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A new fossil species of kiwi (Aves: Apterygidae) from the mid-Pleistocene of New Zealand

Alan James Drummond Tennyson^{1*}, Barbara Mizumo Tomotani^{1,2}

¹Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington 6140, New Zealand.

²Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, The Netherlands.

*Corresponding author: AlanT@tepapa.govt.nz

<https://orcid.org/0000-0001-6374-6924>

<https://orcid.org/0000-0002-8855-4803>

Abstract

We describe *Apteryx littoralis* sp. nov., a new species of kiwi based on a 1-million-year-old tarsometatarsus from shallow marine sediment in the North Island of New Zealand. The fossil is very similar to the tarsometatarsi of living kiwi species, most closely resembling *Apteryx rowi* and *A. mantelli* in size and shape, but differs in being stouter, with proportionally narrower proximal and distal ends. The new fossil is the second oldest known record of kiwi. It demonstrates a relatively conservative kiwi morphology since the mid-Pleistocene.

<http://zoobank.org/References/cefc907d-0c1d-44dc-83c5-5799f5d6d3d2>

Keywords: *Apteryx littoralis* sp. nov.; *Apteryx rowi*; *Apteryx mantelli*; tarsometatarsus

Introduction

Kiwi are an enigmatic and threatened bird group, unique to New Zealand, with six living taxa recognised (Tennyson et al. 2003). Very little is known about the origin and evolution of kiwi (note that ‘kiwi’ can refer to single or multiple birds because ‘s’ is not used to denote plural nouns in the Māori language). The ratite group of birds, which includes kiwi and moa, were long regarded as ancient lineages whose flightless ancestors were isolated by the break-up of Gondwana (Cracraft 1974). Under that scenario, these birds had about 80 million years to evolve in isolation on Zealandia but since the 1990s genetic research has increasingly indicated that the ancestors of kiwi and moa arrived more recently by flying (Sibley and Ahlquist 1991; Cooper et al. 1992; Haddrath and Baker 2001; Phillips et al. 2010). The closest relatives of kiwi are Madagascar’s extinct elephant birds (Phillips et al. 2010; Mitchell et al. 2014), with the split between their ancestors thought to be about 50 million years ago, which supports the suggestion that the ancestors of kiwi flew to Zealandia and subsequently evolved flightlessness. Further evidence of ancestral kiwi flying to Zealandia was provided by kiwi fossils from the Early Miocene (16–19 million years ago) of New Zealand, which represent much smaller and possibly volant birds (Worthy et al. 2013). Subsequent studies have supported the sister relationship between kiwi and elephant birds but have suggested that the split between these taxa occurred about 54 or 62 million years ago (Grealy et al. 2017; Yonezawa et al. 2017), again raising the possibility that ancestral kiwi did not need to reach Zealandia by flight (Tennyson 2010).

Overall, while modern kiwi taxa are well represented in the late Pleistocene/Holocene (Worthy 1997b), the fossil record of kiwi remains extremely poor. The only other possible ancient ‘kiwi’ records (Worthy and Holdaway 2002) are ‘footprints’ from the uppermost Miocene (Hutton 1899 plate XLV;

Fleming 1979, GNS Science CD49) but these are probably not footprints, despite their superficial appearances (AJDT pers. obs.). Until 1998 the oldest known kiwi fossils were only c.50,000 years old (from Tuarangi Cave, South Canterbury) and were all similar to modern kiwi taxa (Worthy 1997b). Thus, the transition between the Miocene proto-kiwi and recent species remains unknown. When the kiwi crown group emerged continues to be debated with recent genetic studies concluding that it was either within the last 3.85 million years (Weir et al. 2016) or within the last 12–14 million years (Grealy et al. 2017; Yonezawa et al. 2017).

Here we describe the first kiwi fossil to bridge the gap between the Miocene fossil record and the modern fauna: a new species of kiwi from the mid-Pleistocene.

Material and methods

The fossil tarsometatarsus of an unidentified kiwi species was collected in 1998 at a site near Marton in the North Island of New Zealand. Previously this site had produced a small but significant fossil bird fauna, including a large rail (*Pleistorallus flemingi* Worthy 1997a), as well as unidentified remains of moa and another smaller rail taxon (Worthy 1997a).

We took the following measurements of the new tarsometatarsus: total length, distal width, proximal width and mid-shaft width, using digital callipers (0.01 mm precision, rounded to the nearest 0.1 mm). While the fossil was largely complete, it had a small amount of damage on its extremities. This damage did not affect measurements of the shaft width but the total length, proximal width and distal width could not be measured with complete accuracy. To estimate the amount of missing bone, we compared these areas of the fossil with bones from living taxa under a microscope. We concluded that very little bone was missing: using callipers, a maximum of 0.5–2 mm for any measurement. Our data analyses are thus based on the minimum size (for all measurements) and the maximum estimated size for total length, proximal width and distal width.

To compare the fossil with other currently known kiwi taxa, we also measured the tarsometatarsus of 161 kiwi specimens, recent and fossil, deposited in the collections of the Museum of New Zealand Te Papa Tongarewa (NMNZ), as well as the Auckland (AIM) and Canterbury Museums (CMC). We measured 6 specimens of *A. a. australis*, 12 *A. haastii*, 8 *A. a. lawryi*, 56 *A. mantelli*, 59 *A. owenii* and 20 *A. rowi* (see Appendix 1).

Osteological nomenclature follows Baumel and Witmer (1993) and Livezey and Zusi (2007). Taxonomic nomenclature for extant kiwi follows Tennyson et al. (2003).

Due to the degree of overlap in measurements of the tarsometatarsus of kiwi taxa, we performed a statistical comparison of the taxa consisting of three steps: (1) firstly, we used a Principal Component Analysis (PCA) including all measurements to detect whether the different kiwi taxa would cluster based on their tarsometatarsus measurement and which taxon would be more similar to the fossil. (2) Secondly, we used a Linear Discriminant Analysis on the Principal Components 1 and 2 to test whether the Marton fossil would be classified within the cluster of one of the existing taxa and whether some of the other taxa would be classified within the Marton fossil category. For this analysis we only included the taxa with the most similar measurements to the fossil based on the PCA: *A. mantelli*, *A. rowi* and *A. owenii*. We divided our dataset into a training and a test dataset (one and two thirds of the data, respectively) and ran one test including the Marton fossil and a second one without the fossil to assess the accuracy of the model classification. 3) Finally, we compared the distance of each measured specimen to the centre of the cluster of each taxon to assess the similarity of the Marton fossil with the different taxa.

Systematic Palaeontology

Class **Aves** Linnaeus, 1758

Order **Apterygiformes** Haeckel, 1866

Family **Apterygidae** Gray, 1840

Genus ***Apteryx*** Shaw, 1813

Apteryx littoralis sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:>

Holotype. NMNZ S.36731.

Etymology. The fossil was found on an ancient marine shore (= littoral); additionally, the species was probably restricted to a coastal region due to volcanic activity in the central North Island.

Description. A largely complete left tarsometatarsus with a small amount of damage on the extremities, particularly to the hypotarsus (see Figure 1). Mineralisation has turned the bone light brown, as are previous bones recovered at this locality (Worthy 1997a). It partly broke when found in the field so required minor reconstruction and hardening with polyvinyl butyral. Measurements: see Table 1 and Appendix 1.

Differential Diagnosis. The fossil is a typical *Apteryx* tarsometatarsus, differing from the tarsometatarsus of other kiwi species by being stouter, with proportionally narrower proximal and distal ends. The relatively narrow width across the trochleas suggests that the toes were less splayed than those of modern kiwi taxa. In modern kiwi the narrowest distal tarsometatarsus width is found in *A. owenii* (see Table 1). Apart from these broad differences in shape, the bone also shows a larger, deeper *sulcus extensorius* (Figure 1) in comparison to all other taxa. *A. owenii* have the deepest *sulcus extensorius* of extant taxa.

A. littoralis sp. nov. was probably about the size of *A. mantelli* and *A. rowi* because its tarsometatarsus was similar in length to the tarsometatarsi of these taxa (see Table 1). The fossil was shorter than the tarsometatarsi of *A. haastii*, *A. a. australis* and *A. a. lawryi* and longer than that of *A. owenii*.

Classification. Given its size and shape, the new fossil could only belong to the Order Apterygiformes (kiwi). Comparison with the extensive NMNZ collections ruled out all other bird orders. This included an especially detailed comparison with the tarsometatarsi of Gruiformes (rails, cranes and allies) (see Appendix 2 for list of specimens compared) because of the superficial similarity of their tarsometatarsi to that of kiwi, and because two taxa of rail, but no kiwi, had been identified from the Marton fossil site previously (Worthy 1997a). Within the Gruiformes only the tarsometatarsi of rails might be confused with those of kiwi. The tarsometatarsi of kiwi have an anterior proximal medial ridge slightly higher than the lateral ridge, whereas in rails the lateral ridge is clearly higher than the medial ridge. Unlike in kiwi, the lateral ridge continues to be prominent distally in rails. In rails, the medial *foramen vasculare proximale* is always proximal to its lateral counterpart, whereas these are more evenly positioned in kiwi. Also, kiwi have a relatively longer *trochlea metatarsi* II than rails. In kiwi, the distal end of this trochlea extends beyond the proximal end of the *incisura intertrochlearis lateralis*, whereas in rails, the distal end of the *trochlea metatarsi* II does not extend beyond the proximal end of this *incisura intertrochlearis* (except in rare examples, e.g. *Porphyrio*). This character makes the *incisura intertrochlearis medialis* relatively larger in kiwi than in rails. In rails, the *cotyla medialis* is clearly proximal to the *cotyla lateralis*, whereas in kiwi these cotyles are more evenly positioned. Rails usually have a very prominent *fossa metatarsi* I, but like most kiwi, the Marton fossil has a relatively indistinct fossa. In combination, these features make the tarsometatarsus of a kiwi much more symmetrical.

The bones of the large rail *Pleistorallus flemingi* (femur NMNZ S.34497 and tibiotarsus S.34498) from the same Marton fossil site were re-examined to confirm that these did not belong to a kiwi because they are from a bird about the same size as the new tarsometatarsus and Worthy (1997a) did not compare them with kiwi bones. The femur has the relatively shallow *fossa poplitea* of rails, while this fossa is much deeper in the femora of kiwi. The tibiotarsus shows a high, thin *crista cnemialis* typical of rails, but unlike that found in kiwi. Anteriorly, the distal *condylus lateralis* is wider than the *condylus*

medialis, which is typical of rails, whereas they are of similar width in kiwi. There is a *pons supratendineus*, found in all rails, but not in kiwi. Thus, we confirm that those bones belong to a rail rather than a kiwi.

Comparative analysis. The tarsometatarsus of *Apteryx littoralis* sp. nov. has a unique morphology. It differs in size and shape in comparison to all other known kiwi taxa (Figures 1, 2 a–d, Table 1).

When all taxa were compared, the first two principal components explained 98% of the variance. The only modern kiwi taxon that can be reliably identified from the tarsometatarsus, not clustering with the others, is *A. owenii*; bones of other modern *Apteryx* cannot be reliably separated using shape or size characters (Worthy 1997b; see Figure 2f). While the other kiwi taxa overlap considerably in their measurements, *A. littoralis* sp. nov. was distinct from all taxa, not clustering with any of them (Figure 2 e, f).

The linear discriminant analysis had an overall misclassification rate of 20.46%, when comparing *A. littoralis* sp. nov. with *A. rowi*, *A. mantelli* and *A. owenii* and about 18.60% when the fossil was not included. The model containing all kiwi correctly assigned *A. littoralis* sp. nov. to its own taxon and only classified a single specimen of *A. owenii* as *A. littoralis* sp. nov. (1% error), while, in comparison 8% of the specimens were incorrectly classified as *A. mantelli* and *A. rowi* was incorrectly classified as a different taxon 73% of the time. Thus, the model did not classify the *A. littoralis* sp. nov. fossil within one of the existing clusters, supporting the conclusion that the specimen has unique morphology (Figure 3) and represents a distinct species.

Finally, the difference between *A. littoralis* sp. nov. and the three morphologically closest taxa was also evident when we calculated the distance of the points to the centre of the 95% confidence ellipse of each species. Although this method has to rely on using the single fossil value (thus, with an unknown sample distribution), the minimum distance between *A. littoralis* sp. nov. and the centre of the ellipse was always larger than the maximum distance of a bird classified as belonging to each of those three species and the centre of their respective ellipse (Figure 3, Table 2).

Type locality. ‘Morrison’s Farm Gully’, north of Marton, North Island, New Zealand, (40°0’16.8’’S 175°21’54.2’’E).

Geological context, stratum and age. The fossil was found in a c.1 m deep coarse sand layer, within a series of unconsolidated cobble, sandstone and mudstone layers, many with abundant intertidal and subtidal marine molluscs and pumice pebbles. The fossil was found c. 15 m above the present-day stream, c.5 m above the farm road and 20 cm above the base of the 1 m deep fossiliferous layer. It was in the Kaimatira Pumice Sand (part of the Potaka tephra) of the Kai-Iwi Group, Lower Castlecliffian, mid-Pleistocene (about 1 million years old) (see New Zealand Fossil Record Number S22/f162; (Worthy

1997a). At the time of deposition of the kiwi bone, the site was coastal shoreline, being either an exposed beach or a more sheltered environment (Worthy 1997a). The fact that the bones at this site have been found as isolated elements with their extremities worn (Worthy 1997a), indicates that they were washed around in water before final deposition.

Discussion

This first record of a mid-Pleistocene kiwi closes the extensive temporal gap between flightless modern and ancestral flighted kiwi species. The overall similarity of the bone of the new fossil species to that of modern taxa suggests that the fossil taxon had a similar ecology to its modern relatives and that it was certainly flightless. Worthy (1997a) speculated that the contemporary terrestrial environment of the area where the fossil was deposited may have included tall, wet, closed canopy forests – a habitat that modern kiwi commonly inhabit (Marchant and Higgins 1990). Thus, we can speculate that mid-Pleistocene kiwi were not only similar in size and appearance to modern kiwi but also lived in similar environments.

Most genetic and phylogenetic studies indicate that crown kiwi taxa evolved within the last 3.85 million years, with splits between *A. australis* and *A. rowi/A. mantelli*, *A. rowi* and *A. mantelli*, and *A. haastii* and *A. owenii* all occurring in the Pleistocene (Weir et al. 2016). If this was the case then *A. littoralis* sp. nov. lived during a period of high kiwi speciation. In contrast, Yonezawa et al. (2017) concluded that all species level splits in modern kiwi occurred at least 3.55 million years ago, which was backed up by Grealy et al. (2017) who concluded that the split between sister taxa *A. haastii* and *A. owenii* occurred 4.15 million years ago. This could indicate that the ancestors of *A. littoralis* sp. nov. diverged from their nearest relatives several million years ago.

Although superficially the fossil is most similar morphologically to *A. rowi* and *A. mantelli*, the similarity and amount of overlap between the skeletal morphology of modern kiwi taxa makes it very difficult to infer phylogenetic relationships between the different taxa, even among modern birds. Therefore, morphology alone does not allow us to infer the fossil taxon's systematic position or whether or not it supports the various molecular clock estimates for kiwi divergence times (Sibley and Ahlquist 1991; Baker et al. 1995; Burbidge et al. 2003; Weir et al. 2016; Grealy et al. 2017; Yonezawa et al. 2017).

For flightless taxa-like kiwi, separation between the North and South Islands of New Zealand was/is a major barrier separating lineages. Weir et al. (2016) suggested that kiwi originated on the South Island with the oldest colonisation of the North Island at either 1.1 or 1.6 million years ago after the islands joined. A similar evolutionary history was suggested for moa (Bunce et al. 2009). Under this scenario, ancestors of *A. littoralis* sp. nov. could have arrived from the south a few 100,000 years earlier. The

two islands were connected for long periods after the time that *A. littoralis* sp. nov. was alive (Lewis et al. 1994; Worthy and Holdaway 2002). Thus, its descendants potentially could have walked between these landmasses before the current physical isolation between the islands occurred.

However, the last million years has been a tumultuous period in New Zealand's geological history, with extensive volcanism, tectonic uplift and several glacial cycles (Shane 1994; Weir et al. 2016). As kiwi are relatively poor dispersers and the country's geological history led to many allopatric kiwi lineages; these factors have made kiwi lineages vulnerable to extinction (Weir et al. 2016). The basin where the Marton fossil site occurs would have been particularly vulnerable to volcanic events, e.g. the one million year old Potaka tephra (in which the kiwi fossil was found) was an ignimbrite that originated from the central North Island and left widespread deposits in the region (Shane 1994). The eruption of the Taupo volcano 26,500 years ago covered much of the North Island in ash, with about 0.5 m falling in the Marton region (Wilson 2001). The habitat devastation that such events caused may have been enough to wipe out a local kiwi population and, if the taxon's range was already small, then it is plausible that this resulted in its complete extinction. This might explain why the unusual features of the *A. littoralis* sp. nov. tarsometatarsus are not found in modern taxa.

The Marton fossil provides evidence backing a dynamic recent evolutionary history for kiwi, as suggested by genetic studies (Weir et al. 2016). Similarly, the unique large rail also from the Marton fossil site indicates a dynamic history in the evolution of Gruiformes in New Zealand (Worthy 1997a).

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Figures

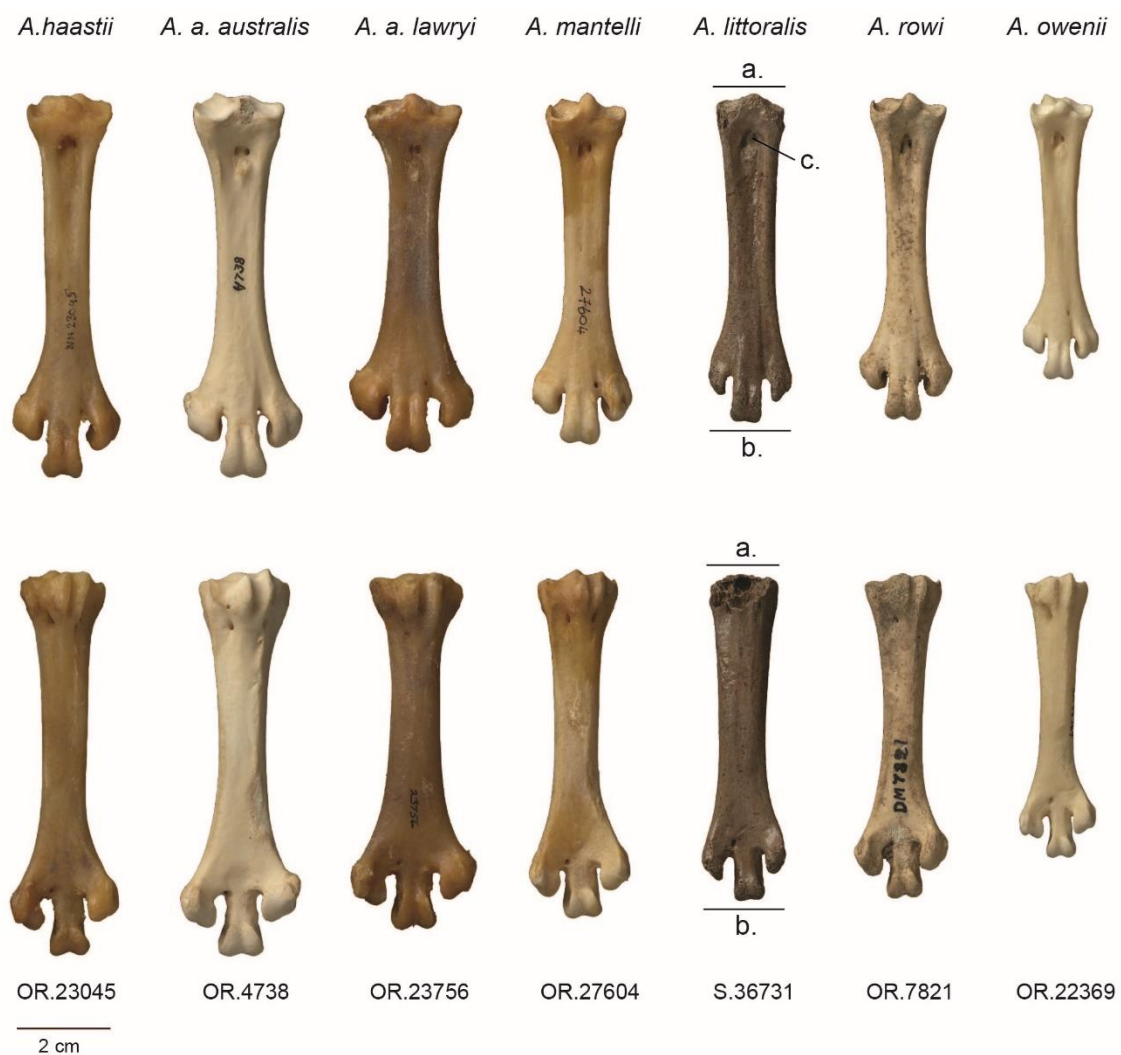


Figure 1: Dorsal view (above) and ventral view (below) of the tarsometatarsus of all kiwi taxa analysed in this study (all specimens in NMNZ). The differential diagnosis characters are marked on the figure: a) narrower proximal end, b) narrower distal end and narrow width across the trochlea, c) deeper sulcus extensorius.

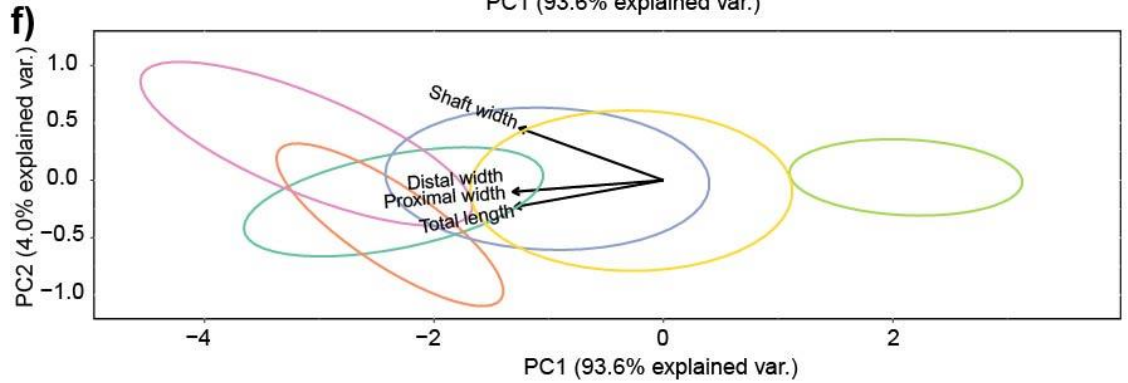
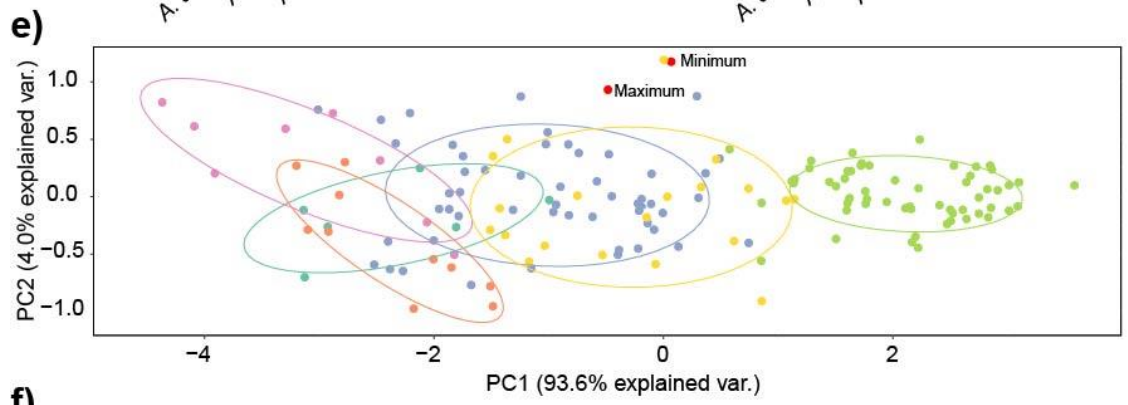
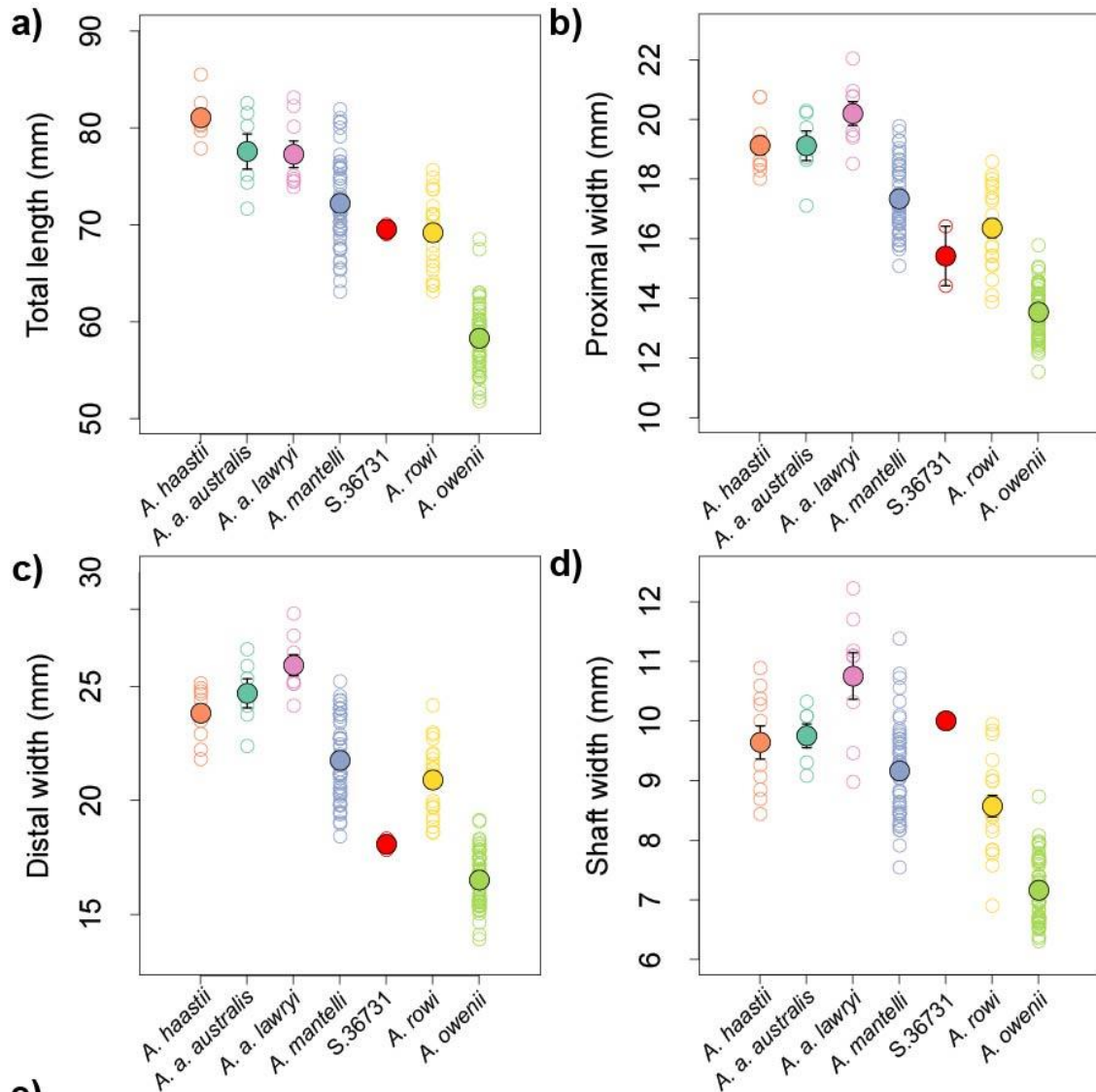


Figure 2: Plots showing the measurements of the kiwi taxa analysed. (a) tarsometatarsus length; (b) proximal width; (c) distal width; (d) shaft width; (e) biplot with scores of the principal components 1 and 2 showing the clustering of the different taxa relative to the Marton fossil (using either the minimum or maximum estimated values); (f) projection of the principal component vectors (loadings) onto the PC1-PC2 biplot showing the direction of the measurement vectors. Colours represent different taxa. Filled circles represent a mean (Figs a–d) or a single value (Fig. e), while open circles (Figs a–d) represent the individual measurements used to calculate the mean. For the Marton kiwi, the mean and individual points are based on the minimum and maximum possible value for each measurement. Error bars (Figs a–d) indicate standard errors. Ellipses (Figs e and f) are normal data ellipses (68% probability for each group).

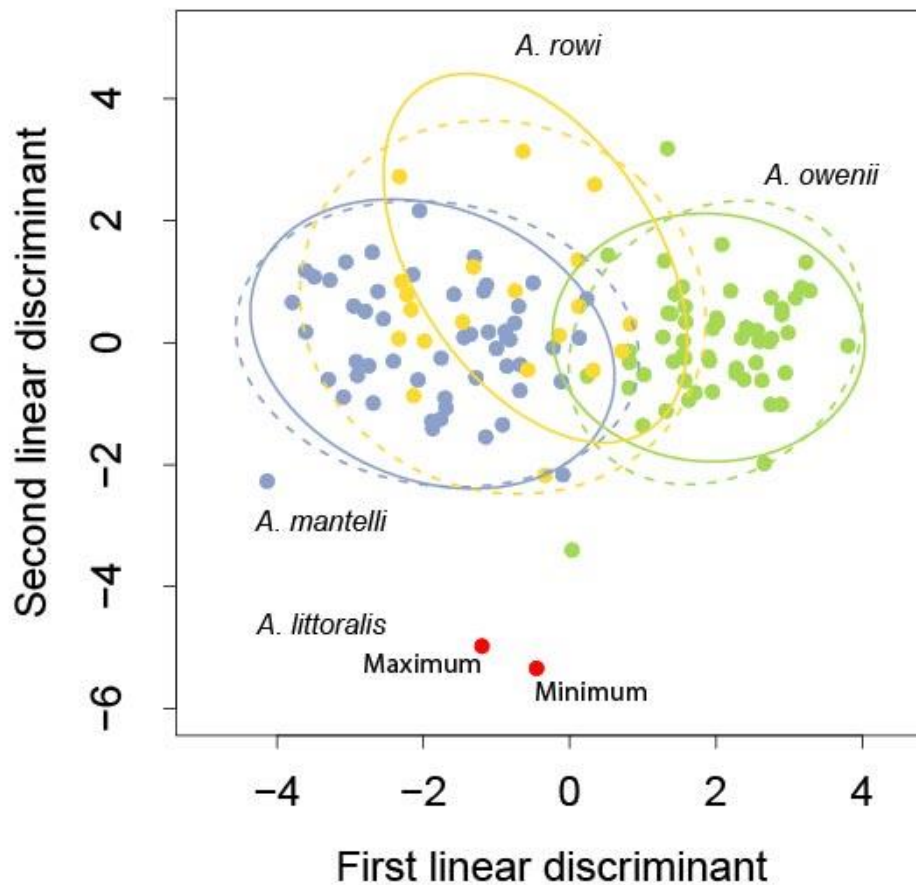


Figure 3: Biplot showing the results of the linear discriminant analysis for *A. mantelli* (blue), *A. rowi* (yellow), *A. owenii* (green) and the Marton fossil (red) and the distance of the Marton fossil to the centre of the ellipses as described in Table 2. With the exception of the Marton fossil, each point represents a single specimen and ellipses are 95% confidence ellipses for each group. Dashed ellipses represent our original classification while solid line ellipses represent the model classification.

Tables

Table 1: Measurements (in mm) of skeletal elements of the holotype of *Apteryx littoralis* sp. nov., compared with measurements of other *Apteryx* taxa. The table contains the means \pm standard error (sample size) [range] of each kiwi taxon analysed and the minimum and, where appropriate, possible maximum dimensions for the Marton fossil.

	S.36731	<i>A. a. australis</i>	<i>A. haastii</i>	<i>A. a. lawryi</i>	<i>A. mantelli</i>	<i>A. owenii</i>	<i>A. rowi</i>
Total length	Min: 69.0 Max: 70.0	77.5 ± 1.81 (6) [71.6 - 82.5]	81.0 ± 0.63 (10) [77.9 - 85.5]	77.2 ± 1.38 (8) [73.9 - 83.1]	72.2 ± 0.62 (53) [63.1 - 81.9]	58.3 ± 0.44 (58) [51.8 - 68.5]	69.2 ± 0.92 (20) [63.1 - 75.6]
Distal width	Min: 17.8 Max: 18.3	24.6 ± 0.64 (6) [22.4 - 26.6]	23.8 ± 0.37 (10) [21.8 - 25.1]	25.9 ± 0.46 (8) [24.1 - 28.2]	21.7 ± 0.24 (53) [18.4 - 25.2]	16.5 ± 0.37 (58) [13.9 - 19.1]	20.9 ± 0.37 (20) [18.6 - 24.1]
Proximal width	Min: 14.4 Max: 16.4	19.1 ± 0.50 (6) [17.1 - 20.3]	19.1 ± 0.31 (10) [18 - 20.7]	20.2 ± 0.40 (8) [18.5 - 22.0]	17.3 ± 0.16 (53) [15.1 - 19.8]	13.5 ± 0.11 (58) [11.5 - 15.8]	16.3 ± 0.32 (20) [13.9 - 18.6]
Shaft width	Min: 10.0	9.8 ± 0.20 (6) [9.1 - 10.3]	9.6 ± 0.28 (10) [8.4 - 10.9]	10.8 ± 0.39 (8) [9.0 - 12.2]	9.2 ± 0.11 (53) [7.5 - 11.4]	7.2 ± 0.07 (58) [6.3 - 8.7]	8.6 ± 0.18 (20) [6.9 - 9.9]

Table 2: Distance between the centre of the 95% confidence ellipses of *A. mantelli*, *A. owenii* and *A. rowi* and a) the Marton fossil and b) the individual specimen of *A. mantelli*, *A. owenii* or *A. rowi* furthest from the ellipse centre of its species.

Species	<i>A. mantelli</i>	<i>A. owenii</i>	<i>A. rowi</i>
Distance to the centre of the ellipse			
a) Minimum distance of Marton fossil to each ellipse centre	5.01	6.42	5.95
b) Individual specimen furthest from their respective ellipse centre	3.21	2.29	3.14

Appendix 1

List of kiwi tarsometatarsi measured for this study.

Museum	Registration	Classification	TotLength	ProxWidth	DistWidth	ShaftWidth
NMNZ	OR.4738	<i>A. a. australis</i>	81.5	19.7	25.3	10.1
NMNZ	OR.20995b	<i>A. a. australis</i>	80.2	20.3	25.9	10.3
NMNZ	OR.21035	<i>A. a. australis</i>	71.6	17.1	22.4	9.1
NMNZ	OR.22115	<i>A. a. australis</i>	74.3	18.7	24.1	10.1
NMNZ	OR.27238a	<i>A. a. australis</i>	82.5	20.2	26.6	9.7
NMNZ	OR.27965	<i>A. a. australis</i>	75.1	18.6	23.7	9.3
CMC	AV.5341	<i>A. haastii</i>	80.3	18.0	23.5	9.1
CMC	AV.14547	<i>A. haastii</i>	81.2	20.7	23.8	10.9
CMC	AV.16091	<i>A. haastii</i>	80.6	20.7	24.4	10.0
CMC	AV.31538	<i>A. haastii</i>	85.5	19.5	24.8	10.3
CMC	AV.31539	<i>A. haastii</i>	80.2	18.3	21.8	8.7
NMNZ	OR.955	<i>A. haastii</i>	77.9	19.3	25.1	10.6
NMNZ	OR.23038	<i>A. haastii</i>	79.7	18.5	22.2	8.4
NMNZ	OR.23045	<i>A. haastii</i>	81.0	18.6	22.9	9.3
NMNZ	OR.27156	<i>A. haastii</i>	81.3	19.1	24.9	10.4
NMNZ	OR.27983	<i>A. haastii</i>	82.5	18.5	24.6	8.9
CMC	AV.3317	<i>A. a. lawryi</i>	74.4	18.5	25.1	9.0
CMC	AV.14447	<i>A. a. lawryi</i>	75.0	19.6	25.2	11.1
CMC	AV.32404	<i>A. a. lawryi</i>	80.1	20.8	28.2	11.7
CMC	AV.32617	<i>A. a. lawryi</i>	82.2	20.9	27.2	11.2
CMC	AV.36638	<i>A. a. lawryi</i>	73.9	19.4	25.1	10.3
NMNZ	OR.23591	<i>A. a. lawryi</i>	74.5	19.5	24.1	9.5
NMNZ	OR.23756	<i>A. a. lawryi</i>	74.7	20.7	26.5	11.1
NMNZ	OR.26398	<i>A. a. lawryi</i>	83.1	22.0	25.8	12.2
NMNZ	S.36731 Max	<i>A. littoralis</i> sp. nov.	70.0	16.4	18.3	10.0
NMNZ	S.36731 Min	<i>A. littoralis</i> sp. nov.	69.0	14.4	17.8	10.0
AIM	LB.202	<i>A. mantelli</i>	74.4	17.5	22.7	9.8
AIM	LB.550	<i>A. mantelli</i>	76.4	18.5	23.7	9.6
AIM	LB.610	<i>A. mantelli</i>	67.4	17.5	21.2	9.3
AIM	LB.610	<i>A. mantelli</i>	67.5	17.5	21.3	9.5
AIM	LB.1202	<i>A. mantelli</i>	81.0	18.9	24.2	9.6
AIM	LB.1570	<i>A. mantelli</i>	74.8	18.2	25.2	10.8
AIM	LB.2182	<i>A. mantelli</i>	77.2	18.2	24.0	10.6
AIM	LB.7289	<i>A. mantelli</i>	75.8	17.9	24.0	9.4
AIM	LB.8395	<i>A. mantelli</i>	65.5	15.6	19.0	7.5
AIM	LB.10445	<i>A. mantelli</i>	73.1	17.4	21.9	9.5
AIM	LB.10514	<i>A. mantelli</i>	74.7	18.4	22.3	9.9
AIM	LB.11268	<i>A. mantelli</i>	72.8	17.2	21.5	9.1
AIM	LB.11519	<i>A. mantelli</i>	69.5	16.7	19.4	8.6
AIM	LB.11734	<i>A. mantelli</i>	69.3	16.8	19.8	8.3

AIM	LB.14035	<i>A. mantelli</i>	76.5	17.7	23.8	9.8
AIM	LB.14145	<i>A. mantelli</i>	66.1	16.0	19.4	8.3
AIM	LB.14280	<i>A. mantelli</i>	71.2	16.5	22.0	10.3
AIM	LB.14507	<i>A. mantelli</i>	75.0	17.0	23.8	10.1
AIM	LB.14630	<i>A. mantelli</i>	71.3	16.6	21.5	9.8
NMNZ	OR.11243	<i>A. mantelli</i>	70.3	16.3	21.1	8.8
NMNZ	OR.13588	<i>A. mantelli</i>	79.1	19.8	24.0	9.2
NMNZ	OR.13590	<i>A. mantelli</i>	76.1	19.3	23.8	9.3
NMNZ	OR.13591	<i>A. mantelli</i>	75.8	19.0	22.7	9.6
NMNZ	OR.14964	<i>A. mantelli</i>	70.9	17.2	21.2	9.7
NMNZ	OR.15277	<i>A. mantelli</i>	71.1	17.0	21.0	8.2
NMNZ	OR.16198	<i>A. mantelli</i>	69.5	16.2	20.6	8.6
NMNZ	OR.17204	<i>A. mantelli</i>	72.3	18.1	22.7	9.2
NMNZ	OR.17205	<i>A. mantelli</i>	74.0	18.6	23.4	10.7
NMNZ	OR.17206	<i>A. mantelli</i>	67.8	17.1	20.1	8.5
NMNZ	OR.17207	<i>A. mantelli</i>	81.9	19.3	24.6	9.5
NMNZ	OR.17208	<i>A. mantelli</i>	66.3	16.7	19.8	8.8
NMNZ	OR.17209	<i>A. mantelli</i>	71.6	17.1	21.9	8.8
NMNZ	OR.17210	<i>A. mantelli</i>	71.3	18.6	23.5	10.1
NMNZ	OR.17212	<i>A. mantelli</i>	75.7	16.7	21.1	9.1
NMNZ	OR.17213	<i>A. mantelli</i>	70.3	16.7	20.8	9.0
NMNZ	OR.17342	<i>A. mantelli</i>	69.9	15.9	20.5	8.6
NMNZ	OR.17343	<i>A. mantelli</i>	65.3	15.8	19.0	8.5
NMNZ	OR.17344	<i>A. mantelli</i>	80.5	18.8	24.3	11.4
NMNZ	OR.23047	<i>A. mantelli</i>	80.6	18.3	22.4	8.8
NMNZ	OR.23048	<i>A. mantelli</i>	69.6	17.1	21.7	8.6
NMNZ	OR.24640	<i>A. mantelli</i>	68.6	16.2	20.2	7.9
NMNZ	OR.24984	<i>A. mantelli</i>	72.6	18.5	22.7	8.4
NMNZ	OR.27406	<i>A. mantelli</i>	63.1	15.8	18.4	9.3
NMNZ	OR.27604	<i>A. mantelli</i>	72.4	17.1	21.1	9.2
NMNZ	OR.28615	<i>A. mantelli</i>	80.0	19.6	24.4	9.3
NMNZ	OR.28616	<i>A. mantelli</i>	71.5	16.6	21.2	8.2
NMNZ	OR.29282	<i>A. mantelli</i>	68.9	16.8	19.9	9.2
NMNZ	OR.29374	<i>A. mantelli</i>	76.0	18.2	22.9	9.7
NMNZ	OR.29746	<i>A. mantelli</i>	70.3	15.8	19.8	8.4
NMNZ	S.909	<i>A. mantelli</i>	71.6	16.5	20.3	8.2
NMNZ	S.35720	<i>A. mantelli</i>	69.7	16.2	20.3	8.2
NMNZ	S.35720	<i>A. mantelli</i>	64.2	15.1	19.5	8.6
NMNZ	S.48340	<i>A. mantelli</i>	67.5	16.5	20.4	8.5
AIM	LB.687	<i>A. owenii</i>	57.7	13.1	15.9	6.7
AIM	LB.9427	<i>A. owenii</i>	55.6	12.6	15.0	7.1
AIM	LB.12246	<i>A. owenii</i>	67.4	14.9	17.5	8.7
NMNZ	OR.6306	<i>A. owenii</i>	57.7	14.1	16.3	7.0
NMNZ	OR.6307	<i>A. owenii</i>	56.3	13.5	16.7	7.1

NMNZ	OR.6312	<i>A. owenii</i>	52.7	12.1	15.4	6.6
NMNZ	OR.6315	<i>A. owenii</i>	53.0	12.4	15.5	6.4
NMNZ	OR.6316	<i>A. owenii</i>	54.2	12.6	15.2	6.7
NMNZ	OR.6320	<i>A. owenii</i>	56.6	13.0	15.7	6.7
NMNZ	OR.6321	<i>A. owenii</i>	57.6	13.9	16.4	7.3
NMNZ	OR.6322	<i>A. owenii</i>	59.6	14.1	17.2	7.7
NMNZ	OR.6323	<i>A. owenii</i>	56.3	12.7	15.3	7.0
NMNZ	OR.6324	<i>A. owenii</i>	55.0	12.7	15.6	7.0
NMNZ	OR.6325	<i>A. owenii</i>	54.4	12.7	15.6	6.7
NMNZ	OR.6326	<i>A. owenii</i>	51.8	11.5	14.1	6.3
NMNZ	OR.22369	<i>A. owenii</i>	60.2	13.3	16.1	7.1
NMNZ	OR.22404	<i>A. owenii</i>	62.9	14.5	17.8	8.0
NMNZ	OR.22535	<i>A. owenii</i>	61.9	14.2	17.8	8.0
NMNZ	OR.23036	<i>A. owenii</i>	68.5	15.0	18.3	7.4
NMNZ	OR.23044	<i>A. owenii</i>	56.7	12.6	16.4	7.6
NMNZ	OR.23214	<i>A. owenii</i>	61.4	14.0	16.9	7.7
NMNZ	OR.23719	<i>A. owenii</i>	58.4	13.0	15.5	6.8
NMNZ	OR.24414	<i>A. owenii</i>	55.9	12.4	16.1	7.2
NMNZ	OR.24415	<i>A. owenii</i>	54.9	12.2	15.1	6.9
NMNZ	OR.24416	<i>A. owenii</i>	59.7	13.6	16.7	7.7
NMNZ	OR.25100	<i>A. owenii</i>	61.0	13.9	17.7	7.4
NMNZ	OR.25794	<i>A. owenii</i>	58.9	13.6	17.5	7.9
NMNZ	OR.29420a	<i>A. owenii</i>	62.6	14.0	17.4	8.1
NMNZ	OR.30306	<i>A. owenii</i>	63.0	14.4	18.1	7.9
NMNZ	S.24478	<i>A. owenii</i>	59.4	14.5	19.1	7.0
NMNZ	S.24478	<i>A. owenii</i>	59.5	13.7	16.9	7.7
NMNZ	S.27784	<i>A. owenii</i>	55.7	12.3	15.7	6.6
NMNZ	S.27784	<i>A. owenii</i>	61.8	13.2	16.3	6.7
NMNZ	S.32705	<i>A. owenii</i>	62.7	14.4	18.2	7.9
NMNZ	S.32721	<i>A. owenii</i>	55.2	12.9	15.4	6.7
NMNZ	S.33365	<i>A. owenii</i>	60.7	13.6	16.4	7.2
NMNZ	S.33365	<i>A. owenii</i>	58.2	12.7	15.5	6.6
NMNZ	S.33756	<i>A. owenii</i>	58.5	13.8	17.9	7.7
NMNZ	S.33781	<i>A. owenii</i>	54.2	12.8	14.6	7.0
NMNZ	S.33781	<i>A. owenii</i>	57.5	13.3	13.9	6.5
NMNZ	S.34466	<i>A. owenii</i>	60.1	13.3	16.6	6.7
NMNZ	S.34527	<i>A. owenii</i>	52.1	12.8	15.3	6.6
NMNZ	S.34527	<i>A. owenii</i>	54.7	13.3	15.6	6.5
NMNZ	S.34527	<i>A. owenii</i>	59.8	14.6	17.4	7.6
NMNZ	S.34527	<i>A. owenii</i>	59.8	13.9	17.4	7.3
NMNZ	S.34527	<i>A. owenii</i>	57.5	14.0	16.3	6.9
NMNZ	S.34527	<i>A. owenii</i>	59.0	14.5	16.7	7.4
NMNZ	S.34527	<i>A. owenii</i>	58.0	13.3	15.8	6.6
NMNZ	S.34527	<i>A. owenii</i>	58.1	14.3	16.9	7.7

NMNZ	S.34527	<i>A. owenii</i>	59.3	14.1	17.2	7.3
NMNZ	S.34527	<i>A. owenii</i>	54.3	12.5	15.3	6.4
NMNZ	S.34527	<i>A. owenii</i>	58.9	13.5	17.1	6.5
NMNZ	S.34527	<i>A. owenii</i>	60.3	14.5	17.5	7.3
NMNZ	S.34527	<i>A. owenii</i>	57.0	13.2	15.8	6.7
NMNZ	S.36244	<i>A. owenii</i>	57.5	15.1	18.0	7.6
NMNZ	S.37291	<i>A. owenii</i>	56.6	14.0	15.4	6.8
NMNZ	S.40715	<i>A. owenii</i>	60.1	14.0	17.8	7.4
NMNZ	S.46008	<i>A. owenii</i>	61.3	15.8	19.1	7.8
NMNZ	OR.7817	<i>A. rowi</i>	75.6	17.4	22.7	9.3
NMNZ	OR.7819	<i>A. rowi</i>	71.9	17.5	22.0	9.9
NMNZ	OR.7821	<i>A. rowi</i>	67.8	16.2	19.7	8.5
NMNZ	OR.7824	<i>A. rowi</i>	69.2	15.8	22.0	7.8
NMNZ	OR.7825	<i>A. rowi</i>	65.7	14.6	18.8	8.2
NMNZ	OR.7831	<i>A. rowi</i>	67.0	15.1	20.0	6.9
NMNZ	OR.7834	<i>A. rowi</i>	71.1	16.8	21.6	9.0
NMNZ	OR.7835	<i>A. rowi</i>	63.1	15.7	19.1	9.8
NMNZ	OR.7840	<i>A. rowi</i>	65.3	13.9	18.6	7.8
NMNZ	OR.27241a	<i>A. rowi</i>	73.6	17.8	24.1	9.1
NMNZ	OR.27243a	<i>A. rowi</i>	73.7	18.1	21.4	8.7
NMNZ	S.18458	<i>A. rowi</i>	63.7	15.1	19.8	8.5
NMNZ	S.22136	<i>A. rowi</i>	64.1	16.3	19.3	7.6
NMNZ	S.23211	<i>A. rowi</i>	70.9	18.0	23.0	9.8
NMNZ	S.24476	<i>A. rowi</i>	71.1	17.3	21.3	8.2
NMNZ	S.24542	<i>A. rowi</i>	74.8	17.8	22.9	9.0
NMNZ	S.24588	<i>A. rowi</i>	63.8	14.1	18.6	7.8
NMNZ	S.24589	<i>A. rowi</i>	70.3	15.4	21.1	8.4
NMNZ	S.24738	<i>A. rowi</i>	66.2	15.4	19.7	8.4
NMNZ	S.46139	<i>A. rowi</i>	74.0	18.6	21.8	8.6

Appendix 2

List of non-kiwi tarsometatarsi compared with tarsometatarsus NMNZ S.36731. All specimens are registered in NMNZ.

Dinornithiformes, *Megalapteryx didinus* S.23843; Galliformes, *Gallus gallus* OR.15145; Anseriformes, *Tadorna variegata* OR.16472; Podicipediformes, *Podiceps cristatus australis* OR.16594; Sphenisciformes, *Eudyptes sclateri* OR.668; Procellariiformes, *Diomedea b. bulleri* OR.24200; Pelecaniformes, *Stictocarbo p. punctatus* OR.24431; Ciconiiformes, *Botaurus poiciloptilus* OR.11836; Falconiformes, *Falco novaeseelandiae* OR.23909; Charadriiformes, *Catharacta antarctica lonnbergi* OR.24699; Columbiformes, *Hemiphaga chathamensis* OR.22818; Psittaciformes, *Strigops habroptilus* OR.23032; Cuculiformes, *Scythrops novaehollandiae* OR.25345; Strigiformes, *Ninox a. albifacies* S.36303; Apodiformes, *Aegotheles novaeseelandiae* S.36387, *Hirundapus c. caudacutus* OR.24234; Coraciiformes, *Todiramphus sancta vagans* OR.13669; Passeriformes, *Corvus moriorum* S.962.

Gruiformes: Psophiidae, *Psophia crepitans* OR.1490; Aptornithidae: *Aptornis otidiformis* OR.8129, *Aptornis defossor* S.23267; Rallidae: *Lewinia muelleri* OR.25556, *Gallirallus philippensis assimilis* OR.23821, *Gallirallus dieffenbachii* S.30037, *Gallirallus australis greyi* S.573, *Gallirallus a. australis* OR.14994, *Gallirallus australis hectori* OR.25361, *Gallirallus australis scotti* OR.18327, *Cabalus modestus* S.31755, *Capellirallus karamu* S.23241, *Diaphorapteryx hawkinsi* OR.7997, *Porzana t. tabuensis* OR.20984, *Porzana pusilla affinis* OR.24417, *Gallinula ventralis* OR.22100, *Gallinula tenebrosa* OR.24520, *Gallinula hodgenorum* S.33724, *Porphyrio m. melanotus* OR.24252, *Porphyrio mantelli* S.28440, *Porphyrio hochstetteri* OR.24641, *Fulica atra australis* OR.24566, *Fulica prisca* S.33721, *Fulica chathamensis* S.26519.