	8.4	8.6	7.5	–	9.5
Croc L1	42273	R hum	119.4	–	17.4	–	8.3	6.9	16.5	–
Croc L1	42274	pR hum	–	23.3	18.1	8.2	–	–	–	–
Croc L1	42275	dL hum	–	–	–	–	–	–	17.9	10.2
Croc L1	42810	dL hum	–	–	–	–	–	–	18.8	10.6
HH1a	40475	pL hum	–	–	–	8.4	–	–	–	–
HH1a Holotype	42794	R hum	122.9	25.2	18.8	8.4	9.6	8.0	17.5	10.1
HH1a	42796	dR hum	–	–	–	–	–	–	18.1	10.2
HH1a	42313	dR hum	–	–	–	–	–	–	15.8	–

TL, total length; PW max, maximum proximal width; PW dt-bc, proximal width from dorsal tubercle to bicipital crest; Depth ch, depth caput humeri; SWmax, maximum shaft width at mid-length; SWmin, minimum shaft width in caudal view; DW, greatest distal width; Depth dc, depth dorsal condyle.

Table 5 Measurements for coracoids (cor) referred to *Miotadorna* gen. nov.

Site	Cat No. MNZ S	Element	Cor L1	Cor L2	Cor L3	Cor L4	W hum fac	W scap cotyla
Croc Site L1	42271	L cor	–	35.2	11.1	35.0	6.1	4.4
Croc Site L1	42217	R cor	47.4	34.4	12.2	34.7	6.4	4.5
Croc Site L1	42235	R cor	–	35.9	11.9	36.3	6.9	5.4
HH1a	40093	R cor	–	37.9	~12.0	–	6.9	4.6
HH1a	42795	R cor	46.4	33.6	11.9	33.9	6.8	4.5
Croc Site L1	42808	R cor	~53	38.6	14.0	–	7.3	5.7

Abbreviations: Cor L1, medial length from acrocoracoid to medial angle; Cor L2, length from procoracoid by scapular cotyla along the medial facies to sternal facet; Cor L3, length from scapular cotyla to the top of the humeral facet; Cor L4, length from procoracoid by scapular cotyla to the medial angle; W hum fac, width of humeral facet; W scap cotyla, width of scapular cotyla.

Table 6 Summary statistics for measurements (mm) of *Tadorna variegata* and data for other modern species (specimens listed on pp. 6–7, Comparative Material).

	Hum L	Hum PW	Hum PW 2	Hum SW	Hum DW	Cor L1	Cor L2	Cor L3	Cor L1/humL	Cor L2/humL
Mean	126.4	25.4	19.5	8.6	18.3	53.5	37.9	13.4	0.427	0.303
Standard Deviation	6.32	1.28	1.05	0.42	1.03	2.67	1.77	0.67	0.007	0.006
Minimum	118.6	23.6	18.1	7.9	16.8	49.7	35.2	12.7	0.416	0.294
Maximum	136.7	26.9	20.8	9.2	19.5	57.1	40.5	14.3	0.436	0.311
Count	11	11	11	11	11	10	10	10	10	10
<i>T. tadornoides</i> ANWC 22240	113.8	24.7	–	8.0	18.0	51.4	–	–	0.452	–
<i>T. tadornoides</i> MNZ 27367	125.9	27.3	20.1	8.5	19.1	56.8	40.0	14.2	0.451	0.318
<i>T. tadorna</i>	101.8	21.8	15.2	7.8	15.0	47.5	33.8	12.5	0.467	0.332

Abbreviations: Hum L, length of humerus; Hum PW, proximal width of humerus in the latero medial plane; Hum PW2, humerus width from dorsal tubercle to the end of the humeral head; Hum SW, shaft width at midlength; Hum DW, distal width of humerus; Cor L1, medial length from acrocoracoid to medial angle; Cor L2, length from procoracoid by scapular cotyla along the medial facies to sternal facet; Cor L3, length from scapular cotyla to the top of the humeral facet.

(3) a moderately inflated ventral edge to the supracoracoidal sulcus; (4) an acute medial angle; (5) ventrally the blade is convex and bound laterally by a weak ridge; (6) the ventral sternal facet is not prominent. Measurements are given in Table 5, with the size range indicated by specimens in Figs 9A and 9B.

Coracoids of *Tadorna* differ from the fossil in that they do not have a pneumatic foramen penetrating the acrocoracoid, the ventral surface of the sternal blade is flattened, not convex, and the ventral sternal facet is prominent. In *Tadorna variegata*, *T. tadornoides* and *T. tadorna*, but not in *T. radjah*, the supracoracoidal sulcus is excavated under the

humeral facet as well as under the ridge leading to the clavicle facet and the dorsal lobe of the clavicle facet is prominent and overhangs the supracoracoidal sulcus. In *T. radjah*, the clavicle facet is less prominent, the acrocoracoid does not overhang the shaft medially and the shaft is slender.

Coracoids of *Alopochen*, unlike all other extant tadornines, have an area of pneumatic foramina, rather than a discrete single foramen, within the acrocoracoid that is centred under the dorsal lobe of the clavicle facet rather than between the dorsal and ventral lobes of that facet. As a result, the dorsal lobe of the clavicle facet does not obstruct the extension of the supracoracoidal sulcus under the head

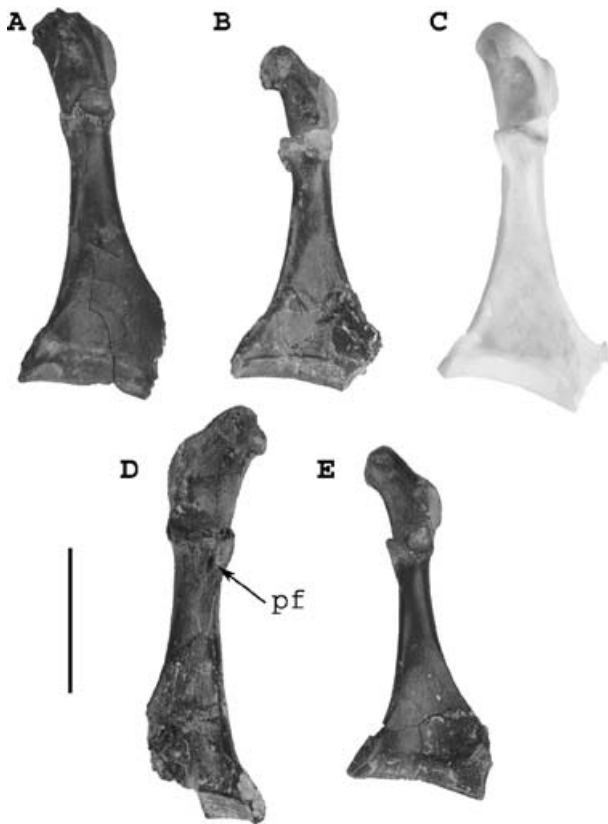


Figure 9 Comparison of fossil and Recent anatid coracoids as follows: **A**, *Miotadorna sanctibathansi* gen. et sp. nov., MNZ S42808; **B**, *M. sanctibathansi* gen. et sp. nov., MNZ S42795; **C**, *Tadorna variegata* MNZ 16501, Recent; **D**, anatid subfamily undetermined MNZ S42797; **E**, *Dunstanetta johnstoneorum* gen. et sp. nov., paratype MNZ S42481. Abbreviations: pf, procoracoidal foramen. Scale bar = 20 mm.

as it does in *Miotadorna*. Otherwise coracoids of *Alopochen* differ from the fossil in that the supracoracoidal sulcus has a marked excavation under the humeral facet and its medial edge is thick, the ventral sternal facet is prominent and the ventral face of the blade is flat not convex. Coracoids of *Chloephaga* lack pneumatic foramina in the acrocoracoid.

Anatidae, Subfamily undetermined

The presence of an anatid larger than *Miotadorna sanctibathansi* is indicated by a left coracoid, MNZ S42797, that is larger (length = 57.5 mm, SW = 7.16 mm, scapular facet – top humeral facet = 14.3 mm) than those referred to *Miotadorna*. It also differs markedly by the presence of a well defined procoracoidal foramen and in having a proportionally larger humeral end so that least shaft width is at mid length, rather than closer to the humeral end (Fig. 9D). The shape of the fossil is similar to that of anserines and it shares with *Cereopsis* and *Cnemiornis* the presence of a procoracoidal foramen (otherwise found only in anhimids and *Anseranas* among extant anseriforms), but it differs from all anserines and also *Miotadorna* in that it lacks a large pneumatic foramen penetrating the acrocoracoid under the clavicle facet. There is instead a very small foramen below the dorsal clavicle facet. The fossil coracoid differs

markedly from that of *Anseranas*, which is of similar size and robustness, in that the procoracoid is relatively smaller, the procoracoidal foramen does not open to the shaft interior, dorsally the blade lacks a large pneumatic fossa (that is also present in anhimids) and medially the margin is compressed to a thin flange and is not thick above the medial angle. At present the affinities of this anatid are unknown.

The other specimen listed below is of similar size and may represent this taxon or a large specimen of *Miotadorna*, but is too worn to determine whether a procoracoidal foramen is present. At the present time, no humeri are known that are of appropriate size for the taxon represented by this coracoid. The existence of this anatid, which is slightly larger than *Miotadorna*, reveals the probability that not all other skeletal elements of large anatids would necessarily be correctly referred to *Miotadorna*.

MATERIAL. MNZ S42797, L coracoid, HH1a. Possibly MNZ S40456, worn R coracoid, HH1a.

Subfamily ?ANATINAE Leach, 1820

Tribe *incertae sedis*

Genus *DUNSTANETTA* gen. nov.

TYPE SPECIES. *Dunstanetta johnstoneorum* gen. et sp. nov., by monotypy.

ETYMOLOGY. After the high mountain range that overlooks the fossil site.

DIAGNOSIS. An anatid distinguished from all other anatids by the following suite of characters. It is the size of *Stictonetta* or smaller individuals of *Miotadorna*. The humerus has a broad flat impression of *m. brachialis anticus* in a shallow brachial depression that extends close to the ventral margin of the bone, such that the intervening shaft width is less than half the width of the facet for the attachment of the anterior articular ligament. The ventral facies of the humerus is essentially flat and at right angles to the plane of the adjacent brachial depression, with the attachment for the superficial pronator muscle forming a large deep pit, more so than in any compared taxa, centrally located and extending from a point level with, to a point slightly proximad of, the top of the facet for the attachment of the anterior articular ligament. The coracoid has the acrocoracoid penetrated by a single large pneumatic foramen located between the ventral and dorsal lobes of the clavicle facet, which is thus notched; the shaft is slender; the medial angle is acute. The tarsometatarsus is relatively short with proportions similar to that of *Somateria* or *Mergus serrator*, it has broad ends and a narrow shaft that is about as wide as deep and trochlea II is strongly recurved plantarly.

REMARKS. Among anatids, only anserines, some tadornines (*Alopochen* and *Miotadorna*), *Aix*, *Cairina* and *Callonetta leucophrys* (Vieillot, 1816) have pneumatic foramina penetrating the acrocoracoid (Livezey, 1991). In *Cairina* and *Aix* (although some individuals of *A. galericulata* lack any foramina e.g. MNZ 27368), the area of pneumatic foramina is large and extends under the whole acrocoracoid. In *Alopochen* the foramen lies under the dorsal clavicle facet and *Miotadorna* is similar to *Dunstanetta* with the foramina

between the lobes of the clavicle facet. The narrow shaft of the coracoid and the short tarsometatarsus with expanded ends and recurved trochlea for digit 2 in *Dunstanetta* is, however, unlike that in any anserine or tadornine. The absence of a proximal end to the humerus precludes any further refinement of the relationships of this taxon intergenerically.

Dunstanetta johnstoneorum gen. et sp. nov.

(Figs 7C, 8C, 9E)

HOLOTYPE. MNZ S41007, distal L humerus (Figs 7C, 8C).

LOCALITY AND HORIZON. Home Hills Station, Site 2 (HH2), true left side Manuherikia River, Otago, (44° 54' 28"S; 169° 51' 30"E). Bed HH2c, ca. 17 cm thick sand layer about 21.3 m above the base of the Bannockburn Formation, Manuherikia Group, Early–Middle Miocene, 19–16 Ma.

MEASUREMENTS OF HOLOTYPE. Distal width = 15.4 mm, shaft width at proximal end of brachial fossa = 9.1 mm, depth of dorsal condyle = 9.3 mm.

PARATYPES. MNZ S42481 a complete R cor (Fig. 9E), MNZ S42482 R ulna, MNZ S42483 L tmt lacking distal end, MNZ S42484 R tmt, MNZ S42485 pedal phalanx RII.1; all from HH2a.

ETYMOLOGY. Named after Ann and Euan Johnstone of Home Hills Station, on which the type locality lies.

DIAGNOSIS. As for the genus.

COMPARATIVE DESCRIPTION. The preserved elements of *Dunstanetta* show that, compared to other Manuherikia anatids, it is larger than the species of *Manuherikia* and the following taxon (*Matanas*) and smaller than *Miotadorna* or the undetermined taxon described above.

The humerus of *Dunstanetta* has a uniquely deep and large point of attachment for the superficial pronator muscle. However, the other features, such as a shallow brachial depression with the adjacent medial surface at right angles to it, are individually seen in many diverse anatid taxa: e.g. *Tadorna*, *Stictonetta*, *Somateria*, *Chenonetta* and some *Anas* spp. The ventral epicondyle of *Dunstanetta* is short and broad with the attachment for the superficial pronator muscle centrally located on the ventral surface, as seen in *Cairina*, but unlike in *Somateria* and *Mergus* where the ventral epicondyle is very elongate and the pit for attachment for the superficial pronator muscle is located towards the cranial side. In the more specialised divers *Oxyura* and *Biziura*, the pit is indistinct and lies at the cranial margin of the ventral facies and the epicondyle is even more elongate.

In *Miotadorna*, for which some examples of distal humeri are only slightly larger than *Dunstanetta*, the brachial depression is deeper and more widely separated from the medial margin and the attachment for the superficial pronator muscle is a shallower pit.

The associated coracoid, apart from having a pneumatic acrocoracoid, has the following unique combination of characters: the ventral and dorsal lobes of the clavicle facet are separated by a notch; the acrocoracoid is compressed lateromedially and overhangs the shaft medially; the dorsal clavicle facet is not protuberant into the supracoracoidal sulcus; the ventral medial edge of the supracoracoidal sulcus is thin; the supracoracoidal sulcus is not excavated under the humeral

facet; there is no procoracoidal foramen; the medial angle is acute; the ventral surface of the sternal end is evenly convex with no ridge along the lateral side; the dorsal sternal facet is broad and extends over most of the blade width, but the ventral sternal facet is small. The acrocoracoid is only pneumatic in *Cairina*, *Aix*, *Callonetta leucophrys*, some tadornines (such as *Miotadorna* and *Alopochen*) and *Cereopsis* and other anserines, however, the broad sternal end and narrow shaft of the coracoid of the fossil is unlike that of these taxa. In most diving ducks (*Oxyura*, *Biziura*, *Aythya*, *Mergus*, *Somateria*) the acrocoracoid does not overhang the shaft medially as it does in the fossil. The fossil coracoid has neither the deep fossa on the ventral surface of the sternal end found in *Dendrocygna*, *Thalassornis* and *Stictonetta*, nor the shallow one of *Mionetta*, *Oxyura*, *Nettapus*, *Malacorhynchus* and *Hymenolaimus*. In *Mionetta*, the acrocoracoid is not pneumatic, the dorsal lobe of the clavicle facet protrudes into or overhangs the supracoracoidal sulcus, the ventral surface of the sternal blade has a marked hollow in it and the ventral sternal facet is prominent.

The associated tarsometatarsi have similar proportions to those of *Somateria mollissima*. They feature a narrow shaft about as wide as deep with abruptly expanded ends; the extensor sulcus, deep proximally and extending to about mid-length, is bound by a ridge laterally but not medially; the trochlea II is rotated plantar-caudally to the extent that the whole articular surface is distad to TIII; the intercotylar knob does not extend above the cotylae. The narrow shaft differs markedly from the wider than deep state seen in *Cairina*, *Stictonetta* and *Oxyura*. The tarsometatarsus of *Stictonetta* is very different in that the extensor sulcus is deep, bound by high ridges both laterally and medially and extends distally to the foramen vasculare distale.

REFERRED MATERIAL. MNZ S41008, R fem lacking proximal end.

MEASUREMENTS. See Table 7. Measurements of coracoid (MNZ S42481): medial length = 46.0 mm, length from scapula cotyla to top of acrocoracoid = 16.7 mm, scapular facet to top of humeral facet = 11.4 mm, width of humeral facet = 5.9 mm, shaft width = 4.4 mm, width of sternal articulation = 20.2 mm.

REMARKS. The holotype and referred femur were found about 2 years before the associated type series but came from the same place. The paratype series was found in a 20 cm wide exposure of HH2c and are probably parts of a single individual, which because of their uniqueness are associated with the holotype. The nearest bird bones elsewhere

Table 7 Measurements (mm) of *Dunstanetta johnstoneorum* gen. et sp. nov.

Element	Cat No. MNZ S	Length	PW	SW (min)	DW	Depth T3
Ulna	42482	89.8	10.4	5.2	–	–
Femur	41008	51 (est.)	–	4.4	12.5	–
Tmt	42483	46.1	11.1	4.6	10.8	7.6
Hum	41007	–	–	–	15.3	–

PW, proximal width in the lateromedial plane; SW (min), minimum shaft width; DW, distal width; T3, trochlea III.

in this layer were several metres distant. The femur is different to the common species in HH1a and as it is of appropriate size for the humerus, is referred to the present new species. It lacks the proximal end, but the shaft is narrow and dorsoventrally bent, it has a large deep popliteal fossa bound by a narrow ridge medially, while the distal end features a markedly expanded fibular condyle. The associated ulna has a deep *impressio brachialis* that forms a right angle with the medial facies but is otherwise unremarkable.

The above femoral characters and the short tarsometatarsus with strongly recurved TII are features normally associated with diving behaviours in anatids so *Dunstanetta johnstoneorum* was probably a diving duck. However, it differed from the highly specialised diving ducks, e.g. *Oxyura*, in not having a broad tarsus. The combined features of the coracoid distinguish it from all known anatids, but its proportions are more similar to anatines than anserines or tadornids. Similarly, the shortened tarsometatarsus of *Dunstanetta*, with a strongly recurved TII, is more like those of anatines than the more elongate bone of tadornines and anserines, in which TII and TIV have closer to equal distal extent. This combination of features suggests *Dunstanetta* may have affinity with anatids such as *Chenonetta* and *Hymenolaimus* or other anatines, exclusive of *Aythya*, *Mergus* and *Oxyura*, but its affinities remain obscure and will probably remain so until a proximal humerus is found.

Subfamily ANATINAE Leach, 1820

Tribe ?ANATINI Leach, 1820

Genus *MATANAS* gen. nov.

TYPE SPECIES. *Matanas enrighti* gen. et sp. nov., by monotypy.

ETYMOLOGY. A combination of the name of the creek, Mata, beside which the type locality lies and *Anas*, a duck. The gender is feminine.

DIAGNOSIS. An anatid about the size of *Hymenolaimus malacorhynchos* (Gmelin, 1789) defined by the following combination of features of the humerus: not elongate, proportioned as in *Anas*; deltoid crest concave dorsally; dorsal tubercle elevated; capital shaft ridge extends to beside dorsal tubercle; broad dorsal part to the pneumotricipital fossa; ventral pneumotricipital fossa pneumatic, opens internally; shaft does not taper distally; the brachial depression has a small narrow impression of *brachialis anticus* that forms a noticeable sulcus distomedially and is bound medially by a broad rounded ridge; the pit for the attachment of the superficial pronator muscle is proximad of the facet for the attachment of the anterior articular ligament and located centrally on the ventral facies; the attachment for anterior articular ligament is elevated and rotated distally; the ectepicondylar prominence extends well proximad of the dorsal condyle; the dorsal condyle in cranial view overlaps ventrally the ventral condyle on its proximal side to leave a relatively narrow space between it and the facet for the attachment of the anterior ligament.

REMARKS. That the humerus is not elongate precludes a close relationship with *Anseranas*, *Dendrocygna* and *Thalassornis*. The presence of a dorsal pneumotricipital fossa is derived with respect to *Anseranas*, *Dendrocygna* and *Thalassornis*. The open pneumatic ventral pneumotricipital fossa ex-

cludes a close relationship of *Thalassornis*, *Dendrochenines*, *Malacorhynchus*, *Oxyura*, *Biziura* and *Aythya* (wherein all it is closed) with *Matanas*. The presence of the plesiomorphic features of a capital shaft ridge, concave deltoid crest and raised dorsal tubercle excludes a relationship with *Anas* and its near relatives, which all have the derived states (no capital shaft ridge, flat-convex deltoid crest, dorsal tubercle flush with shaft). The proportions of the humerus are similar to that found in *Chenonetta* or *Anas* and not elongate as in tadornines. Furthermore, the deltoid crest is relatively short and does not extend well distad of the bicapital crest as in tadornines, while the size of the humerus is smaller than all tadornines except *Tadorna radjah*.

The combination of humeral characters of prominent capital shaft ridge, concave deltoid crest, elevated dorsal tubercle and open ventral pneumotricipital fossa found in *Matanas* are also found in *Stictonetta naevosa* (Gould, 1841), *Hymenolaimus* and *Chenonetta*. However, in *Matanas*, the *proc. supracondylaris dorsalis* (ectepicondylar prominence), while lacking the projection seen in *Dendrocygna*, is located farther proximally than in *Stictonetta* or *Hymenolaimus* and is distinctly proximad of the dorsal condyle. *Hymenolaimus* further differs by the head being deeply excavated under its caudal surface resulting in the capital groove being interrupted by a distinct ridge at its dorsal end, whereas in *Matanas* the head is not undercut caudally, although the dorsal part of the pneumotricipital fossa is much deeper than the adjacent capital groove. In addition, *Hymenolaimus* has a wider space between the dorsal condyle and the facet for the anterior articular ligament.

Chenonetta shares with *Matanas* the proximal position of the ectepicondylar prominence, but differs as it has a weak capital shaft ridge in *C. jubata* (Latham, 1802), or one that is secondarily enhanced by flightlessness in *C. finschi* (Beneden, 1875), that does not extend up to beside the dorsal tubercle (Worthy & Olson 2002). Also, in *Chenonetta*, the dorsal condyle does not overlap the ventral condyle in cranial view to the same extent, so that the space between it and the facet for the attachment of the anterior articular ligament is wider.

All three genera (*Hymenolaimus*, *Chenonetta* and *Stictonetta*) have been problematic as to their taxonomic placement. While *Stictonetta* is generally regarded as relatively primitive, both *Hymenolaimus* and *Chenonetta* are variably placed within or outside of anatines but are often allied to tadornines (Johnsgard 1968; Marchant & Higgins 1990; Sraml *et al.* 1996; Livezey 1997b; Donne-Goussé *et al.* 2002; Worthy & Olson 2002). Certainly, the proximal position of the ectepicondylar prominence in *Matanas* and *Chenonetta* is seen in *Tadorna*, but no other compared taxa. The available evidence suggests *Matanas* may be more closely related to *Chenonetta* among extant taxa and so could be a relatively primitive member of Anatini. However, discovery and referral of other elements will be crucial to the further refinement of the relationships of this taxon.

Matanas thus differs markedly from sympatric and similar-sized *Manuherikia* in the pneumatic ventral pneumotricipital fossa, lesser excavation of the dorsal part of the pneumotricipital fossa, by the brachial depression being separated from the medial margin by a broad rounded ridge and by the proximal location of the ectepicondylar prominence (*sensu* Howard 1929: fig. 20). *Matanas enrighti* is much smaller than *Dunstanetta johnstoneorum*.

***Matanas enrighti* gen. et sp. nov.** (Figs 4A, C, 5A, C, 6C)

HOLOTYPE. MNZ S42281, left humerus with deltoid crest broken, *crus dorsale fossae* and the distal margin of the bicapital crest broken and the distal condyles worn (Fig. 4A, 5A).

LOCALITY AND HORIZON. Croc Site L1, in 3 m cliff north side of small hill left side Mata Creek, Otago, New Zealand, (44° 53' 22"S; 169° 50' 16"E). Layer 1, a 10 cm thick silty-sand layer, ca. 3.5 m above the Dunstan/Bannockburn contact, Manuherikia Group, early–Middle Miocene, 19–16 Ma.

DISTRIBUTION. Croc Site L1; Layer HH1a, Manuherikia River, Otago.

MEASUREMENTS OF HOLOTYPE. Length = 84.8 mm, depth of head = 6.3 mm, mid-shaft width 6.2 × 5.5 mm, distal width = 11.8 mm.

PARATYPES. MNZ S42704, dR hum, HH1a, (DW = 11.7 mm, depth of dorsal condyle = 6.6 mm: Figs 4C, 5C).

ETYMOLOGY. After Mr Jack Enright, who owns the station on which the type locality lies.

DIAGNOSIS. As for genus.

REMARKS. A single left coracoid (MNZ S42312, HH1a, Fig. 6C) represents an anatid about the size of *Manuherikia lacustrina* and smaller than *Dunstanetta*, so may belong to *Matanas*. This specimen is more robust and slightly shorter than those referred to *M. lacustrina* and differs from them as follows: the acrocoracoid markedly overhangs the medial margin, the dorsal and ventral lobes of the clavicle facet are not markedly notched, the supracoracoidal sulcus extends as a deep pneumatic pocket up under the dorsal clavicle facet; the shaft is robust and aligned markedly medially relative to the sternal facet, the ventral sternal facet is robust and prominent. Its measurements are: medial length = 37.2 mm, length to top of procoracoid = 27.4 mm, least shaft width = 4.74 mm, width sternal articulation 16.25 mm. It differs markedly from most taxa, except *Miotadorna* and *Dunstanetta*, by the deep pneumatic pocket in the acrocoracoid and it differs from all tadorines by the acrocoracoid markedly overhanging the shaft medially and by its short stouter form. It further differs from dendrochenines, *Stictonetta* and *Malacorhynchus* in lacking a marked hollow on the ventral surface of the blade. While the pneumatic acrocoracoid is very different to the non-pneumatic state of *Stictonetta*, *Hymenolaimus* and *Chenonetta* as well as of *Malacorhynchus*, *Matanas* shares with these taxa the overhanging acrocoracoid.

Order ACCIPITRIFORMES Vieillot, 1816

Family ACCIPITRIDAE Vigors, 1824

Genus and species indet. (Fig. 10A)

MATERIAL. MNZ S42811, dL tibiotarsus, Croc Site L1, (Fig. 10A); MNZ S42490, dR ulna, HH2c.

MEASUREMENTS. MNZ S42811, DW = 14.2 mm (across condyles). MNZ S42490, SW maximum near distal end = 7.6 mm, length *cond. dorsalis ulnaris* = 12.4 mm, width



Figure 10 St Bathans fossils compared to Recent taxa. **A**, accipitrid gen. and species indet. MNZ S42811, dL tib; **B**, *Aquila audax* MNZ 25643, dL tib, Recent; **C**, ?Aptornithid gen. et sp. indet. MNZ S42623 phalanx IV.1; **D**, *Aptornis otidiformis* MNZ S42995, phalanx IV.1, Holocene fossil; **E**, *Macropygia amboinensis phasianella* MNZ27230, R ulna, Recent; **F**, columbid gen. et sp. indet. MNZ S42430, dR ulna, HH1a; Scale bar = 20 mm.

dorsal ulnar condyle = 11.2 mm. In ventral view the width across the *sulcus intercondylaris* = 9.0 mm.

REMARKS. In cranial aspect MNZ S42811 is relatively unworn, but posteriorly the condyles are worn to the level of the intercondylar area. The side of the medial condyle is worn but the base of the central prominence is visible. This fragment is readily identified as an accipitrid tibiotarsus by the distinct shape of the *pons supratendineus* over the centrally placed *canalis extensorius* and the shallow depth of the condyles, but few features allowing generic attribution are preserved. The area laterad of the supratendinal bridge and above the lateral condyle has a distinct shallow fossa not found in *Circus* but seen in eagles (*Aquila*, *Haliaeetus*). In cranial view, the medial condyle extends proximally to a point medial of the extensor canal, whereas in *Circus*, *Aquila* and *Haliaeetus* it ends proximally with no overlap of the extensor canal. In size, this fossil represents an accipitrid about the size of a large female extinct Eyles's harrier *Circus eylesi* Scarlett, 1953 (e.g. MNZ S33635, tibiotarsus DW = 15.9 mm) which is the largest known *Circus* species, but it is smaller than a male wedge-tailed eagle *Aquila audax* (Latham, 1802), e.g. MNZ 25956, tibiotarsus DW = 19.7 mm.

The distal ulna MNZ S42490 is from an accipitrid and is shaped most like *Aquila audax*, especially in the more elongate dorsal ulnar condyle. It lacks pneumatic foramina as found in *Gyps* or *Aegyptius*. Both *Haliaeetus leucogaster* (Gmelin, 1788), e.g. MNZ 27059, and the golden eagle *Aquila chrysaetos* (Linnaeus, 1758), e.g. MNZ 15894, have a relatively short dorsal ulnar condyle that is about as long



Figure 11 Comparison of fossil rail (Rallidae) bones (**B, C, E, F, G, I, J, K**) to those of a Recent individual *Gallirallus philippensis assimilis* MNZ 23800 (**A, D, H**). **B, C**, new sp. 1 pR hum, MNZ S42665; **F, G**, new sp. 1 dL hum, MNZ S42872; **E**, new sp. 1 R femur, MNZ S42870; **I**, new sp. 1 dR tt (small specimen), MNZ S42248; **J**, new sp. 1 dR tt (big specimen), MNZ S42869; **K**, new sp. 2 pR fem, MNZ 42638; Scale bar = 20 mm; **C** and **F** at 2x scale.

as it is wide. The *incisura tendinosa* is broad and long and thus more similar to *Aquila* than *Circus*, in which it is narrow. This fossil is from a larger bird than a large fossil *Circus eylesi* (MNZ S33635) but is smaller than a male *Aquila audax* (MNZ 25956).

Both fossils document the existence of an accipitrid larger than most *Circus* hawks but smaller than the wedge-tailed eagle *Aquila audax*. Until more complete material is found and comparisons are possible with a wider array of Accipitridae, the relationships of this fossil will remain unknown.

Order GRUIFORMES Bonaparte, 1854

Family ?APTORNITHIDAE Bonaparte, 1856

Genus and species indet. (Fig. 10C)

MATERIAL. MNZ S42623, pedal phalanx R IV.1, HH1a (Fig. 10C).

MEASUREMENTS. L = 25.7 mm, PW = 13.2 mm, proximal height = 10.4 mm, DW = 8.4 mm, distal height = 8.4 mm.

REMARKS. This phalanx is proportionally shorter than those of all anatids, ciconiiforms and phoenicopteriforms and very different in shape to those of accipitrids. Its proportions are similar to this element in gruiforms and the shape of this specimen is very similar to that of the giant extinct *Aptornis*. It is slightly smaller than this phalanx in the North Island

Aptornis otidiformis (Owen, 1844) (Fig. 10D). We thus tentatively refer MNZ S42623 to the Aptornithidae.

Family RALLIDAE Rafinesque, 1815

Genus indet.

New species 1 – magn. *Gallirallus striatus* or *G. philippensis assimilis* (Fig. 11B, C, E–G, I, J)

MATERIAL. 115 elements. All specimens, except one femur (MNZ S42870) and two carpometacarpi, are incomplete and size dimorphism is present in most elements. 3 premaxillae: S42357, S42827, S42857; 5 mandibles: S40955, S42473, S42660, S42672, S42847; 9 quadrates: S42403, S42404, S42503, S42575, S42666, S42667, S42692, S42840, S42846; 3 scapulae: S40951, S42251, S42668; 9 coracoids: S40953, S42673, S42674, S42675, S42694, S42834, S42844, S42848, S42871; 17 humeri: S40946, S40952, S42293, S42301, S42402, S42407, S42408, S42474, S42664, S42665, S42676, S42786, S42789, S42839, S42859, S42865, S42872; 5 ulnae: S42303, S42693, S42790, S42849, S42858; 1 radius S42576; 9 carpometacarpi: S40947, S40954, S40981, S42472, S42695, S42816; S42843, S42845, S42864; 2 wing phalanges: S42670, S42835; 6 femora: S42294, S42406, S42411, S42659, S42669, S42870; 34 tibiotarsi: S40106, S40107, S40108, S40444, S42224, S42225, S42247, S42248, S42291, S42295, S42299, S42300, S42302, S42339,

S42401, S42476, S42477, S42478, S42479, S42573, S42661, S42662, S42691, S42696, S42699, S42787, S42837, S42838, S42861, S42863, S42866, S42867, S42868, S42869; 12 tarsometatarsi: S40442, S40499, S42405, S42489, S42495, S42503, S42555, S42690, S42791, S42814, S42836, S42862.

New species 2 – magn. *Gallirallus philippensis goodsoni* (Fig. 11K)

MATERIAL. 1 quadrate: S.40957; 2 femora: S.42658, S.42785.

REMARKS. Rails are the most abundant taxon after anatids in the St Bathans Fauna. We have referred 118 bones to at least two taxa based on morphology and size variation. Only one major element, a femur (MNZ S42870), is complete, making it difficult to define size ranges or to associate different elements to a taxon. In the following discussion we use *Gallirallus* for the barred wing rails following Olson (1973) and Dickinson (2003).

The leg bones, especially tibiotarsi, indicate that the most common species (new sp. 1) was about the size of the slaty-breasted rail *Gallirallus striatus* (Linnaeus, 1766) e.g. MNZ 25709 or the banded rail *Gallirallus philippensis assimilis* (G. R. Gray, 1843) with distal tibiotarsus widths having a non-overlapping bimodal size distribution over the ranges 4.4–5.4 and 5.4–6.2 mm. By way of comparison, the modern *G. p. assimilis* from New Zealand, which does not have a noticeable bimodal size distribution in our specimens, although it is sexually dimorphic in size (Livezey 2003), ranges from 5.2 mm (MNZ 22107) to 6.3 mm (MNZ 23802).

For all other elements, one or two size classes predominate as for tibiotarsi and so are referred to the same taxon. There are relatively few femora and tarsometatarsi, but most are of expected size, given the distal widths of tibiotarsi. The complete femur (MNZ S42870) is of similar length to that of *G. striatus* but is slightly more robust at each end: L = 46.0 mm, PW = 8.0 mm, SW = 3.0 mm, DW = 7.6 mm (Fig. 11E).

All pectoral girdle elements are smaller than predicted, given the common fossil taxon had legs the size of *G. striatus* or *G. p. assimilis*. The partial rail humeri include seven similar in size to that of the Chatham Island rail *Cabalus modestus* (Hutton, 1872), e.g. MNZ S30115, or *Porzana* species such as the spotless crane *Porzana tabuensis* (J. F. Gmelin, 1789), e.g. MNZ 23823, while 10 are slightly larger specimens, about the size of humeri of the Auckland Island rail *Dryolimnas muelleri* (Rothschild, 1893) e.g. MNZ 25556. The widths of the proximal humeri from the ventral end of the capital groove to the dorsal tubercle range from 4.0 mm (MNZ S42665, S42786) to 4.5 mm (MNZ S42664, S42789). All 16 fossil outer wing elements are also small. For example, carpometacarpi range in total length from 12.2 mm (MNZ S42816) to 15.3 mm (MNZ S40981) with proximal widths of 3.2 mm (MNZ S42816) to 3.9 mm (MNZ S40947).

In shape, the proximal humeri resemble those of the flightless *Cabalus* far more than those of any volant rails, small or large, such as *G. philippensis*, *G. striatus*, the black-tailed native-hen *Gallinula ventralis* Gould, 1837 (e.g. MNZ 22100, 22101), or the Virginia rail *Rallus limicola* Vieillot, 1819 (e.g. MNZ 27336). The fossils feature a shallow non-pneumatic (rather than excavated) ventral pneumotricipital

fossa, a short bicipital crest (rather than one extending further distally down the humeral shaft), a low rounded (rather than more protuberant) humeral head and a narrow shaft that is ridged caudally, which are all features indicative of a flightless species (Livezey 2003: table 63, features A, B, E and M/N, respectively). To this we add the feature of the deltoid crest being rotated farther over the cranial surface, so accentuating the prominence of the dorsal tubercle. Therefore, new sp. 1 was flightless and had very reduced wings and a dimorphic size range. Sexual size dimorphism is especially prevalent in flightless rails (Livezey 2003: 94, 349).

The second fossil species (new sp. 2) is slightly larger than new sp. 1 and similar in size to the tropical banded rail *G. philippensis goodsoni* (Mathews, 1910–1911) e.g. MNZ 25269. The quadrate (MNZ S40957) is notably stouter than the other fossil quadrates. It has a particularly short ‘shaft’ leading to the process containing the quadratojugal socket, when compared with that of *G. philippensis*, the weka *G. australis* (Sparman, 1786), *Porzana* and *Gallinula ventralis*; the otic process is more stocky with a shallower *incisura intercapitularis* than that found in *G. philippensis*, *G. australis* and *Porzana* and is even stouter than the fairly stout process of *G. ventralis*. This larger quadrate probably indicates some generic diversity in the fossil rail fauna. The femora (MNZ S42658: PW = 8.5 mm, SW = 4.0; MNZ S42785: PW = 8.0 mm) are flat ventrally at the level of the trochanter and so lack the narrow ridge on the shaft laterad of a deep medially open sulcus as in new sp. 1 and they have a more rounded lateral facies at the distal end of the trochanter.

The fragmentary nature of the rail fossils precludes much discussion on phylogenetic relationships at this stage. All post-cranial bones are most similar to *Gallirallus* species, with none having any affinity to gallinules. However, some comments on the relationships can be made based on the skull fragments, which are presumed to belong to new sp. 1. The premaxilla tips (MNZ S42357, S42827, S42857) and mandible tips (MNZ S42473, S42672) are noticeably deeper and a little larger, but most closely resemble those of *G. philippensis* and resemble to a lesser extent, those of *G. australis*, *Dryolimnas muelleri*, *Porzana* and *G. striatus*. They are considerably more truncated than the long premaxilla and mandible tips of *Cabalus modestus* and *Rallus limicola* and not as broad as those of *Gallinula*. The *crista tomalis* of the premaxilla is sharp, as in *Gallirallus*, *Rallus*, *Cabalus*, *Dryolimnas*, *Porzana* and *Gallinula*, not flat and broad occlusally, as in Hawkins’ rail *Diaphorapteryx hawkinsi* (Forbes, 1892a) and the extinct Fiji rail *Vitirallus watlingi* Worthy, 2004 (Worthy 2004b) e.g. MNZ S37543. The bill fragments and the three partial posterior mandibles (MNZ S40955, S42660 and S42847) suggest that new sp. 1 had a stouter bill than that found in modern similar-sized (based on legs) *Gallirallus* species, e.g. *G. striatus* or *G. p. assimilis*.

The quadrates referred to new sp. 1 have a very prominent pterygoid articulation (MNZ S42403, S42667), an elongate mandibular articular surface (MNZ S40503, S42403, S42667 and S42846) and a relatively slender and flattened otic process (MNZ S42403, S42575, S42666, S42667, S42692, S42840 and S42846) with a deep *incisura intercapitularis* (*sensu* Howard 1929: 315). The prominent pterygoid articulation is similar to that found in *Porzana* and *Gallirallus* but is unlike that found in *Gallinula*. The otic processes of the fossils are most like those of *Gallirallus* – the processes

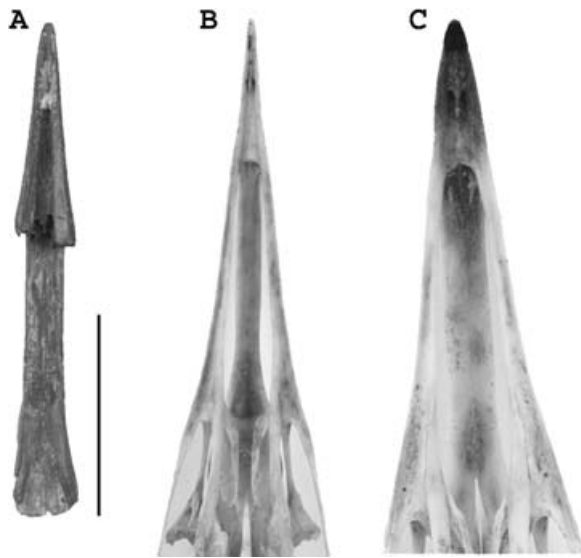


Figure 12 Gull (Laridae) premaxilla in occlusal view. **A**, ?Laridae, gen. et sp. indet. fossil MNZ S42681; **B**, *Larus bulleri* MNZ 25098, Recent; **C**, *Larus dominicanus* MNZ 24270, Recent. Scale bar = 20 mm.

are not quite as elongate as those found in *Porzana* or as stout as those of *Gallinula*. The elongate mandibular articular surface of the fossils is similar to that found in *G. australis* and close in shape to that of *Porzana* and *G. philippensis* but is relatively unlike the short articular surface found in *Gallinula*. Thus, among the compared taxa, the fossils have most similarity to those of *Gallirallus*.

All of the fossils represent fairly small taxa, none being larger than *G. philippensis*. Thus the Manuherikia rail fauna appears to have lacked larger species, of which there was a considerable diversity in the Recent fauna of New Zealand, e.g. *G. australis*, *Diaphorapteryx*, *Gallinula*, *Porphyrio* and *Fulica* species (Holdaway *et al.* 2001).

Order CHARADRIIFORMES Huxley, 1867

Family ?LARIDAE Rafinesque, 1815

Genus and species indet. (Fig. 12A)

MATERIAL. MNZ S42736, premaxilla, HH1a; MNZ S42681, premaxilla, HH1a (Fig. 12A); MNZ S41058, proximal end R scapula, Croc Site L1.

MEASUREMENTS. MNZ S42736, total length = 47.7 mm, symphyseal length = 19.0 mm (tip is worn); MNZ S42681, total length = ~50.0 mm, symphyseal length = 21.7 mm.

REMARKS. Both premaxillae MNZ S42736 and MNZ S42681 are referred to Laridae based on their overall similarity to gulls, more so than to any other taxon. They feature a *rostrum maxillare* with the following features: it is shorter than the *os nasale*; it has a downcurved tip; and it has flattened sides resulting in an acute rather than broadly rounded dorsal surface. The premaxillae are thus similar to galliralline rails, which also have a shorter maxillary rostrum than the supporting *os nasale*, but have a broadly dorsally-rounded maxillary rostrum and generally not such a decurved tip. Terns e.g. *Sterna bergii*, which is the most similar tern to the fossil, have a longer maxillary rostrum than the *os na-*

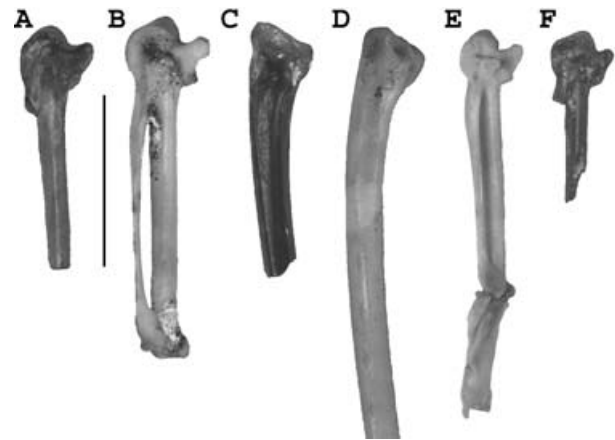


Figure 13 Charadriiform bones. **A**, fossil pL cmc MNZ S42434; **B**, *Charadrius bicinctus* MNZ 24688, L cmc, Recent; **C**, fossil pL ulna MNZ S42807; **D**, *C. bicinctus* MNZ 24688, L ulna, Recent; **E**, *Calidris ruficollis* MNZ 23292, L cmc, Recent; **F**, fossil pL cmc MNZ S42415. Scale bar = 10 mm.

sale. The fossils indicate a species slightly smaller than *Larus dominicanus* Lichtenstein, 1823 (e.g. MNZ 24270: Fig. 12C) but they feature a straighter and more elongate bill tip that is very similar in shape, although larger, to that of *L. bulleri* Hutton, 1871 (e.g. MNZ 25098: Fig. 12B). Unlike the bill of *L. dominicanus*, but like that of *L. bulleri*, on the fossil premaxillae the *crista tomalis* is thickened along its length (Fig. 12A). This feature is generally lacking in gulls, but is a feature of some birds that manipulate prey in their bills, e.g. *Phalacrocorax* species, so perhaps these gulls were fish eaters. *Larus bulleri* preys on a variety of food, including insects captured aerially (Higgins & Davies 1996).

The scapula, MNZ S41050, has the rather featureless shape of charadriiforms and is of appropriate size to belong to the bird that the above premaxillae are derived from.

Family, genus and species undetermined (Fig. 13)

MATERIAL. Three bones from Croc Site Layer 1 are from a very small charadriiform the size of a red-necked stint *Calidris ruficollis* (Pallas, 1776) e.g. MNZ 23292: MNZ S42416, a fragment of a pR hum; MNZ S42415, a pL cmc (Fig. 13F); MNZ S42435, a pL cmc.

Eight mainly fragmentary bones are from a charadriiform that differs little from the New Zealand banded dotterel *Charadrius bicinctus* Jardine & Selby, 1827, e.g. MNZ 23889 or 24688: MNZ S42413, dR ulna, Croc Site L1; MNZ S42807, pL ulna, HH1a (Fig. 13C); MNZ S42434, pL cmc, Croc Site L1 (Fig. 13A); MNZ S42877, pL cmc, HH2c; MNZ S42414, pR scap, Croc Site L1; MNZ S42850, L scap, HH1a; MNZ S42860, ant stern, HH1a; MNZ S42475, R cor, Croc Site L1.

REMARKS. These few bones, assigned on the basis of overall similarity, are sufficient to indicate the presence of at least two small waders in the fossil fauna. The genus *Calidris* includes the smallest waders in the world and the fossil is of similar size to *C. ruficollis*, one of the smallest species in the genus. More diagnostic material is required to determine whether the genera *Calidris* and *Charadrius* were indeed a part of the fauna.

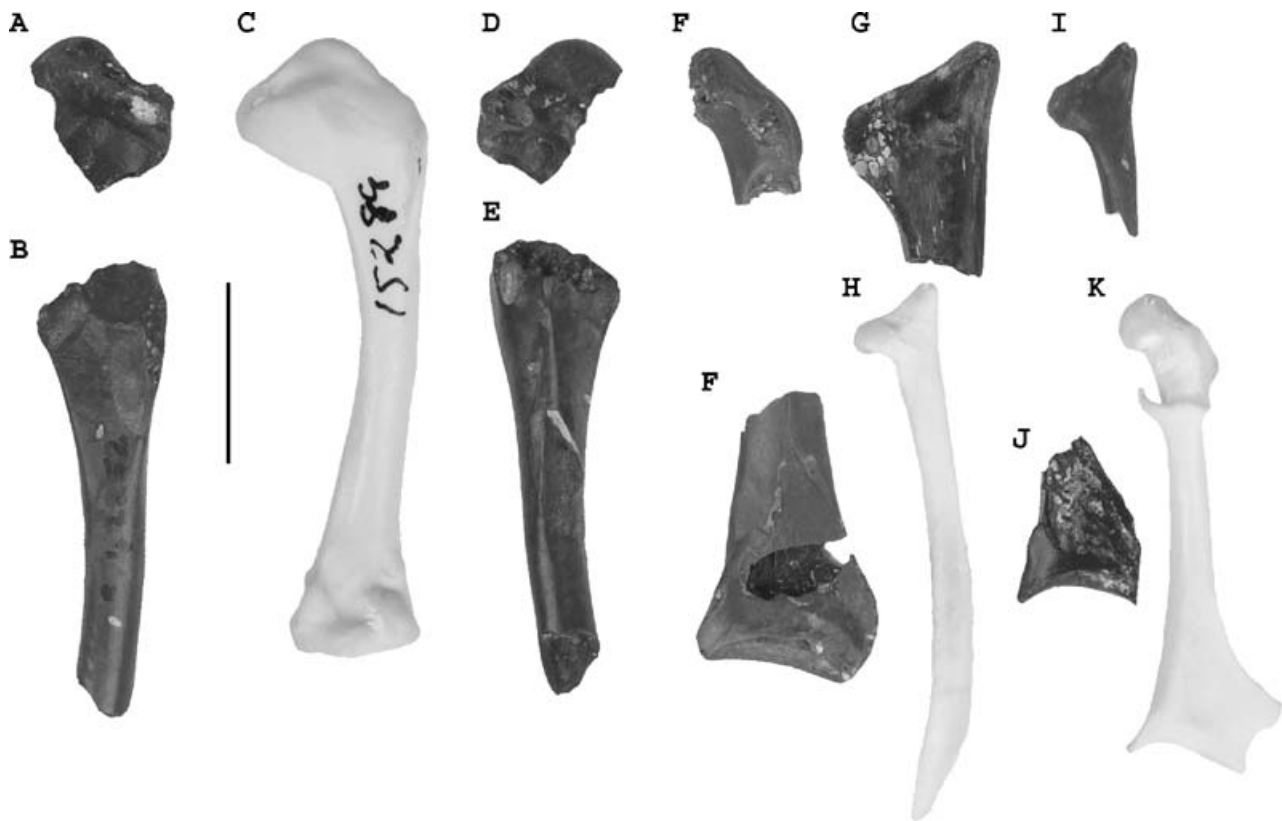


Figure 14 Representative fossil parrot bones, Psittacidae gen. et sp. indet., from St Bathans compared to those of Recent *Cyanoramphus unicolor* MNZ 15289 (C, H, K). A, D, small species, MNZ S42854 pR hum; B, E, small species, MNZ S42252 shaft L hum; C, MNZ 15289 L humerus; F, medium-sized species, MNZ S42550 humeral and sternal parts R cor; G, large species, MNZ S42246 L scap; H, MNZ 15289 L scap; I, small species, MNZ S42833 L scap; J, small species, sternal end R cor MNZ S42855; K, MNZ 15289 R cor. Scale bar = 10 mm.

Order COLUMBIFORMES Latham, 1790

Family COLUMBIDAE Illiger, 1811

Genus and species indet. (Fig. 10F)

MATERIAL. MNZ S42430, dR ulna, HH1a.

MEASUREMENTS. Dorsoventral SW = 3.04 mm, length of *cond. dorsalis ulnaris* = 5.26 mm, width of *cond. dorsalis ulnaris* = 5.60 mm.

REMARKS. MNZ S42430 is referred to Columbidae because of the following features: the dorsal condyle is as long as it is wide and distinctly concave across the base of its caudal face, in distal view the caudal face of the dorsal condyle and the dorsal facies form a right angle and the shaft has prominent *papillae remigales caudales*. It is of similar size to *Ptilinopus magnificus* (MNZ 27278). Of the taxa in the Australasian–southwest Pacific region, it is thus bigger than all other *Ptilinopus* species, all *Phaps* and *Gallicolumba* species and it is similar in size to some *Macropygia*, *Columba* and smaller *Ducula* species. The carpal tuberculum is short and robust, as in the brown cuckoo-dove *Macropygia amboinensis phasianella* (Temminck, 1821) (MNZ 27230: Fig. 10E) and *Ptilinopus* spp., rather than it being longer, as in the feral pigeon *Columba livia* Gmelin, 1789 (MNZ 14973). The spacing of the caudal remigal papillae is most similar to *Ducula* (e.g. the Pacific pigeon *D. pacifica* (Gmelin, 1789): MNZ 27340), albeit from a smaller bird, indicating a more

elongate and straighter ulna than in *M. a. phasianella* or in the Wompoo fruit dove *Ptilinopus magnificus* (Temminck, 1821), which otherwise are of comparable size.

A distal ulna is insufficiently diagnostic to assign to any genus within columbids, so this fossil indicates only that a medium-sized pigeon was present in the fauna.

Order PSITTACIFORMES Wagler 1827

Family PSITTACIDAE Rafinesque, 1815

Genus and species indet. (Figs 14A, B, D–F, G, I, J)

MATERIAL. Sixteen fossils represent a parrot about the size of the crimson rosella *Platycercus elegans* (Gmelin, 1788), e.g. MNZ 26998, or the Antipodes parakeet *Cyanoramphus unicolor* (Lear, 1831), e.g. MNZ 15289 (Figs 14C, H, K).

A shaft and part proximal L humerus (MNZ S42252) from Croc Site L1 (Figs 14B, E) is most similar to parrots in that the insertion point for the principle part of the tendon of *M. supracoracoideus* is a recessed pit, not a ‘*tuberculum dorsale*’, that is flush with the dorsal surface of the deltoid crest, and in that there is a tuberosity on the *margo caudalis* just distad of the base of the said pit. The base of the deltoid crest is thick and the cranial surface adjacent to the proximal end of the deltoid crest has a shallow fossa typical of parrots. The fossil differs from *Platycercus*, *Cyanoramphus* and *Nestor* in that the bicipital crest joins to the shaft at a shallow angle, not at near right angles. It is similar to *Nestor*

and *Cyanoramphus* in the presence of a distinct ridge aligned slightly obliquely on the shaft caudally. A part proximal R humerus (MNZ S42854) from HH1a (Figs 14A, D) preserves part of the head, the complete bicapital crest and the ventral tubercle and is similar to *Cyanoramphus*.

Two sternal ends of R coracoids from HH1a, MNZ S42855 (with a width across sternal facet of 7.0 mm; Fig. 14J) and MNZ S42663, differ markedly from all compared species in that the medial angle is less acute and has a large flange extending above it.

Other bones provisionally referred to this taxon are: MNZ S42833, L scap, HH1a, width across articular surfaces = 6.2 mm (Fig. 14I); MNZ S42615, dL ulna, HH1a; MNZ S42671, dL ulna, HH1a; MNZ S42832, dL ulna, HH1a; MNZ S42409, pL cmc, Croc Site L1, proximal width 5.1 mm; MNZ S42480, R cmc, Croc Site L1, length 24.8 mm, approximate proximal width 5.1 mm; MNZ S40447, last thoracic vertebra, HH1a (this fossil has a deeper lateral fossa in the *corpus vertebrae* than in the compared platycercines); MNZ S42723, pR fem, HH1a, proximal width = 5.46 mm, proximal depth = 3.0 mm; MNZ S42784, dR tib, HH1a, distal width = c. 5.8 mm, width at tendinal bridge = 4.7 mm; MNZ S42853, dL tib, HH1a, width at tendinal bridge = 4.6 mm; MNZ S42614, trochlea metatarsi III of R tmt, HH1a; MNZ S42856, trochlea III and part of distal end including distal foramen of L tmt, HH1a.

Two specimens represent a parrot slightly smaller than the North Island kaka *Nestor meridionalis septentrionalis* Lorenz, 1896, e.g. MNZ 26892. The dR femur MNZ S42400, Croc Site L1, distal width = 9.5 mm, is referred to Psittaciformes on general similarity to platycercine femora. It differs in having a lower ridge bounding the popliteal fossa medially, but is similar to *Cyanoramphus* in having a shallow fossa above the *trochlea fibularis* and a large *impressio ansae m. iliofibularis* that is separated from the fibula trochlea. In *Nestor*, the fossa above the fibular trochlea is very deep and the *impressio ansae m. iliofibularis* abuts the fibular trochlea. The unconnected humeral and sternal ends of a R coracoid, MNZ S42550 (Fig. 14F), HH1a, apparently broken during excavation, do not articulate but have similar preservation and derive from the same small lot of sediment concentrate and so are assumed to be the fragmented parts of a single bone. The sternal end differs markedly from all compared Recent species in that the medial angle is less acute and has a large flange extending above it and so is similar to the smaller fossil parrot types. Proximally, the acrocoracoid has large pneumatic foramina, as in *Cyanoramphus* but unlike *Nestor*.

One specimen (MNZ S42246, pL scapula, Croc Site L1; Fig. 14G) represents an even larger species, similar in size to the kea *Nestor notabilis* Gould, 1856, e.g. MNZ 22028.

REMARKS. The available material indicates that at least three species of parrots were present in the St Bathans Fauna. The form of the coracoids (S42550, S42663 and S42855), is unlike that of any parrots examined so far and since all are similar, this indicates that the small and medium-sized taxa may be congeneric. The fossil coracoids have a relatively deep *impressio m. sternocoracoidei*, which form is approached in the platycercine taxa examined, but is unlike the very shallow impression found in *Cacatuidae*. In contrast, the coracoid flange above the medial angle is similar to that in *Cacatua galerita* (Latham, 1790) but this feature was not seen in any platycercine taxon. The form of the scapulae also indicates

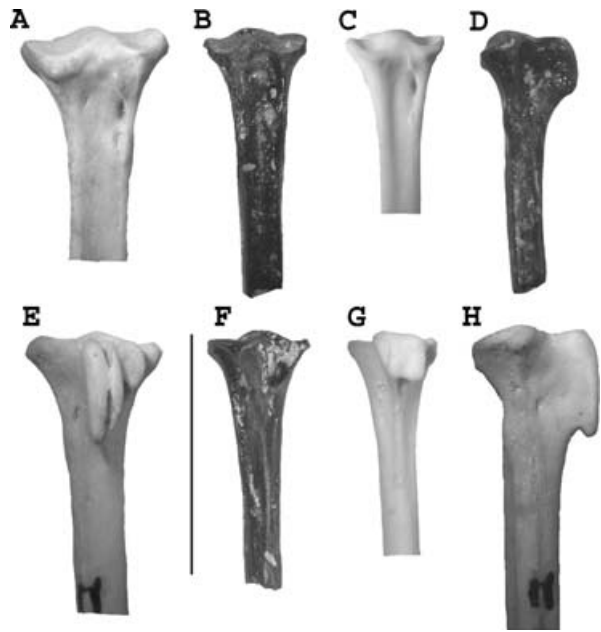


Figure 15 Tarsometatarsi of owl nightjars *Aegotheles* sp. **A–D** in dorsal view, **E–H** in plantar view. **A, E, H**, *A. novaezelandiae*, MNZ S1002, Recent; **B, D, F**, *Aegotheles* sp., fossil, MNZ S42800; **C, G**, *Aegotheles cristatus* MNZ 26990, Recent. Scale bar = 10 mm.

that the fossil taxa differ from *Cacatuidae*, whose members have scapulae with pneumatic foramina in the acromion. Platycercine taxa have scapulae that lack pneumatic fossae and are thus like the fossils, however until more complete material and wider comparisons have been made, it would be premature to accept any relationship between this group and the fossils.

Order AEGOTHELIFORMES Simonetta, 1967

Family AEGOTHELIDAE Bonaparte, 1853

The family Aegothelidae has usually been listed in Caprimulgiformes but much recent work, reviewed by Sangster (2005), supports the sister-group relationship of Aegothelidae (owllet-nightjars) and Apodiformes (swifts and hummingbirds) to the exclusion of other members of Caprimulgiformes, first proposed by Mayr (2002a, 2003). Sangster (2005) used *Daedalornithes* as the new name for this clade, but it requires elevation of Aegothelidae to ordinal status as first recognised by Simonetta (1967).

Genus AEGOTHELES Vigors & Horsfield, 1827

Aegotheles sp. indet. (Figs 15B, D, F)

MATERIAL. MNZ S42800, proximal right tarsometatarsus lacking lateral side of hypotarsus, HH1a.

MEASUREMENTS. Proximal width = 4.3 mm; proximal depth = 4.1 mm; least shaft width = 1.6 mm; preserved length = 11 mm, which is likely to be less than half of the total length.

REMARKS. This fossil is identified as *Aegotheles* because of the following combination of features: lateral and medial cotyla overhang shaft to equal extent; hypotarsus is composed

of two main ridges separated by an enclosed canal; there is a deep broad *fossa parahypotarsalis medialis* within which the medial vascular foramen opens level with the distal end of the hypotarsus as a small hole; the intercotylar eminence is low and rounded, only slightly elevated above the cotylar margins; anteriorly, the extensor sulcus is shallow with a large medial proximal vascular foramen sited just proximad of a large, ovate, elevated *tuberositas m. tib. cranialis* that abuts the medial facies; the shaft (although incompletely preserved) is apparently gracile and elongate, with the anterior facies flat and the posterior facies convex.

All members of Apodiformes have very short and gracile tarsometatarsi that differ markedly from those of *Aegothales*.

Members of Caprimulgiforms, to which *Aegothales* have been generally allied, differ as follows. Podargidae, e.g. *Podargus strigoides* (Latham, 1802) e.g. MNZ 27001, differ by their much larger size, short stout tarsometatarsi with two small centrally placed proximal vascular foramina in the extensor sulcus and by having a hypotarsal structure of two principle canals and three ridges, of which the medial ridge is shorter than the middle one.

The Caprimulgidae, e.g. *Eurostopodus mystacalis* (Temminck, 1826) e.g. MNZ 27369 and 27370, and *E. argus* (Hartert, 1892) e.g. MNZ 27371, also differ greatly from *Aegothales* in tarsometatarsal structure. They have short stout tarsometatarsi with a single centrally placed opening in the extensor sulcus from which lateral and medial proximal vascular foramina open interiorly, the *tuberositas m. tib. cranialis* is centrally placed in the extensor sulcus, the shaft is concave posteriorly with a prominent medial crest, but the hypotarsus has a single canal as in aegothelids.

The fossil is slightly larger than the tarsometatarsus of *Aegothales cristatus* (Shaw, 1790) e.g. MNZ 26990 (Figs 15C, G), 22103, and is smaller than those of *A. novaezealandiae* (Scarlett, 1968) (Figs 15A, E, H) or *A. savesi* Layard & Layard, 1881 (specimens from Pindai Cave, Testpit 4, spits 22–24, 21 July 2003, MNZ unreg). It further differs from *A. cristatus* and is similar to *A. novaezealandiae* and *A. savesi* in that the medial hypotarsal ridge is higher or extends more plantarly than the rest of the hypotarsus (*A. cristatus* has a flat plantar surface to the hypotarsus). The medial hypotarsal ridge is elongate, at least twice as long as the medial ridge (as in *A. novaezealandiae*, but unlike *A. cristatus* where they are of equal length and *A. savesi* where the medial is only a little longer than the lateral ridge). The fossil differs from *A. savesi* in that the medial parahypotarsal fossa is smaller, being of similar extent to that in *A. novaezealandiae*.

Family APODIDAE Olphe-Gaillard, 1887

Genus COLLOCALIA Gray, 1840

Collocalia sp. indet. (Fig. 16A)

MATERIAL. MNZ S42799, R ulna, HH1a.

MEASUREMENTS. Total length = 11.2 mm; PW = 2.9 mm; SW = 1.4 mm; DW = 2.4 mm.

REMARKS. This ulna is from an apodid swift and is very much smaller than that from either of the chaeturines: *Hirundapus caudacutus* (Latham, 1802) (e.g. MNZ 21833) or *H. cochinchinensis* (Oustalet, 1878) (e.g. MNZ 25710)



Figure 16 Right ulnae of swiftlets *Collocalia* sp. **A**, *Collocalia* sp. fossil, MNZ 42799; **B**, *C. spodiopygia*, MNZ 26799, Recent. Scale bar = 5 mm.

and much smaller than the apodine swift *Apus affinis* (Gray, 1830) (e.g. MNZ 24340). It is similar in size and form to collocaline swiftlets *Collocalia* species (of which *Aerodromus* is here considered a synonym, following Boles (2001) and Steadman (2002)), especially in the short acromion (more anteriorly directed and longer in *Apus*), presence of a shallow fossa on the lateral facies below the *cond. ventralis* (lacking in *Apus*) and in the shape of the *tuber. lig. collateralis ventralis*, which in the fossil is widest medially and narrows dorsally (in *Apus* it is broad over the medial–dorsal extent). The fossil is slightly longer and more stout than *C. spodiopygia* (Peale, 1848) (e.g. MNZ 26799, Fig. 16B: TL = 10.6 mm; THW colln, Fiji 5 June 1997, TL = 10.9 mm) and *C. esculenta* (Linnaeus, 1758) (MNZ 23002, TL = 10.1 mm; MNZ 22993, TL = 10.4 mm; MNZ 22991, TL = 10.3 mm). It is substantially smaller than the ulnae of the mountain swiftlet *Collocalia hirundinacea* Stresemann, 1914, e.g. AU9481, V347 TL = 13.6 mm, AU9481, V348 TL = 13.7 mm and AU9481, V349 TL = 13.3 mm, from Papua New Guinea. The fossil differs in form, with the ventral condyle being relatively more elongate dorsoventrally than in the modern taxa compared. The channel separating the dorsal cotyla from the olecranon (which opens into the dorso-caudal part of the ventral cotyla) is also relatively wider and deeper than in the modern taxa. In the fossil, the brachial impression is relatively shallow, as in *C. esculenta*, and unlike the deeper condition of *C. spodiopygia*.

Recently, *Collocalia buday* Boles, 2001 was described from the Oligo–Miocene of Australia. It is a large species, larger than all compared *Collocalia* species (Boles 2001) so, while comparative elements are not yet available, the New Zealand fossil derives from a smaller species. Boles (2001) presented data indicating that *C. maxima* (Hume, 1878), *C. brevirostris* (Horsfield, 1840) and *C. inexpectata* (Hume, 1873) are a little larger than *C. spodiopygia* and thus are

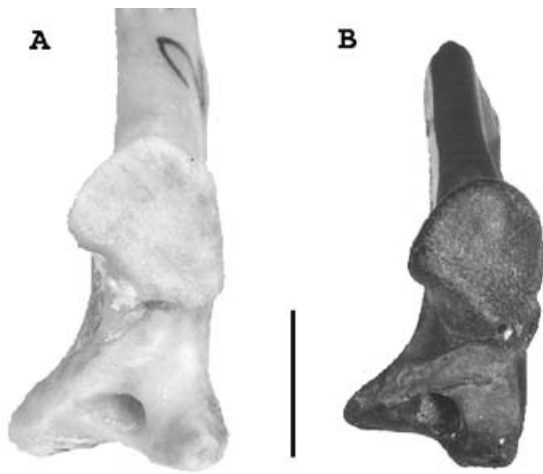


Figure 17 Passerine right scapulae. **A**, *Strepera graculina* MNZ 27326, Recent; **B**, fossil MNZ S41061. Scale bar = 5 mm.

likely to have similar ulnae length as the fossil described here. Until wider comparisons are possible, all that can be determined of this fossil is that a collocaline swiftlet was part of the St Bathans Fauna.

Order PASSERIFORMES Linnaeus, 1758

Family CRACTICIDAE Amadon, 1943

Genus and species indet. (Fig. 17B)

MATERIAL. MNZ S41061, R scapula, Croc Site L1.

REMARKS. This well preserved passerine scapula is referred to the Cracticidae because of the combination of the following characters: (1) the acromion is short and robust; (2) the angle of a line linking the acromion with the lateral side of the coracoid tubercle and the lateral side of the humeral articular facet is about 90°; (3) there is a large pneumatic foramen in the base of the coracoid tubercle between it and the acromion.

The scapula in species within Callaeidae (New Zealand wattlebirds), Corcoracidae (Australian mudnesters) and Corvidae (crows and jays), which include relatively large taxa, such as the fossil represents, all lack such a pneumatic foramen. An exception is the white-winged cough *Corcorax melanorhamphos* (Vieillot, 1817), which in some individuals has a small foramen, e.g. MNZ 27034, but in others does not e.g. MNZ 27035. However, the acromion of the coughts extends well dorsad of the coracoid tubercle, unlike in the fossil.

Within the Australasian fauna, some taxa are known to have a similarly placed fossa. These include the meliphagids, e.g. pied honeyeater *Certhionyx variegatus* Lesson, 1830 e.g. MNZ 26996, New Caledonian friarbird *Philemon diemenensis* (Lesson, 1831) e.g. MNZ 22996 and the red wattlebird *Anthochaera carunculata* (Shaw, 1790) (Walter Boles, pers. comm., 28 June 2004), but not the New Zealand *Prosthemadera*, *Anthornis* and *Notiomystis*. The pachycephalids e.g. rufous whistler *Pachycephala rufiventris* (Latham, 1802) e.g. MNZ 26997, grey shrike-thrush *Colluricincla harmonica* (Latham, 1802) (Walter Boles, pers. comm., 28 June 2004) and the New Zealand piopio *Turnagra*

spp, Turnagridae e.g. MNZ 1390 (these are allied to pachycephalids by Schodde & Mason 1999: 432) also have a large fossa. Lastly, some monarchines have a similar fossa e.g. southern shrikebill *Clytorhynchus pachycephaloides* Elliot, 1870 and magpie-lark *Grallina cyanoleuca* (Latham, 1802) e.g. MNZ 27036. All of these taxa are very much smaller birds in groups that are not known to have any members as large as that represented by the fossil. Also, in all these taxa, the acromion is elongate and flattened unlike the fossil, except for *Philemon* which differs markedly in having a short acromion but which is still flattened lateromedially and has a very large coracoid tubercle that is about twice the size of the acromion.

There are only four Australasian families with relatively large taxa that were found to have a pneumatic foramen in the scapula. The lyrebirds, Menuridae (*Menura novaehollandiae* Latham, 1802 e.g. MNZ 27159), have variation in the size of the pneumatic foramen both within and between individuals (pers. obs; Walter Boles, pers. comm., 28 June 2004). However, the shape of the lyrebird's scapula differs markedly from cracticids, with the coracoid tubercle extending markedly above the lateral facies and the acromion being relatively longer and flattened.

The bowerbirds Ptilinorhynchidae include no taxa as large as the fossil, but several species were found to have large pneumatic foramina in the scapula e.g. the satin bowerbird *Ptilinorhynchus violaceus* (Vieillot, 1816) e.g. MNZ 16048, green catbird *Ailuroedus crassirostris* (Paykull, 1815) and fawn-breasted bowerbird *Chlamydera cerviniventris* Gould, 1850 (Walter Boles, pers. comm., 28 June 2004). The scapula of *Ptilinorhynchus violaceus* differs in shape from cracticids, with the acromion being more produced dorsally such that a line linking the acromion, the tip of the coracoid tubercle and the lateral margin of the humeral articular facet forms a wide angle.

Birds of paradise (Paradisaeidae) have not been widely examined by us, but this is a highly tropical group whose centre of diversity is in the mountains of Papua New Guinea and for which there are only four species in tropical northern Australia (Schodde & Mason 1999). However, the scapula of at least some species has a large pneumatic foramen e.g. trumpet manucode *Manucodia keraudrenii* (Lesson & Garnot, 1826) and magnificent riflebird *Ptiloris magnificus* (Vieillot, 1819) (Walter Boles, pers. comm., 28 June 2004). The scapula of *Manucodia* is very different to cracticids and is shaped more like that of *Corvus* (which differ in lacking a pneumatic foramen), with the acromion positioned well dorsad of the coracoid tubercle so that the angle of the line linking the acromion with the lateral side of the coracoid tubercle and the lateral side of the humeral articular facet is about 120°. Moreover, the acromion of *Manucodia* is lateromedially flattened and the coracoid tubercle is relatively small.

The butcherbirds Cracticidae, which includes Australian magpies and currawongs, is the only other family whose members have a large pneumatic foramen in the scapula. Cracticids have recently been included as a subfamily in Artamidae by Schodde & Mason (1999), but here we follow Dickinson (2003). The scapula of the white-breasted woodswallow, *Artamus leucorhynchus melaleucus* Wagler, 1827 e.g. MNZ 22995 and the dusky woodswallow, *A. cyanopterus* (Latham, 1802) e.g. MNZ 27033, have a short and not flattened acromion as in cracticids, but they lack a pneumatic foramen.

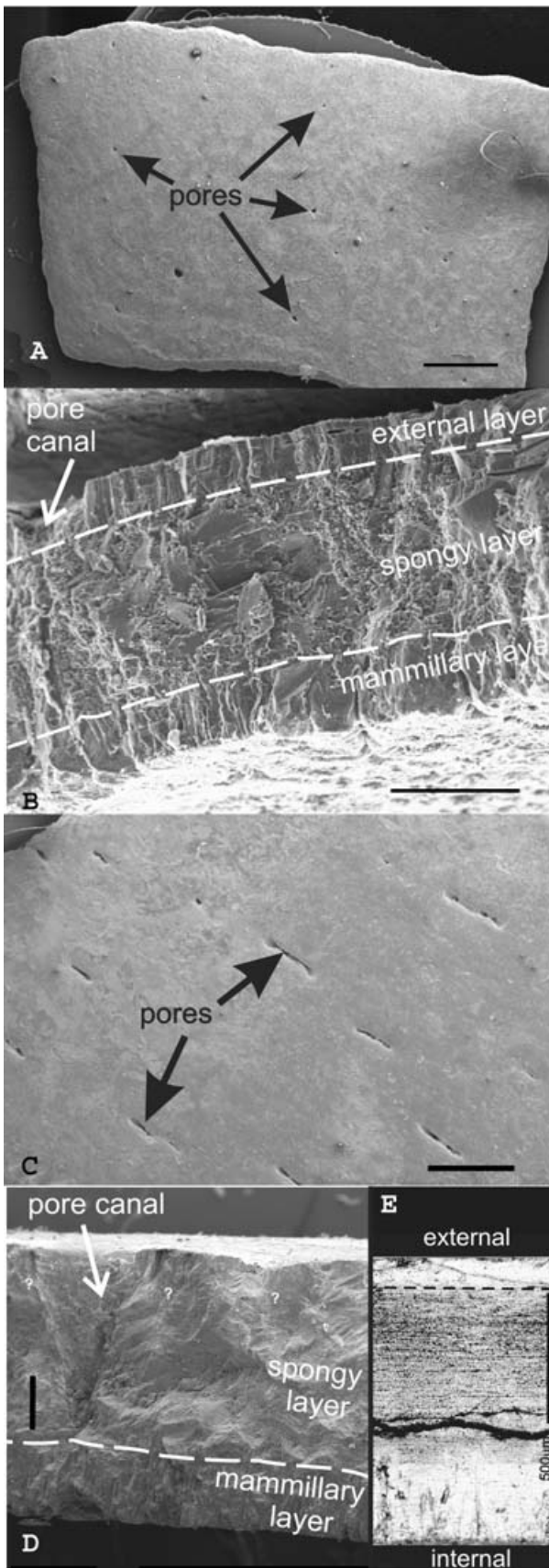


Figure 18 Avian eggshell from the St Bathans Fauna. **A**, Scanning electron micrograph (SEM) showing the general appearance of the thin eggshell; **B**, SEM of a cross-section of the thin (?anatid) eggshell

The butcherbirds *Cracticus* species e.g. *C. torquatus* (Latham, 1802) e.g. MNZ 27037, are notably smaller than other cracticids, but they have similar-shaped scapulae to those of species in other genera in the family. The species in *Gymnorhina* and *Strepera* have scapulae of similar size to the fossil, which measures 7.3 mm from the acromion to the ventral side of the humeral articular facet. In *Gymnorhina tibicen* (Latham, 1802) e.g. MNZ 16060, 12256, 13695, 11404, 23534 and 24235, the acromion is a little more hooked dorsally than in *Strepera graculina* (Shaw, 1790) e.g. MNZ 27326 and 27030, or in the fossil. In both *Gymnorhina* and *Strepera*, the coracoid tubercle varies considerably in shape, as does the size of the pneumatic fossa, but in all specimens examined it protrudes above the lateral facies. In the fossil it does not.

This fossil strongly suggests that a cracticid of similar size to an Australian magpie or currawong was present in the fauna.

Passerine family, genus, species indet.

MATERIAL. Ten bones are referred to passerines, family and species indeterminate, as follows: MNZ S42250, Croc Site L1, dL tmt; MNZ S42433, Croc Site L1, pL tmt; MNZ S42535, Croc Site L1, pR cmc; MNZ S42815, Croc Site L1, dR tmt; MNZ S40448, HH1a, dR tmt; MNZ S40956, HH1a, pL cmc; MNZ S42340, HH1a, dR tmt; MNZ S42806, HH1a, dR tmt; MNZ S42842, HH1a, dL ulna; MNZ S42852, HH1a, mandible tip.

REMARKS. A minimum of two taxa based on size are represented. MNZ S42815 is the largest and represents a bird about the size of a tui *Prosthemadera novaeseelandiae* (Gmelin, 1788). The rest could derive from a single species and are from a bird about the size of a North Island saddleback *Philesturnus rufusater* (Lesson, 1828).

Bird, family, genus, species indet.

MATERIAL. Several bone fragments (40968, S42245 and S42812) are from moa-sized birds, as indicated by shaft cortex thicknesses of ca. 4.0, 3.5 and 4.0–4.5 mm, respectively. MNZ S42812 could be a fragment of a right tibiotarsus, preserving the fossa for the unfused astragalus in a juvenile bird. Whatever their true identity, these fragments reveal a bird larger than any considered above.

Avian eggshell – family, genus, species indet.

MATERIAL. Avian eggshell is common in the Bannockburn Formation, but most is thin (<0.5 mm) and presumed to be from the abundant anatids in the deposit. It has the usual neognath structure of three prominent layers: (1) a mammillary zone, 28% of thickness, (2) a squamatic zone (spongy layer), 54% of thickness and (3) an external zone, 18% of thickness (Figs 18A & B).

showing three prominent layers; **C**, SEM of the external surface of the ?moa eggshell showing the characteristic elongate pores and smooth surface; **D**, SEM of a broken section of the ?moa eggshell showing the structure; **E**, thin section of the ?moa eggshell showing structure. Scale bars: **A**, **C** = 1 mm; **B**, **D** = 100 μ m.

Table 8 Specimens of relatively thick eggshell that represent a bird the size of a small moa (Aves: Dinornithiformes).

MNZ No.	Site name		Thickness (mm)
S 40935	Croc Site, layer 1	1 frag	0.95
S 40936	Vinegar Hill	8 frags	1.00, 1.10, 0.90, 0.90, 1.10, 1.06, 1.10, 1.10
S 40937.1	HH1b	1 frag	0.86
S 40937.2	HH1b	1 frag	1.68
S 40938.1-3	HH1b	3 parts 1 frag	1.10
S 40938.4	HH1b	1 frag	0.90
S 40938.5-7	HH1b	3 parts 1 frag	1.14
S 40939	HH1b	1 frag	1.12

Avian eggshell – Dinornithiformes, family, genus, species indeterminate

Avian eggshell, greater than 0.8 mm thick is rare in the Banockburn Formation, with most falling in a single thickness class (Table 8). This shell is 0.86–1.14 mm thick (mean = 1.02 mm, standard error = 0.0269, $n = 14$) and is of appropriate size to be from a small moa. It has a mammillary zone of 30% of the shell thickness in which the mammillae are higher than wide, a well defined squamatic zone of 65% of the shell thickness with a weakly horizontally aligned structure and a poorly defined external zone that is only 5% of the shell thickness, at maximum, with a smoothly homogeneous structure (Figs 18D & E). Externally the surface is smooth with slit-like, elongate branching pores (Fig. 18C). This structure is identical to that seen in moa (Aves, Dinornithiformes: Tyler 1957; Tyler & Simkiss 1960; Zelenitsky & Modesto 2003) and the thickness is similar to that found in smaller moa taxa (Gill 2000). A single piece is much thicker at 1.68 mm (Table 8) and appears to have a second spongy layer under a distinct external layer. It is unclear whether this is a result of diagenesis or indicates a distinct taxon.

REMARKS. The thicker shell fragments support the contention that moa ancestors were present in the environment about Lake Manuherikia in the Early–Middle Miocene, despite the lack of definitive osseous fossils (although the large bone fragments discussed above could be from moa). The thickness of these egg fragments indicates the presence of a bird as large as the moa *Anomalopteryx*, which suggests that this presumed moa precursor was already of giant stature and flightless.

DISCUSSION

The significance of the New Zealand Miocene avifauna

Procellariiformes

The diving petrel *Pelecanoides miokuaka* is by far the oldest representative of the Pelecanoididae known. At 15–20 million years old it is the first Miocene record of the family and 10–15 million years older than the previous oldest fossil record for this family in the early Pliocene (Olson 1985a). All four modern petrel (Procellariiformes) families (albatrosses – Diomedidae; fulmars, gadfly petrels, prions and shearwaters – Procellariidae; stormpetrels – Hydrobatidae; diving petrels – Pelecanoididae) now have a Miocene

fossil record (Warham 1996). Olson (1985a) described the Pliocene fossils (from South Africa) as a new species *Pelecanoides cymatotrypetes*, stating that it ‘differs only in minor details from living species of *Pelecanoides*.’ The fact that the well-preserved distal humerus of *P. miokuaka* appears relatively similar to modern taxa and the extinct Pliocene species is little different from modern forms, shows that the family diverged from other Procellariiformes at least by the early Miocene and has maintained a highly stable morphology to the present day. Viot *et al.* (1993) interpreted molecular data to infer that diving petrels originated as a distinct lineage before the Early Miocene. Penhallurick & Wink (2004) suggested from molecular data that the extant *Pelecanoides* species have a common origin no younger than 45.8 Ma. *Pelecanoides miokuaka* certainly indicates the genus existed at about 20 Ma.

The finding of a diving petrel at the Miocene lake site suggests that the species was breeding nearby. Petrels are pelagic marine species that only come ashore to nest and do not utilise freshwater bodies (Warham 1996). The probability of finding a petrel bone in a lake deposit seems low, unless there were large numbers of petrels nesting in the land adjacent to the lake. Thus the modern importance of petrels as major contributors of marine nutrients to terrestrial ecosystems (Worthy & Holdaway 2002) is probably a longstanding feature of New Zealand’s history.

Anseriformes

In Australia, the oldest anatid fossils are known from the late Oligocene–Miocene lacustrine deposits of the Lake Eyre and Tarkarooloo basins of central Australia (Vickers-Rich 1991) but the material remains undescribed. All nine extinct taxa named by de Vis from Pliocene–Pleistocene deposits have been referred to modern taxa by Olson (1977b) and no other extinct anatids have been described from Australia. No extant taxa are known from pre-Pliocene deposits (Vickers-Rich 1991; T.H.W., pers. obs.).

The most well known ducks of the Lower Miocene of the northern Hemisphere are relatively primitive forms that do not belong in *Anas*. The early Miocene *Dendrochen robusta* Miller, 1944 from South Dakota (USA), was made the type genus of Dendrocheninae by Livezey & Martin (1988). The similarly primitive anatid from North America *Anas* (= *Querquedula*) *integra* (Miller, 1944), also from the Lower Miocene of South Dakota, was transferred to *Dendrochen* by Cheneval (1987). The unusual swan-sized diver *Paranyroca magna* Miller & Compton, 1939, of the early Miocene of South Dakota, was placed in a monotypic family Paranyrocaidae by Miller & Compton (1939) on account of the hypotarsus having only two ridges, but it was later demoted to a subfamily of Anatidae (Brodkorb 1964). However, that this taxon is known only from tarsometatarsi precludes an understanding of its true relationships to other anatids, if indeed it is an anseriform.

In Lower to Middle Miocene sediments from Europe, the most well known anatid is *Anas blanchardi* Milne-Edwards, 1863. Cheneval (1983, 1987) recognised that this and associated anatids from Saint-Gérard-le-Puy did not belong in the genus *Anas* and placed them in the genus *Dendrochen*. Livezey & Martin (1988) restudied *Anas blanchardi* and erected a new genus for it – *Mionetta* – in the subfamily Dendrocheninae (taxonomically placed after

Dendrocygninae and before Thalassorninae). Of the two taxa found with *M. blanchardi*, the relatively rare, larger taxon *Anas consobrina* Milne-Edwards, 1867–71 was considered to be based on large individuals of *Mionetta blanchardi*, while the smaller *Anas natator* Milne-Edwards, 1867–71 was transferred to *Mionetta* (Livezey & Martin 1988).

Other than these dendrochenines, all Early Miocene anatids fall mainly in the anserine clade. Anserines are represented in the Lower Miocene of Europe by *Cygnopterus alphonsi* Cheneval, 1984 and *Cygnavus senckenbergi* Lambrecht, 1931, with both genera having their origin in the Oligocene (Cheneval 1987; Mlíkovský 2002). However, Mlíkovský (2002) synonymised *C. alphonsi* with *C. senckenbergi*. *Anas robusta* Milne-Edwards, 1867–71 (based on a *Branta*-sized distal humerus from Sansan, France), was placed in *Anserobranta?* by Cheneval (1987), but later transferred to *Mionetta* (Mlíkovský 2002). It is not like *Mionetta*, however, especially in the short distal extent of the flexor process (in which it is most similar to *Cygnus*), the conformation of the brachial fossa and that the space between the dorsal condyle and the facet for the attachment of the anterior ligament is greater than the width of the facet (Cheneval 1987: pl. 1, fig. 1), not less than as in Dendrocygnini (Woolfenden 1961:6), so we prefer to leave it identified as an anserine in *Anserobranta?*. The true swans *Cygnus*, do not appear in Europe until the mid-Miocene, with *Cygnus atavus* (Fraas, 1870: Mlíkovský 2002), although Lambrecht (1933) considered this taxon should be in *Anser*. *Cygnus* appears in North America in the Late Miocene, with *Cygnus mariae* Bickart, 1990. Geese, such as *Anser*, appear in the Late Miocene in Europe (Howard 1964) and *Anser* and *Branta* both appear in the Late Miocene of North America (Bickart 1990), but are preceded by *Presbychen abavus* Wetmore, 1930 from the Miocene of California (Howard 1964).

The tadorines are first known with certainty in Europe with the appearance of the genus *Tadorna* in the early Pliocene in Europe (Mlíkovský 2002). However, an earlier arrival in Europe is possible if Mlíkovský's (2002) referral of *Anserobranta tarabukuni* Kuročkin & Ganea, 1972, based on a proximal carpometacarpus from the Late Miocene, to *Alopochen* is correct. Olson (1985b) reported Tadornini from the Middle Miocene Calvert Formation of Maryland, USA and undescribed fossils similar to *Tadorna* from the Middle Miocene of Germany. The latter, from the Nördlinger Ries, remain undescribed (P. Ballmann, pers. comm., 24 November 2004). Lambrecht (1933: 368) briefly described *Anser scaldii*, wrongly attributing it to van Beneden (Mlíkovský 2002: 125), on the basis of a humerus 129 mm long that he said was like *Tadorna casarca*, from the middle Miocene of Belgium. We await descriptions of *Anser scaldii* and the Nördlinger Ries 'tadornid' to see if they represent middle Miocene occurrences of tadornids in Europe.

There are few other genera of anatids recognised from Europe's Early–Middle Miocene. Mlíkovský (2002) erected *Oxyura doksana* on a cranial end of a left coracoid from the Czech Republic. However, this generic attribution may be in doubt, as the cranial ends of *Oxyura* coracoids do not differ significantly from those of many anatid genera, including the dendrochenine taxa *Mionetta* and *Manuherikia*, and even differ little from those of *Anas chlorotis*.

In the Anatinae, other than species of '*Anas*', there is only the single species *Aythya chauvirae* Cheneval, 1987 from Sansan, France, based on a femur, but whose type

series includes a complete coracoid, a proximal and a distal humerus, a proximal and a distal ulna and distal femur (Cheneval 1987). We note that the holotype, as figured in Cheneval (1987: pl. 1, fig. 7a,b) lacks the lateral expansion of the fibular condyle typical of *Aythya*. Other than this, a deep popliteal fossa is shared by diving taxa and other taxa, e.g. *Malacorhynchus*. Of the referred specimens examined by T.H.W. and A.J.D.T., the distal right femur MNHN Sa10279 lacks the fibular condylar area, but the bone has a straight shaft and so lacks the marked ventral bend seen in the distal third of *Aythya* femora. The proximal end shaft of a right humerus (MNHN Sa10275) has a prominent capital shaft ridge unlike any *Aythya*. The second referred humeral specimen (MNHN Sa1280), a distal left humerus, is from a considerably smaller bird than MNHN Sa10275, so much so that it is unlikely to be the same taxon. There are no features on this specimen that allow referral to *Aythya* to the exclusion of other taxa: it is, in contrast, similar to the dendrochenine taxa described herein. Similarly, the referred distal right ulna MNHN Sa1279 lacks features to refer it unambiguously to *Aythya*. We conclude that *Aythya chauvirae* Cheneval, 1987 is unlikely to be an *Aythya* and may well be a dendrochenine and that the hypogeum comprises two taxa.

The species *Aythya* (= *Fuligula*) *arvernensis* (Lydekker, 1891), reported as in need of reassessment by Cheneval (1987), was included in the synonymy of *Mionetta blanchardi* by Mlíkovský (2002). The taxa *Anas velox* Milne-Edwards, 1867–71 (whose lectotype is a right carpometacarpus) and *Anas sansaniensis* Milne-Edwards, 1867–71 (whose lectotype is a distal left tibiotarsus) are both doubtfully correctly placed in *Anas* (Mlíkovský 2002), a conclusion we agree with as these elements are of insufficient diagnostic utility for generic attribution. The referred coracoid of *Anas velox* has 'à fosse pneumatique profonde et à bord externe de la facette glénoïdale épais' (Cheneval 1987), but it cannot be in the genus *Anas* because coracoids of *Anas* lack pneumatic foraminae of any kind within the acrocoracoid, as this description suggests and as is shown in Cheneval (1987: pl. 1, fig. 3). Mlíkovský (2002: 118) synonymised *Anas meyerii* Milne-Edwards, 1867–71, which Howard (1964) considered indeterminate to genus, with *A. velox*.

The species *Anas oligocaena* Tugarinov, 1940 from the upper Oligocene of Siberia, was referred to *Dendrochen?* by Cheneval (1987). *Anas creccoides* Beneden, 1871 from the early Oligocene of Belgium is considered indeterminate and relegated to *Aves incertae sedis* (Brodkorb, 1962: 707). *Anas basaltica* Bayer, 1882 from the early Oligocene of Czechia is an indeterminate heron (Mlíkovský 2002: 70). *Anas skalicensis* Bayer, 1882 is based on bones indeterminate at the ordinal level (Mlíkovský 2002: 251). *Anas risgoviensis* Ammon, 1918 from the Middle Miocene of Germany, is considered as genus *incertae sedis* by Mlíkovský (2002: 125). *Anas isarensis* Lambrecht, 1933 (based on a scapula) and *Anas eppelsheimensis* Lambrecht, 1933 (based on a cranial fragment of a coracoid), both from the late Miocene of Germany, are regarded as *Anatidae incertae sedis* (Mlíkovský 2002: 124). *Anas luederitzensis* Lambrecht, 1929 based on a proximal humerus from southwest Africa has a closed ventral pneumotricipital fossa (Howard, 1964), so does not belong in *Anas*. Therefore, the genus *Anas* Linnaeus, as now defined e.g. Livezey (1997b), is not certainly known from any time earlier than or in the Miocene.

The most extensive Lower Miocene anatinid fauna known to date was that from Saint-G erand-Le-Puy (Cheneval 1987). It comprises four species: the dendrochenines *Mionetta blanchardi* (which includes *M. consobrina*) and *M. natator*, the anserine *Cygnopterus alphonsi* (Cheneval 1987) and ?*Anserobranta robusta* (as *Mionetta robusta*, in Ml kovsk  2002). The mid-Miocene fauna from Sansan also contains four taxa (Cheneval 1987): the anserine ?*Anserobranta robusta*, *Aythya chauvirae*, which herein we suggest is a possible dendrochenine, and *Anas? velox* (which includes *Anas* [= *Aythya*] *meyerii*) and *Anas? sansaniensis*. Cheneval (1987) suggested that the changed taxon composition between these faunas indicated the evolution of anatids from the Lower to mid-Miocene towards a fauna with a modern aspect. This would only be true if the presence of *Aythya* is confirmed by future analysis.

Recently, Noriega (1995) has described a humerus from the Upper Miocene of Argentina as the first record of the Dendrocheninae in the southern Hemisphere. It lacks the proximal end above the external tuberosity but has the main diagnostic features seen in *Manuherikia* and at > 92 mm long with a DW = 12.5 mm, it is a bigger bird than *M. lacustrina*.

Thus the St Bathans Fauna, with six anatinid taxa, is the most diverse Early–Middle Miocene anatinid fauna now known. This St Bathans fauna allows some observations on anatinid evolution in general. It contains no modern genera of anatids – notably *Anas*, *sensu stricto*, is absent, as noted for European faunas by Livezey & Martin (1988) and data herein. As *Anas* has not been recorded from sites older than Middle Miocene in Australasia, Europe or North America, it is possible that this genus had yet to evolve. The absence of *Cygnus*, amid otherwise abundant anatinid bones in the St Bathans Fauna, indicates that it was not a member of the Early–Middle Miocene New Zealand avifaunas. Moreover, there is no evidence of *Cygnus* in Australia until the Pliocene (Vickers-Rich 1991; T.H.W., A.J.D.T., pers. obs.), indicating a northern hemisphere origin for swans. In contrast, the presence of *Miotadorna* in the St Bathans Fauna indicates tadornines have a long history in the Australasian region, possibly predating their appearance in Europe and, therefore, suggesting that tadornines could have evolved in the southern hemisphere. However, as a cautionary note, it is observed that no pre-Pliocene fossil record exists in Australasia for *Anseranas* (Anseranatidae), the dendrocynines, the anserines *Cereopsis* and *Cnemiornis* and *Stictonetta*, despite them all being the most primitive members of the Recent fauna (Livezey 1986, 1989, 1996a, 1997b; Worthy *et al.* 1997), nor is there a pre-Pliocene fossil record for any other extant anatinid in the region.

The phylogenetic position of *Malacorhynchus* has been problematic, with Livezey (1997b) considering the composition of the Tribe Malacorhynchini and its inclusion in Anatinae provisional. Sraml *et al.* (1996) found that, based on a strict consensus tree of mitochondrial DNA data, *Malacorhynchus* was the sister taxa to *Biziura* and close to *Dendrocynna*. When we examined the skeletal characters of the humerus of both *M. membranaceus* and *M. scarletti*, we found that they both have all the diagnostic features of the Dendrocheninae as given in Livezey & Martin (1988) and as discussed herein, and differ in no appreciable way. Moreover, the coracoids of *Malacorhynchus* are very similar to those of *Mionetta*, especially in the presence of a distinct depression on the ventral surface of the blade (contra Livezey 1996b), also shared with *Stictonetta*. This indicates support for the

primitive location of *Malacorhynchus* advocated by Sraml *et al.* (1996). Livezey (1986) found *Malacorhynchus* to be a highly derived tadornine but in a more extensive analysis (Livezey 1996b) found its placement unresolved. Future analyses of dendrochenine relationships should include *Malacorhynchus* among compared taxa.

Accipitriformes

The Quaternary fauna of New Zealand included a large eagle *Harpagornis moorei* Haast, 1872, in addition to a harrier *Circus eylesi* Scarlett, 1953 and a falcon *Falco novaeseelandiae* Gmelin, 1788. It is tempting to speculate that the two fossils reported herein may be from a precursor of *Harpagornis*, however, they are too incomplete to provide data on this question.

The fossil record of Australia is known to include eagles up to the size of *Aquila audax* and as old as the late Oligocene–Miocene, from lacustrine deposits in Central Australia (Ngapakaldi and Ngama local faunas) and from Riversleigh in northwestern Queensland (Vickers-Rich 1991), but the material remains undescribed.

Elsewhere in the world, accipitrids have an extensive fossil record dating back to the late Eocene or early Oligocene, with uncontested modern genera appearing first only in the mid-Miocene (Olson 1985b).

Gruiformes

One of the most distinctive elements of the New Zealand avifauna is the enigmatic gruiform *Aptornis*. Due to extreme specialisation and devolution from a flight capacity, its relationships are obscure and unresolved (e.g. Olson 1985b; Weber & Hesse 1995; Houde *et al.* 1997; Livezey 1998). It has obviously been a long-time member of the New Zealand avifauna, but its fossil record until now has been restricted to the late Quaternary and so the report herein of a fossil that may represent an ancestral form is significant. However, a phalanx is not very revealing and we await the discovery of more diagnostic elements that might have bearing on the evolutionary history of this taxon.

The gruiforms in the St Bathans Fauna are otherwise only represented by rallids, as is the case in modern New Zealand. Rail fossils are abundant but fragmentary, nevertheless two taxa are apparent. Both are small: the biggest being the size of a banded rail *Gallirallus philippensis*. Both appear to be most similar to members of the *Gallirallus* group, with no evidence of gallinules and coots, which prefer aquatic habitats, so might have been expected as fossils. This contrasts with the modern fauna, where highly derived and endemic gallinules and coots were components of the Recent fauna and several taxa had evolved to become among the largest of their kind in the world, e.g. *Fulica prisca* Hamilton, 1893, *F. chathamica* Forbes, 1892b, *Porphyrio mantelli* (Owen, 1848), *P. hochstetteri* (A.B. Meyer, 1883). A surprising aspect of the Early Miocene fauna is the observation that the most abundant rail species present was apparently flightless and markedly sexually dimorphic in size. The flightless taxon indicates that flightless rails were a feature of both the Miocene and Recent faunas of New Zealand (Worthy & Holdaway 2002).

Olson (1985b) described the Tertiary record of rails as meagre and largely uninformative, with the first referred taxa to the family dating from the lower Eocene, but all based on

fragmentary isolated bones. Not until the upper Oligocene–Early Miocene from deposits in France, are there taxa known from adequate diagnostic material, e.g. *Rallicrox* Lambrecht, *Palaeoramides* Lambrecht, *Paraortygometra* Lambrecht, but these lack modern analysis and their relationships remain undetermined, despite having morphologies not significantly different from modern rallids (Olson 1985b). Recently Mayr & Smith (2001) described two species in the new genus *Belgirallus* from the early Oligocene of Belgium, while Fischer (1997) described *Rupelrallus* from the early Oligocene of Germany. From continental deposits younger than mid-Miocene, all rallid material has been assigned to modern genera (Olson 1985b).

In Australia, rails occur in late Oligocene–Early Miocene beds in central Australia (Ngapakaldi and Ngama local faunas) and at Riversleigh (Vickers-Rich 1991). A flightless gallinule has been recently described by Boles (2005) from the Oligo–Miocene of Riversleigh, but the other Tertiary forms remain undescribed. The New Zealand record thus complements others but we await more complete material for more adequate comparisons and diagnoses.

Charadriiformes

Boev (2000) reported a gull (Larinae, genus indet.) from the Lower Miocene of western Bulgaria and summarised the fossil record of the group. *Larus elegans* Milne-Edwards, 1867–71 [1868] and *Larus totanoides* Milne-Edwards, 1867–71 [1868] (both from the late Oligocene–Early Miocene of France and transferred to the new genus *Laricola* by Mlíkovský (2002)), are the oldest undisputed gull taxa, if it is accepted that *Larus desnoyersii* Milne-Edwards, 1863, has closer affinity to Stercorariidae (Olson 1985b). *Larus raemdonckii* Beneden, 1871 (from the lower Oligocene of Belgium), was transferred to *Puffinus*. *Larus dolnicensis* Švec, 1980, as noted by Olson (1985b), is not a gull and was transferred to *Mioglareola* in the Glareolidae (Mlíkovský 2002). *Larus pristinus* Shufeldt, 1915 is from the Lower Miocene of Oregon, but Olson (1985b) considered the generic attribution doubtful. However, *Gaviota niobrara* Miller & Sibley, 1941 is a larid from the mid-Miocene of Nebraska (Olson 1985b) and Olson & Rasmussen (2001) recorded *Larus* sp. from the Middle Miocene Pungo River Formation. Thus gulls do have a wide, though sparse, distribution in the Lower–Middle Miocene and could be expected in New Zealand.

There are many fossils named and unnamed attributed to Charadriiformes (Olson 1985b; Mlíkovský 2002). If the very small taxon reported here is a *Calidris* sandpiper, it would compliment an Early Miocene record of the genus (Mlíkovský 2002). The family Charadriidae is reported from two European Miocene records but the genus *Charadrius* itself has only a Pliocene–Recent distribution in Europe (Mlíkovský 2002). Several other small waders, described from the Early–Middle Miocene of Europe (*Totanus larteanus* Milne-Edwards, 1863; *T. grivensis* Ennouchi, 1930; *T. majori* Lydekker, 1893; *T. minor* Ennouchi, 1930 and *Tringa gracilis* Milne-Edwards, 1867–71 [1868]), are all considered genus *incertae sedis* by Mlíkovský (2002), but indicate a diversity of waders at this time. Most recently, Ballmann (2004) has erected four new species within the new genus *Miroliia*, which was referred to Calidridinae, from the Nördlinger Ries of the Middle Miocene in Germany. Charadriiforms of

up to Miocene age are known from Australia (Vickers-Rich 1991: 760) but none have been distinguished at family level yet. Ballmann (2004) considered that entire elements representing several parts of the post cranial skeleton and cranial elements were needed to evaluate subfamilial affinities and in the absence of, especially, whole humeri and other diagnostic remains, the New Zealand fossils certainly cannot yet be assigned to subfamily or genera.

Columbiformes

Pigeons and doves have a fossil record in Australia extending back to the late Oligocene–Early Miocene, from lacustrine deposits at Lake Palankarina (Etadunna Formation) and Lake Pinpa (Namba Formation) of central Australia (Vickers-Rich 1991) but the material is undescribed. Elsewhere in the world, the fossil record of columbids is meagre (Olson 1985b; Becker & Brodkorb 1992). The fossil *Columba calcaria* Milne-Edwards 1867–1871, from the Lower Miocene at Saint-Gérard-le-Puy in France, is now considered to be a sandgrouse (Pteroclididae), as *Gerandia calcaria* (Mlíkovský 2002). An abundant small dove from the Thomas Farm Local Fauna, Early Miocene 18–19 Ma, of Florida (Olson 1985b) has been recently described in a modern genus, as *Columbina prattae* Becker & Brodkorb (1992). Australasia has about 30 breeding species (including three recently extinct) in 15 genera (Higgins & Davies 1996; Holdaway *et al.* 2001). Considering this diversity and the early fossil record in Australia, an Early Miocene New Zealand record of Columbidae is not unexpected, but the relationships of the fossil will remain obscure until better material is available.

Psittaciformes

Parrots have an old fossil record in Europe, with stem-group representatives (including Pseudasturidae) present in the Lower Eocene (Olson 1985b; Dyke & Cooper 2000; Mayr 2001, 2002b). Crown-group taxa first appear in Lower Miocene European sites, with *Archaeopsittacus verreauxi* (Milne-Edwards 1867–1871) the best known of a variety of taxa (Olson 1985b; Mayr & Göhlich 2004). From the Miocene of North America, there is a single taxon described (Olson 1985b; Mayr & Göhlich 2004).

Fossil parrots are rare in the Australian Tertiary (Vickers-Rich 1991), despite the proliferation of taxa in the Recent fauna. The oldest Australian record is of Cacatuidae from the Early Miocene or late Oligocene deposits at Riversleigh (Boles 1993a).

Aegotheliformes

Aegothelids, in the form of *Quipollornis koniberi* Vickers-Rich & McEvey, 1977, have a mid-Tertiary fossil record in Australia, dated to 13.5–17 Ma (Vickers-Rich & McEvey 1977; Vickers-Rich 1991). The ten Recent species of *Aegothales* occur in the Australasian region from the Maluku Islands (1 sp.), through Papua New Guinea (7 spp.), Australia (*A. cristatus*), New Caledonia (*A. savesi*) and (recently extinct) in New Zealand (*A. novaezealandiae* (Scarlett, 1968)). Mitochondrial DNA studies indicate that the group is monophyletic, with *A. savesi* and *A. novaezealandiae* being weakly associated as sister taxa and together are the most primitive members of the group and are not sister taxa to *A. cristatus*, as geography might lead one to infer (Dumbacher *et al.* 2003).

An aegothelid from the Lower–Middle Miocene of New Zealand indicates a long history of the group in New Zealand, as could have been predicted from the distant phylogenetic relationship between *A. novaezealandiae* and *A. savesi*, its closest relative, and other taxa (Dumbacher *et al.* 2003).

Apodidae

Swifts are unknown as breeding taxa in New Zealand, so the Miocene fossil adds a novel (presumably breeding) bird family to the country's past fauna.

Boles (2001) described *Collocalia buday* from late Oligocene to ?Early–Middle Miocene deposits at Riversleigh, northwestern Queensland. This taxon, based on three humeri, a tarsometatarsus and a coracoid, was larger than other compared *Collocalia* species and is the oldest record of the family Apodidae in Australia and of Collocaliini in the world.

The presence of a *Collocalia* species in New Zealand about the same time is thus not unexpected. Also, its presence supports the postulated subtropical–tropical environment indicated by palaeofloral studies (Pole & Douglas 1998; Pole *et al.* 2003), as *Collocalia* (26 species, including *Aerodramus* as a synonym), is now a member of tropical faunas from Southeast Asia, through the Philippines, Indonesia, Melanesia, northern Australia and Oceania as far as the Marquesas (Higgins 1999; Steadman 2002).

Passeriformes

Little can be said about the passerine record of the St Bathans Fauna at this stage, other than to note that at least three species were present. There is no fossil evidence yet for the New Zealand endemic families Acanthisittidae, Turnagridae and Calleatidae in the Miocene. The only fossil that can so far be associated with any taxon, is a scapula which we consider to be very similar to that of currawongs and Australian magpies. These are members of the Australian Cracticidae, although the introduced Australian magpie is a familiar member of the current New Zealand avifauna.

Notable absences

At the present time there is no evidence in the St Bathans Fauna for other waterbirds such as grebes (Podicipidae) and flamingos (Phoenicopteridae and Palaelodidae), despite a late Oligocene–Miocene record for these groups in Australia (Vickers-Rich 1991). Anhingids, despite being a member of the Recent Australian fauna, lack a pre-Pliocene fossil record there (Vickers-Rich 1991) and as yet have not been found in the St Bathans fauna. Cormorants (Phalacrocoracidae) have a Miocene record in Australia from undescribed material (Vickers-Rich 1991), but are another notable absence, contra Peat (2002), from the St Bathans Fauna considering their high diversity in the Recent fauna of New Zealand. There is also no evidence in the St Bathans Fauna for herons (Ardeidae), storks (Ciconiidae), or ibises and spoonbills (Threskiornithidae), which is as expected since these groups are absent in pre-Pliocene deposits in Australia (Vickers-Rich 1991).

Worldwide significance of the New Zealand Miocene fauna

The St Bathans Fauna includes the first terrestrial avifauna of Tertiary age described for New Zealand. The comprehensive review by Fordyce (1991) showed that the New Zealand avian

fossil record included mainly penguins (Sphenisciformes) with a few bony-toothed birds (Pelagornithidae). Fordyce (1991) reported undescribed anatids from near St Bathans in the Manuherikia Group that were discovered by Barry Douglas and Jon Lindqvist in 1980 (Douglas *et al.* 1981; Douglas 1986). A few other Middle–Late Miocene aged bones were reported from freshwater limestone deposits in the Waitaki Valley (Fordyce 1991), but like the Manuherikia bones, they remained undescribed. The large moas (Aves: Dinornithiformes) only have a fossil record extending to 2.5 million years ago (Worthy *et al.* 1991). In contrast to this poor Tertiary record, the late Quaternary record is extraordinarily rich (Worthy & Holdaway 2002).

The Manuherikia Group sediments (16–19 Ma, Altonian, Early–Middle Miocene) were deposited shortly after much of New Zealand re-emerged from an Oligocene marine transgression. Maximum coverage of the land occurred in the Oligocene–earliest Miocene when perhaps only 18% of the present land area remained (Cooper & Cooper 1995). With the onset of renewed tectonism and lowering sea level in the Early Miocene, land area rapidly increased thereafter. The Oligocene transgression was postulated to be a time of evolutionary stress on the fauna, a bottleneck, during which diversity of terrestrial biota would have been markedly reduced (Cooper & Cooper 1995) and mitochondrial DNA evidence for moas, kiwis (Apterygidae) and wrens (Acanthisittidae), has provided evidence for radiations in these groups since the Miocene. Cooper & Cooper (1995) and Campbell & Landis (2001) further suggested that the Oligocene transgression was the reason that terrestrial mammals and snakes are not now present in New Zealand, noting that they may have been present once. Such reasoning applies to other groups such as the Chelidae turtles and the lungfishes (Ceratodontidae).

If this scenario is correct, then an Early Miocene fauna in New Zealand should reflect one recently released from ecological constraint and may be one of restricted diversity, or one having close affinity to Australian faunas, assuming dispersal of taxa from that continent enabled colonisation of a depauperate land. However, as this initial investigation of the avifauna reveals, there is no lack of diversity indicated, with five genera and six species of waterfowl, at least, and a wide range of other bird families represented. This St Bathans Fauna shows few similarities to similar-aged Australian faunas in terms of faunal composition. There, bird faunas were dominated by the mihirungs Dromornithidae (Murray & Vickers-Rich 2004) casuariids, common flamingos, palaelodids and anatids, as well as by rarer megapodiids, charadriiforms (including Burhinidae), pelicans, falconiforms, gruiforms, columbids, psittaciforms and passeriforms (Vickers-Rich 1991; Boles 1993*a, b*, 1995; Boles & Ivison 1999). Some taxa are common to both regions: *Pelecanoides*, *Aegothales*, *Collocalia* and Cracticidae, but among the common waterfowl of the St Bathans Fauna, there are no described Australian equivalents and we have seen none among undescribed material. Among vertebrates in the Manuherikia Group St Bathans Fauna, birds dominate unquestionably, and do so in groups known today, but there were several bats, skinks and geckos, sphenodontids and a crocodylian. Except for the crocodylian and the sphenodontid to remind us of the ancient gondwanan connection, the overall impression is that by Manuherikian time, the fauna had acquired its Recent bird-dominated New Zealand character – the St Bathans Fauna already had a distinctive

Table 9 Summary of taxa from the St Bathans Fauna.

Family	Genus	Species	Croc Site L1	HH1a	HH2
?Dinornithidae	Genus indet.	Sp. indet.	Y	Y	
Pelecanoididae	<i>Pelecanoides</i>	<i>miokuaka</i>	Y		
Anatidae	<i>Manuherikia</i>	<i>lacustrina</i>	Y	Y	Y
		<i>minuta</i>	Y	Y	Y
	<i>Miotadorna</i>	<i>sanctibathansi</i>	Y	Y	
	<i>Dunstanetta</i>	<i>johnstoneorum</i>			Y
	<i>Matanas</i>	<i>enrighti</i>	Y	Y	
	Genus indet.	Sp. indet.		Y	
Accipitridae	Genus indet.	Sp. indet.	Y		Y
?Aptornithidae	Genus indet.	Sp. indet.		Y	
Rallidae	Genus indet.	Sp. indet. 1	Y	Y	Y
		Sp. indet. 2		Y	
Laridae	Genus indet.	Sp. indet.	Y	Y	
'wader'	Genus indet.	Sp. indet. 1	Y		
		Sp. indet. 2	Y	Y	
Columbidae	Genus indet.	Sp. indet.		Y	
Psittacidae	Genus indet.	Sp. indet. 1	Y	Y	
		Sp. indet. 2		Y	
		Sp. indet. 3	Y		
Aegothelidae	<i>Aegotheles</i>	Sp. indet.		Y	
Apodidae	<i>Collocalia</i>	Sp. indet.		Y	
Passeriforms	Cracticidae, Genus indet.	Sp. indet. 1	Y		
	Genus indet.	Sp. indet. 2	Y		
		Sp. indet. 3	Y	Y	

Abbreviations: Sp., species; indet., indeterminate; Y, yes.

New Zealand flavour to it. Therefore, it is evident that a diverse terrestrial vertebrate fauna passed through the postulated Oligocene bottleneck and certainly there is no evidence to support the theory of a complete drowning of proto-New Zealand during this period of high sea levels, as suggested by Campbell & Landis (2001). The presence of a crocodylian, the swiftlet *Collocalia* sp., and probable abundant parrots, are in keeping with a subtropical environment reconstructed from macro- and microfloral studies (Pole *et al.* 2003).

CONCLUSION

In the subtropical environs of the Lower–Middle Miocene Lake Manuherikia, waterfowl dominated the avifauna, with at least six species in five genera (Table 9). Tadornines perhaps ancestral to *Tadorna*, were present, but there were no modern genera and no anserines. Other modern waterbirds, such as shags and grebes would have been expected in the fossil fauna but were apparently absent. Living in the surrounding habitats were two diminutive rails (one of which was flightless) and at least one large gruid (perhaps a fore-runner to *Aptornis*), but there is no evidence yet for herons, ibises, flamingos or storks. Other fossil birds included several parrots, an owl nightjar, a swiftlet and a range of passerines, including a currawong-like species. There is no evidence yet for the presence of any of the Recent endemic passerine families. Aerial predators included a medium-sized accipitrid, but there is no evidence yet for owls or falcons. The absence of several other bird families from the fossil fauna (such as kiwis, kingfishers, cuckoos), may be due to preservational biases (e.g. few small arboreal bird species are represented) or may reflect what were natural rarities around

Lake Manuherikia and it should not be taken as evidence of the absence of these taxa from the Miocene of New Zealand. Moas were probably present but are only represented by egg-shell and possibly by bone fragments to date. However, these indicate that moas were large, presumably flightless, birds in the Early–Middle Miocene. Lastly, as in modern New Zealand, petrels were present, with a diving petrel *Pelecanoides miokuaka* presumed to be nesting near Lake Manuherikia. New Zealand at last has a non-marine mid-Tertiary avifauna.

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