

The Holocene fossil waterfowl fauna of Lake Poukawa, North Island, New Zealand

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ABSTRACT: Lake Poukawa, in Hawke's Bay, North Island, New Zealand, has a number of lacustrine deposits of early to late Holocene age on its margins. A total of 13 475 anatid bones from these sites were examined to reveal minimum numbers of individuals as follows: *Anas superciliosa* 332, *A. chlorotis* 442, *A. rhynchotis* 157, *Aythya novaeseelandiae* 158, *Tadorna variegata* 6, *Chenonetta finschi* 28, *Oxyura* n.sp. 19, *Malacorhynchus scarletti* 16, *Cygnus atratus* 66, *Biziura delautouri* 3, *Mergus australis* 2. Four bones of *Cnemiornis gracilis* are presumed to be from a Pleistocene site. The fossils of *Anas rhynchotis* reveal that this species was a resident in the prehuman avifauna. Descriptive diagnoses are given for humeri, ulnae, carpometacarpi, scapulae, coracoids, femora, tibio-tarsi, and tarsometatarsi of all mainland New Zealand anatids except *Cygnus*, *Cnemiornis*, and *Biziura*.

KEYWORDS: Anatidae, Holocene fossil assemblages, bone descriptions, Lake Poukawa, Hawke's Bay, New Zealand.

Introduction

New Zealand has a rich late Quaternary fossil avifauna derived from cave, dune, and swamp deposits (Worthy & Holdaway 2002, and references cited therein). Most deposits are less than 30 000 years old and the older ones are mainly from cave deposits. Cave deposits are primarily of pitfall origin, but several important ones were accumulated by avian predators, mainly *Sceloglaux albifacies* (Gray, 1844) (laughing owl) and *Falco novaeseelandiae* Gmelin, 1788 (New Zealand falcon). Dune deposits are sparsely distributed around the coastline and are all of late Holocene age. Swamp deposits are mostly those that accumulated in springs, where birds, mainly moa, were mired in the surrounding soft sediments or drowned in the spring itself. Lacustrine deposits are very rare, with only Pyramid Valley in North Canterbury (Holdaway & Worthy 1997, Worthy & Holdaway 1996) and Marfell's Beach (Worthy 1998) producing avifaunas in the South

Island. As a result, the fossil record of lacustrine birds in New Zealand is relatively poor, and it is for this reason that species like dabchicks and grebes have very limited fossil records in New Zealand (Millener 1991), rather than their being recent colonists. The endemic waterfowl *Biziura delautouri* Forbes, 1892 (New Zealand musk duck) and *Malacorhynchus scarletti* Olson, 1977 (Scarlett's duck) were probably primarily lacustrine species, and the rarity of fossils of these species is also mostly due to a lack of lacustrine deposits (Worthy & Gill 2002, Worthy 2002a). In the North Island, a huge and largely undescribed fossil avifauna obtained from deposits around Lake Poukawa (see Fig. 1) by T.R. Price *et al.* has great potential to reveal insights into the former lacustrine faunas of New Zealand.

Excavations at a number of sites spanned the period 1960–1980. Sites N141/I and N141/II (hereafter referred to as Sites I and II, respectively), on the edges of the natural outflow channel from Lake Poukawa, were briefly described by Price (1963, 1965). At Site I, about 75 sq m of

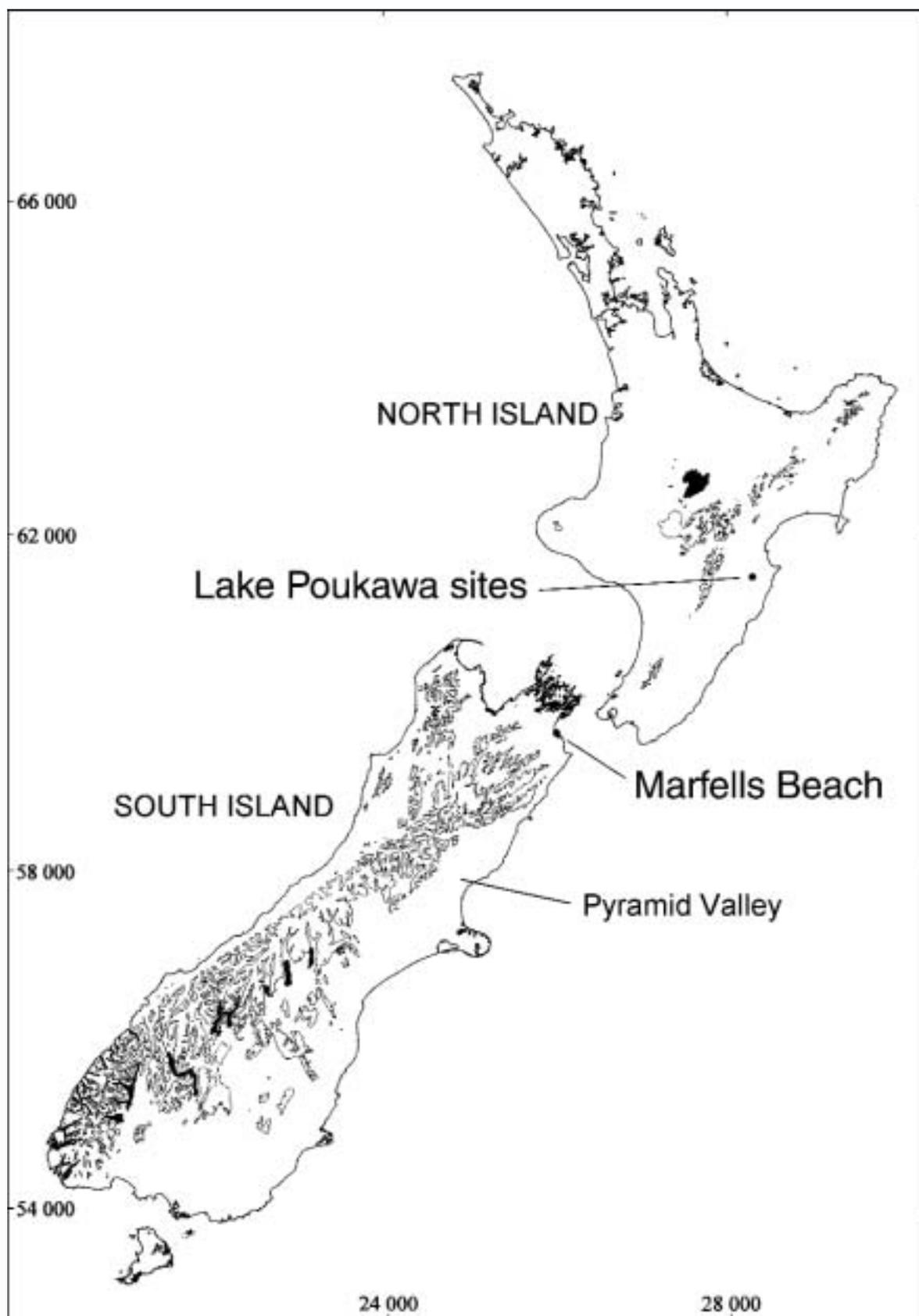


Fig. 1 Locality of Lake Poukawa in New Zealand. The NZMS 260 map grid is indicated on the border. The 1000 m contour lines are shown and major lakes are shaded.

stream bed, 164 sq m of stream bank, and about 115 sq m on the headland were excavated. At Site II, about 200 sq m of stream bed and adjacent bank were excavated. Price interpreted the faunal deposits on the stream bank and in the stream bed as primarily associated with the middens on the headland, and concluded that people had occupied the area prior to the Waimihia eruption.

McFadgen (1979) examined this contentious claim using site N141/XII (hereafter called Site XII), which Price considered displayed a similar history of deposition to that seen in sites I and II. McFadgen concluded that the Māori middens indicated occupation on parts of the site 150–300 years ago and that most of the fauna was of natural origin, occurring mainly either between the Taupo Ignimbrite (1850 yrs BP) and the Waimihia Tephra (3300 yrs BP) or below the latter (tephra nomenclature and dates follow Froggatt & Lowe 1990). The tephtras at Poukawa have been studied and identified by Puller (1965) and Howorth *et al.* (1980). Environmental studies of the Lake Poukawa palaeovegetation by McGlone (1978) and Pocknall & Millener (1984) also found no evidence of humans in the Poukawa catchment below the Taupo Ignimbrite. Nine radiocarbon dates on moa bones from Price's excavations (Anderson 1989, Appendix B) indicated that the deposits extended to at least 7246 years old, supporting the chronology given in Horn (1983).

Despite Price's (1963, 1965) record of substantial faunas from Sites I and II, no analysis of these has yet been published and Horn's (1983) analysis is the only one available for Site XII. However, the fauna provides notable records for some species, e.g. parts of two individual *Pelecanus conspicillatus* Temminck, 1824 (Australian pelican) (Scarlett 1966, Rich & van Tets 1981, Gill & Tennyson 2002) and the largest series of bones of *Biziura delautouri* (Scarlett 1969, Worthy 2002a).

Horn's (1983) analyses of 12 403 bones of birds other than moas from about 3500 sq m in Site XII indicated 23 waterbirds, 26 terrestrial species, and 4 seabirds, making it one of the most diverse faunas ever recorded in New Zealand. Among the taxa Horn listed, *Biziura* and *Mergus australis* Hombron & Jacquinot, 1841 (New Zealand merganser) were notable on account of their national rarity. Horn also reported *Oxyura australis* Gould, 1836 (blue-billed duck) and *Dupetor flavicollis* (Latham, 1790) [now *Ixobrychus*] (black bittern) from New Zealand for the first time, though for the latter Millener (1991) suggested these remains might be from *Ixobrychus novaeseelandiae* (Potts, 1871) (New Zealand little bittern), and it is to this latter

taxon that they are now accepted as belonging (Turbott 1990, Holdaway *et al.* 2001). Worthy (in press) has confirmed the presence of *Oxyura* in the fauna, contra Millener (1991: 1329), but the material represents a new species distinct from the Australian form.

The Poukawa collection was subsequently gifted to the National Museum of New Zealand (now the Museum of New Zealand Te Papa Tongarewa) by the Hastings Cultural Centre (per Mr Ray Dixon, Director), Mr David Buddo, and Mr Peter Horn in July 1982, and the bones identified and catalogued by Dr Philip R. Millener in 1982–83. However, Millener had left unidentified several thousand anatid bones. For this project, the identity of these and all previously identified anatid bones from the entire Poukawa collection was reassessed. This led to the discovery of several bones that I identified as *Oxyura*, which are described elsewhere (Worthy in press). The purpose of this contribution is to reveal the composition of the complete waterfowl fauna from the late Holocene deposits of Lake Poukawa. For completeness, the very few bones – but significantly two *Biziura* bones – from these excavations that found their way into the Canterbury Museum collections are also included.

Methods Abbreviations

Institutions

AM, Australian Museum, Sydney, Australia; 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.

Skeletal elements and descriptive terms

The following abbreviations apply to single and plural usage of the elements: Cmc, carpometacarpi; Cor, coracoids; Fem, femora; Hum, humeri; Rad, radii; Tib, tibiotarsi; Tmt, tarsometatarsi.

Anatomical nomenclature for specific bone landmarks follows Baumel & Witmer (1993), with Latin names given at first mention and English equivalents thereafter. Some common terms are abbreviated as follows: *artic.* for *articularis*; *cond.* for *condylus*; *proc.* for *processus*; *tub.* for *tuberculum*. MNI stands for minimum number of individuals, while NISP is number of identified specimens.

Avian taxonomy follows Turbott (1990), as modified by Holdaway *et al.* (2001).

Measurements

Measurements were made with Tesa® dial callipers and rounded to 0.1 mm. L: 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*. P: proximal width in the lateromedial plane; femora were measured from the *caput femoris* through the mid-depth point of the

collum femoris to the lateral side. S: shaft width at mid-length (except for tibiotarsi, where it is the minimum value) in a lateromedial plane. D: distal width. Tibiotarsi AL: length measured from the proximal articular surfaces to the *cond. lateralis*. Tibiotarsi P: measured across the articular surface. Tarsometatarsus D was measured at right angles to the shaft.

Comparative material

The following comparative material was used. All is modern except that for *Mergus australis* and *Chenonetta finschi*:

Oxyura australis Gould, 1836 blue-billed duck: CM Av31408, Lake Cowal, New South Wales, Australia; AM O65518, Taronga Zoo, Australia.

Malacorhynchus membranaceus (Latham, 1801) Australian pink-eared duck: MNZ 23880, MNZ 23881.

Aythya novaeseelandiae (Gmelin, 1789) New Zealand scaup: CMAv22382, CMAv22413; MNZ 8726, MNZ 13685, MNZ 16588, MNZ 16589, MNZ 17001, MNZ 17002, MNZ 17003, MNZ 23144, MNZ 24245.

Aythya australis (Eyton, 1838) Australian white-eyed duck: AM O65772, New South Wales, Australia.

Anas chlorotis G.R. Gray, 1845 brown teal: MNZ 14978, MNZ 15628, MNZ 15935 = CMAv31828, MNZ 18898, MNZ 21544, MNZ 22086, MNZ 22802, MNZ 22806, MNZ 24535, MNZ 24536, MNZ 24537, MNZ 25105, MNZ 25106, MNZ 26630, MNZ 26631, MNZ 26940a, MNZ 26941a, MNZ 26942a, MNZ 26943a, MNZ 26944a, MNZ 26945a, MNZ 26946, MNZ 26947, MNZ 26949, MNZ 26950a, MNZ 26951a, MNZ 26952a; THW colln, male, Great Barrier Island, Feb. 1985.

Anas gracilis Buller, 1869 grey teal: MNZ 19351, MNZ 19348, MNZ 19301, MNZ 19322, MNZ 13688, MNZ 19323, MNZ 26815 (ex 24545), MNZ 18099, MNZ 19324; CM Av36764.

Anas superciliosa Gmelin, 1789 grey duck: MNZ 13686, MNZ 15030, MNZ 16586, MNZ 18132, MNZ 16476, MNZ 17341, MNZ 17261, MNZ 16698, MNZ 16584, MNZ 24607.

Anas rhynchos (Gould, 1856) Australasian shoveler: MNZ 17000, MNZ 18971, MNZ 16591, MNZ 24588, MNZ 24589; CM Av36112, CM Av19237, CM Av19117, CM Av19238.

Hymenolaimus malacorhynchos (Gmelin, 1789) blue duck: MNZ 16699, MNZ 23924.

Mergus australis Hombron and Jacquinot, 1841 New Zealand merganser: MNZ S30046, MNZ S31777 – collections of fossils from Chatham Island.

Chenonetta finschi (Van Beneden, 1875) Finsch's duck: individual skeleton in THW collection from Hodge Creek Cave, Mt Arthur, collected 25 May 1995; other skeletons in MNZ, notably S35885.

Tadorna variegata (Gmelin, 1789) paradise shelduck: MNZ 16501.

Examples of all other extant anatids mentioned were examined in the collections of the MNZ. Extinct taxa were identified with the characters previously described as follows: *Biziura* (Worthy 2002a), *Oxyura* n.sp. (Worthy in press), *Malacorhynchus scarletti* (Worthy 1995, Worthy & Gill 2002), and *Chenonetta finschi* (Worthy & Olson 2002).

Site localities

In the specimen lists, sites N141/I, N141/II, and N141/XII are referred to hereafter as sites I, II, and XII, respectively. All three sites are along the old outflow

channel, on the northern margin of Lake Poukawa in Hawke's Bay, New Zealand (see Fig. 1). Sites I and II are located at NZMS 260 series map reference V22/296525, or 39° 46' 24"S, 176° 43' 54"E, and Site XII is at the map reference V22/283523, or 39° 46' 34"S, 176° 43' 0"E.

Identification of specimens

Between the time of excavation and the arrival of the collection in the National Museum of New Zealand, many elements of the more rare or interesting taxa were removed from the bags carrying their associated data, and were associated by taxon. As a result, hundreds of bones have



Fig. 2 View of proximal end of humeri of (A) *Oxyura* n.sp. MNZ S18056, (B) *Aythya novaeseelandiae* MNZ 24245, and (C) *Anas chlorotis* MNZ 25105 to reveal the internal structure of the bicipital foramen. The open nature, with foramina to the bone interior, is clearly visible in *Anas*, compared to the walled-off nature of the foramen in *Aythya* and *Oxyura*.

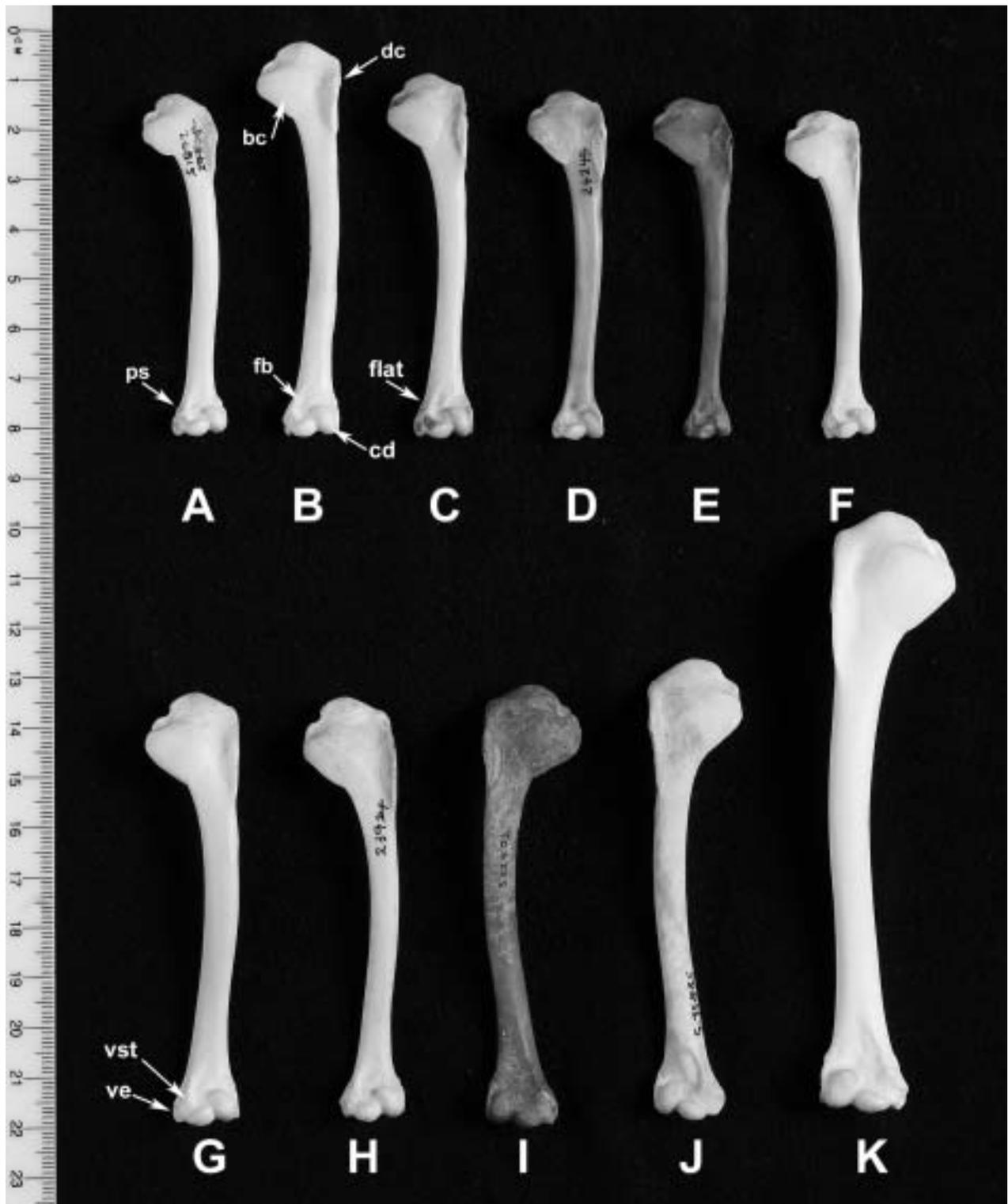


Fig. 3 Left humeri in cranial aspect: (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S41259; (F) *Mergus australis* MNZ S30046; (G) *Anas superciliosa* MNZ 13686; and (H) *Hymenolaimus malacorhynchos* MNZ 23924. Right humeri in cranial aspect: (I) *Malacorhynchus scarletti* MNZ S22402; (J) *Chenonetta finschi* MNZ S35885; and (K) *Tadorna variegata* MNZ 16501. Note flat ventral facies in *A. rhynchos* (C) (abbreviations: bc, bicipital crest; cd, dorsal condyle; dc, deltoid crest; fb, brachial fossa; ps, attachment *pronator superficialis*; ve, ventral epicondyle; vst, ventral supracondylar tubercle. Scale in cm).

no site or collection data other than 'Poukawa'. As the recorded stratigraphy of sites I, II, and XII indicate a similar age range for each of the faunas and as they are geographically close, lying on the shore of the same lake, for this analysis I consider all bones to be derived from a single 'Poukawa' fauna. These bones are 21 715 lots derived from all Poukawa sites catalogued in the Museum of New Zealand S register up until S41604. The few anatid bones recorded from minor sites whose locations are unknown except that they are around Lake Poukawa (e.g. Hall Site VII – 4/2 *Cygnus*, Hall Site X – 1/1 *Cygnus*, and John's Spring V – 2/1 *Cnemiornis gracilis* and 1/1

Anas superciliosa') do not materially affect the analysis. In addition, the two important *Biziura* specimens in CM Av34501 are included.

Previous to this study, many thousands of the bones of smaller anatids were not identified, or only identified as 'anatid'. All anatid bones from the Price Collection in the fossil bird collection of the Museum of New Zealand Te Papa Tongarewa, taken from various sites about Lake Poukawa, were reassessed for their species identity. Also, all the lots of unidentified material from each collection unit (square and spit) were checked for identifiable bones, and if such were found, they were catalogued.

Differential species diagnoses for bones of *Anas superciliosa*, *A. chlorotis*, *A. gracilis*, *A. rhynchotis*, *Mergus australis*, New Zealand *Oxyura* n.sp., *Aythya novaeseelandiae*, *Tadorna variegata*, *Malacorhynchus scarletti*, *Hymenolaimus malacorhynchus*, and *Chenonetta finschi*

The identification of anatid bones is relatively difficult and there are no relevant keys for New Zealand taxa. Diagnostic characters have either not been described previously or are scattered through numerous papers, so I include the following section to indicate how the bones were identified in order to assist future work. I restrict the following differential diagnoses to the above listed taxa as *Cygnus atratus* is larger and very different from all. Bones of *Biziura delautouri* are distinct and were described in Worthy (2002a). Of the included species, no bones were referred to *Anas gracilis* from within the Poukawa collections, but as the species was recorded from the late Holocene of Pyramid Valley, South Island (Holdaway & Worthy 1997), and those identities are still taken as valid, it is considered below. Only four bones of *Cnemiornis gracilis* were found in the Poukawa deposits, but as this species is very distinct (Worthy *et al.* 1997), it is unlikely to be confused with those of other anatids and so is not considered below. Summary statistics for measurements of the species of *Anas* and *Aythya novaeseelandiae* are given in Appendix 1, of fossil New Zealand *Oxyura* in Appendix 2, and of *Malacorhynchus scarletti* in Appendix 3. Summary statistics for measurements of *Chenonetta finschi* are given by Worthy (1988, 1997).

Humeri (Figs 2, 3, 4, and 5)

The humerus is the most useful postcranial element for distinguishing anatid taxa. The humeri of *Anas gracilis*,

A. chlorotis, *A. rhynchotis*, *Aythya novaeseelandiae*, and *Oxyura* n.sp. have overlapping length distributions. Similarly, humeri of the larger *Malacorhynchus scarletti*, *Hymenolaimus malacorhynchus*, *Anas superciliosa*, and *Chenonetta finschi* also have overlapping length distributions. That the ventral part of the *fossa pneumatica* (tricipital fossa) is 'open' to the bone interior, via a large *foramen pneumaticum* – that is, it is not closed off by a continuous sheet of bone, but rather has many pneumatic foramina to the inside of the bone – characterises all *Anas* species, *Mergus*, *Hymenolaimus*, *Chenonetta*, and *Tadorna* (see Fig. 2). Since this fossa opens into the *crista bicipitalis* it will be referred to as the bicipital fossa hereafter. In taxa with an open fossa, if a probe is slid along the humeral shaft up into the bicipital fossa it meets a ledge, whereas if the fossa is occluded, such a probe would follow a continuous flat surface right to the proximal end of the bicipital fossa. *Malacorhynchus*, *Oxyura*, and *Aythya* have closed bicipital fossae.

Of the smaller taxa, humeri of *Oxyura* and *Aythya* are at once distinguished by the closed bicipital fossa (see Fig. 2). In addition, the distal ends of *Aythya* and *Oxyura* humeri differ from those of *Anas* by having a much deeper *fossa m. brachialis*, which is bound by a prominent ridge medially and tends to be aligned more towards the shaft than across it (see Fig. 3).

In *Aythya*, the attachment point of the *pronator brevis* (Howard 1929: Fig. 21) or of the *M. pronator superficialis*

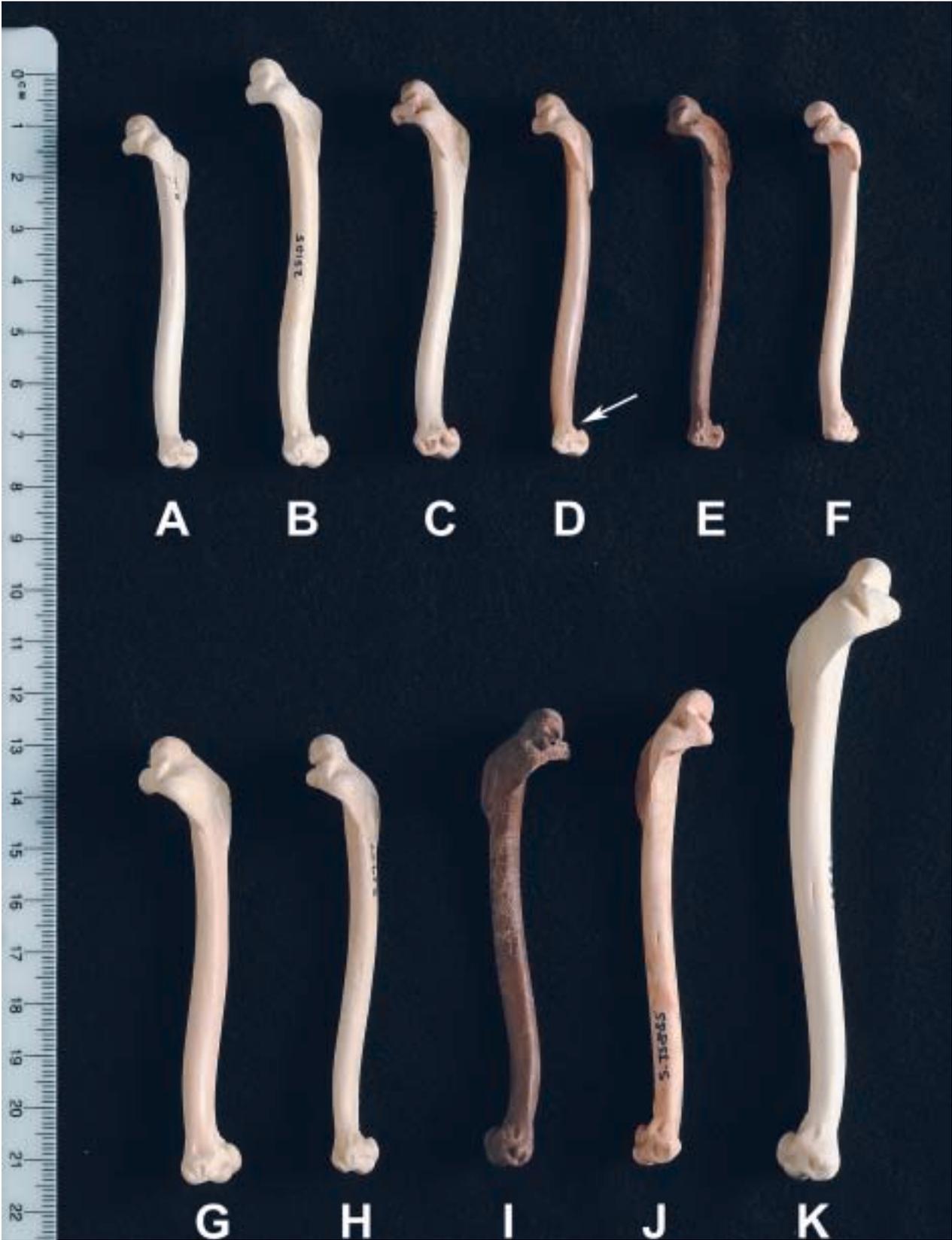


Fig. 4 Humeri in ventral aspect. Specimens as for Fig. 3. Note point of attachment of *M. pronator superficialis* arrowed in D (scale in cm).

is lower than it is in *Anas* species, being further distad than the proximal point of the triangular-shaped *tuberculum supracondylare ventrale* (ventral supracondylar tubercle, otherwise known as the attachment point of the anterior articular ligament (Howard 1929: Fig. 21)), and the medial shaft surface above the ventral supracondylar tubercle is much more constricted than it is in *Anas*. In *Aythya*, the flat face of the ventral supracondylar tubercle faces somewhat distally and in ventral view forms a distinct triangle with the shaft proximad of it, and its proximal margin is level with that of the *condylus dorsalis* (see Figs 3 and 4).

The humerus of *Oxyura* is most similar to that of *Aythya novaeseelandiae* but differs in several significant features. Proximally, the *tuberculum dorsale* is more elevated above the flat bone surface on the adjacent ventral side. The *caput humerus* (head) is more greatly excavated under its caudal surface. The *incisura capitalis* (capital groove) is interrupted by a distinct ridge at its dorsal end (no ridge in *Aythya*). The distal margin of the *crista bicipitalis* joins to the shaft at a steep angle (much shallower angle in *Aythya*). The *tuberculum ventrale* is situated lower in relation to the capital groove, so that the proximal margin of the bicipital fossa in caudal view slopes distally towards the tip of the ventral tubercle. Distally, the shaft immediately above the brachial fossa is more constricted than in *Aythya*. The ventral supracondylar tubercle is larger, extending further proximally than the dorsal condyle, its flat face is parallel to the shaft (not tilted distally as in *Aythya*), and the attachment point of the *M. pronator superficialis* is not distinct, having merged with the margin of the ventral supracondylar tubercle.

The humerus of *Mergus australis* is similar in size to that of *Anas chlorotis*. It is characterised by having a pronounced ridge (capital shaft ridge) on the *margo caudalis*, an elevated dorsal tubercle adjacent to which the head is deeply undercut caudally, a concave dorsal surface to the *crista deltopectoralis*, an open bicipital fossa, a distinct attachment point of the *M. pronator superficialis* that is situated level with the top of the ventral supracondylar tubercle, and a larger brachial fossa that is more deeply excavated adjacent to the ventral supracondylar tubercle.

The humeri of the smaller *Anas* species (*A. chlorotis*, *A. gracilis*, and *A. rhynchotis*) all have an open bicipital fossa, lack an elevated dorsal tubercle, and have a convex dorsal surface to the deltoid crest (see Fig. 5). They differ

from each other as follows. The humeral shaft in *A. chlorotis* is thinner and more sinuous than it is in similar sized *A. rhynchotis* or *A. gracilis*. In *A. chlorotis*, the shaft is compressed on its caudal surface to form a ridge on the *margo caudalis*, unlike other volant *Anas* species. Other weak-flying or non-flying species have a similar ridge, e.g. *A. marecula* and *A. aucklandica*, so I consider this feature to be a pseudo-capital shaft ridge as seen in *Chenonetta finschi* and not homologous to the similar structure seen in e.g. *Tadorna*. In *A. chlorotis* and in *A. rhynchotis*, the distal margin of the bicipital crest forms a relatively straight line from the shaft that intersects the shaft in a shallow angle, whereas in *A. gracilis* this margin is convex and meets the shaft much more abruptly, nearly at right angles. In *A. chlorotis*, the deltoid crest is less robust or thinner along its base, and the brachial fossa is larger and is deeper medially than it is in *A. rhynchotis*, in which the latter is always shallow.

Viewed from the distal end, the *epicondylus ventralis* is directed ventrocranially in *Anas rhynchotis*, whereas in *A. chlorotis*, it is directed more caudally. For *A. chlorotis* this results in the tubercle that is located centrally in the epicondyle being prominent and obscuring the caudal margin of the epicondyle when the humerus is viewed cranially with the caudal surface of both condyles lying on a flat surface. In contrast, in *A. rhynchotis* in cranial view the entire margin of the epicondyle is visible. Described another way, in *A. chlorotis*, a line drawn across the caudal surface from the *proc. flexorius* to the dorsal condyle forms a right angle with the alignment of the ventral epicondyle compared to an acute angle in *A. rhynchotis*. The alignment of the ventral epicondyle results in the medial shaft surface at the level of the ventral supracondylar tubercle being curved in *A. chlorotis*, but flattened in *A. rhynchotis*. The alignment of the ventral epicondyle in *A. gracilis* is similar to that of *A. chlorotis*. The brachial fossa is longer and deeper in *A. chlorotis* than it is in *A. rhynchotis*, in which it is noticeably small and shallow adjacent to the flat, broad surface above the ventral supracondylar tubercle.

The head of *Anas chlorotis*, in caudal view, does not overhang the proximal margin of the capital groove, whereas in *A. rhynchotis* and *A. gracilis* it does, creating a marked alcove within the profile of the incisura notch. Viewed from the proximomedial angle, the capital groove is relatively wider in *A. chlorotis* than it is in *A. rhynchotis* and *A. gracilis*. These characteristics of the head are somewhat subjective, so were not used on their own to identify bones.

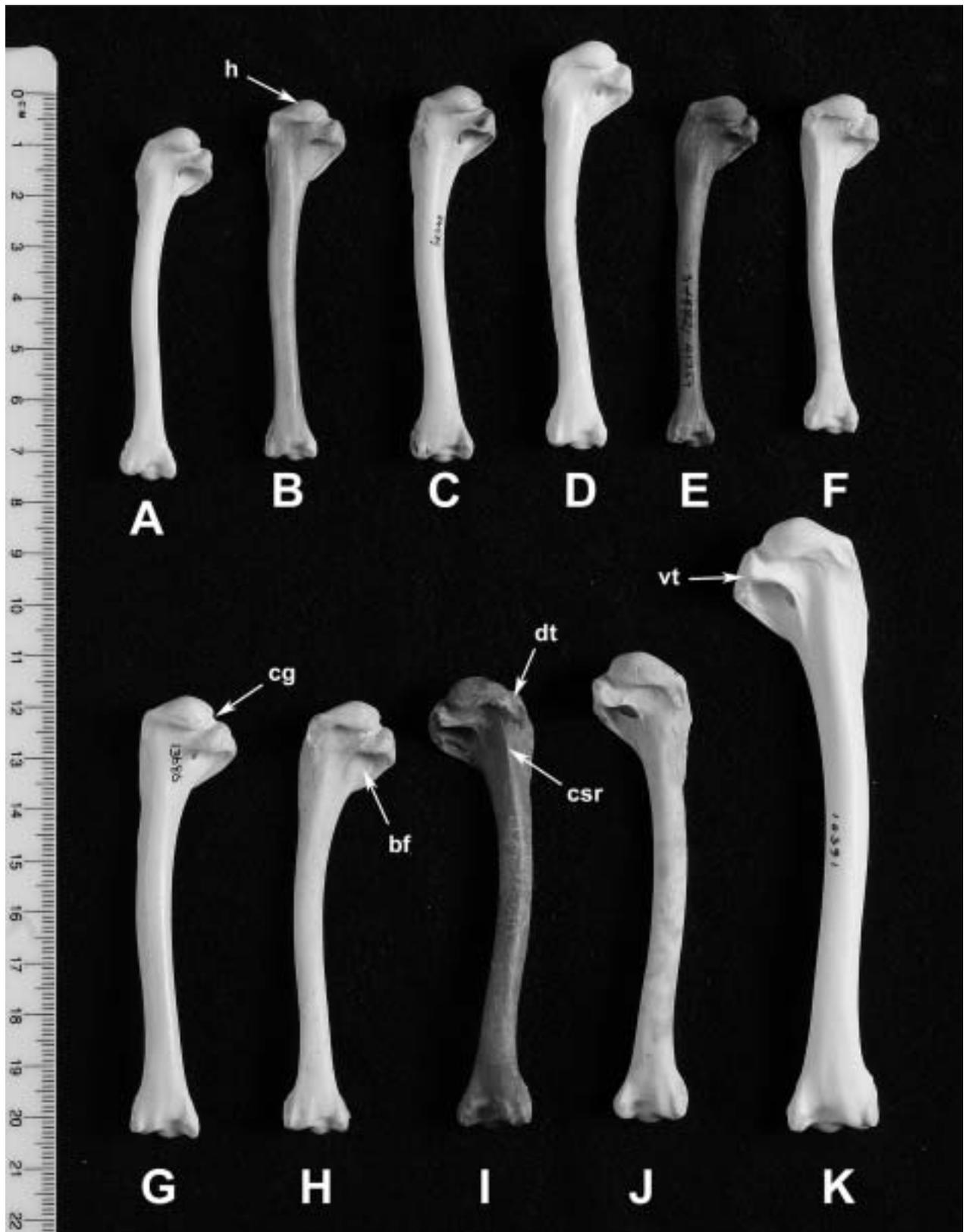


Fig. 5 Humeri in caudal aspect. Specimens as for Fig. 3 (abbreviations as for Fig. 3, and: bf, bicipital fossa; cg, capital groove; dt, dorsal tubercle; csr, capital shaft ridge; h, head; vt, ventral tubercle. Scale in cm).

Humeri of the larger ducks *Anas superciliosa*, *Hymenolaimus malacorhynchos*, *Chenonetta finschi*, and *Malacorhynchus scarletti* are larger than the above discussed taxa. Those of *A. superciliosa* have a typical *Anas* form, with an open bicipital fossa, a non-elevated dorsal tubercle, no capital shaft ridge, and a shallow brachial fossa with a flat shaft mesad to it on which the attachment point of the pronator brevis is centrally placed on the ventral facies and proximad of the ventral supracondylar tubercle. The ventral supracondylar tubercle faces distally and its proximal margin is level with that of the dorsal condyle.

Humeri of *Malacorhynchus scarletti* have a markedly sigmoid shaft, a prominent capital shaft ridge, an elevated dorsal tubercle, a concave dorsal surface to the deltoid crest, and a closed bicipital fossa. In addition, the face of the ventral supracondylar tubercle is aligned with the shaft, not directed distally as in *Anas superciliosa* (Worthy 1995, Worthy & Gill 2002).

The humeri of *Hymenolaimus* are on average slightly smaller than those of *Anas superciliosa* and, like *Anas*, have an open bicipital fossa. However, they differ in that they have a marked capital shaft ridge, an elevated external tuberosity, a concave dorsal surface to the deltoid crest, a head that is more deeply excavated under its caudal surface (resulting in the capital groove being interrupted by a distinct ridge at its dorsal end), a distinct attachment point of the *M. pronator superficialis* that is centred level with the top of the ventral supracondylar tubercle rather than just above as in *Anas*, and an ovoid brachial fossa that is aligned along the shaft rather than at 45 degrees across it.

Humeri of *Chenonetta finschi* have an elevated dorsal tubercle, a concave dorsal surface to the deltoid crest, an open bicipital fossa, and a pseudo-capital shaft ridge. The face of the ventral supracondylar tubercle is directed distally, the attachment point of the pronator brevis is centrally placed on the ventral facies and just proximad of the ventral supracondylar tubercle, and the shaft above it is markedly constricted (Worthy & Olson 2002).

Ulnae (Fig. 6)

The ulnae of the various New Zealand *Anas* spp. are partially separated by size, but those of *A. chlorotis*, *A. gracilis*, and *A. rhynchotis* overlap in length (see Appendix 1). The ulnae of *Anas* spp. are curved such that the plane of the *margo caudalis* from the distal end forms a straight line for less than half of the total length, whereas more than the distal half of the ulna of *Oxyura* and *Aythya* is straight.

Ulnae of *Anas chlorotis* tend to have relatively larger proximal and distal ends compared to those of similar length of *A. gracilis*. The *impressio brachialis* is deeper in *A. chlorotis* than it is in *A. gracilis*, *A. rhynchotis*, or *A. superciliosa*, and it forms a near right angle with the *margo cranialis*. In ventral aspect, the width of the brachial impression extends more than halfway to the caudal margin at a point just below the *tuberculum ligamentosa collateralis ventralis* in *A. chlorotis*, and less than halfway in *A. rhynchotis* and *A. gracilis*. The shaft is generally somewhat stouter in *A. rhynchotis* than it is in *A. chlorotis*. In *A. rhynchotis* in ventral view, the *tuberculum carpale* is less pointed and the *cond. dorsalis ulnaris* is more inflated and more robust along its length than in *A. chlorotis*.

The ulnae of both *Aythya novaeseelandiae* and New Zealand *Oxyura* are similar to each other, and are more slender and straighter than those of *Anas* spp. In both, the ventral margin of the *cotyla ventralis* is straight, forming a near right angle with the cranial margin, whereas in *Anas* spp. the *cotyla* is rounded ventrally. *Aythya* ulnae are longer (59.3–63.2 mm versus 51–57 mm) and stouter than those of New Zealand *Oxyura*. In *Aythya*, the dorsal ulnar condyle, in dorsal view, tends to be longer than it is wide; in New Zealand *Oxyura* it is about as wide as it is long, yet it is not as short nor does it end so abruptly proximally as it does in *O. australis*. In *Aythya*, the carpal tuberculum is stouter dorsoventrally than it is in *Oxyura*.

The ulnae of *Mergus* are of similar size and proportions to those of *Anas chlorotis*. The *tuber. carpale* is more robust and the *incisura tuberculi carpalis* is not as deep as in *A. chlorotis*, but in general ulnae of both taxa are likely to be confused.

The ulnae of *Malacorhynchus scarletti* are of similar length and curvature to those of *Anas superciliosa*, but have a more slender shaft. *M. scarletti* differs markedly, however, in that the brachial impression is deep and forms a right angle with the cranial surface, whereas it is shallow and curved in *A. superciliosa*. There is a prominence on the cranial surface under the ventral *cotyla* and adjacent to the brachial impression of *M. scarletti*, which is lacking in *A. superciliosa*. The *olecranon* is much more pointed in *Malacorhynchus* than it is in *Anas* and, as in *Aythya* and *Oxyura*, the ventral and cranial margins of the ventral *cotyla* are straight and meet at a right angle, not curved as in *Anas*. Distally, the carpal tuberculum has a sharp, proximally directed crest running to the cranial surface, which is lacking in *Anas*.

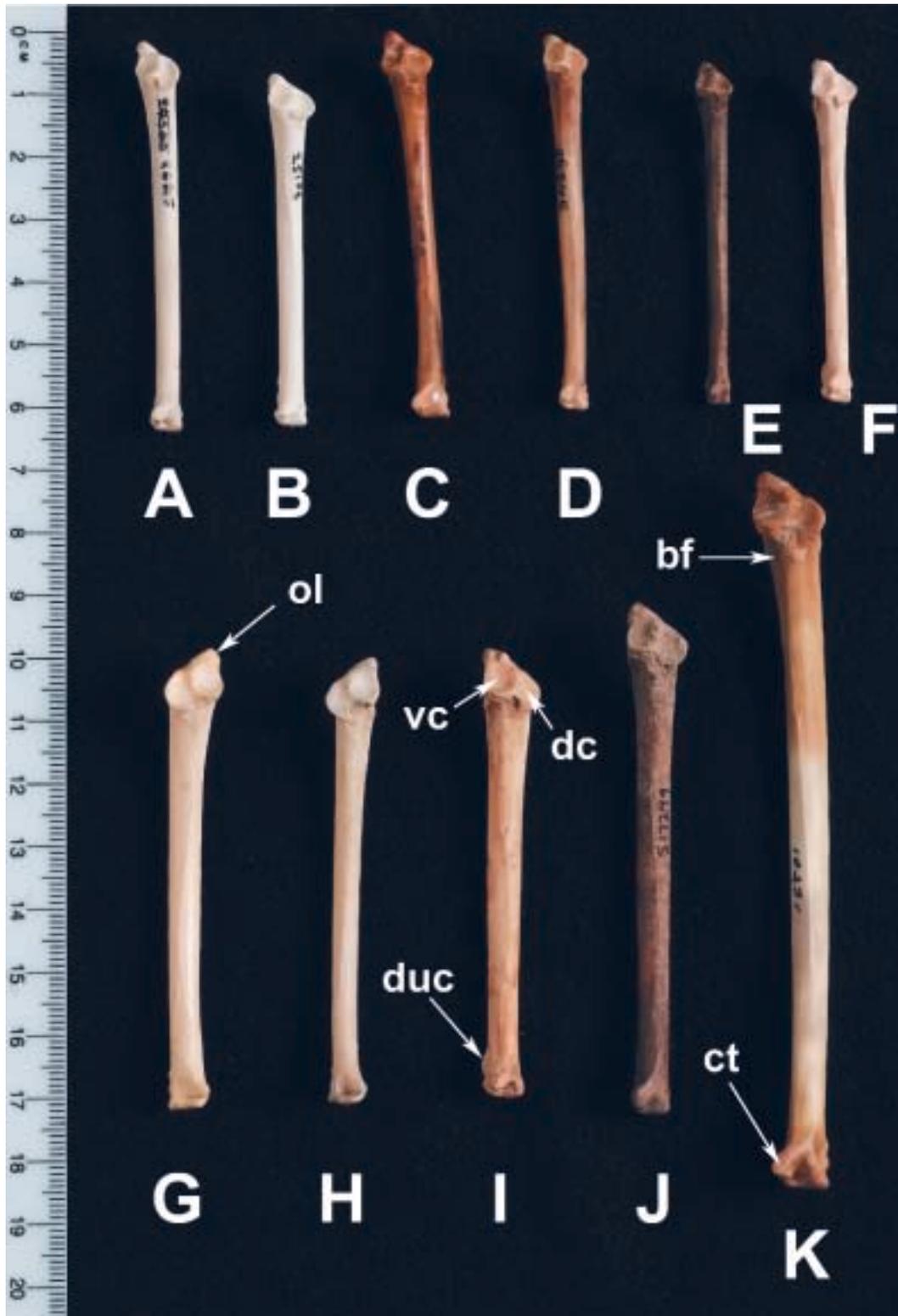


Fig. 6 Left ulnae in medial aspect: (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S20180; and (F) *Mergus australis* MNZ S30046. Right ulnae: (G) *Anas superciliosa* MNZ 13686; and (H) *Hymenolaimus malacorhynchos* MNZ 23924. Left ulnae: (I) *Chenonetta finschi* MNZ S35885; (J) *Malacorhynchus scarletti* MNZ S17299; and (K) *Tadorna variegata* MNZ 16501 (abbreviations: bf, brachialis impression; ct, carpal tubercle; dc, dorsal cotyla; duc, dorsal ulna condyle; ol, olecranon; vc, ventral cotyla. Scale in cm).

The ulnae of *Hymenolaimus* are of similar length to those of *Anas rhynchotis*, but uniquely are very dorsoventrally flattened on the distal end. The *margo caudalis* and *facies ventralis* in species of *Anas* meet distally in a right angle, with a shallow groove between the *incisura tendinus* and the *tuber. carpale*. In contrast, in *Hymenolaimus* the area between the *incisura tendinus* and the *tuber. carpale* forms a deeply grooved articular facet for the *os carpi radialis*. The net result of this is that the dorsoventral depth of the distal end is about 55% of the caudo-cranial depth. Proximally, the *facies artic. radialis* is more elongate and is pointed (in *Anas* spp., it is shorter than it is wide at the junction with *cotyla dorsalis* and is rounded distally). The *impressio brachialis* is relatively deep and the ventral corner of the *cotyla ventralis* is produced into an acute point (rounded in *Anas*, and at right angles in *Aythya*).

Ulnae of *Chenonetta finschi* are also of similar length to those of *Anas superciliosa*, but differ in that they have a less elevated olecranon and a much more robust carpal tuberculum, which is flattened over its proximal margin. *Tadorna* ulnae are much larger and unlikely to be confused with any other species.

Carpometacarpi (Fig. 7)

The carpometacarpi of *Anas* spp. are similar in shape and differ mainly in size among the taxa discussed herein. The *os metacarpale minus* is evenly curved along its length and joins to the *os metacarpale majus* at a point opposite the distal base of the *proc. alularis*. In posterior view, the ventral rim of the *trochlea carpalis* is aligned somewhat dorsally rather than being in line with the *os metacarpale majus*, so that it forms a dorsally convex curve with the ventral ridge of the proximal end of the minor metacarpal. In the teal, *Anas gracilis* and, to a greater extent, *A. chlorotis*, the ventral ridge of the proximal end of the minor metacarpal is elevated into a crest that links to the ventral rim of the carpal trochlea. In *A. superciliosa* and *A. rhynchotis*, this ridge is not elevated into a crest and the 'saddle' between the minor metacarpal and the carpal trochlea is rounded. Carpometacarpi of *A. gracilis*, *A. rhynchotis*, and *A. chlorotis* have length ranges that broadly overlap. Those of *A. gracilis* are distinctively slender and elongate, more so than either those of *A. chlorotis* or *A. rhynchotis*. *A. chlorotis* carpometacarpi are distinguished by having a relatively bigger proximal end on which the *proc. extensorius* is often enlarged by a rugosity, and a stouter major metacarpal with a short *synostosis metacarpale distalis*. The rugosity on the

extensor process is functional in derivation, being related to the use of the wings in fighting. The carpometacarpi of *A. rhynchotis* have a relatively slender major metacarpal with an elongate distal metacarpal synostosis and a round junction of the minor metacarpal and the carpal trochlea. Those of *A. superciliosa* are larger than any of *A. rhynchotis* but are otherwise similar.

The carpometacarpi of *Aythya novaeseelandiae* are distinct from those of any *Anas*, as they are shorter and the minor metacarpal joins to the major metacarpal distad of the alular process, creating a distinctive 'neck'. The ventral rim of the carpal trochlea is not aligned with the major metacarpal and so is like *Anas* in this respect.

No New Zealand *Oxyura* carpometacarpi have been identified. However, from the structure of *O. australis* and what is known of the other wing elements of the New Zealand bird, it is likely that they will be smaller than those of *Aythya novaeseelandiae* and differ from that taxon by the following features. They will have a straight minor metacarpal whose ventral ridge proximally joins to the ventral rim of the carpal trochlea in a straight line (not forming a dorsally convex curve as in *Aythya*), and the distal metacarpal synostosis will be shorter.

The carpometacarpi of *Mergus* are similar in size and proportions to those of *Aythya*, but the carpal trochlea is dorsoventrally thicker, the extensor process is more ventrally rotated and is more squared cranially, the pisiform process is large and blunt but does not overhang the *fovea carpalis cranialis* (it does in *Aythya* and is pointed), and ventrally the minor metacarpal abuts the internal rim of the carpal trochlea (it joins to the shaft further distad in *Aythya*, creating a 'neck').

The carpometacarpus of *Malacorhynchus scarletti* has not been securely identified. However, on the basis that *Malacorhynchus humeri* and ulnae of similar length to those of *Anas superciliosa* are more slender, the nine carpometacarpi (MNZ S3315, MNZ 3495, MNZ 17553, MNZ 18036, MNZ 18609, MNZ 19340, MNZ 19372, MNZ 19398, MNZ 20045) previously catalogued as *A. superciliosa* are referred to *Malacorhynchus*. They differ from *A. superciliosa* in the following ways: (i) when lying at rest on a flat surface with ventral side uppermost, the extensor process is directed ventrally (in *A. superciliosa*, it is parallel to the surface); (ii) they are more gracile than similar length *A. superciliosa* bones; (iii) the length of the shaft between the proximal end of the intermetacarpal space and the alular process is relatively longer than in

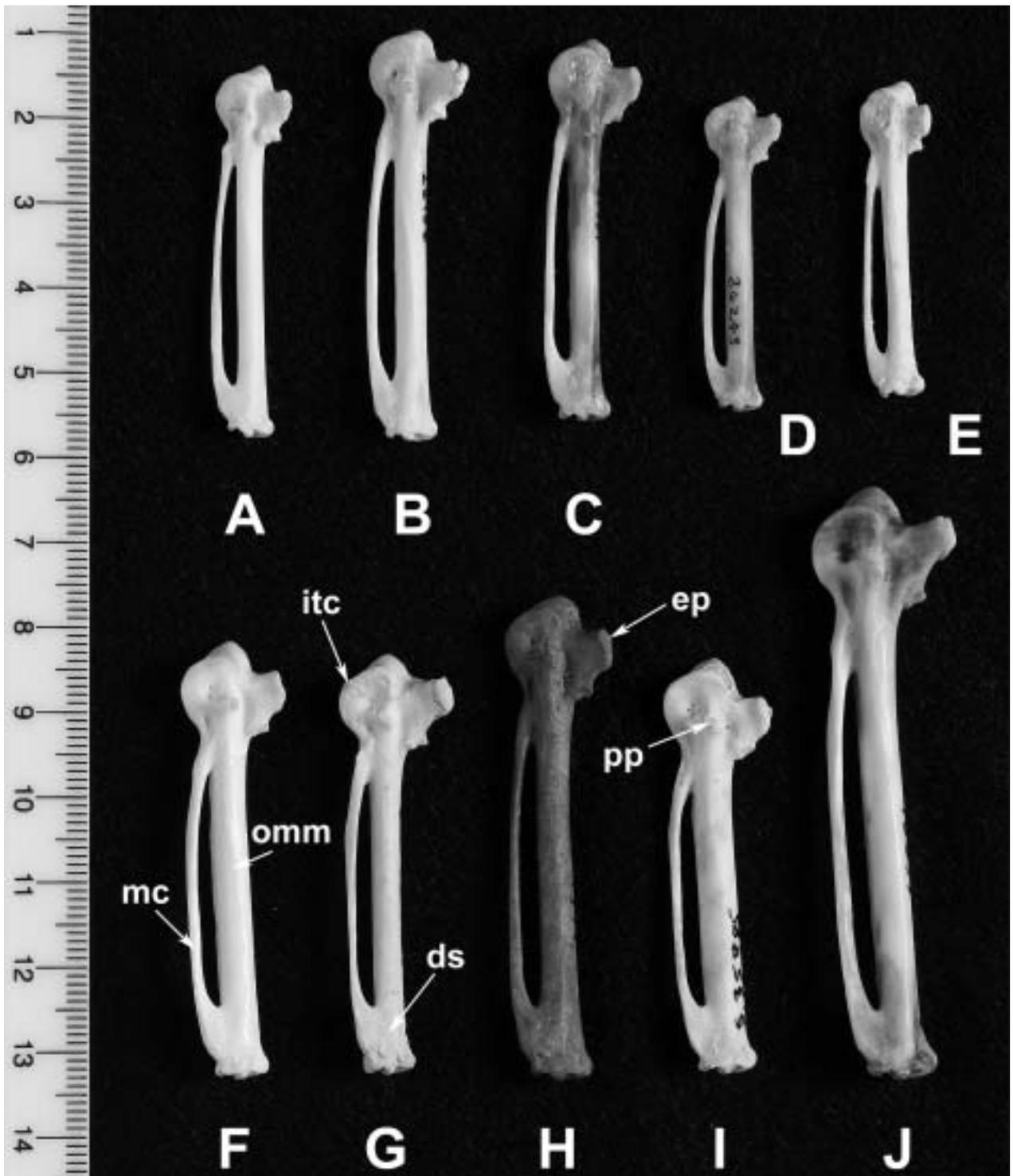


Fig. 7 Left carpometacarpals in ventral aspect: (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Mergus australis* MNZ S30046; (F) *Anas superciliosa* MNZ 13686; (G) *Hymenolaimus malacorhynchus* MNZ 23924; (H) *Malacorhynchus scarletti* MNZ S19372; (I) *Chenonetta finschi* MNZ S35885; and (J) *Tadorna variegata* MNZ 16501 (abbreviations: ds, distal synostosis; ep, extensor process; itc, internal rim carpal trochlea; pp, pisiform process; omm, major metacarpal; mc, minor metacarpal. Scale in cm).

A. superciliosa bones and is slightly less than the width immediately distad of the alular process (in *A. superciliosa*, this length is very much less than the width distad of the alular process); (iv) the distal metacarpal synostosis is shorter than in *A. superciliosa*; (v) the proximal end of the minor metacarpal is not grooved externally (in *A. superciliosa* there is a distinct groove); (vi) the outer edge of the minor metacarpal (in ventral aspect) at its proximal synostosis forms a relatively straight line that diverges only slightly from the shaft (in *A. superciliosa*, it forms an arc that is initially quite divergent from the shaft at the proximal end); and (vii) the external rim of the carpal trochlea is notched distally by a groove opening to the *fovea carpalis caudalis* and is only slightly elevated between this groove and the shaft (in *A. superciliosa*, there is a distinct prominence between the groove and the shaft). The three specimens MNZ S3315, MNZ 3495, and MNZ 20045 are referred with less certainty to *Malacorhynchus* as they conform with *A. superciliosa* in characters (i) and (v), but are otherwise like the other listed specimens.

Carpometacarpi of *Hymenolaimus*, while as long as those of *Anas rhynchotis*, differ mainly in the larger extensor process, which normally contributes at least half of the total width (markedly less than half in *A. rhynchotis* or *A. superciliosa*). The carpal trochlea is more deeply grooved between the internal and external rims than in *Anas*, proximally the minor metacarpal has a distinct tuberosity and the distal metacarpal synostosis is relatively shorter than in *Anas*.

The carpometacarpi of *Chenonetta finschi* broadly overlap in length with those of *Anas superciliosa*, but are relatively stouter, the ventral rim of the proximal minor metacarpal is elevated into a crest that links to the rim of the carpal trochlea, and the distal synostosis is shorter.

Carpometacarpi of *Tadorna variegata* are longer than those of the other taxa discussed. They have a relatively more elongate extensor process, the carpal trochlea is concave between the rims over its proximal extent, and the *fossa supratrochlearis* opens via a wide notch to the *facies ulnocarpalis* (relatively much smaller in *Chenonetta finschi*).

Coracoids (Fig. 8)

In *Anas* (*A. chlorotis*, *A. gracilis*, *A. rhynchotis*, and *A. superciliosa*), the *proc. acrocoracoideus* overhangs the shaft medially, forming a wide angle in dorsal aspect (not at right angles). The *sulcus m. supracoracoidei* usually has a shallow fossa that is little excavated under the *facies artic. humeralis*.

The latter extends up to and beneath the dorsal part of the *facies artic. clavicularis*, which forms a rounded lobe overhanging the sulcus. In rare examples of both *A. superciliosa* and *A. chlorotis*, this fossa is more deeply excavated from the humeral facet right to the medial margin of the acrocoracoid past the ventral clavicular facet. In *A. rhynchotis*, however, the supracoracoidal sulcus is deeply excavated under the ridge between the humeral facet and the dorsal clavicular facet: the excavation never extends past the clavicular facet. The acrocoracoid in *A. chlorotis* is less produced beyond the humeral facet, such that if a line is drawn from the point where the acrocoracoid overhangs the shaft across to the top of the humeral facet, the height above the point of the dorsal clavicular facet is less than the width medial of this point, as compared with greater height in *A. gracilis*, *A. rhynchotis*, and *A. superciliosa*. In *Anas*, the *proc. procoracoideus* is directed medially so that the dorsal edge is slightly directed towards the acrocoracoid and is pointed (not thickened). The *angulus medialis* is acute, with the ventral and dorsal surfaces meeting in a sharp crest (often produced as a flange) that extends from the medial angle up the shaft a distance equivalent to twice the height of the *facies artic. sternalis*. The medial angle is usually more pointed in *A. chlorotis* than in *A. rhynchotis*, *A. gracilis*, or *A. superciliosa*. The *proc. lateralis* in *Anas* is produced as a flange that forms a right angle with the sternal facet and an obtuse angle with a thickened point above the lateral side of the sternal facet.

The coracoid in *Aythya* differs from *Anas* in that the acrocoracoid does not protrude medially from the line of the shaft, the supracoracoidal sulcus is markedly excavated under the humeral facet, the dorsal lobe of the clavicular facet is prominent and pointed and overhangs the supracoracoidal sulcus, and the depth of the bone medially of the supracoracoidal sulcus is very much greater than in similar-sized *Anas* coracoids. Also, the ventral surface mesad of the humeral facet is markedly convex leading to the acrocoracoid, rather than more or less flat as in *Anas* (especially so in *A. chlorotis*). The lateral process is less produced laterally, forming a more obtuse angle than in *Anas*.

The coracoid of New Zealand *Oxyura* is similar to that of *Aythya* in that the acrocoracoid does not overhang the shaft. However, unlike *Aythya* there is no excavation in the supracoracoidal sulcus and the dorsal lobe of the clavicular facet is poorly developed. The humeral facet is distinct, being produced abruptly from the shaft just above the scapular cotyla, and it is nearly as wide as it is long, rather than tapering to the shaft and longer than wide as in

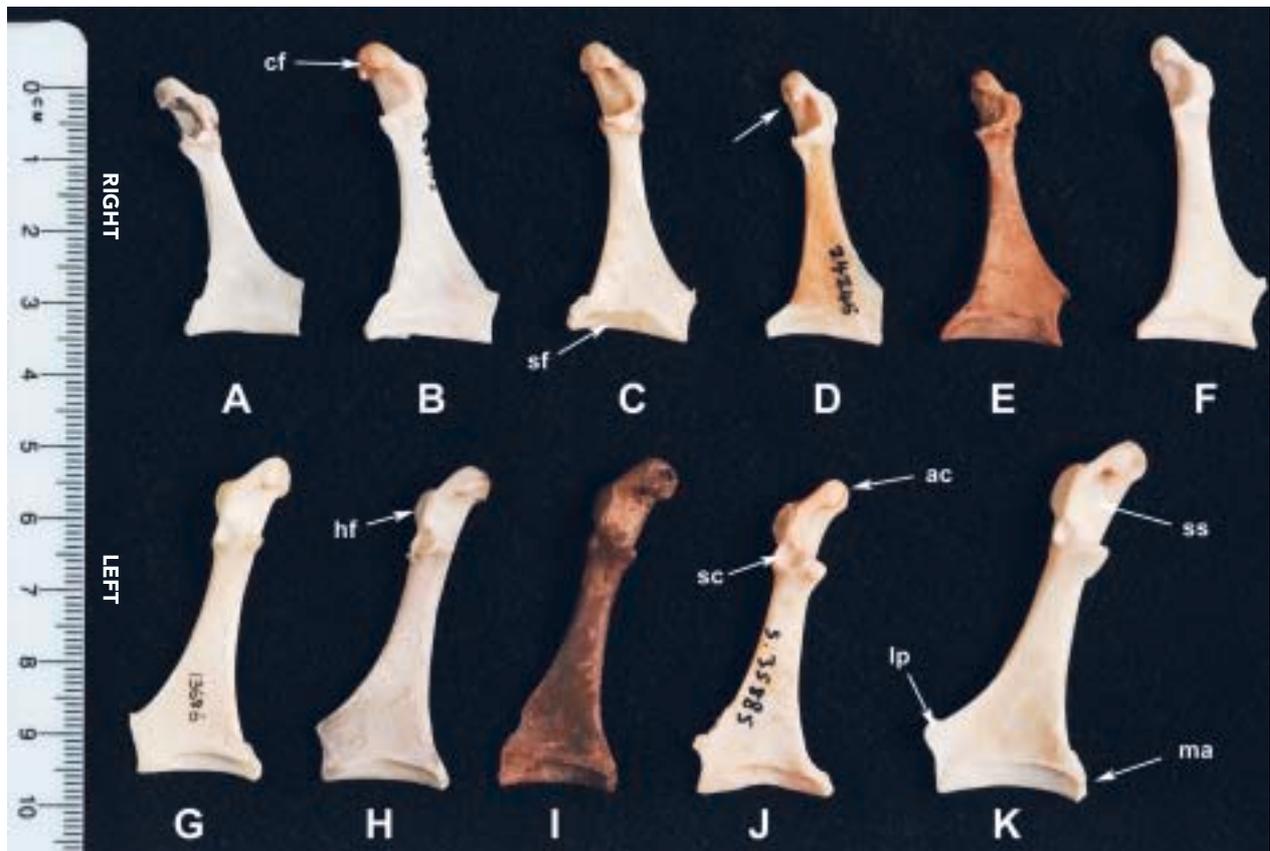


Fig. 8 Right coracoids in dorsal aspect: (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S18506; (F) *Mergus australis* MNZ S30046. Left coracoids in dorsal aspect. (G) *Anas superciliosa* MNZ 13686; (H) *Hymenolaimus malacorhynchos* MNZ 23924; (I) *Malacorhynchus scarletti* MNZ S21082; (J) *Chenonetta finschi* MNZ S35885; and (K) *Tadorna variegata* MNZ 16501. Note prominent dorsal lobe of clavicular facet in *Aythya* (abbreviations: ac, acrocoracoid; cf, clavicular facet; hf, humeral facet; lp, lateral process; ma, medial angle; sc, scapular cotyla; sf, sternal facet; ss, supracoracoidal sulcus. Scale in cm).

Aythya. The alignment of the coracoid differs from that in *Anas* or *Aythya*: if the coracoids are aligned with the sternal facets, those of *Anas* and *Aythya* have the humeral end directed medially, whereas that of *Oxyura* is directed more or less at right angles to the sternal end. The sternal end of the coracoid in New Zealand *Oxyura* is relatively broader below a thinner shaft than in *Aythya*. The lateral process is produced as an acute, somewhat sternally directed, point above the lateral end of the sternal facet, which is also produced as an acute point. The sternal facet is broader than in *Aythya* and widest centrally. The medial angle is acute and is connected to the shaft by a sharp crest.

Coracoids of *Mergus* are similar in shape to those of *Aythya* in that the acrocoracoid does not overhang the shaft medially (as it does in all *Anas* spp.). Unlike *Aythya*,

the coracoid of *Mergus* has a distinct point on the lateral process so that the lateral margin of the process is concave. The dorsal lobe of the clavicular facet is not as robust as in *Aythya* and does not point sternally, nor does it extend below the humeral facet (in *Aythya* it is pointed sternally and extends below the level of the humeral facet). In *Mergus*, the shape of the supracoracoidal sulcus as defined in dorsal view by the top of the procoracoidal process and the ridge mesad of the humeral facet forms an open 'C' (nearly a right angle in *Aythya*).

The coracoids of *Malacorhynchus scarletti* are of similar size to those of *Anas superciliosa*, but differ as follows: the acrocoracoid in dorsal view is wider and more rounded above the supracoracoidal sulcus; the shaft sternally of the cotyla scapularis in dorsal view has parallel sides (they diverge

in *Anas*); the *impressio m. sternocoracoidei* is more concave and the small intermuscular ridges extending from the medial side in it are directed more along the bone than across it and are more pronounced than in *Anas*; the medial angle is less acute and has a robust crest leading to the shaft; ventrally, the sternal facet below the medial angle is more robust, forming a prominent ridge above the surface of the bone; there is a distinct depression in the middle of the ventral surface mesad of the intermuscular line; and the ventral intermuscular line marks an abrupt change in the plane of the ventral surface to the medial surface above the lateral process, whereas this area is evenly curved in *Anas*.

The coracoids of *Hymenolaimus* are very similar to those of *Anas* and overlap those of *A. rhynchosotis* in size. The main differences are that the medial angle lacks a flange above it as in *Anas* spp., and the clavicular facet is concave between prominent ventral and dorsal lobes.

The coracoids of *Chenonetta finschi* are shorter and more robust than those of either *Anas superciliosa* or *Malacorhynchus scarletti*. The medial angle is much further produced medially and the lateral process has an acute projection above the sternal facet that is also acutely pointed laterally. The sternal facet is more concave than in *A. superciliosa* or *M. scarletti*.

Coracoids of *Tadorna variegata* are generally larger than those of other species, with the exception that those of smaller females may overlap those of larger *Anas superciliosa*. Both are very similar, but coracoids of *Tadorna* are thicker, especially through the shaft, and the acrocoracoid does not overhang the shaft medially as much as it does in *A. superciliosa*. The dorsal clavicular facet is more pointed and overhangs the supracoracoidal sulcus in *Tadorna*. The procoracoid process is not as pointed and is directed more at right angles to the shaft (not slightly towards the acrocoracoid as in *Anas*), and the procoracoid process has a notch interpreted as an open procoracoidal foramen (*Anas* does not have either a procoracoidal foramen or a notch). The intermuscular lines in the *impressio m. sternocoracoidei* are aligned more towards the humeral end in *Tadorna* than across the bone as in *Anas*. The medial angle is less pointed in *Tadorna* than in *Anas*.

Scapulae (Fig. 9)

Scapulae were first separated on size into small and larger anatis: small included *Aythya novaeseelandiae*, *Anas chlorotis*, and *Anas rhynchosotis*, and is presumed to include New Zealand *Oxyura*; large included *Anas superciliosa*,

Chenonetta finschi, and *Malacorhynchus scarletti*. In all *Anas* scapulae, the blade markedly widens posterior of a prominent tubercle on the *facies lateralis* of the *collum scapulae* (neck).

Scapulae of *Anas chlorotis* were identified by the following combination of characters: *corpus scapulae* markedly curved ventrally; *acromium* produced as a triangular point to form a concave hollow between it and *tuberculum coracoideum* on the anterior margin; in lateral view, the dorsal margin of the acromium deviates upwards slightly from the line of the dorsal margin of the shaft between it and the blade, before curving proximally; on the lateral face of the acromium the *facies artic. clavicularis* is a raised triangular tubercle that may be weakly or strongly defined; and the anterior end of the *facies costalis* is flat and lacks marked hollows.

Scapulae of *Anas rhynchosotis* differ most notably from those of *A. chlorotis* in that the acromium is further produced proximally, such that its dorsal and ventral margins are nearly parallel and the tip is rounded. In lateral view, the acromium is directed upwards from the dorsal margin of the shaft only slightly, and the costal face of the anterior end is medially convex and lacks marked hollows.

Scapulae of *Anas superciliosa* have an acromium that is elevated dorsally above the line of shaft, and the lateral tubercle on the acromium is of variable height but is highest caudad of the tip. There is a distinct elongate rugosity dorsal to, and extending caudad of, the humeral articular facet, and there is either no crest or a weak crest dorsally on the medial surface behind the acromium. Additionally, the blade maintains the same height caudad of the lateral tuberosity, and the coracoid tubercle is level with a line linking the acromium and the humeral articular facet.

Scapulae of *Aythya novaeseelandiae* also have a prominent tubercle on the lateral face of the neck, but they differ most from like-sized *Anas chlorotis* by the form of the acromium, which is directed markedly upwards from the dorsal line of the shaft, has near parallel sides, and is rounded at the tip. In addition, the acromium has a flat cranial face and does not form a hollow between its tip and the coracoid tubercle on the anterior margin; this results in the coracoid tubercle extending beyond a line connecting the anterior points of the acromium and the humeral articular facet, unlike in *Anas*, in which all three connect in a straight line. Finally, in *Aythya novaeseelandiae* the blade does not markedly widen posterior of the tubercle on the lateral face of the neck and the costal face lacks hollows.

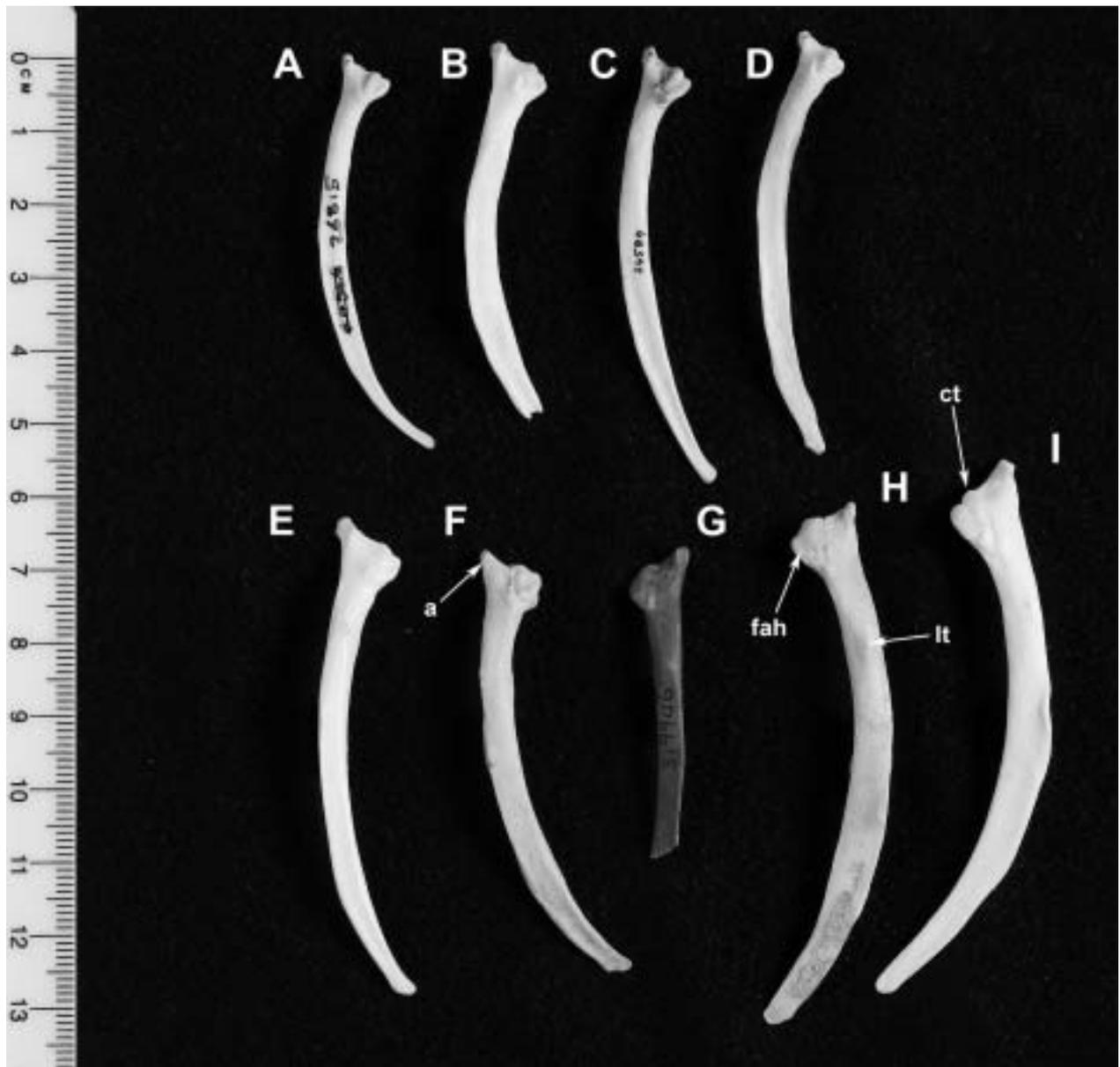


Fig. 9 Right scapulae in lateral aspect: (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Anas superciliosa* MNZ 13686; and (F) *Hymenolaimus malacorhynchos* MNZ 23924. Left scapulae: (G) *Malacorhynchus scarletti* MNZ S19906; (H) *Chenonetta finschi* MNZ S35885; and (I) *Tadorna variegata* MNZ 16501 (abbreviations: a, acromion; fah, articular facet for humerus; lt, lateral tubercle; ct, coracoid tubercle. Scale in cm).

The scapulae of *Mergus* are similar in size to those of *Aythya* and *Anas chlorotis* but differ most from them in that they lack the tubercle on the lateral surface of the shaft. They differ further in that the acromium, while produced into an elongate point as in *Aythya* (*Anas* has a broader based, shorter acromium), is directed anteriorly (not upwards from the dorsal line of the shaft as in *Aythya*), forming a deep notch cranially between it and the coracoid tubercle (very shallow and flat in *Aythya*). Also, the blade does not markedly widen posterior of the neck on the lateral face, and the humeral articular facet is very little produced ventrally, so the lateral ventral profile is only very slightly concave distally of the humeral facet (markedly so in *Anas*). On the ventrolateral face just caudad of the humeral facet is an elongate fossa not seen in *Anas*, but which is about twice as long as a similar feature in *Aythya* and *Oxyura*.

Scapulae of *Oxyura australis* have a marked hollow on the costal face of the neck just caudad of the acromium. They also differ from the above small waterfowl in that the humeral articular facet is directed further ventrally, rather than being roughly on a plane with the surface immediately above it as in *Anas*. There is an elongate crest (not a tubercle) on the lateral face and the least height of the shaft is caudad of, rather than at or anterior of, this point (as in *Anas* and *Aythya*). Additionally, the shaft through the lateral crest tends towards a distinctly triangular shape in section rather than an oval. It is assumed that scapulae of New Zealand *Oxyura* would have similar features, but no scapulae with such features were located.

Scapulae of *Chenonetta finschi*, like *Oxyura*, have the least height of blade caudad of the tubercle on the lateral face, and the blade expands greatly in height over the caudal half. In lateral view, the dorsal surface deviates upwards from the line of the shaft towards the acromium (point of inflexion) at the caudal margin of the humeral articular facet, whereas in *Anas superciliosa* the point of inflexion is much further anterior, essentially at the base of the acromium itself and by the clavicular articular facet. Finally, the coracoid tubercle extends well beyond a line connecting the anterior margin of the acromium and the humeral articular facet, and there is no distinct lateral crest above the humeral articular facet.

In *Malacorhynchus scarletti*, the acromium in lateral view is not directed dorsally from the line of the shaft as in *Anas superciliosa*, and in medial view there is a distinct crest dorsally immediately caudad of the acromium (crest

absent or very weak in *A. superciliosa*). The triangular tubercle on the lateral surface of the acromium is strongly marked and highest close to the tip (situated caudad of the tip of the acromium and generally relatively smaller in *A. superciliosa*). Also, the blade does not expand in height caudally and there is no distinct lateral tuberosity dorsad of the humeral articular facet.

In *Hymenolaimus*, the prominent tubercle on the lateral facet of the blade present in *Anas* is replaced by an elongate crest, but otherwise scapulae are very similar to those of *Anas rhynchotis*. However, the anterior part of the humeral articular facet is less well developed and so is not separated from the coracoid tubercle by a notch as in *Anas*, and the coracoid tubercle therefore protrudes beyond a line linking the acromium and the humeral facet.

Femora (Figs 10 and 11)

The shaft is straight in all *Anas* species, whereas those of *Aythya*, *Mergus*, and *Oxyura* are markedly bent dorsoventrally. Femora of *Anas chlorotis*, *A. rhynchotis*, and *A. superciliosa* have overlapping length distributions, but those of *A. gracilis* are smaller.

In *Anas chlorotis*, the femora are very stout, having relative (to their length) much greater distal, shaft, and proximal widths than do *A. rhynchotis* or *A. superciliosa*. In *A. chlorotis*, the *linea intermus. caudalis* is prominent over the middle third of the shaft (there is no crest between it and the *crista supracondylaris medialis*) and it continues proximally as a crest on the medial side of the shaft aligned towards the femoral ball. This proximal extension is more weakly developed in *A. gracilis*. In *A. chlorotis*, the *fossa poplitea* is relatively shallow and bound by a sharp crest medially. The shaft mesad of this crest is flat (not concave as in *Malacorhynchus*, in which the popliteal fossa is also much deeper and the crest higher and thinner). The *trochanter femoris* in *A. chlorotis* and *A. gracilis* is slightly concave to flat in lateral view, in contrast to convex in *A. rhynchotis*. In *A. gracilis*, the crest of the trochanter overhangs the pretrochanteric surface, whereas there is no such overhang in *A. chlorotis* or *A. rhynchotis*.

The femora of *Anas superciliosa* are usually longer than those of *Anas chlorotis*, but have similar shaft and distal widths (see Appendix 1), and are thus similar in shape to those of *A. rhynchotis*.

The femora of *Aythya novaeseelandiae* are characterised by features commonly seen in diving ducks: a dorsoventrally bent shaft; a deep popliteal fossa bound by a robust ridge



Fig. 10 Femora in cranial aspect (ABCGH – right sides; DEFIIJK – left sides): (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S5976; (F) *Mergus australis* MNZ S30046; (G) *Anas superciliosa* MNZ 13686; (H) *Hymenolaimus malacorhynchos* MNZ 23924; (I) *Malacorhynchus scarletti* MNZ S10342; (J) *Chenonetta finschi* MNZ S35885; and (K) *Tadorna variegata* MNZ 16501 (abbreviations: b, femoral ball; ct, trochantal crest; t, trochanter. Scale in cm).

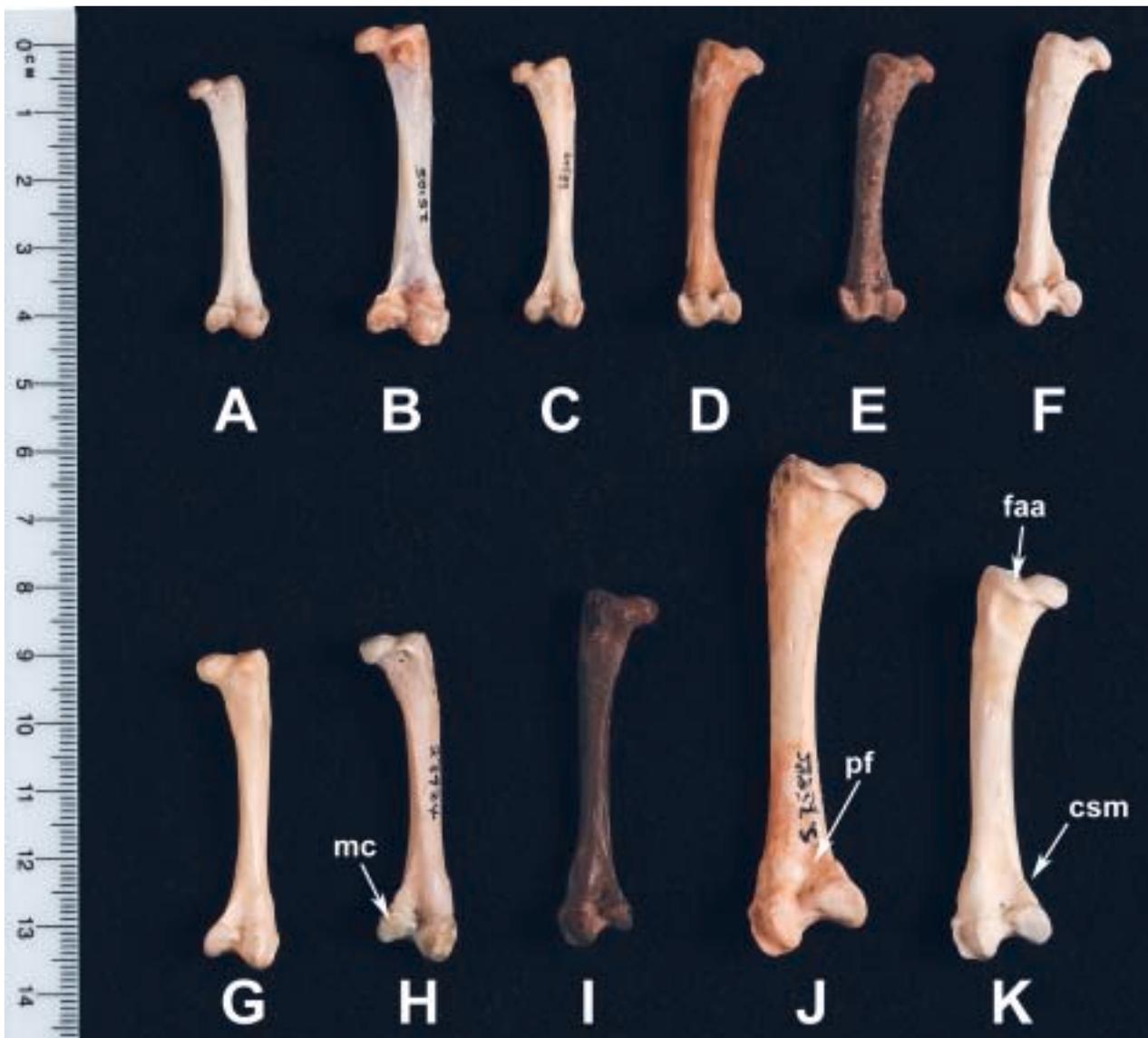


Fig. 11 Femora in caudal aspect. Specimens as for Fig. 10 (abbreviations: csm, *crista supracondylaris medialis*; faa, articular facet for antitrochanter; mc, medial condyle; pf, popliteal fossa. Scale in cm).

medially; and a low trochanter, such that the depth is not much greater than the depth of the *caput femoris* (head). The trochanter extends further proximad than the head. The shaft is narrowest at a point level with the proximal end of the popliteal fossa, but shaft depth at this point is distinctly greater than shaft width. The *crista trochanteris* does not overhang the cranial surface. The caudal surface below the *facies artic. antitrochanterica* is flat.

The femora of New Zealand *Oxyura* are of similar length to those of *Aythya novaeseelandiae* and share features associated with diving habits. However, *Oxyura* femora are much more robust, with markedly wider proximal and distal ends. The head extends further proximally in the New Zealand form (but not in *O. australis*) so that it can exceed the height of the trochanter, the antitrochanteric articular facet protrudes over a marked hollow on the caudal surface, and the trochanteric ridge overhangs the cranial surface, forming a distinct concavity. On the lateral surface of the shaft adjacent to the distal end of the femoral trochanter, there is a distinct prominence. Distally, the proximal border of the *crista tibiofibularis*, when viewed in lateral aspect, forms a right angle with the shaft and is large (it curves to the shaft in *Aythya* and is much smaller). Similarly, the proximal border of the *trochlea fibularis* in lateral aspect has a flat surface that is much larger than in *Aythya*. The popliteal fossa is larger than in *Aythya*. The proximal margin of the *condylus medialis* is distinctly stepped up from the medial supracondylar crest, forming a ledge in medial aspect, and the medial surface of the medial condyle has a marked tuberosity on it; both of these features are lacking in *Aythya*.

The femora of *Mergus* are very similar in morphology to those of *Oxyura*. They differ in that they have a wider rotular groove, they lack the prominent tubercle on the lateral face at a point level with the distal margin of the trochanter, a deep fossa is excavated under the trochanter on the cranial surface (shallow in *Oxyura*), and the popliteal fossa is deeper.

Malacorhynchus femora (e.g. CM Av14697 from Pyramid Valley; MNZ S2411, MNZ 7192, MNZ 10342, MNZ 16252 from Poukawa) are distinguished from those of *Anas superciliosa* by the following characters and are referred to *M. scarletti* because of their expected shape, surmised from the tibiotarsi description below. These femora are of similar length to those of *A. superciliosa* but have a relatively narrower distal end as predicted from the narrow proximal end of the referred tibiotarsi. The

condylus lateralis extends further distally past the medial condyle than it does in *Anas*. The shaft is noticeably narrower than in similar length *A. superciliosa* femora, and in caudal view its sides are noticeably parallel for about 50% of its length centred on the midlength point (cf. 30% in *Anas*). The ridge laterally bounding the popliteal fossa is more compressed than in *Anas*, and it leads proximally to a marked prominence on the caudal surface level with the proximal end of the *tuber. m. gastrocnemialis lateralis* that is absent in *Anas*.

The femora of *Hymenolaimus* are of similar size and proportions to those of *Anas superciliosa* and thus relatively large for its wing bones, which are shorter than those of *A. superciliosa*. They differ most from those of *A. superciliosa* in that they have a much deeper popliteal fossa and the antitrochanteric articular facet markedly overhangs the caudal surface

Femora of *Chenonetta finschi* and *Tadorna variegata* are much larger than those of *Anas*, *Aythya*, *Oxyura*, and *Malacorhynchus*, and may be confused with each other as they overlap in size. They differ in that in lateral aspect the cranial margin of the trochanteric ridge in *Tadorna* appears to bend and become parallel to the shaft, so that it meets the proximal surface in a right angle, whereas in *Chenonetta* it remains straight further proximally and meets the proximal surface at an acute angle. Distally, the popliteal fossa is deeper in *Chenonetta*, and the *crista supracondylaris medialis* extends as a sharp crest to a point level with the *tuberculum m. gastroc. lat.*, rather than ending distad of it as in *Tadorna*.

Tibiotarsi (Fig. 12)

The tibiotarsi of all *Anas* spp., *Aythya*, and *Oxyura* are of broadly similar size (see Appendix 1). Within *Anas*, the shape of the tibiotarsus is similar. Those of *A. gracilis* and *A. rhynchotis* are smallest and have a similar size range. *A. rhynchotis* differs from *A. gracilis* in that it has a tendency to have a narrower shaft, especially in terms of least shaft width near the distal end, and the tuberosity on the medial surface opposite the top of the *crista fibularis* is longer. In addition, the *condylus lateralis* is linked to the cranial surface of the shaft by a robust short ridge rather than the compressed sharp crest that extends further proximally as seen in teal (*A. gracilis*, *A. chlorotis*).

Tibiotarsi of *Anas chlorotis* are a little longer than those of *A. rhynchotis* and *A. gracilis* but are noticeably stouter, especially in the diameter of the proximal articular surface,

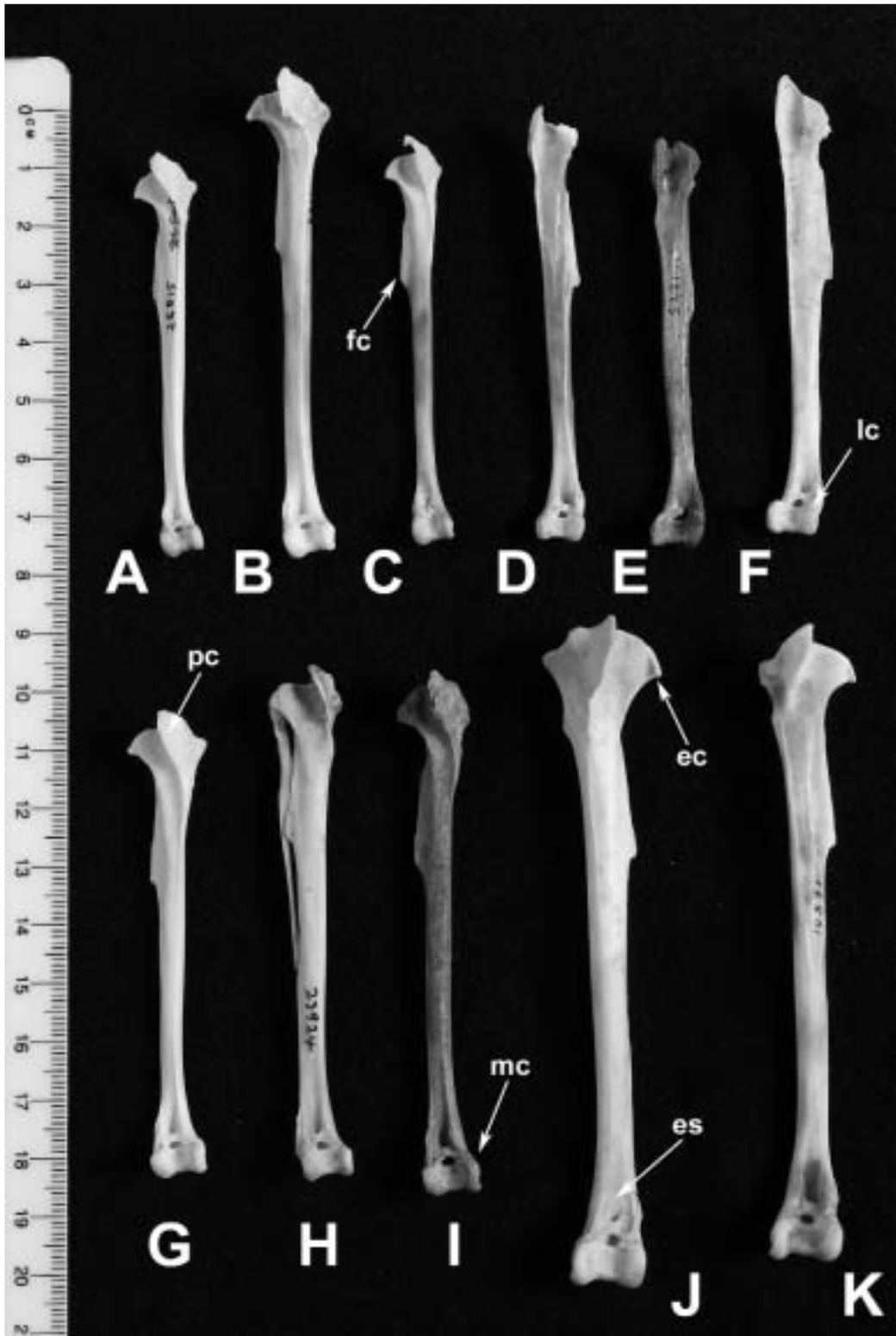


Fig. 12 Tibiotarsi in cranial aspect (ABCGHI – right sides; DEFJK – left sides): (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchotis* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S22175; (F) *Mergus australis* MNZ S30046; (G) *Anas superciliosa* MNZ 13686; (H) *Hymenolaimus malacorhynchos* MNZ 23924; (I) *Malacorhynchus scarletti* MNZ S41079; (J) *Chenonetta finschi* MNZ S35885; and (K) *Tadorna variegata* MNZ 16501 (abbreviations: ec, ectocnemial crest; es, extensor sulcus; fc, fibular crest; lc, lateral condyle; mc, medial condyle; pc, procnemial crest. Scale in cm).

at least shaft width, and for the width and depth of the distal end. The support strut for the *crista cnemialis lateralis* (ectocnemial crest) extends to a point level with the top of the fibular crest (ends above it in *A. gracilis* and *A. rhynchotis*). Tibiotarsi of *A. superciliosa* are larger than those of *A. chlorotis* but in shape are closest to that of *A. rhynchotis*.

Tibiotarsi of *Aythya novaeseelandiae* differ markedly from those of *Anas* in that they have a very flat cranial surface bound by a sharp crest medially opposite the fibular crest. The ectocnemial crest is not hooked distally as in *Anas*, and the *crista cnemialis cranialis* (procnemial crest) is directed more proximally. While the shaft may have similar relative stoutness to that of *Anas chlorotis*, the proximal end is relatively narrower and the notch on the caudal face of the *area interarticularis* opens caudally rather than caudolaterally as in *Anas*. Distally, the depths of the medial and lateral condyles are about equal, whereas in *Anas* the depth of the medial condyle markedly exceeds that of the lateral condyle. On the lateral surface adjacent to the *sulcus extensorius*, the *tuberculum retinaculi m. fibularis* is large and above it the surface curves steeply caudally, so that the depth from the extensor sulcus to the laterocaudal surface is shallow. In contrast, the *tuberculum retinaculi m. fibularis* is smaller in *Anas* and there is a distinct lateral surface, so that the depth from the extensor sulcus to the caudal surface is deeper.

Tibiotarsi of the New Zealand *Oxyura* are most similar to those of *Aythya novaeseelandiae*, but slightly shorter and the shaft is markedly broader and more flattened cranially. The ridge extending down the medial face of the cranial surface below the procnemial crest is markedly better developed and bulges medially from the line of the shaft to define a noticeable hollow in the proximal cranial surface of the shaft. The distal end is markedly larger and more inflected medially, with a much broader and flat-bottomed extensor sulcus. Unlike *Anas* or *Aythya*, the medial condyle has a large, centrally placed prominence on its face.

Tibiotarsi of *Mergus* are most similar to those of *Oxyura*, especially in the very flattened shaft and greatly developed cnemial crests. However, the distal end is not nearly as expanded and lacks the prominent tubercle medially. Proximally, the procnemial crest is not as produced above the articular surface but is more expanded anteriorly in front of the shaft. While the procnemial crest continues as a ridge down the medial side of the anterior face of the shaft, this ridge lacks the marked medial inflection seen

in *Oxyura*, and the cranial face lacks the marked hollow adjacent to this inflexion seen in *Oxyura*.

Tibiotarsi of *Malacorhynchus scarletti* were identified among Lake Poukawa *Anas superciliosa* tibiotarsi in November 2002. A right tibiotarsus (MNZ S41079) is the most complete specimen and is referred to *Malacorhynchus* because it is basically an enlarged version of *M. membranaceus*. It is characterised by its slender shaft, by a narrower and shallower proximal articular surface than in *A. superciliosa*, and by a fibular crest that in anterior aspect is well defined proximally by a notch between it and the lateral articular surface, so that the diameter there is markedly less than at any point across the fibular crest (in *Anas superciliosa*, the lateral profile of the fibular crest continues in a straight line up to the lateral articular surface and the base of the ectocnemial crest with only a slight hollow, such that the diameter just above the fibular crest is the same as at points across the fibular crest). Medially and opposite the proximal end of the fibular crest, there is a marked prominence, the *impressio lig. collateralis medialis* (much less of one in *A. superciliosa*), and the *crista patellaris* is much more elevated above the articular surfaces and is less robust along its crest than it is in *A. superciliosa*. Finally, the proximal articular surface has a deep *fossa retropatellaris* medially adjacent to a deep lateral *incisura tibialis* laterally (both much deeper than in *A. superciliosa*). Distally, its shape differs little from that of *A. superciliosa*.

Summary measurements for *Malacorhynchus scarletti* are given in Appendix 3, but measurements of MNZ S41079 compared to those of MNZ 13686, a recent *Anas superciliosa* (in brackets), show some of the above differences: total length, 89.4 mm (80.0); length from proximal articular surface, 83.1 mm (75.6); length from distal end fibular condyle, 55.5 mm (49.7); width of proximal articular surface, 9.3 mm (9.1); diameter above fibular crest, 5.9 mm (7.0); mid-shaft width, 4.4 mm (4.4); least shaft width, 4.0 mm (3.8); distal width, 9.6 mm (8.9); depth of medial condyle, 10.1 mm (10.0); depth of lateral condyle, 8.5 mm (8.5).

The tibiotarsus of *Hymenolaimus* is similar to that of *Anas superciliosa* but has a slightly more elongate shaft, and the shaft just proximad of the distal end is relatively wider to house a wider and deeper extensor sulcus. The procnemial crest extends onto the shaft as a more accentuated sharper ridge (compared to *Anas*) that extends beyond the level of the fibular crest. The *fossa retropatellaris* is deeper, and the proximal articular surfaces are excavated



Fig. 13 Tarsometatarsi in dorsal aspect (ABC – left sides; D–J – right sides): (A) *Anas gracilis* MNZ 26815; (B) *A. chlorotis* MNZ 25105; (C) *A. rhynchos* MNZ 24589; (D) *Aythya novaeseelandiae* MNZ 24245; (E) *Oxyura* n.sp. MNZ S22176; (F) *Mergus australis* MNZ S30046; (G) *Anas superciliosa* MNZ 13686; (H) *Hymenolaimus malacorhynchos* MNZ 23924; (I) *Chenonetta finschi* MNZ S35885; and (J) *Tadorna variegata* MNZ 16501 (abbreviations: df, distal foramen; es, extensor sulcus; lc, lateral cotyla; mc, medial cotyla; TII, trochlea II; TIV, trochlea IV. Scale in cm).

posteriorly in a fossa that is not divided by an obvious ridge linking the shaft to the base of the *facies artic. medialis* as in *Anas*, thus the *fossa flexoria* is not clearly separated from the *impressio lig. collateralis medialis*.

Tibiotarsi of *Chenonetta finschi* are much larger than those of *Anas superciliosa* and can only be confused with those of *Tadorna variegata*. However, the latter are generally longer, with a more slender shaft. Distally, both are very similar, differing mainly in that in *Tadorna* the extensor sulcus is broader and flat-bottomed, and its lateral margin merges with the *facies lateralis* in a sharp crest. Proximally, the caudal–medial margin is very angular in *Chenonetta* as opposed to well-rounded in *Tadorna*. On the cranial surface, the area between the fibular crest and the *facies medialis* is only slightly convex in *Tadorna*, versus markedly convex in *Chenonetta*. Finally, in *Chenonetta* the ectocnemial crest is supported by a narrow strut that extends down to a point anterior of, but level with, the top of the fibular crest, whereas the crest is smaller, and its strut more robust and shorter, in *Tadorna*.

Tarsometatarsi (Fig. 13)

The tarsometatarsi of the smaller *Anas* species are similar in shape and are also broadly similar in size (see Appendix 1). All have a broad, relatively deep *sulcus extensorius*, bound by ridges of equal height on either side. The dorsal opening of the *foramen vasculare distale* is relatively small, and opens via a small foramen into the *incisura intertrochlearis lateralis* and via a large one into the *fossa supratrochlearis plantaris*. *Trochlea metatarsi II* is characteristically raked plantarly so that in dorsal view its most distal extreme is level with the base of the *incisura intertrochlearis lateralis*. The *crista medialis hypotarsi* is largest and about twice the length of the lateral hypotarsal ridge (IV), and it forms an angle with the shaft (in medial view) greater than 90 degrees. Tarsometatarsi of *A. gracilis* and *A. rhynchotis* are smaller and more slender than those of other *Anas*, and both are relatively smaller in relation to wing element size than are those of *Anas chlorotis*, which is a similar sized bird. That of *A. gracilis* is more elongate than that of *A. rhynchotis*. Those of *A. chlorotis* and *A. superciliosa* overlap in length ranges, but in similar sized bones those of *A. chlorotis* are distinguished by a relatively narrower proximal end and, while the distal width is similar, the trochleae are smaller. Notably, the trochleae have a shallower depth as seen from the distal end. The larger trochleae in *A. superciliosa*, combined with a shaft width that is narrower and least close to

the distal end, results in there being more lateral deflection of trochlea IV.

Tarsometatarsi of *Aythya novaeseelandiae* differ markedly from those of *Anas*. They are relatively much shorter, the extensor sulcus is bound by a much higher ridge laterally than medially, and the trochlea II is further raked back plantarly so that its most distal extreme in dorsal view is markedly proximad of the lateral intertrochlear groove. Further, the trochlea II is longer than it is deep and the hypotarsal ridges I to IV are of similar length.

Tarsometatarsi of the New Zealand *Oxyura* are of similar length and shape to those of *Aythya*, but differ markedly in their broader widths, relatively shallower shaft, larger distal vascular foramen, much more inflected *cotyla medialis* that bounds a marked sulcus between it and the medial hypotarsal ridge (no such sulcus in *Aythya*), and medial hypotarsal ridge that wraps laterally behind the adjacent intermediate ridge.

The tarsometatarsi of *Mergus* have proportions more similar to those of *Anas chlorotis*, rather than being short as in *Aythya* and *Oxyura*, and they lack the markedly expanded ends of *Oxyura*. Distally, the end of the medial hypotarsal ridge and the shaft form a right angle as in *Oxyura*, but differ from *Aythya* and *Anas*, in which the hypotarsal ridge drops at a less abrupt angle to the shaft. All trochleae are larger, especially deeper plantar–dorsally, than in like-sized *A. chlorotis* tarsometatarsi, and the furrow on trochlea II is directed more medially in dorsal aspect. Nevertheless, *Mergus* tarsometatarsi are most likely to be confused with those of *A. chlorotis*.

The tarsometatarsus of *Malacorhynchus scarletti* has not yet been securely identified.

The tarsometatarsi of *Hymenolaimus* are more elongate, with a more slender shaft, than those of *Anas superciliosa*, to which they are similar in overall size. The medial hypotarsal ridge slopes to the shaft (not abruptly or hooked distally), the medial cotyla lies markedly proximad of the *cotyla lateralis*, and the small canal linking the dorsal opening of the *foramen vasculare distale* to the *incisura intertrochlearis medialis* is, uniquely among compared taxa, open dorsally.

The tarsometatarsi of *Chenonetta finschi* are larger than those of *Anas superciliosa* and markedly more robust. They are further distinguished by the unusual feature of trochlea II and IV diverging at about equal angles, with trochlea II extending distad of the lateral intertrochlear groove.

Tarsometatarsi of *Tadorna variegata* are much longer than those of *Chenonetta finschi*, although they have similar proximal and distal widths. As in *Anas*, trochlea IV does not diverge much from the line of the shaft and trochlea II's most distal extent is just level with the beginning of the lateral intertrochlear groove. They further differ from *Chenonetta* in that the medial hypotarsal ridge continues distally of the hypotarsus and lowers gradually to the shaft.

Results

Species composition among anatids in the Poukawa faunas

Most of the bones examined were clearly of natural origin, removed from the peaty sediments of the lake bed or its outflow channel. A very few were obviously derived from the overlying middens, as indicated by their lighter colour, more recent age (as indicated by a shiny, fresh, or less leached appearance), greenstick fractures (often resulting from the removal of the ends of the bone), and coatings of charcoal-rich sediment. All such bones were from Layer 1, the uppermost layer, but most Layer 1 bones were of natural origin. The bones of natural origin were also often broken, but breaks were randomly situated, though usually in the weakest sections (e.g. mid-shaft), and were never of a greenstick type. Because the excavation procedures did not clearly separate midden material from the underlying natural deposits, all avifaunal material is analysed together here.

The 21 715 catalogued lots from Poukawa contain at least 23 643 bones. A total of 11 393 anatid bones had their identity confirmed at least to generic level and a further 2082 bones remain identified as 'Anatidae' only (see Table 1). The latter category mainly comprises small taxa, and the bones included are either undiagnostic elements or are worn or broken, thus lacking diagnostic features. Some bones are identified as 'cf.' a taxon, e.g. '*Anas* cf. *A. chlorotis*', which means that they are considered most similar to *Anas chlorotis*. For the following analyses, bones labelled with a taxon name prefixed by cf. are considered to be that taxon. Because of the differential diagnostic utility of various elements, MNI here is based mainly on humeri. In primarily aquatic waterfowl, humeri are the most robust bone in the skeleton and for this reason alone dominate this assemblage. The exceptions here are the very robust femora of the more terrestrial *Chenonetta finschi* that contributes most to MNI. But except for this

species, humeri best reveal the MNI and hence the relative frequency of each species in the fauna.

In terms of NISP (number of identifiable specimens), *Anas superciliosa* dominated the assemblage, with 3607 bones, although this represents just 332 individuals (see Table 1). *Anas chlorotis* (NISP = 3051), in contrast, had an MNI of 442. This difference resulted from the larger size of bones of *A. superciliosa*, which enabled more elements to be identified, e.g. partial ulnae could be identified if from *A. superciliosa*, but if from a small species proximal and distal parts were left unidentified, as fragmentary *A. chlorotis* and *A. rhynchotis* ulnae could not be differentiated; furthermore, if slightly worn, partial ulnae of *Aythya* might not be separable from those of the smaller *Anas* species. It is probable that the original frequency of *Anas chlorotis* was even higher, as most bones in the category '*Anas* sp. small' are likely to be of this taxon. At about half the frequency of *A. superciliosa*, the smaller *A. rhynchotis* and *Aythya novaeseelandiae* had a very similar representation in the fauna, with MNIs of 157 and 158 respectively. No bones of *Anas gracilis* were identified.

Seven more taxa complete the waterfowl assemblage at Poukawa. Of these, *Cygnus atratus* dominated, with 1908 bones but an MNI of just 66. The uniquely large size of its bones meant that phalanges and vertebrae were usually identified for this species and not for any other waterfowl. The relatively large terrestrial *Chenonetta finschi* was the next most abundant, with 287 bones and an MNI of 28. The two highly aquatic specialist species *Malacorhynchus scarletti* and *Oxyura* n.sp. had about equal frequency, with MNIs of 16 and 19 respectively. The large *Tadorna variegata* was relatively rare, with just 54 bones for an MNI of 6. *Biziura delautouri* was rare, with only 17 bones (MNI = 3), and *Mergus australis* was very rare, with only four bones identified, of which two are left femora. *Cnemiornis septentrionalis* was represented by just four bones, two from an unrecorded site and two from John's Spring V. Their preservation is different from most Poukawa bones and it is likely they are of late Glacial age, as were the Te Aute bones (Worthy 2000). The relative proportions of waterfowl MNI from Poukawa is shown in Fig. 14.

In Table 1, data for the two grebes are included so as to compare the relative frequency of these still extant taxa with the extinct waterfowl. *Poliiocephalus rufopectus* (New Zealand dabchick) was relatively rare in the fauna, with NISP = 104 for an MNI of 11. *Podiceps cristatus* (great crested grebe) was even rarer, with only 34 bones and an MNI of 6.

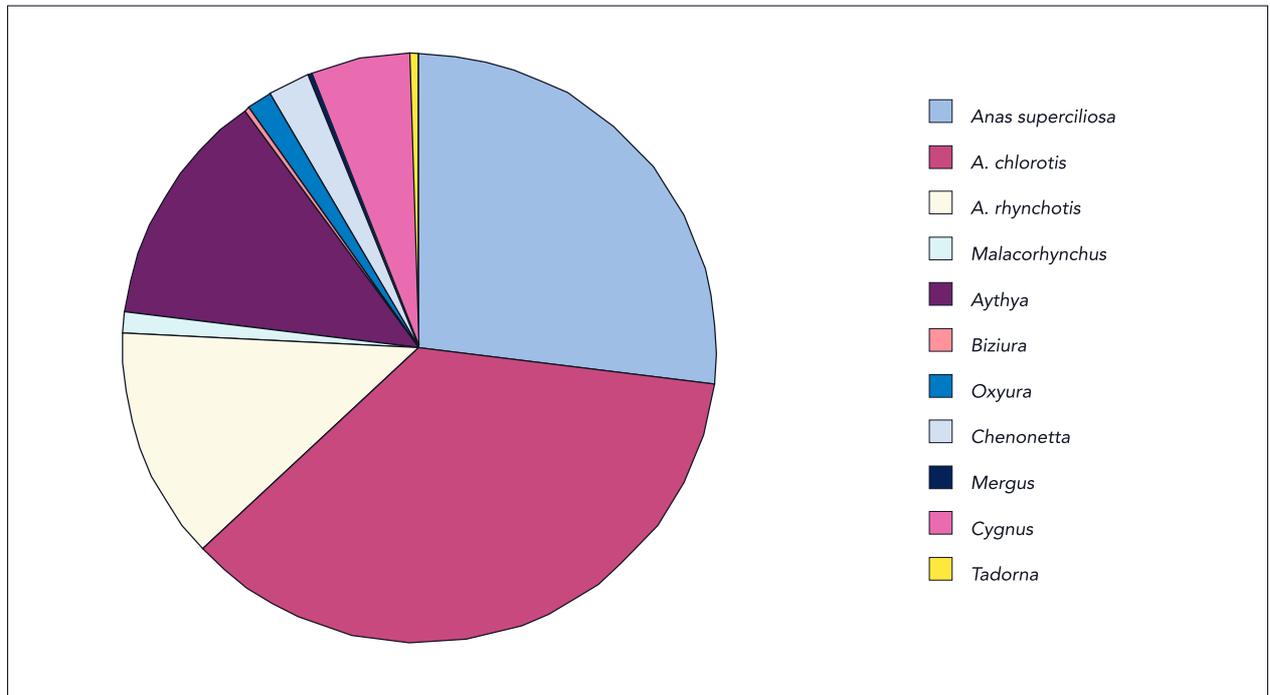


Fig. 14 Pie chart showing the relative frequency of waterfowl taxa from the whole Poukawa fauna. *Cnemiornis* is excluded, as it is assumed the four bones are of late Pleistocene age.

Lake Poukawa *Cygnus*

The large sample of swan bones from Lake Poukawa allows meaningful statistics of bone measurements to be ascertained for the swans found prehistorically in New Zealand and a comparison with those from Marfells Beach (Worthy 1998), which is the only other sample analysed (see Appendix 4). Mean values for the samples of swan bones from Lake Poukawa and Marfells Beach do not differ substantially. Mean values of bone measurements from the fossil sites are plotted as a proportion of those of first, a modern female, and second, a male *Cygnus atratus* with similar ratios of other available individuals (see Fig. 15).

The lines linking the data from the fossil populations largely parallel other lines in the figure, indicating that the birds had similar proportions to the modern individuals. The observation that some sections of the line may either rise or fall for different individuals (e.g. where the female is the reference, the lines linking coracoids and femora or tibiotarsi and tarsometatarsi) indicates that the relative proportions of these elements is variable between individuals. The data suggest that the leg bones of the fossil populations are on average larger than expected given

their wing bone lengths. However, apparently relatively shorter wing bones (notably ulnae and humeri) and longer leg bones can be explained as a taphonomic issue. The longer wing bones are those most likely to be broken, whereas the leg bones are more robust and even the larger ones are likely to survive intact, resulting in lower mean values for wing bones than predicted from leg bones. This can only really be tested with data from associated bones of individuals, and MNZ S5504 is the only such specimen. Its lengths plotted as ratios in Fig. 15 show that this bird had similar proportions to the modern black swan, as did individuals in Marfells Beach (Worthy 1998). These data support the contention that the New Zealand species of *Cygnus* during the Holocene was *C. atratus* (Worthy 1998).

Discussion

In the above analyses, the avifaunas from the various sites around Lake Poukawa are combined. The great majority of specimens is derived from three sites, which all have a similar stratigraphy, indicating an early to late Holocene

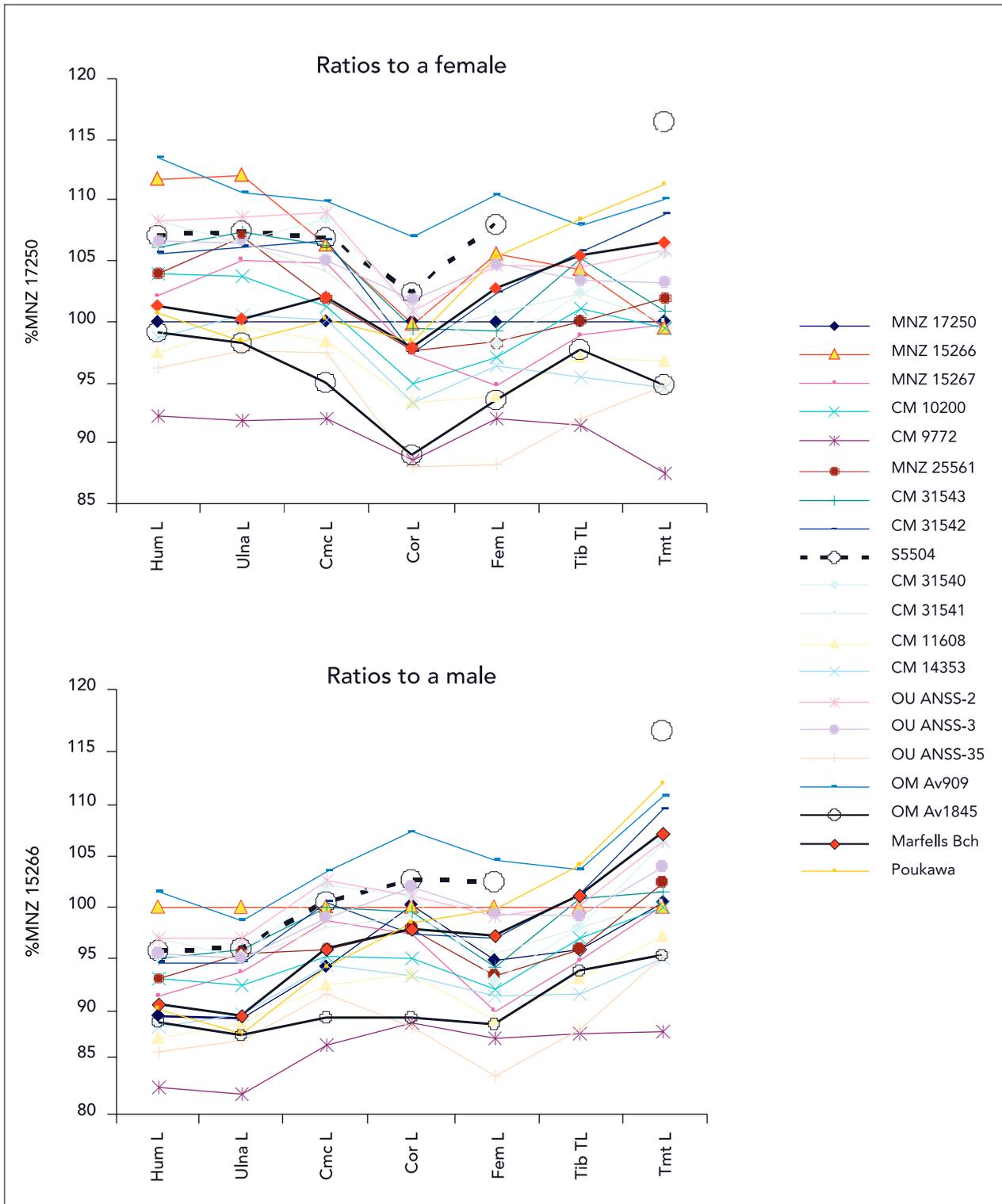


Fig. 15 A ratio diagram showing data for various modern individuals and the mean values for the fossil populations from Lake Poukawa and Marfells Beach as proportions of the length values for a small female (MNZ 17250) and a large male *Cygnus atratus* (MNZ 15266), whose data is shown as 100%. Values below the horizontal line are smaller and those above it larger than the reference individual. In the graph for the male, that most values for femora drop relative to adjacent bones indicates the reference male had a relatively long femur compared to most birds in the analysis. In contrast, when the data was based on the female it became apparent that some birds had relatively smaller, and some relatively larger, femora; similar results were found for tarsometatarsi.

Table 1 Summary data for anatid bones from Lake Poukawa fossil sites derived from Price's collections (abbreviations as in 'Methods', plus the following: dL, distal left; pL, proximal left; dR, distal right; pR, proximal right).

Taxon	NISP	L hum	dL hum	pL hum	R hum	dR hum	pR hum	Total MNI
<i>Anas superciliosa</i>	410	17	16	14	22	14	15	37
<i>Anas cf. A. superciliosa</i>	3197	158	114	84	161	134	93	295
Total <i>A. superciliosa</i>	3607	175	130	98	183	148	108	332
<i>Anas chlorotis</i>	764	141	66	13	165	61	11	226
<i>Anas cf. A. chlorotis</i>	2287	154	78	28	135	81	23	232
Total <i>A. chlorotis</i>	3051	295	144	41	300	142	34	442
<i>Anas rhynchotis</i>	363	87	50	6	91	58	17	149
<i>Anas cf. A. rhynchotis</i>	509	6	6	0	2	6	1	12
Total <i>A. rhynchotis</i>	872	93	56	6	93	64	18	157
<i>Anas sp. small</i>	422	74	8	138	62	7	106	82(212) ^A
<i>Aythya novaeseelandiae</i>	978	111	47	38	100	35	36	158
<i>Tadorna variegata</i>	54	0	0	2	2	2	1	4(6) ^B
<i>Malacorhynchus scarletti</i>	84	10	4	6	8	3	2	16
<i>Biziura delautouri</i>	17	0	0	0	3	0	0	3
<i>Oxyura n. sp.</i>	105	13	6	0	9	2	3	19
<i>Chenonetta finschi</i>	287	8	3	4	10	1	4	14(28) ^C
<i>Mergus australis</i>	4	0	0	0	0	0	0	2
<i>Cygnus atratus</i>	1908	35	31	28	33	24	30	66
<i>Cnemiornis gracilis</i>	4	0	0	0	0	0	0	2
Anatidae	2082	96	13	93	98	14	72	112 (189) ^D
Total bones	13 475							MNI = 1424
<i>Poliiocephalus rufopectus</i>	104	8	2	3	5	1	5	11
<i>Podiceps cristatus</i>	34	1	0	1	1	2	0	3(6) ^E

A Here, the MNI is based on complete bones plus distal part(82), because in the determined small anatids the distal humerus is usually identified, leaving many proximal ends unidentified.

B While MNI is given for humeri for comparison's sake, when humeral shafts are factored into the analysis, MNI is 6.

C While MNI on humeri is 14, it is 28 based on femora.

D MNI is best derived from whole plus distal fragments (112), as distal parts were usually identified to taxon and proximal parts were not, and thus this lower MNI better reflects the contribution these bones make to the total anatid fauna.

E While MNI on humeri is 3, it is 6 based on tibiotarsi.

(<7000 yr) age for most of the bones. One exception appears to be the John's Spring V site, where the moa fauna and other bones are preserved differently and look similar to those derived from the nearby Te Aute site, which is late Pleistocene in age (Worthy 2000). That John's Spring V is the only Poukawa site with *Euryapteryx curtus* and *Cnemiornis* also supports a late Pleistocene age for its fauna. The anatid fauna from Lake Poukawa is otherwise virtually solely derived from sites I, II, and XII, located less than 1 km apart on the same side of the same 1 km-wide lake, and thus can be considered as part of a single fauna. The identity of 13 475 anatid bones has been reviewed here, a number that is greater than all those reported for the entire non-moa avifauna by Horn (1983). Analysis of other sections of the avifauna is yet to be carried out, but there are at least 23 643 bones, so anatids account for about 57% of the fauna.

Twelve anatid species are represented as fossils in the Poukawa avifaunas. The only species known from the North Island that are not represented are *Hymenolaimus malacorhynchos* (blue duck) and *Anas gracilis* (grey teal). *Hymenolaimus* is primarily a river specialist that requires riffles or rapids (Marchant & Higgins 1990), so is not expected on a shallow lake with no substantial inflows and only slow-moving outflows. While wing bones of *Anas gracilis* might be indistinguishable from the smaller ones of *A. chlorotis*, the very small leg bones of *A. gracilis* are diagnostic and none was present. It therefore seems that *A. gracilis* was absent from Lake Poukawa in the late Holocene, contra to its reported abundance by Horn (1983). However, I re-examined the four bones reported by Holdaway & Worthy (1997) from Pyramid Valley and their identity as *A. gracilis* seems secure. What is not certain is their exact age, but even if they are older than 100 years, they may represent an earlier irruption of the species into New Zealand that failed to establish, such as occurred with *Aythya australis* (white-eyed duck) in the nineteenth century (Turbott 1990). *Anas gracilis* were not reported by the first observers in New Zealand and appear to have self-established, with first records in 1866 and irregular influxes since then (Turbott 1967: 220, Marchant & Higgins 1990: 1269).

Cnemiornis gracilis can be dismissed from further consideration from the Holocene fauna as being of late Pleistocene age and thus not coeval with the other anatids. *Mergus australis* (New Zealand merganser) is a coastal marine species and the two individuals represented are certainly

only vagrants. This species has never been reported in freshwater sites in New Zealand before.

Of the 10 species living together on Lake Poukawa prehistorically, *Anas chlorotis* (brown teal) dominated the avifauna in terms of MNI, with 442 individuals (see Fig. 14). This abundance in Lake Poukawa, and that in fossil deposits generally in New Zealand from a range of sites and habitats (Worthy 2002b), indicates that *A. chlorotis* was the most abundant duck in prehuman New Zealand. *Anas superciliosa* (grey duck), with 332 individuals, was next most abundant, then *Aythya novaeseelandiae* (scaup) and *Anas rhynchos* (Australasian shoveler), with 157 and 158 individuals respectively. As these ducks are of similar size to *Anas chlorotis*, these data suggest that brown teal were perhaps twice as numerous as other duck species on this shallow, peaty, forest-lined lake. The identification of *Anas rhynchos* bones in Lake Poukawa runs contra to recent faunal analyses, such as Holdaway & Worthy (1997) and Worthy & Holdaway (2002), in which this species was considered to be a recent immigrant. The Poukawa data clearly demonstrate that *A. rhynchos* were a common part of the New Zealand avifauna over at least the last several thousand years.

Cygnus atratus (black swan), which because of its large and recognisable bones had a large number of identified elements (1908), was much less numerous, with just 66 individuals. *Chenonetta finschi* (Finsch's duck) was the next most abundant, with 287 bones and a MNI of 28. This figure is much lower than values for the typical aquatic species and lower than numbers for terrestrial taxa such as *Gallirallus australis* (weka) or *Hemiphaga novaeseelandiae* (New Zealand pigeon). *Chenonetta finschi* was primarily a terrestrial species (Worthy & Holdaway 2002) that preferred the lower rainfall zones of eastern rainshadow areas. Its abundance in a fauna has been taken to indicate the presence of vegetation mosaics of grassland, shrubland, and forest (Worthy 1999, Worthy & Holdaway 2002). The closed podocarp broadleaf forest dominated by matai inferred from pollen profiles by McGlone (2002) would not normally be associated with high numbers of *C. finschi*, and indeed an MNI of 28 is likely to be a low proportion of the terrestrial component of the Poukawa avifauna. That there were some *C. finschi* present indicates the proximity of suitable habitat, probably on the surrounding hills.

Five other waterfowl taxa were each rare in the fauna. *Tadorna variegata* (paradise shelduck) was present at all

levels in the deposits but was rare, with 54 bones or just six individuals. This species is primarily omnivorous, but grazing is an important foraging mode (Marchant & Higgins 1990). The frequency data suggest that the surrounds of the lake did not afford suitable forage for it – this can be predicted from the floral reconstructions of McGlone (2002), which show that a podocarp forest surrounded the lake. While *T. variegata* aggregates in moulting flocks on lakes, the lack of a hillside rising from the water's edge and the lack of grazing habitat probably made Lake Poukawa unsuitable for the species (Marchant & Higgins 1990).

The identification of a stiff-tailed duck *Oxyura* sp. partially vindicates the claims of Horn (1983), but the bones represent a New Zealand endemic species first recognised during this study and that is now extinct (Worthy in press). The New Zealand *Oxyura* n.sp. was smaller than its Australian counterpart (see Appendix 2) and was represented by 105 bones and 19 individuals. *Malacorhynchus scarletti* (Scarlett's duck) was a large duck (see Appendix 3) the size of *Anas superciliosa*. Its remains were comparatively rare, with 84 bones for 16 individuals, and it was thus probably about as abundant as the *Oxyura* n.sp. The Poukawa collections have revealed tibiotarsi of this species for the first time, along with a good series of other elements (femora, coracoids, ulnae, and carpometacarpi) for which identification features were not certain before (Worthy 1995). However, tarsometatarsi remain unidentified for this species. The presence of juvenile bones of both *Oxyura* and *Malacorhynchus* indicate that both these taxa bred on Lake Poukawa.

Particularly rare is *Biziura delautouri* (New Zealand musk duck), with only three individuals. Its rarity may perhaps be explained by the shallow peaty water of Lake Poukawa, which was not its preferred habitat. Presently, Lake Poukawa is usually less than 1 m deep (McGlone 2002), and allowing for recent drainage it was probably 1–2.5 m deep during deposition of the fossils. *B. lobata* of Australia, the congener of *B. delautouri*, prefers deep water with stable conditions and abundant aquatic flora (Marchant & Higgins 1990), conditions that may more likely have been found in many other lakes in New Zealand.

In order to assess the meaning of the frequency data for the apparently rare taxa, the data for *Poliiocephalus rufopectus* (New Zealand dabchick) and *Podiceps cristatus* (crested grebe) were totalled. They had 104 and 34 bones

respectively, or MNIs of 11 and 6. *Poliiocephalus* normally defend a breeding territory, and thus on small lakes only two to three pairs or small family groups are seen (Marchant & Higgins 1990), although they do aggregate as flocks on selected lakes outside of the breeding period. Similarly, *Podiceps* occur as sedentary pairs on a given lake, and so perhaps only a pair would have lived at a time on Lake Poukawa. Thus, these data might suggest that if Lake Poukawa had only a pair or two of normally breeding birds, and that these resulted in a sample of only about 100 bones in a total avifaunal sample in some 6000 years, then perhaps a similar frequency for *Oxyura* and *Malacorhynchus* in the original fauna was likely. If so, then only a pair or two of both *Oxyura* n.sp. and *Malacorhynchus* may have lived on this lake at any one time. These data show that in similar fossil sites, in order to detect what might be only an infrequent species, large samples are needed – the 13 475 anatid bones recorded here are only about half the total fossil avifauna sample and they did not reveal large numbers of these rare taxa!

These data allow better interpretation of rare taxa in smaller samples or in total fossil faunas of New Zealand. They clearly suggest that the presence of taxa such as *Malacorhynchus scarletti* and *Biziura delautouri* in some archaeological sites, e.g. Marfells Beach (Worthy 1998) and Wairau Bar (Scofield *et al.* 2003), is significant given that even these 'large' faunas are much smaller (less than a tenth) of the Poukawa fauna. As most archaeological faunas are very much smaller (usually less than 200–300 identifiable bones), the chances of detecting any uncommon species in the source avifauna are very small. Thus, the mere presence of taxa such as *Malacorhynchus* and *Biziura* in archaeological faunas, and of similarly rare taxa such as *Cnemionis*, *Aptornis* (adzebills), and *Porphyrio mantelli* (North Island takahē), means that these were undoubtedly important but likely uncommon components of the habitats surrounding those sites. In addition, their presence in the middens clearly indicates that hunting was a significant factor in their extinction.

Poukawa reveals better than any other site in New Zealand that the fossilisation process is a rare occurrence, which combined with collection biases means that the detection of species formerly uncommon in the environment is a serendipitous event indeed.

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Appendices

Appendix 1

Summary statistics for measurements (mm) of long bones and selected ratios for various recent anatids to illustrate features mentioned in the text (specimens used listed in 'Comparative material'; abbreviations as in 'Methods').

Anas superciliosa.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Rad L	Rad D	Cmc L	Cmc P	Cor L
Mean	90.76	19.87	7.316	14.18	77.73	9.654	5.23	9.705	71.84	6.665	55.41	12.6	48.24
Standard error	0.905	0.186	0.105	0.193	0.965	0.113	0.099	0.127	0.973	0.086	0.81	0.139	0.546
Standard deviation	2.861	0.587	0.333	0.611	3.051	0.357	0.314	0.402	3.078	0.272	2.56	0.439	1.727
Minimum	86.1	18.6	6.8	13.1	72.8	8.9	4.8	9.0	67.0	6.2	51.8	12.0	45.1
Maximum	94.4	20.4	7.9	14.9	81.7	10.0	5.8	10.2	75.9	7.0	59.1	13.2	50.7
Count	10	10	10	10	10	10	10	10	10	10	10	10	10

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib AL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	50.1	10.54	4.464	11.12	85.17	79.91	8.84	4.13	8.89	43.92	9.4	4.44	9.291
Standard error	0.573	0.151	0.067	0.154	1.288	1.149	0.08	0.06	0.09	0.847	0.11	0.08	0.099
Standard deviation	1.811	0.479	0.213	0.486	4.074	3.632	0.26	0.19	0.29	2.395	0.32	0.25	0.297
Minimum	46.9	9.9	4.1	10.3	79.7	74.7	8.2	3.8	8.3	41.4	8.8	4.0	9.0
Maximum	52.2	11.3	4.8	11.7	92.8	85.7	9.0	4.4	9.2	47.8	9.9	4.8	10.0
Count	10	10	10	10	10	10	10	10	10	8	8	9	9

	HumL/FemL	UlnaL/FemL	TmtL/FemL	TibL/FemL
Mean	1.812	1.5517	0.87806	1.69963
Standard error	0.0112	0.0123	0.01168	0.014
Standard deviation	0.0354	0.0388	0.03303	0.04428
Minimum	1.7542	1.469	0.83451	1.62159
Maximum	1.8675	1.5997	0.93542	1.79775
Count	10	10	8	10

Anas rhynchos.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Rad L	Rad D	Cmc L	Cmc P	Cor L
Mean	75.84	16.45	5.92	11.96	64.19	8.08	4.16	8.35	59.58	5.39	46.49	11.25	41.93
Standard error	0.733	0.143	0.076	0.114	0.649	0.101	0.116	0.066	0.620	0.035	0.528	0.103	0.494
Standard deviation	2.200	0.428	0.229	0.341	1.947	0.303	0.348	0.198	1.755	0.100	1.585	0.310	1.482
Minimum	72.3	15.6	5.6	11.4	61.2	7.5	3.6	8.0	56.9	5.3	43.3	10.8	40.2
Maximum	78.9	17.0	6.3	12.5	67.2	8.5	4.9	8.6	62.2	5.5	48.3	11.7	44.2
Count	9	9	9	9	9	9	9	9	8	8	9	9	9
CV	2.90	2.60	3.87	2.85	3.03	3.75	8.37	2.37	2.94	1.85	3.41	2.76	3.53

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib AL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	40.83	8.63	3.58	8.92	71.43	66.70	7.21	3.18	7.31	36.28	7.69	3.78	7.66
Standard error	0.421	0.090	0.050	0.130	0.792	0.798	0.087	0.048	0.094	0.339	0.087	0.095	0.078
Standard deviation	1.264	0.256	0.149	0.389	2.096	1.596	0.261	0.145	0.281	1.017	0.262	0.285	0.233
Minimum	39.9	8.3	3.4	8.3	69.6	65.0	6.8	3.0	6.9	34.7	7.2	3.5	7.3
Maximum	43.1	9.0	3.8	9.6	75.2	68.8	7.7	3.4	7.7	37.8	8.1	4.4	8.0
Count	9	8	9	9	7	4	9	9	9	9	9	9	9
CV	3.10	2.96	4.16	4.37	2.93	2.39	3.62	4.57	3.84	2.80	3.41	7.55	3.04

	HumL/FemL	UlnaL/FemL	TmtL/FemL	TibL/FemL
Mean	1.8583	1.5729	0.8889	1.7615
Standard error	0.0160	0.0152	0.0052	0.0064
Standard deviation	0.0480	0.0457	0.0157	0.0169
Minimum	1.8005	1.5151	0.8665	1.7390
Maximum	1.9369	1.6300	0.9086	1.7927
Count	9	9	9	7
CV	2.58	2.91	1.77	0.96

Anas gracilis.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Rad L	Rad D	Cmc L	Cmc P	Cor L
Mean	69.17	14.47	5.14	10.60	60.58	7.03	3.67	7.12	55.95	4.91	42.91	9.49	36.17
Standard error	0.677	0.132	0.081	0.149	0.439	0.060	0.068	0.125	0.468	0.072	0.444	0.086	0.334
Standard deviation	2.141	0.417	0.257	0.470	1.389	0.191	0.214	0.395	1.481	0.227	1.404	0.271	1.057
Minimum	65.4	14.0	4.7	9.8	58.1	6.8	3.4	6.6	52.7	4.5	40.6	9.0	35.2
Maximum	72.3	15.2	5.5	11.5	62.9	7.4	4.0	8.0	58.1	5.2	45.2	9.8	38.4
Count	10	10	10	10	10	10	10	10	10	10	10	10	10

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib AL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	38.11	7.60	3.19	8.29	66.44	63.11	6.58	2.92	6.74	35.37	7.20	3.27	7.15
Standard error	0.350	0.121	0.044	0.084	0.730	0.734	0.065	0.069	0.066	0.467	0.058	0.063	0.072
Standard deviation	1.106	0.382	0.140	0.266	2.308	2.322	0.204	0.219	0.210	1.477	0.184	0.200	0.227
Minimum	36.4	7.0	3.0	7.9	63.1	59.6	6.2	2.6	6.5	33.1	6.9	3.0	6.7
Maximum	40.1	8.1	3.5	8.9	69.4	66.5	6.9	3.4	7.2	37.5	7.4	3.6	7.4
Count	10	10	10	10	10	10	10	10	10	10	10	10	10

	HumP/L	UlnaP/L	Ulna S/L	Ulna D/L	Radius D/L	CMC P/L	Tib S/L
Mean	0.209	0.116	0.061	0.118	0.088	0.221	0.046
Standard error	0.002	0.001	0.001	0.002	0.001	0.002	0.001
Standard deviation	0.006	0.005	0.004	0.007	0.004	0.008	0.004
Minimum	0.202	0.109	0.054	0.110	0.080	0.212	0.039
Maximum	0.219	0.121	0.066	0.130	0.093	0.234	0.052
Count	10	10	10	10	0	10	10

	HumL/FemL	UlnaL/FemL	TibTL/FemL	TmtL/FemL
Mean	1.815	1.590	1.743	0.928
Standard error	0.010	0.008	0.012	0.006
Standard deviation	0.033	0.024	0.036	0.020
Minimum	1.753	1.558	1.690	0.897
Maximum	1.857	1.624	1.798	0.961
Count	10	10	10	10

Anas chlorotis.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Rad L	Rad D	Cmc L	Cmc P	Cor L
Mean	70.47	15.66	5.49	10.84	57.83	7.36	3.98	7.75	53.39	5.45	41.59	11.23	37.21
Standard error	0.588	0.149	0.058	0.090	0.597	0.083	0.060	0.130	0.520	0.076	0.521	0.203	0.334
Standard deviation	3.113	0.790	0.305	0.477	2.671	0.382	0.268	0.580	2.547	0.370	2.328	0.908	1.766
Minimum	63.6	14.3	4.9	10.0	51.7	6.5	3.4	5.8	47.8	4.8	37.2	9.7	33.7
Maximum	79.4	17.5	6.0	11.7	64.9	8.0	4.4	8.5	60.3	6.4	48.6	13.3	41.5
Count	28	28	28	28	20	21	20	20	24	24	20	20	28
CV	4.42	5.04	5.55	4.40	4.62	5.18	6.75	7.49	4.77	6.80	5.60	8.09	4.75

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib AL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	43.42	9.71	4.13	10.44	75.84	71.14	8.53	3.96	8.12	40.75	8.74	4.18	8.90
Standard error	0.273	0.129	0.056	0.112	0.570	0.565	0.131	0.068	0.064	0.328	0.100	0.059	0.108
Standard deviation	1.419	0.670	0.292	0.583	2.611	2.525	0.586	0.313	0.295	1.502	0.459	0.271	0.495
Minimum	40.6	8.1	3.5	9.1	69.9	65.4	7.4	3.1	7.5	37.3	8.0	3.6	7.8
Maximum	47.6	11.2	4.7	11.8	83.2	78.3	9.5	4.5	8.7	44.1	10.0	4.7	9.9
Count	27	27	27	27	21	20	20	21	21	21	21	21	21
CV	3.27	6.89	7.08	5.58	3.44	3.55	6.87	7.90	3.64	3.69	5.26	6.49	5.57

	HumP/L	UlnaP/L	Ulna S/L	Ulna D/L	Radius D/L	CMC P/L	Tib S/L
Mean	0.2223	0.1275	0.0688	0.1340	0.1020	0.2700	0.0557
Standard error	0.001	0.001	0.001	0.002	0.001	0.004	0.001
Standard deviation	0.007	0.005	0.004	0.008	0.005	0.016	0.004
Minimum	0.2099	0.1165	0.0608	0.1034	0.0891	0.2401	0.0445
Maximum	0.2454	0.1350	0.0765	0.1437	0.1092	0.3087	0.0633
Count	28	20	20	20	24	20	20

	HumL/FemL	UlnaL/FemL	TmtL/FemL	TibL/FemL
Mean	1.6223	1.3274	0.9368	1.7435
Standard error	0.0052	0.0056	0.0026	0.0037
Standard deviation	0.0269	0.0251	0.0120	0.0170
Minimum	1.5658	1.2734	0.9197	1.7212
Maximum	1.6695	1.3655	0.9603	1.7931
Count	27	20	21	21

Aythya novaeseelandiae.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Rad L	Rad D	Cmc L	Cmc P	Cor L
Mean	72.1	15.4	5.2	10.4	61.1	7.1	4.0	6.9	57.3	4.6	38.2	9.1	38.3
Standard error	0.779	0.144	0.068	0.074	0.441	0.055	0.101	0.121	0.499	0.049	0.220	0.052	0.397
Standard deviation	2.463	0.456	0.214	0.234	1.463	0.181	0.335	0.401	1.577	0.156	0.730	0.172	1.257
Minimum	69.0	14.8	4.9	10.0	59.3	6.9	3.8	6.5	55.1	4.4	37.4	8.8	36.2
Maximum	76.7	16.1	5.5	10.7	63.2	7.4	4.9	8.0	59.3	4.9	39.2	9.4	40.2
Count	10	10	10	10	11	11	11	11	10	10	11	11	10

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	43.1	9.9	4.0	9.6	74.2	7.4	3.6	8.0	34.6	8.1	4.1	8.4
Standard error	0.581	0.093	0.053	0.153	0.680	0.069	0.044	0.112	0.355	0.129	0.052	0.126
Standard deviation	1.839	0.293	0.168	0.484	2.255	0.228	0.147	0.373	1.122	0.407	0.163	0.398
Minimum	40.3	9.5	3.8	8.6	71.8	7.0	3.3	7.5	33.0	7.0	3.8	7.8
Maximum	46.0	10.4	4.3	10.0	79.7	7.7	3.8	8.9	37.1	8.4	4.3	9.1
Count	10	10	10	10	11	11	11	11	10	10	10	10

	Hum P/L	Ulna P/L	Ulna S/L	Ulna D/L	Radius D/L	CMC P/L	Tib S/L	HumL/FemL	UlnaL/FemL	TmtL/FemL	TibL/FemL
Mean	0.214	0.115	0.065	0.113	0.080	0.238	0.048	1.675	1.422	0.805	1.727
Standard error	0.0015	0.0008	0.0016	0.0022	0.0008	0.0013	0.0005	0.0128	0.0127	0.0068	0.0122
Standard deviation	0.0047	0.0025	0.0052	0.0073	0.0026	0.0042	0.0017	0.0406	0.0403	0.0215	0.0385
Minimum	0.208	0.111	0.060	0.107	0.076	0.232	0.045	1.618	1.374	0.760	1.691
Maximum	0.221	0.119	0.079	0.133	0.084	0.245	0.051	1.758	1.489	0.843	1.807
Count	10	11	11	11	10	11	11	10	10	10	10

Appendix 2

Summary statistics for measurements (mm) of bones of *Oxyura* n.sp. from Poukawa deposits (abbreviations as in 'Methods').

Humeri – specimens MNZ S1081, MNZ 1115, MNZ 2107, MNZ 3277, MNZ 3370, MNZ 3527, MNZ 3777, MNZ 3778, MNZ 4104, MNZ 4553, MNZ 5915, MNZ 8942, MNZ 9745, MNZ 9746, MNZ 10077, MNZ 10731, MNZ 11218, MNZ 11316, MNZ 12165, MNZ 12425, MNZ 12638, MNZ 13685, MNZ 13686, MNZ 13687, MNZ 13730, MNZ 15650, MNZ 15952, MNZ 20191, MNZ 20228, MNZ 20605, MNZ 41025, MNZ 41259. Ulnae – specimens MNZ S2398, MNZ 4512, MNZ 5316, MNZ 8653, MNZ 9727, MNZ 10917, MNZ 11118, MNZ 11634, MNZ 12107, MNZ 15697, MNZ 16618, MNZ 16732, MNZ 18178, MNZ 19128, MNZ 20617, MNZ 20180, MNZ 22179.

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D
Mean	65.50	14.38	4.01	8.72	55.55	6.15	3.45	6.52
Standard error	0.482	0.133	0.035	0.058	0.468	0.111	0.054	0.119
Standard deviation	1.805	0.516	0.183	0.288	1.750	0.384	0.207	0.476
Minimum	61.6	13.5	3.6	7.8	51.2	5.4	3.0	5.6
Maximum	68.4	15.5	4.4	9.3	58.3	6.6	3.9	7.0
Count	14	15	27	25	14	12	15	16

Coracoids – specimens MNZ S3363, MNZ 3781, MNZ 8933, MNZ 9444, MNZ 11212, MNZ 11404, MNZ 12163, MNZ 13722, MNZ 13773, MNZ 16176, MNZ 16972, MNZ 18056, MNZ 22439 (fas = facies articularis sternalis). Femora – specimens MNZ S1082, MNZ 1091, MNZ 4515, MNZ 5976, MNZ 10436, MNZ 10437, MNZ 11739, MNZ 11741, MNZ 12855, MNZ 13635, MNZ 13809, MNZ 16696, MNZ 17025, MNZ 18288.

	Cor L	Cor S	Cor width fas	Fem L	Fem P	Fem S	Fem D
Mean	36.72	3.82	16.31	41.28	10.07	3.77	10.20
Standard error	0.492	0.059	0.306	0.214	0.049	0.029	0.076
Standard deviation	1.476	0.219	0.809	0.741	0.183	0.107	0.229
Minimum	34.6	3.5	15.1	40.1	9.7	3.6	9.7
Maximum	38.3	4.1	17.2	42.7	10.3	4.0	10.6
Count	9	14	7	12	14	14	9

Appendix 2, continued

Tibiotarsi – specimens MNZ S1083, MNZ 2247, MNZ 4298, MNZ 5776, MNZ 8348, MNZ 9632, MNZ 9976, MNZ 13688, MNZ 16540, MNZ 22170, MNZ 22172, MNZ 22173, MNZ 22174, MNZ 22175 (Tib D is measured from the face of the lateral condyle, rather than from the prominence in the central proximal region of the condyle, which would markedly increase distal width and which homologous protuberance is located more anteriorly in *Aythya*). Tarsometatarsi – specimens MNZ S8684, MNZ 13358, MNZ 14692, MNZ 22176, MNZ 22178, MNZ 22177.

	Tib TL	Tib AL	Tib P	Tib S mid	Tib S min	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	69.08	66.12	8.39	4.52	3.84	8.96	34.18	9.30	5.09	8.36
Standard error	0.580	0.796	0.121	0.049	0.034	0.095	0.474	0.150	0.145	0.129
Standard deviation	0.820	1.593	0.342	0.163	0.101	0.232	0.948	0.260	0.354	0.223
Minimum	68.5	64.6	7.8	4.3	3.7	8.7	33.0	9.1	4.5	8.1
Maximum	69.7	68.3	8.8	4.7	4.0	9.4	35.0	9.6	5.4	8.5
Count	2	4	8	11	9	6	4	3	6	3

Appendix 3

Summary statistics for measurements (mm) of bones of *Malacorhynchus scarletti* from Poukawa deposits (abbreviations as in 'Methods').

Humeri – specimens MNZ S1276, MNZ 1823, MNZ 2379, MNZ 5145, MNZ 5492, MNZ 7584, MNZ 5714, MNZ 5736, MNZ 7599, MNZ 10080, MNZ 10477, MNZ 10478, MNZ 10966, MNZ 11447, MNZ 12190, MNZ 13119, MNZ 14153, MNZ 17097, MNZ 17226, MNZ 17655, MNZ 19400, MNZ 19505, MNZ 19506, MNZ 19531, MNZ 20758, MNZ 21656, MNZ 22402. Coracoids – specimens MNZ S1939, MNZ 16632, MNZ 21082, MNZ 21541 (sf-acrocor = length from scapular facet to tip of acrocoracoid).

	Hum L	Hum P	Hum S	Hum D	Cor L	Cor S	Cor D	Sf-acrocor
Mean	85.65	18.29	5.87	12.96	46.16	4.87	17.00	16.38
Standard error	1.431	0.333	0.127	0.177	0.428	0.123	—	0.120
Standard deviation	3.504	0.998	0.539	0.770	0.741	0.246	—	0.239
Minimum	80.4	16.7	4.9	11.6	45.3	4.6	17.0	16.0
Maximum	89.8	19.8	6.7	14.3	46.7	5.2	17.0	16.6
Count	6	9	18	19	3	4	1	4

Ulnae – specimens MNZ S2630, MNZ 7588, MNZ 8345, MNZ 11283, MNZ 15583, MNZ 17299, MNZ 17596, MNZ 19186, MNZ 20599, MNZ 22165, MNZ 22266, MNZ 41398. Carpometacarpal – specimens MNZ S3315, MNZ 3495, MNZ 17553, MNZ 18036, MNZ 18609, MNZ 19340, MNZ 19372, MNZ 19398, MNZ 20045.

	Ulna L	Ulna P	Ulna S	Ulna D	Cmc L	Cmc P
Mean	77.49	8.82	4.62	9.54	54.74	11.99
Standard error	1.124	0.186	0.108	0.222	0.657	0.298
Standard deviation	2.754	0.557	0.324	0.667	1.971	0.843
Minimum	73.0	7.7	4.1	8.3	51.5	10.7
Maximum	81.3	9.5	5.1	10.1	57.0	13.1
Count	6	9	9	9	9	8

Appendix 3, continued

Femora – specimens MNZ S2411, MNZ 7192, MNZ 10342, MNZ 15315, MNZ 16252. Tibiotarsi – specimens MNZ S2502, MNZ 10355, MNZ 11684, MNZ 15119, MNZ 15133, MNZ 17300, MNZ 41079, MNZ 41405.

	Fem L	Fem P	Fem S	Fem D	Tib L	Tib AL	Tib P	Tib S mid	Tib D
Mean	50.97	10.05	4.05	10.70	89.26	80.03	8.95	4.35	8.90
Standard error	0.937	0.456	0.129	0.447	—	1.017	0.313	0.047	0.186
Standard deviation	1.875	0.791	0.289	0.894	—	2.690	0.626	0.124	0.454
Minimum	48.4	9.3	3.6	9.7	89.3	75.3	8.3	4.1	8.3
Maximum	52.4	10.9	4.3	11.6	89.3	83.2	9.6	4.5	9.6
Count	4	3	5	4	1	7	4	7	6

Appendix 4

Summary statistics for measurements (mm) of bones of *Cygnus atratus* from Lake Poukawa. Mean and *n* values for Marfell's Beach fossils from Worthy (1998).

	Hum L	Hum P	Hum S	Hum D	Ulna L	Ulna P	Ulna S	Ulna D	Cmc L	Cmc P	Cor L
Mean	232.52	41.42	12.98	28.14	212.42	18.74	9.39	17.94	107.60	25.66	74.03
Standard error	2.15	0.45	0.09	0.19	2.29	0.17	0.13	0.25	1.06	0.29	0.66
Standard deviation	11.15	2.37	0.66	1.40	9.98	0.83	0.62	1.30	6.39	1.80	3.44
Minimum	210.0	38.2	11.7	24.9	190.0	16.6	8.3	15.8	94.2	22.0	67.7
Maximum	257.0	50.7	14.4	30.8	232.0	20.2	10.9	21.3	119.7	29.7	80.0
Count	27	28	50	55	19	23	22	27	36	40	27
Marfell's Beach	233.71	43.18	14.00	28.08	216.29	18.07	9.52	17.80	109.51	25.68	73.6
Marfell's Beach <i>n</i>	7	10	8	9	14	15	15	14	26	21	24

	Fem L	Fem P	Fem S	Fem D	Tib TL	Tib AL	Tib P	Tib S	Tib D	Tmt L	Tmt P	Tmt S	Tmt D
Mean	93.74	23.22	10.89	25.94	189.90	185.90	20.43	10.91	22.43	107.06	23.16	9.35	21.84
Standard error	0.77	0.22	0.10	0.22	2.59	1.87	0.21	0.11	0.20	0.84	0.17	0.08	0.26
Standard deviation	5.38	1.45	0.69	1.54	8.20	8.57	1.00	0.65	1.32	5.48	1.07	0.57	1.47
Minimum	84.2	19.1	9.0	23.2	174.0	169.0	18.8	9.6	19.8	95.0	21.1	8.2	18.0
Maximum	109.8	27.6	12.9	30.4	205.0	202.0	22.8	12.4	27.7	118.3	25.5	10.6	24.9
Count	49	45	52	50	10	21	22	37	43	43	40	48	33
Marfell's Beach	91.33	23.52	10.67	25.34	184.58	—	19.56	10.78	20.66	102.39	22.13	9.31	21.74
Marfell's Beach <i>n</i>	28	28	33	25	5	—	9	12	24	32	29	30	24