Miocene fossils show that kiwi (*Apteryx*, Apterygidae) are probably not phyletic dwarves

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Abstract — Until now, kiwi (*Apteryx*, Apterygidae) have had no pre-Quaternary fossil record to inform on the timing of their arrival in New Zealand or on their inter-ratite relationships. Here we describe two fossils in a new genus of apterygid from Early Miocene sediments at St Bathans, Central Otago, minimally dated to 19–16 Ma. The new fossils indicate a markedly smaller and possibly volant bird, supporting a possible overwater dispersal origin to New Zealand of kiwi independent of moa. If the common ancestor of this early Miocene apterygid species and extant kiwi was similarly small and volant, then the phyletic dwarfing hypothesis to explain relatively small body size of kiwi compared with other ratites is incorrect. *Apteryx* includes five extant species distributed on North, South, Stewart and the nearshore islands of New Zealand. They are nocturnal, flightless and comparatively large birds, 1–3 kg, with morphological attributes that reveal an affinity with ratites, but others, such as their long bill, that differ markedly from all extant members of that clade. Although kiwi were long considered most closely related to sympatric moa (Dinornithiformes), all recent analyses of molecular data support a closer affinity to Australian ratites (Casuariidae). Usually assumed to have a vicariant origin in New Zealand (*ca* 80–60 Ma), a casuariid sister group relationship for kiwi, wherein the common ancestor was volant, would more easily allow a more recent arrival via overwater dispersal.

Key words: Apterygidae, fossil record, evolution, new species, flightlessness

Introduction

Kiwi (*Apteryx*, Apterygidae) are the most iconic of New Zealand birds. Smallest of the extant ratites, the five species of *Apteryx* now recognised (GILL *et al.* 2010) are all chicken-sized, flightless, nocturnal birds that are superficially convergent on mammals with their fur-like plumage, burrow-breeding behaviour, and dependence on olfactory and tactile rather than optical senses (CALDER 1978). One of the most extraordinary peculiarities of kiwi (kiwi and moa may be both singular and plural because in Māori there is no 's' to denote the plural) is the huge egg that they produce – more than four times the size of that predicted from their body weight – which allows the production of an extremely precocial chick (CALDER 1978). This characteristic led to the hypothesis that kiwi are phyletic dwarfs, as first espoused by CALDER (1978, 1984) and championed by GOULD (1986, 1991). This hypothesis suggested that extant kiwi were the outcome of an evolutionary trajectory of a reduction in body size based on a perceived sister-group relationship with the giant moa

(Dinornithiformes) and a lack of any Cenozoic fossil record.

Ratites (ostrich, rhea, cassowary, emu, elephant bird, moa and kiwi) are flightless palaeognaths with greatly reduced wings, or, in the case of moa, completely lost. In the absence of an informative fossil record, interpretation of ratite origins has been limited to inference from the highly modified extant representatives. In recent decades, ratites have come to be regarded as one of the best vertebrate exemplars of a group with vicariant origins *e.g.*, ROFF (1994), following initial promotion of the idea by CRACRAFT (1974). However, analyses of molecular data, *e.g.*, COOPER *et al.* (2001) and HADDRATH & BAKER (2001), cast doubt on the vicariant origin of various ratite clades with unanimous support for kiwi having a closer relationship to Australian ratites (Casuariidae) than to moa. Thus the first premise underpinning the phyletic dwarfing hypothesis of kiwi origins – a sister-group relationship with moa – is now doubtful. With the divergence of kiwi from casuariids then calculated to have occurred at about 60 Ma, it has been suggested that the occurrence of kiwi in New Zealand required dispersal over a significant oceanic barrier following Zealandia's separation from East Gondwana approximately 80 Ma (MCNAB 1994; COOPER *et al.* 2001). However, it is now recognised that the unzipping of Zealandia (inclusive of New Zealand) from East Gondwana took over 27 Ma, commencing 82 Ma and finishing approximately 55 Ma (GAINA *et al.* 1998; SCHELLART *et al.* 2006). If this was indeed the case, then a vicariant origin for kiwi remains a possibility (TENNYSON 2010). This is especially so given that the most recent estimates for the divergence of kiwi from casuariids continue to support their ancient origin, *e.g.*, 53.5 (95 % CIs 36.9–72.1) Ma, estimated with both external and internal fossil calibrations (PHILLIPS *et al.* 2010), and 73 (95 % CIs 50–100) Ma as estimated in BEAST by HADDRATH & BAKER (2012). But the question arises, was the common ancestor of kiwi and casuariids large and flightless, or was it small and volant as might be predicted by the multiple loss of flight hypothesis invoked for ratites (HARSHMAN *et al.* 2008; PHILLIPS *et al.* 2010)? More recently, even the vicariant origin of moa has been questioned, as molecular analyses suggest multiple independent origins of ratites involving dispersal by volant ancestors and subsequent convergent evolution towards the ratite form (HARSHMAN *et al.* 2008; PHILLIPS *et al.* 2010), although morphological data (JOHNSTON 2011; WORTHY & SCOFIELD 2012) still supports a vicariant origin. It is therefore possible that both moa and kiwi may have dispersed as volant, and therefore small, birds to New Zealand after its separation from East Gondwana.

Resolution of these contrasting hypotheses will be helped by a fossil record that establishes limits such as lineage presence and actual morphological form at crucial times. The fossil history of moa prior to the Quaternary remains elusive, but eggshell and tantalising fragments from the St Bathans Fauna, South Island (WORTHY *et al.* 2007; TENNYSON *et al.* 2010) show that moa ancestors were present and were large birds in the Early Miocene.

The St Bathans Fauna has produced a diverse assemblage of terrestrial vertebrates including leiopelmatid frogs, reptiles including skinks, geckos, turtles and crocodilians, and mammals (JONES *et al.* 2009; LEE *et al.* 2009; WORTHY *et al.* 2006, 2011a, 2011b). The terrestrial vertebrate fauna (non-fish) is however dominated in diversity and abundance by about 40 species of birds, principally of waterfowl (Anatidae), with a minimum of eight taxa in five genera. It includes moa (Dinornithiformes), a tubenose (Procellariiformes), birds of prey (Accipitriformes), several gruiforms (Rallidae), a gull (?Laridae) and other charadriiforms, herons (Ardeidae), a palaelodid (Phoenicopteriformes), pigeons (Columbidae), parrots (Psittaciformes), a swiftlet (Apodidae), an owlet-nightjar (Aegothelidae), and passerines (Passeriformes) (SCOFIELD *et al.* 2010; TENNYSON *et al.* 2010; WORTHY *et al.* 2007, 2009, 2010a, 2010b, 2011c, 2011d). The fauna includes representatives of all the quintessential endemic New Zealand terrestrial vertebrates such as leiopelmatids (WORTHY *et al.* 2011b), sphenodontids (JONES *et al.* 2009), moa (TENNYSON *et al.* 2010), the basal gruiform *Aptornis* (WORTHY *et al.* 2011c), and acanthisittid wrens (WORTHY *et al.* 2010a). It has, however, not revealed any evidence of that most iconic of all New Zealand taxa, the kiwi. This absence is now informed by the discovery of two fossils referrable to Apterygidae. They allow assessment of the phyletic dwarfing hypothesis

and have bearing on when kiwi joined the New Zealand biota.

Material and methods

Nomenclature: We follow GILL *et al.* (2010) for nomenclature of kiwi and use names from specimen labels interpreted via DAVIES (2002) for tinamous. We use the anatomical nomenclature given in BAUMEL *et al.* (1993) and ELZANOWSKI & STIDHAM (2010) and abbreviate common terms as follows: artic., articularis; cond., condyle; m., musculus; proc., processus; tuber., tuberculum.

Abbreviations: AM, Australian Museum, Sydney, New South Wales, Australia; CM, Canterbury Museum, Christchurch, New Zealand; MV, Museum Victoria, Melbourne, Victoria, Australia; NMB, Naturhistorisches Museum, Basel, Switzerland; NMNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NMW, Naturhistorisches Museum, Vienna, Austria; SAM, South Australian Museum, Adelaide, South Australia, Australia; SMF, Forschungsinstitut Senckenberg, Sektion Ornithologie, Frankfurt am Main, Germany. Ma, million years ago.

Comparative material examined: Comparisons were made widely among birds using the skeletal collections of the Australian Museum and South Australian Museum. Following determination of the apterygid affinity of the fossils, detailed observations were made of the following kiwi and tinamou specimens.

Apteryx owenii: SAM B.5051, MV B56009, AMS535, AM A.1980, AM A.1992, AM A.4570; NMNZ OR.22815a; NMNZ OR.23044; NMNZ OR.23717a; NMNZ OR.24415; NMNZ OR.24416; *A. haastii*: MV B40905, CM Av31538; NMNZ OR.19773a; NMNZ OR.23022a; NMNZ OR.23038; NMNZ OR.23045; NMNZ OR.23648a; NMNZ OR.27983; NMNZ OR.28010a; *A. australis*: CM Av14447, CM Av32404, CM Av36637, CM Av36638, CM Av39065, AM O. unregistered; *A. a. australis*: NMNZ OR.22089a; NMNZ OR.27761a; NMNZ OR.27965; *A. a. lawryi*: NMNZ OR.23591; NMNZ OR.23756; *A. mantelli*: CM Av5492; NMNZ DM.909-S; NMNZ OR.13588; NMNZ OR.14964; NMNZ OR.17206; NMNZ OR.17207; NMNZ OR.17208; NMNZ OR.17209; NMNZ OR.17210; NMNZ OR.17211; NMNZ OR.17212; NMNZ OR.17213; NMNZ OR.24640; NMNZ OR.24984; *A. rowi*: CM Av16691, CM Av16717, CM Av16718.

Crypturellus obsoletus, SMF 2148; *C. noctivagus noctivagus*, SMF 11394; *C. tataupa*, SMF 11392; *C. parvirostris*, SMF 2164, SMF 9357, SMF 8184; *C. cinnamomeus*, SMF 2537; *C. undulatus vermiculatus*, SMF 2149; *Eudromia elegans*, NMW 3.071, SMF 9306, SMF 9260, SMF 6111, SMF 5415, SMF 6416, SMF 6298; *Nothoprocta perdicaria*, NMNZ OR.22983, NMW 4.068; *Nothura maculosa*, NMW 1061; *Tinamus major robusta*, SAM B.31339; *T. major major*, NMNZ OR.1433; *T. major*, NMW 4.559; *T.* (*Trachpilmus* Cab.) *robustus*, NMB C.2004; *T. solitarius*, SMF 2150; SMF 2146; *Rhynchotus fasciatus =rufescens*, NMW 161, NMW 160; *R. rufescens*, SMF 2147, NMB 5537.

We describe two fossil bones from the Early Miocene St Bathans Fauna, from Central Otago, New Zealand. The locality details and general stratigraphy of the sites producing this fauna have been described already (WORTHY *et al.* 2007; SCHWARZHANS *et al.* 2012).

We estimated mass for the fossil kiwi based on its femoral circumference using six different algorithms, including four from the literature based on all kinds of birds (ANDERSON *et al.* 1985; CAMPBELL & MARCUS 1992) and ratites (DICKINSON 2007), as well as two newly derived ones based on kiwi and tinamous. Circumference was determined by wrapping a narrow and thin piece of cellotape (or string for extant kiwi specimens in NMNZ) around the mid-shaft and marking the point where it overlapped itself, then measuring the length with callipers. Given apterygids are rather atypical palaeognaths, we also computed algorithms for mass from data for tinamous and for apterygids separately, and used these to estimate the mass of the fossil kiwi. We reasoned that if the fossil taxon was volant the value based on tinamou may be more pertinent but if it were flightless then that based on kiwi would be relevant. Measurements were taken with dial callipers or a graticule in a binocular microscope and rounded to the nearest 0.1 mm.

FIGURE 1. Apterygid right femora. *Proapteryx micromeros* (NMNZ S.53324, A-C, E) and *Apteryx owenii* (MV 56009, D, F), in medial (A), cranial (B), caudal (C, D), and lateral (E, F) views. Scale bars are 10 mm. Numbers refer to family attribution characters.

Systematic Palaeontology

Order Casuariiformes: Cassowaries, Emus and Kiwi
Family Apterygidae G.R. Gray, 1840: Kiwi

The fossil is identified as an apterygid by the following combination of femoral characters (Figs 1, 2): the facies artic. antitrochanterica is convex in cranial-caudal section (1) and lateromedially about same width as the caput femoris (2); in caudal view, the proximal profile has a marked notch between the caput femoris and the facies artic. antitrochanterica (3); the collum femoris is constricted proximodistally and craniocaudally (4); the caudal facies distal to the facies artic. antitrochanterica is flat (5), forming a near right angle with the lateral facies (6), not a curved transition, as in *e.g.* galliforms; the insertion area for the major part of m. obturatorius medialis is on a distinct bulge traversing the caudal facies distolaterally, ending laterally level with the insertion area for m. ischiofemoralis (7); the depth of the crista trochanteris is about twice the depth of the caput femoris (8); the crista trochanteris not extending proximad of the facies artic. antitrochanterica, no fossa trochanteris (9), rounded cranially (10), merges gradually to the corpus femoris distally (11), and lateromedially broad adjacent to the collum femoris such that a narrow groove, less than the diameter of the caput, connects the pretrochanteric surface to the facies artic. antitrochanterica (12); the pretrochanteric surface is shallowly concave cranially, lacking pneumatic foramina (13); the linea intermuscularis cranialis extends to the distal end of the crista trochanteris (14); the area for the insertion of the m. obturatorius lateralis on an elevated bulge, not marked by any scar (15); large sulcus centred on the lateral facies proximally for insertion areas of the m. iliotrochantericus caudalis cranially and the m. iliofemoralis externus caudally (McGowan 1979), is elongate, extending about half the length of the crista trochanteris (16); insertion areas for the mm. iliotrochanterici medius et cranialis form a narrow elongate groove, slightly separated from the insertion area for the m. iliofemoralis externus, extending distally to point level with end of the crista trochanteris (17); insertion area of the m. ischiofemoralis forms a short, broad sulcus, caudal of and overlapping, in the proximodistal plane, the distal end of the insertion area for the m. iliofemoralis externus and the proximal end of the insertion area for the m. iliotrochantericus

medius (18); the corpus femoris is elongate relative to its proximal width (19), arched dorsally at mid-length (20), and bent medially at the distal end of the crista trochanteris, such that the lateral facies beside the trochanter is markedly inclined medially relative to more distal parts (21).

The insertion area for the m. iliotrochantericus caudalis being centred craniocaudally on the lateral facies, not more cranially, may be a synapomorphy of Casuariiformes. Characters 15 and 16 are considered apterygid autapomorphies. Femora of all other birds are further distinguished from those of apterygids by numerous features (see Appendix 1).

Proapteryx gen. nov.

Types species: *Proapteryx micromeros* spec. nov.

Diagnosis: An apterygid distinguished from *Apteryx* by the facies artic. antitrochanterica of the femur having a well-formed lobe overhanging the caudal facies; insertion area for the minor part of the m. obturatorius medialis a marked scar about a third the length of and located proximocaudal to the insertion area of the m. ischiofemoralis, not immediately caudal to it; and by its markedly smaller size with a femoral shaft diameter about half that of *A. owenii*, the smallest *Apteryx* species.

Etymology: Addition of the Latinised Classical Greek prefix προ- (pro-), meaning before, to the scientific name of kiwi (*Apteryx*). *Apteryx* is Latinised Classical Greek and derives from the Greek "α", a prefix indicating to be without or absent, and "πτέρυγας"=wings; neuter noun. Denoting that this taxon precedes *Apteryx* in the geological record.

Proapteryx micromeros spec. nov.
(Figs 1–3)

Holotype: NMNZ S.53324 (Figs 1, 2), right femur missing distal condyles; collected 20 April 2012.

Diagnosis: As for genus.

Etymology: Latinised Classical Greek μικρός (mikros) for small or little and μηρία (meros) for thigh; neuter noun. For the markedly smaller femur than in extant apterygids.

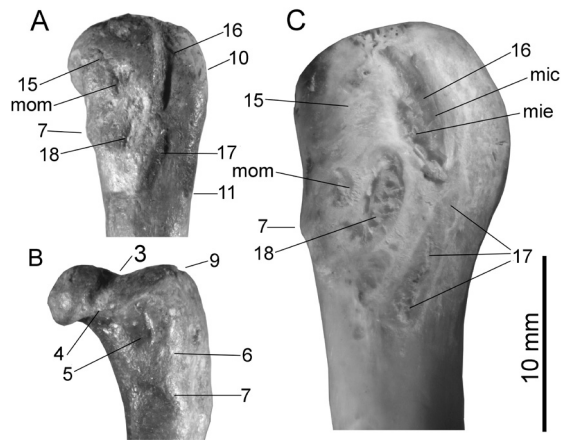**Type locality**: In a clay layer enveloping

FIGURE 2. Apterygid right femora. *Proapteryx micromeros* (NMNZ S.53324, A, B) and *Apteryx owenii* (a small example, SAM B.5095, C), in lateral (A, C), and caudal (B), views. Numbers refer to family attribution characters. Abbreviations: mic, insertion area of m. iliotrochantericus caudalis; mie, insertion area of m. iliofemoralis externus; mom, insertion area of m. obturatorius medialis pars minor.

stromatolites, Site FF1 (LINDQVIST 1994), a fossil stromatolite bed at 44.90359°S, 169.85840°E, Manuherikia River, Otago, New Zealand. Fossil Record Number (FRN) in the archival Fossil Record File of the Geological Society of New Zealand is H41/f0058 (stromatolites) and H41/f0059 (clay draping stromatolites).

Stratigraphy/Age/Fauna: Bannockburn Formation, Manuherikia Group, Early Miocene (Altonian); 19–16 Ma; St Bathans Fauna. The stratigraphic relationship of site FF1 to other Bannockburn Formation exposures is presently unknown but the associated faunas are similar.

Measurements of holotype: Preserved (incomplete) length 42.2 mm, proximal width 8.4 mm, maximum proximal depth 7.6 mm ; shaft width at former mid length 3.6 mm, shaft depth at former mid length 4.0 mm.

Comparison and description: In addition to the listed diagnostic characters, there are few differences between *Proapteryx* and *Apteryx*. The nutrient foramen caudally on the shaft is distinctly proximal to mid-length in *Apteryx*, but near original mid-length in *Proapteryx*. The linea intermuscularis caudalis extends proximally towards the lateral facies laterad of an elongate prominence for the insertion of m. puboischiofemoralis pars medialis (as in Casuariidae). This
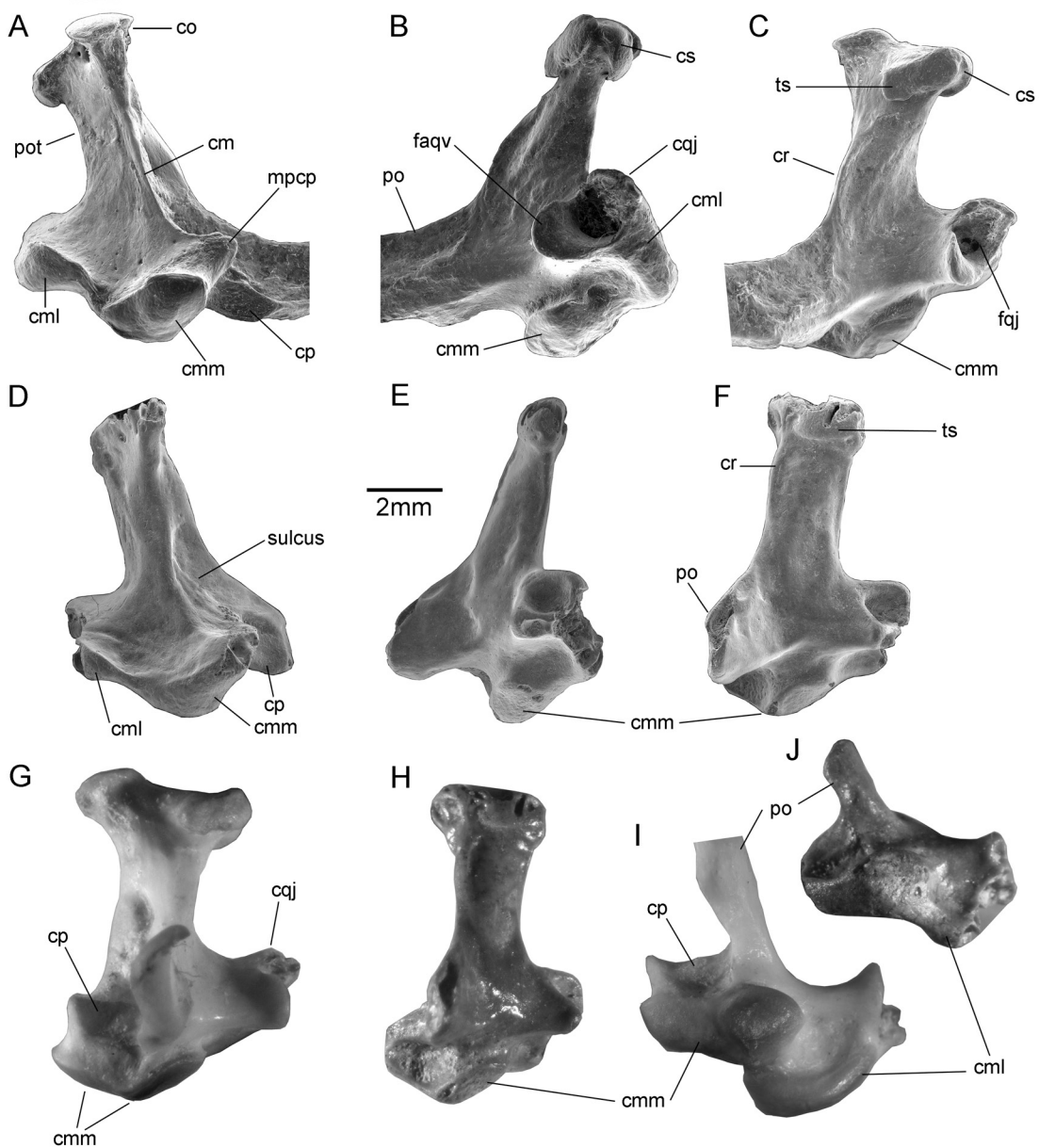
FIGURE 3. Apterygid left quadrates. *Apteryx owenii* (SAM 5051 A-C, G, I) and *Proapteryx micromeros* (NMNZ S.53209, D-F, H, J) in medial (A, D), lateral (B, E), anterolateral (C, F), anterior (G, H) and ventral (I, J) views. Abbreviations: cm, crista medialis; cml, cond. mandibularis lateralis; cmm, cond. mandibularis medialis; co, capitulum oticum; cp, cond. pterygoideus; cqj, cotyla quadrateojugalis; cr, crista; cs, capitulum squamosum; faqv, facies artic. quadrateojugalis ventralis; fqj, fovea quadrateojugalis; mcpc, medial process cond. pterygoideus; po, proc. orbitalis; pot, proc. oticus; ts, tuber. subcapitulare.

prominence in *Proapteryx* is relatively more proximally located, ending level with the caudal bulge that is the insertion area for the major part of m. obturatorius medialis, rather than distal to the crista trochanteris.

Referred specimen: NMNZ S.53209, a left quadrate (Fig. 3).

    Locality of referred specimen: Bed HH1b, 10–15 cm thick sand and cobble layer 9.5–9.58 m above the base of the Bannockburn Formation, Trench Excavation, at 44.90780° S 169.85844° E, Manuherikia River section; FRN is H41/f0103.

    Stratigraphy/Age/Fauna: As for holotype.

    Measurements of referred specimen: Total height from proc. oticum to cond. medialis 9.2 mm; height above cotyla quadratojugalis 4.9 mm.

Comparison and description: The fossil is worn and damaged with the proc. orbitalis lost anterior to the cond. pterygoideus, loss of much of the cond. mandibularis lateralis including the caudoventral rim of the fovea quadratojugalis, and the anteriomedial tip of the cond. mandibularis medialis is worn.

NMNZ S.53209 differs markedly from quadrates of all birds except those of *Apteryx* with which it shares the following combination of features (Fig. 3) and so it is referred to Apterygidae: 1, the head of the proc. oticus is expanded laterally and medially into a broad 'dumbell' shape, about three times wider than long, aligned at right angles to the proc. orbitalis; 2, caudally, there are pneumatic foramina at the base of the capitulum oticum; 3, the capituli oticum et squamosum are linked by a craniocaudally narrow articular surface lacking an incisura intercapitalis; 4, the capitulum squamosum widens laterally and its articular surface extends caudoventrally as a small oval lobe protuberant over the caudal facies; 5, the tuber. subcapitulare on the anterior side of the capitulum squamosum is prominent, robust, and about twice as wide as high; 6, the proc. oticus has a flat caudal facies, straight in lateral aspect, centred above the cond. mandibularis medialis, and forming an angle of approximately 100 degrees with the proc. orbitalis; 7, the crista medialis is acute, extending from the medial prominence of the cond. pterygoideus towards the capitulum oticum, forming the caudal boundary to a deep triangular sulcus without a foramen pneumaticum rostromediale; 8, the corpus lacks pneumatic foramina both caudally and laterally; 9, the cotyla quadratojugalis is very prominent laterally, the fovea quadratojugalis is deep, and the facies artic. quadratojugalis ventralis is proportionately large; 10, the proc. orbitalis is lateromedially thin with a shallow sulcus medially; 11, the cond. pterygoideus is rectilinear, separated by a sulcus from and lies dorsal to the medial half of the cond. mandibularis medialis, broader than high, dorsally convex in section, lateromedially concave, and extends continuously from a prominence medially onto the ventromedial part of the proc. orbitalis; 12, in ventral view, the condyli mandibularis medialis et lateralis are aligned roughly at right angles to the proc. orbitalis; 13, the articular surface of

the cond. mandibularis lateralis is laterocaudal of, narrower than, subparallel to, and overlaps the cond. mandibularis medialis; 14, the cond. mandibularis medialis has two distinct parts: a ventrally convex medial part, and an anterocaudally broader lateral part that extends dorsally onto the lateral facies on the anterior side of the cotyla quadratojugalis.

In addition, NMNZ S.53209 reveals the following features. The preserved dorsal surface of the capitilum squamosum is level with the eroded surface of the capitulum oticum, indicating that the latter was originally slightly more prominent dorsally. Medially, the tuber. subcapitulare abuts a crest linking the capituli to the proc. orbitalis. A deep partially pneumatic sulcus at the base of the capitulum oticum lies medial to this crest. The proc. oticus is robust, extending dorsad of the cotyla quadratojugalis by slightly over half (53 %) of total quadrate height, anterior and caudal borders are subparallel in anterolateral view, being formed respectively from crests extending from the proc. orbitalis to the capituli anteriorly and from the cotyla quadratojugalis to the capitulum squamosum posteriorly. The anterior margin of the proc. oticus meets the dorsal margin of the proc. orbitalis in a broad (approximately 140°) angle level with the dorsal side of the cotyla quadratojugalis. Anterior to the cond. mandibularis lateralis and lateral to the cond. medialis a shallow sulcus undercuts the cotyla quadratojugalis ventrally.

Quadrates of *Apteryx* species differ from NMNZ S.53209 as follows. (1) They are relatively more robust, although the smallest extant species, *A. owenii*, has a similar height (Table 1; Appendix 2). (2) They lack a pneumatic fossa anteriorly under the capitulum oticum. (3) The proc. oticus is relatively shorter with its height above the cotyla quadratojugalis slightly less than half of the maximum dorsoventral height. (4) The laterocaudal margin of the proc. oticus above the cotyla quadratojugalis is more rounded (in NMNZ S.53209, the corpus is notably craniocaudally compressed forming a ridge extending from under the capitulum squamosum down nearly to the cotyla quadratojugalis). (5) The cond. mandibularis medialis is proportionally larger but relatively less protuberant ventrally, and less offset ventrally from the ventral margin

of the base of the proc. orbitalis, creating a deeper sulcus under the cond. pterygoideus. (6) In lateral view, the proc. orbitalis meets the proc. oticus below the dorsal margin of the cotyla quadratojugalis, a result of the more robust ventral half of the quadrate compared to NMNZ S.53209. (7) The tuber. subcapitulare is sometimes (*A. owenii*) not bound medially by a ridge extending from the proc. orbitalis, but in other species, *e.g.*, *A. haastii* and *A. australis*, a ridge is present, as in NMNZ S.53209.

While the fossil quadrate was only similar to those of apterygids among a large range of compared taxa, we present detailed comparisons with three other palaeognath groups, the dinornithiforms because they were previously considered the sister group of kiwi (Cracraft 1974) and the tinamids and extinct lithornithids, because their volant nature makes them or taxa in their lineages potential candidates for the ancestral kiwi in New Zealand via dispersal across oceans (Houde 1988; Phillips *et al.* 2010).

Dinornithiformes. Apart from being considerably larger, moa quadrates differ markedly from those of the fossil and *Apteryx* as follows: proc. orbitalis short, relatively about half the length in kiwi, robust, dorsally convex (not laminar in nature, elongate and concave dorsally); they have a large foramen pneumaticum rostromediale (lacking in *Apteryx*); the capitulum oticum is relatively smaller, more poorly differentiated from the capitulum squamosum, not pneumatic caudally; in ventral view, the articular surfaces of the condyles differ markedly such that the articular facies of the cond. mandibularis medialis has very little medial prominence, and so rather than being lateromedially broad and sub-parallel to the cond. mandibularis lateralis as in kiwi, is craniocaudally elongate and aligned at near right angles to the cond. mandibularis lateralis. The

fossil therefore has little similarity with dinornithiform quadrates.

Lithornithidae. Lithornithids are volant palaeognaths found in the Northern Hemisphere in the Early Tertiary (Houde 1988) and could conceivably have been ancestral to Casuariiformes, which are not known to be older than Late Oligocene *ca.* 24 Ma (Boles 2001). If so, a closer relationship and hence greater osteological similarity with *Apteryx* than to most other ratites might be predicted. We compared images of quadrates of *Lithornis celetius* Houde, 1988 (USNM 290601) with *Apteryx* quadrates. Similarities include: the proc. oticus is dorsally expanded with poorly separated capituli aligned at right angles to the proc. orbitalis, the cond. mandibularis medialis is medially prominent below the saddle-like cond. pterygoideus whose articular facet curves around onto the ventral part of the proc. orbitalis; the proc. orbitalis is relatively low (dorsoventrally) with a sulcus medially. However, the *Lithornis* quadrate differed from *Apteryx* quadrates and the fossil as follows: the proc. oticus is dorsally convex across the capituli, rather than the capituli being separated by a slight hollow; the capitulum oticum is markedly convex dorsally, does not overhang the corpus either posteriorly or anteriorly (not comparable in fossil); the capitulum squamosum is less protuberant laterally; the tuber. subcapitulare is lacking or poorly developed; the cotyla quadratojugalis is located relatively more ventrally, its ventral margin aligned with the ventral margin of the proc. orbitalis, has subequal ventral extent with the cond. mandibularis medialis; the cotyla quadratojugalis is not as protuberant laterally, has a crest extending from the dorsal margin to the corpus at slightly above mid height; the rostromediale facies of the corpus lacks a distinct sulcus at midheight (present in *Apteryx*) where the foramen

TABLE 1. Summary statistics for *Apteryx* species of % TH above cotyla quadrateojugalis from Appendix 2.

	A. mantelli	*A. rowi*	*A. australis*	*A. lawyri*	*A. owenii*	*A. haastii*
Mean	48.6	45.8	47.1	45.0	48.2	45.4
Standard Error	1.08	1.14	1.47	1.34	1.04	1.13
Standard Deviation	3.42	1.98	3.90	3.00	3.28	2.53
Minimum	44.4	43.6	40.9	41.7	42.6	42.5
Maximum	53.5	47.5	50.8	49.4	54.8	49.1
Count	10	3	7	5	10	5

pneumaticum is present in dinornithiforms; and the cond. pterygoideus is not so prominent above the medial side of the cond. mandibularis medialis. Thus, *Lithornis* quadrates differ substantially and in the same way from both *Apteryx* quadrates and the fossil quadrate referred to *Proapteryx*.

Tinamidae. The South American small volant palaeognaths in Tinamidae potentially could be related to the bird represented by this fossil as tinamous render ratites paraphyletic in recent analyses (HARSHMAN et al. 2008; PHILLIPS et al. 2010) and potentially are the sister taxon to moa (PHILLIPS *et al.* 2010). Moreover, the oldest tinamou fossils, clearly recognisable as similar to modern tinamous, are of similar Early Miocene age to the St Bathans Fauna (BERTELLI & CHIAPPE 2005). However, tinamou quadrates differ markedly from those of the fossil and *Apteryx* in having the cotyla quadratojugalis and condyli mandibularis medialis et lateralis displaced caudally relative to the proc. oticus, and the cotyla quadratojugalis more separated vertically from the cond. mandibularis medialis, being located above the base of the proc. orbitalis (see SILVEIRA & HÖFLING 2007: figs 40, 41). Tinamous or their recent ancestors can thus be ruled out as being closely related to the fossil or as ancestral to apterygids.

Assignment to *Proapteryx*

In summary, NMNZ S.53209 is more similar to *Apteryx* than to any other palaeognath group, which supports its referral to the *Apteryx* lineage. While NMNZ S.53209 is most similar to kiwi quadrates among known birds, the above features 2–5 are notable departures from the quadrate form of all extant *Apteryx* species and support the generic distinction based on femoral differences. We tentatively refer NMNZ S.53209 to *Proapteryx micromeros* because it represents a kiwi of similar size to that estimated for the holotype (see below) and it is presently most parsimonious to consider that only one such species is represented in the St Bathans Fauna. With several thousand bird bones having been collected from various sites sourcing this fauna, it seems unlikely that the two apterygid elements collected thus far would belong to separate taxa. The collection of additional material will hopefully confirm this idea.

Mass estimate for *Proapteryx*

The measured femoral circumference of the holotype femur of *Proapteryx* is 12.4 mm. We assessed body mass with several techniques.

Assessment of mass using algorithms based on a range of birds

1. Body mass (W) in g was estimated using the power function $W=0.16C^{2.73}$ (ANDERSON *et al.* 1985; MURRAY & VICKERS-RICH 2004). This equation suggests that a bird with a femoral circumference of 12.4 mm would weigh 154.6 g.

2. We also used equations from CAMPBELL & MARCUS (1992) based on Group AL (all 795 species from diverse families), using Ordinary Least Squares regression (OLS), the intercept is −0.065 and the slope is 2.411: thus $\log_{10}W=2.411\log_{10}C+0.065$ or $W=1.1645C^{2.411}$, and the estimated weight is 502 g.

3. Using the equation based on heavy-bodied (HB) birds using Reduced Major Axis regression (RMA) from CAMPBELL & MARCUS (1992), where the intercept is 0.11 and the slope is 2.268: thus $\log_{10}W=2.268\log_{10}C-0.11$ or $W=0.775427C^{2.268}$, the estimated weight is 234.1 g (95 % CIs 166–337.3 g.

Assessment of mass using only palaeognaths: Because kiwi are palaeognaths and not typical birds and because the above values varied widely, we assessed mass using formulae based only on palaeognaths. Assessing the mass of flightless ratites and the estimating the mass of extinct forms has a sizable literature (see review in DICKISON 2007), however most studies found mass estimates of Apterygidae are not well predicted by algorithms based on other ratites, probably because kiwi measurements lie well outside of the data generating those equations.

4. Ratite-specific algorithms. First we used DICKISON'S (2007) formula from OSL regression of known ratite body mass on bone measurements: $W=0.114815C^{2.83}$. This gives a predicted mass of 142.69 g. This estimate suffers from being based on a data range that does not encompass that for the fossil and further which is biased towards large size of extant ratites and is considerably smaller than other estimates.

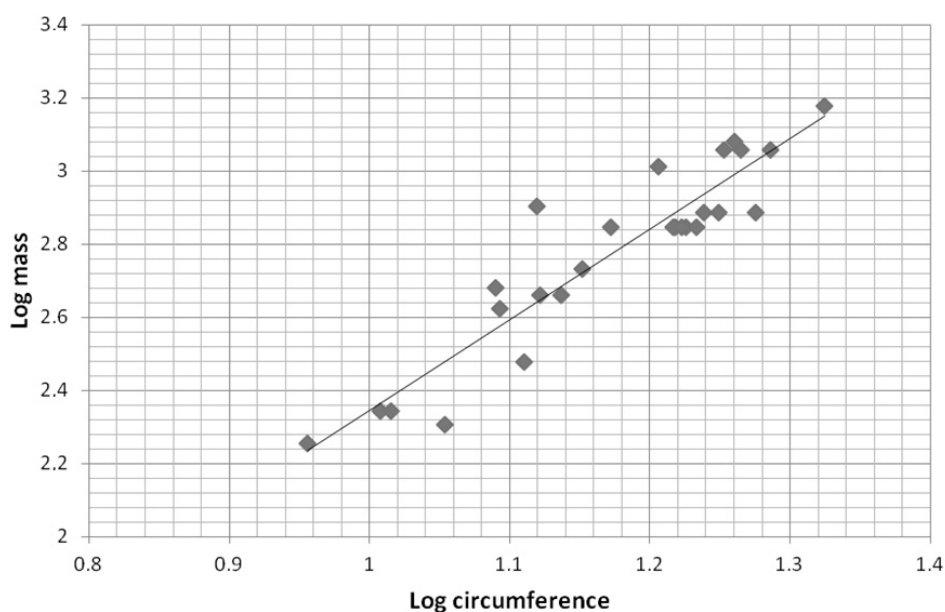**5. Palaeognaths – tinamous.** It is possible *Proapteryx* was volant, so for this reason

FIGURE 4. The least-squares regression of the raw data between the log circumference and log body mass in a sample of 28 tinamous of 14 species from Appendix 3. The coefficient of determination (R^2) was 0.8613.

we compared femoral diameter with mass in the volant and similar-sized palaeognaths, the tinamous (Tinamidae). Using the data in Appendix 3, and Fig. 4, we computed a RMA regression of $\log_{10}W = 2.4639\log_{10}C - 0.1173$ thus $W = 0.763308 \times C^{2.4639}$. This equation suggests the fossil femur with circumference of 12.4 mm was from a bird weighing 377 g (95% CIs 307.2–463.6 g). This predicted mass is greater than the result from the heavy-birds algorithm of Campbell & Marcus (1992), which is consistent with the observation that Tinamidae include some of the more bulky birds among those listed as heavy birds by Campbell & Marcus (1992). We note, however, that this estimate would only be valid if *Proapteryx* was volant and of similar proportions to tinamous.

6. Palaeognaths – apterygids. If *Proapteryx* had body proportions similar to *Apteryx* then an algorithm based on kiwi would be the most accurate way of estimating its mass. We took measurements of femora from 30 individuals of kiwi of known weight in the collection of the National Museum of New Zealand Te Papa Tongarewa (Appendix 5) and generated a kiwi-specific algorithm. The calculated RMA regression equation for kiwi was $\log_{10}W = 2.654307\log_{10}C - 0.56108$ thus $W = 0.274739C^{2.1496}$. This equation suggests that a bird with a femoral circumference of 12.4 mm would weigh 281.9 g (95% CIs 141.2–339.5 g).

These various calculations suggest that the predicted mass of *Proapteryx* probably lay within the range of 234.1 g (95% CIs 166–337.3 g), using Campbell & Marcus's (1992) equation based on heavy-bodied birds, and 377 g (95% CIs 307.2–463.6 g), assuming it was volant and based on tinamou. We note that the equation based on extant kiwi gave an intermediate value of 281.9 g (95% CIs 141.2–339.5 g). It seems the algorithm based on all birds from Campbell & Marcus (1992) probably over-estimated the weight of *Proapteryx* at 502 g. Therefore, *Proapteryx* was markedly smaller than all extant *Apteryx* species (Appendix 4) and similar in mass to the banded rail *Gallirallus philippensis* (Linnaeus).

Discussion

The fossils we describe as *Proapteryx micromeros* reveal, minimally, that a small apterygid species was present in New Zealand, about 19–16 Ma. The holotype femur derives from site FF1, an isolated outlier of the Bannockburn Formation (Lindqvist 1994) whose stratigraphic relationships to bed HH1b 9.5–9.58 m above the base of the Bannockburn Formation in the extensive

Manuherikia River section (Schwarzhans *et al.* 2012) which lies 300 m south, are presently undeterminable, so the two fossils may represent two species. However, we favour conspecificity of these fossils because they indicate a similar-sized bird (see below) and the associated fossils from FF1 are of species found in bed HH1b indicating the same source fauna. The addition of *Proapteryx* to the St Bathans Fauna reveals the assembly of all extant iconic terrestrial vertebrates of New Zealand, *e.g.*, leiopelmatid frogs, *Sphenodon*, moa, *Aptornis*, and acanthisittid wrens (see above), was complete by the Early Miocene: not one has arrived in the subsequent 16 Ma.

The holotype femur reveals that, at an estimated 234.1 g (95 % CIs 166.0–337.3 g) – 377 g (95 % CIs 307.2–463.6 g), *Proapteryx* was only 0.27–0.43 times the mass of the smallest individual (880 g) of the smallest extant kiwi species (*A. owenii*), or 0.2–0.3 times the mass of the approximate modal size (1200 g) of *A. owenii* (Appendix 5). In contrast, the quadrate is about the size of that in a small individual of *A. owenii*, and assuming it reflects skull size, might indicate that *Proapteryx* and *A. owenii* had similar sized skulls. However, *Proapteryx* has a more gracile proc. oticus, which may indicate a shorter bill than in *Apteryx*. The proportion of femur size to quadrate size seen in *Proapteryx* lies intermediate between those observed in similar-sized but distantly related birds such as Banded Rail, *Gallirallus philippensis*, *e.g.*, SAM B36299, and the Australian Little Bittern, *Ixobrychus dubius* (a species that has a relatively large head), *e.g.*, SAM B48804, (height quadrate 7.1 mm and 7.5 mm, respectively, versus 9.2 mm; femur proximal width 8.6 mm and 5.9 mm, respectively, versus 8.4 mm; femur mid shaft width 3.5 mm and 2.3 mm, respectively, vs 3.6 mm). Thus assuming the two bones belong to the same species, *Proapteryx* had a quadrate to femur proportion not greatly different from the Banded Rail. The two fossils, if conspecific, point to a bird with a head only slightly smaller than *A. owenii*, but with proportionally much smaller, more gracile legs, more like those of an average terrestrial bird, rather than with the relatively large legs modern kiwi have.

The presence of *Proapteryx* in the Early Miocene of New Zealand places the apterygid lineage in New Zealand at this time. If, as we prefer to interpret the fossils, only a single taxon is represented, then this taxon was of very small size compared to extant kiwi, being only about 0.195–0.314 times the mass of *A. owenii*, the smallest extant kiwi. We do not know whether *Proapteryx* was the only apterygid present in Zealandia during the Early Miocene, but the large sample size of birds from the St Bathans Fauna, some 5000 specimens, makes the undiscovered presence of another larger apterygid in this local fauna unlikely. However, our samples for this period derive from a single local fauna from one lacustrine environment in a rather large and diverse landscape, so there is a reasonable possibility that other forms existed elsewhere in Zealandia at that time. Despite this, given *Proapteryx* is an undoubted apterygid, it seems reasonable to assume that if its morphology was similar to that of a shared (hypothetical) common ancestor with extant apterygids, then small size was plesiomorphic for the clade. If so, it then follows that since the early Miocene, kiwi have evolved into larger birds with proportionately larger legs. Most terrestrial flightless birds have smaller volant relatives with proportionately smaller legs (Roff 1994; McNab 1994). The small size and slenderness of the femur makes it distinctly possible that *Proapteryx* was volant, supporting an overwater dispersal origin to New Zealand of kiwi that was independent of moa (Roff 1994; Cooper *et al.* 2001; Phillips *et al.* 2010). Further fossils will be required to confirm this suggestion. The divergence of kiwi from casuariids, for which estimates range from 53.5 Ma (Phillips *et al.* 2010) to 73 Ma (Haddrath & Baker 2012) long preceded *Proapteryx* leaving a large gap in the lineage history. This is significant because if *Proapteryx* was volant then the common ancestor of kiwi and Australian casuariids was also likely to have been volant, as is predicted by the multiple loss of flight hypothesis for ratites (Phillips *et al.* 2010). Given that the oldest Australian casuariid fossil presently known, *Emuarius gidju* a species similar to a small emu, is about 25 Ma (Boles 1992), then a ghost lineage in Australia of between 25 and 50 Ma, is inferred, providing more than enough time for the lineage to produce flightless and large species. If *Proapteryx* was flightless, a flightless lineage minimally spanning 16 Ma has to be invoked. The crown radiation of

kiwi has a recent basal divergence most recently estimated at 6.3 Ma (2.3–1.4 Ma, 95 % CIs) in BEAST by Haddrath & Baker (2012). Therefore, if *Proapteryx* was similar to the shared common ancestor with the crown radiation of kiwi and if it were volant, there was minimally a 10 Ma period during which the flightless condition could have been attained and body size of taxa increased. Even more rapid loss of flight and attainment of similar large body size is advocated for such divergent taxa as *Porphyrio* rails in New Zealand over only 1 Ma (Trewick 1997) and for ancestral ducks becoming moa-nalos in Hawaii in just the last 3.6 Ma (Sorenson *et al.* 1999).The phyletic dwarfing hypothesis advocated by Calder (1978, 1984) and Gould (1986, 1991) explains the large size of kiwi eggs as the result of an emu-sized ancestor evolving smaller body size while retaining the large size of the ancestor's egg. Regardless of its position on the volant–flightless continuum, *Proapteryx* reveals that ancestral kiwi were probably small in the Early Miocene. There remains no evidence in the fossil record to support the idea that geologically older kiwi were large like the emu and the cassowary, which are the sister taxa of Apterygidae. If this was so, then whether the ancestor of kiwi arrived in New Zealand vicariantly or by overwater dispersal is irrelevant; it was already small and probably volant – it cannot have been large and flightless like modern casuariids. This reasoning further suggests that the *Apteryx* lineage evolved larger size over the last 19–16 Ma. Thus the super-large egg of kiwi is probably not an historic holdover, but rather is more likely to be the result of adaptive advantage. It results in a highly precocial chick, which on emerging from the egg is independent of adults. We contend that this feature and the nocturnal habits of kiwi are perhaps best interpreted as adaptations to avoid avian predators, including terrestrial *Aptornis* and aerial raptors, both present in the Early Miocene and subsequently (Worthy *et al.* 2007; Worthy *et al.* 2011b), to which the evolution of flightlessness made them more vulnerable. The discovery of *Proapteryx* provides strong evidence to suggest that the origin of *Apteryx* by phyletic dwarfing is probably incorrect and that the opposite is instead more likely, that kiwi are the result of an evolutionary trajectory towards increased body mass during the Neogene and that their large eggs are an evolutionary novelty resulting from development towards extreme precociality.

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Appendix 1

Femoral features distinguishing Apterygidae from other birds.

Other modern birds, with an emphasis on those likely to be related for reasons of geographic proximity, have femora that differ from those of apterygids by the following features, which are considered sufficient to distinguish them, but which are not intended to be a comprehensive list of differences.

Dinornithiformes. All species of moa are vastly larger; facies artic. antitrochantica concave; pattern of ligament insertions proximolaterally differ greatly as follows (terminology after McGowan (1979) with preferred synonyms from Vanden Berge (1982) and Vanden Berge & Sweers (1993) in brackets, although we note McGowan's caveat that size and the presence of few muscles in *Apteryx* can be correlated with impressions on bones): large elongate sulcus for insertions for m. iliotrochantericus posterior (m. iliotrochantericus caudalis), m. gluteus medius et minimus (m. iliofemoralis externus), and m. iliotrochantericus medius et anterior (mm. iliotrochanterici medius et cranialis) shallower, located well craniad, nearly adjacent to cranial margin of crista trochanteris; insertion area for m. ischiofemoralis broad, well separated from the latter, just caudad of centre; impression for m. obturator internus (m. obturatorius medialis) closer to caudal margin, small, just caudad of the insertion area for m. ischiofemoralis; impression for M. obturator externus (m. obturatorius lateralis), shallow, broad.

Casuariidae. Similarities include lack of fossa trochanteris, notably convex facies artic. antitrochantica separated from caput by marked notch and ligamental insertion for m. iliotrochantericus caudalis largest and at mid craniocaudal depth. Differences include markedly larger size and a distinct pattern of sulci for ligamental insertions proximolaterally, interpreted by Patak & Baldwin (1998) as follows: a large oval sulcus at mid-craniocaudal depth for m. iliofemoralis externus, but the bipartite appearance of this sulcus suggests it also houses the insertion for m. iliotrochantericus caudalis; distal to this sulcus lies a circular and deep impression for m. ischiofemoralis; impression for m. obturator externus (=m. obturatorius lateralis), shallow, relatively small, stronger-marked in *Casuarius*.

Tinamidae, Galliformes. Proportions similar, but differ with a well-marked fossa trochanteris; facies artic. antitrochantica concave; impressio m. iliotrochantericus caudalis shallower and more cranially located; insertion area of m. obturatorius lateralis well marked; proximally, caudal and lateral facies meet in even curve; facies artic. antitrochanterica connected via broad groove to cranial surface.

All the following taxa lack a marked notch proximally separating the caput from facies artic. antitrochanterica, have a well-marked impression for m. obturatorius lateralis, and are further distinguished as follows:

Gruiformes (Gruiidae, Otididae, *Rhynochetos jubatus*, and Rallidae). Proportions similar, but have a fossa trochanteris; and lateral facies is markedly convex adjacent to the crista trochanteris.

Ardeidae. Proportions similar, but the shaft lacks dorsal curvature; crista trochanteris craniocaudal depth is much shallower and proximally is lateromedially narrow, so a broad flat groove connects the cranial surface to the facies artic. antitrochanterica.

Anseriforms. Femoral shaft relatively much shorter; caput on shorter neck.

Podicipedidae, Spheniscidae, Procellariiformes, Anhingidae, Phalacrocoracidae, Sulidae, Phaethontidae. Femoral shaft much shorter; craniocaudal depth crista trochanteris subequal or only slightly deeper than caput depth; neck with little or no constriction.

Pelecanidae. Femoral shaft relatively shorter, thinwalled, no dorsal curvature, crista trochanteris shorter, arrangement of insertion areas laterally differs.

Threskiornithidae. Femoral shaft relatively shorter, no dorsal curvature, crista trochanteris relatively short (proximodistally) with little cranial elevation.

Ciconiidae, Phoenicopteridae, Accipitriformes, Cathartidae and Falconidae. Femora as for Theskiornithids, but with pneumatic foramina in cranial pretrochanteric area and linea intermuscularis cranialis extends mesad of crista trochanteris.

Charadriiformes. Shaft lacks dorsal curvature; fossa trochanteris present. In addition, in Haematopodidae, Recurvirostridae, Charadriidae, Laridae, and Glareolidae, linea intermuscularis cranialis extends mesad of and parallel to crista trochanteris.

Columbidae, Psittaciformes, Caprimulgiformes, Cuculidae, Strigiformes, Coraciiformes and Passeriformes. Crista trochanteris cranially low, often with craniocaudal depth subequal to caput depth. Columbidae further differ with a fossa trochanteris and Caprimulgiformes and Strigiformes have crista trochanteris proximodistally shorter, and passed medially by well-marked crista intermuscularis cranialis.

Appendix 2

Measurements (mm) of quadrates of *Apteryx* species. TH is total height. Catalogue numbers starting with OR, DM, and S are all prefixed by NMNZ.

Catalogue number	Taxon	TH (capitulum squamosum – base of cond. medialis)	TH above cotyla quadratojugalis	% TH above cotyla quadratojugalis
DM.492-S	*australis*	11.1	5.6	50.5
OR.4738	*australis*	11.0	4.5	40.9
OR.21035	*australis*	10.5	5.3	50.5
OR.22114	*australis*	11.6	5.5	47.4
OR.22115	*australis*	11.9	5.5	46.2
OR.27965	*australis*	12.0	6.1	50.8
CM Av 39065	*australis*	11.5	5.0	43.2
OR.21415	*haastii*	11.3	5.1	45.1
OR.23045	*haastii*	11.4	5.6	49.1
OR.27983	*haastii*	12.3	5.7	46.3
MV B40905	*haastii*	12.1	5.3	43.8
CM Av31538	*haastii*	12.4	5.3	42.5
OR.21832	*lawryi*	12.1	5.3	43.8
CM Av 14447	*lawryi*	11.7	4.9	41.7
CM Av 32404	*lawryi*	13.5	6.7	49.4
CM Av 36637	*lawryi*	13.0	5.7	43.6
CM Av 36638	*lawryi*	12.0	5.6	46.4
DM.909-S	*mantelli*	11.1	5.9	53.2
OR.23048	*mantelli*	11.1	5.4	48.6
OR.24640	*mantelli*	10.1	5.4	53.5
OR.24984	*mantelli*	11.3	5.8	51.3
OR.27604	*mantelli*	11.3	5.2	46.0
OR.28614	*mantelli*	11.3	5.1	45.1
OR.28615	*mantelli*	11.7	5.2	44.4
OR.28616	*mantelli*	10.8	5.5	50.9
OR.29374	*mantelli*	11.3	5.1	45.1
CM Av 5492	*mantelli*	10.8	5.2	48.1
OR.20990	*owenii*	9.6	4.6	47.9
OR.22369	*owenii*	9.3	4.8	51.6
OR.23214	*owenii*	9.3	5.1	54.8
OR.24414	*owenii*	8.4	4.0	47.6
OR.24415	*owenii*	8.9	4.4	49.4
OR.24416	*owenii*	9.0	4.3	47.8
OR.25100	*owenii*	10.0	4.8	48.0
OR.25794	*owenii*	9.4	4.0	42.6
MV B56009	*owenii*	10.1	4.7	46.2
SAM B5051	*owenii*	9.3	4.3	46.5
CM Av 16691	*rowi*	12.2	5.3	43.6
CM Av 16717	*rowi*	11.0	5.2	47.5
CM Av 16718	*rowi*	12.3	5.7	46.2
USNM 290601	*Lithornis celetius*	10.8	7.6	70.7
S.53209	*Proapteryx*	9.2	4.9	53.3

Appendix 3

Relationship of Tinamidae estimated femoral circumference (using the formula circumference = PI* SQRT(2*((POWER((1/2*SD),2))+(POWER((1/2*SW),2))))) to average weight. SW is width at mid shaft, SD is shaft depth at mid shaft, C is circumference, measurements in mm. Weights were taken from Davies (2002) except for SMF 2147, which was from Queiroz & Cooper (2011).

Reg. No.	Taxa	SW	SD	C	Weight	log C	log mass
SAM B.31339	*Tinamus major robusta*	5.6	5.8	17.9	1140	1.253092	3.056905
NMNZ OR.1433	*Tinamus major major*	4.7	5.5	16.1	1028.5	1.206052	3.012204
NMNZ OR.22983	*Nothoprocta perdicaria*	3.9	4.5	13.2	458	1.121504	2.660865
NMW 4.559	*Tinamus major*	6.1	6.2	19.3	1140	1.286039	3.056905
NMW 1061	*Nothura maculosa*	4.2	4.0	12.9	300	1.110063	2.477121
NMW 3.071	*Eudromia elegans*	5.5	5.0	16.5	703.5	1.217801	2.847264
NMW 160	*Rhynchotus fasciatus = rufescens*	5.6	5.7	17.8	770	1.249215	2.886491
NMW 161	*Rhynchotus fasciatus = rufescens*	6.1	5.9	18.9	770	1.275361	2.886491
NMW 4.068	*Nothoprocta perdicaria*	4.6	4.1	13.7	458	1.136355	2.660865
NMB 5537	*Rhynchotus rufescens*	5.8	5.3	17.3	770	1.238748	2.886491
NMB C.2004	*Tinamus* (*Trachypilmus* Cab.) *robustus*	5.9	5.8	18.4	1140	1.26507	3.056905
SMF 2148	*Crypturellus obsoletus*	4.1	3.7	12.3	480	1.089952	2.681241
SMF 11394	*Crypturellus noctivagus noctivagus*	4.2	4.2	13.2	800	1.119375	2.90309
SMF 11392	*Crypturellus tataupa*	3.4	3.8	11.3	202	1.053995	2.305351
SMF 2164	*Crypturellus parvirostris*	3.0	2.8	9.0	180	0.955935	2.255273
SMF 8184	*Crypturellus parvirostris*	3.5	3.1	10.4	220	1.015069	2.342423
SMF 9357	*Crypturellus parvirostris*	3.4	3.1	10.2	220	1.0081	2.342423
SMF 2537	*Crypturellus cinnamomeus*	3.9	4.0	12.4	419	1.092696	2.622214
SMF 2149	*Crypturellus undulatus vermiculatus*	4.4	4.6	14.2	540	1.151456	2.732394
SMF 2146	*Tinamus solitarius*	5.7	5.9	18.2	1200	1.260642	3.079181
SMF 2150	*Tinamus solitarius*	6.5	6.9	21.1	1500	1.324752	3.176091
SMF 5415	*Eudromia elegans*	5.5	4.9	16.5	703.5	1.216318	2.847264
SMF 6111	*Eudromia elegans*	5.8	5.1	17.1	703.5	1.233381	2.847264
SMF 6416	*Eudromia elegans*	5.6	5.0	16.7	703.5	1.222983	2.847264
SMF 9260	*Eudromia elegans*	5.6	5.1	16.8	703.5	1.225977	2.847264
SMF 9306	*Eudromia elegans*	5.0	4.5	14.9	703.5	1.172044	2.847264
SMF 6298	*Eudromia elegans*	5.4	5.4	16.9	703.5	1.227935	2.847264
SMF 2147	*Rhynchotus rufescens*	5.2	5.2	16.3	747	1.213153	2.873321

Appendix 4

The range in mass values (grams) by sex for *Apteryx* species from Marchant & Higgins (1990) and for *A. rowi* from Tennyson *et al.* (2003).

Species	Males	Females
Apteryx owenii	880–1356	1000–1400
Apteryx mantelli	1820–2590	2090–3270
Apteryx rowi	1575–2250	1950–3570
Apteryx australis lawryi	2300–3060	2700–3600
Apteryx haastii	1215–2320	1530–2718

Appendix 5

Relationship of *Apteryx* femoral circumference to weight of individual recorded at death. (SW is width at mid shaft, SD is shaft depth at mid shaft, circumference is estimated using the formulae PI*SQRT (2*((POWER((1/2*SD),2))+(POWER((1/2*SW),2))))). All specimens are from the Museum of New Zealand Te Papa Tongarewa.

Taxon	Reg no.	SD	SW	Circumference	weight (g)
A. mantelli	DM.909-S	9.6	8.5	25.1607	785
A. mantelli	OR.13588	11	11	29.6656	2428
A. mantelli	OR.14964	10	9	27.0852	1988
A. mantelli	OR.17206	10	9.6	27.0332	1366
A. mantelli	OR.17207	11	10	28.4908	2563
A. mantelli	OR.17208	9.8	9.2	26.13	1729
A. mantelli	OR.17209	11	10	28.1212	2336
A. mantelli	OR.17210	12	11	30.7656	2919
A. mantelli	OR.17211	12	12	32.0138	2495
A. mantelli	OR.17212	11	11	29.9376	2526
A. mantelli	OR.17213	10	8.9	26.4356	930
A. mantelli	OR.24640	9.1	8.6	24.3134	815
A. mantelli	OR.24984	9	9.5	24.948	1055
A. a. australis	OR.22089a	14	12	36.9381	2488
A. a. australis	OR.27761a	13	12	33.6873	3400
A. a. australis	OR.27965	11	10	28.842	2200
A. a. lawryi	OR.23591	11	11	28.8394	2800
A. a. lawryi	OR.23756	12	11	31.1584	4335
A. owenii	OR.22815a	8.4	8	22.497	910
A. owenii	OR.23044	7.8	7.4	20.865	885
A. owenii	OR.23717a	7.7	7.4	20.6809	1285
A. owenii	OR.24415	6.8	6.9	18.5919	670
A. owenii	OR.24416	7.8	7.8	21.2215	875
A. haastii	OR.19773a	9.6	8.5	25.1607	1215
A. haastii	OR.23022a	12	12	32.6507	2232
A. haastii	OR.23038	9.5	9.5	25.8466	1890
A. haastii	OR.23045	12	10	29.9895	2435
A. haastii	OR.23648a	11	11	29.8414	2015
A. haastii	OR.27983	9.6	9.2	25.7611	2550
A. haastii	OR.28010a	12	11	31.3853	2843