

Moa's Ark: Miocene Fossils Reveal the Great Antiquity of Moa (Aves: Dinornithiformes) in Zealandia

ALAN J.D. TENNYSON,*¹ TREVOR H. WORTHY,² CRAIG M. JONES,³
R. PAUL SCOFIELD⁴ AND SUZANNE J. HAND²

¹ Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington, New Zealand
alant@tepapa.govt.nz

² School of Biological, Earth and Environmental Sciences,
University of New South Wales, Sydney NSW 2052, Australia
t.worthy@unsw.edu.au · s.hand@unsw.edu.au

³ Institute of Geological & Nuclear Sciences, PO Box 30–368, Lower Hutt, New Zealand
C.Jones@gns.cri.nz

⁴ Canterbury Museum, Rolleston Ave, Christchurch, New Zealand
pscofield@canterburymuseum.com

ABSTRACT. Fossil eggshell and bone fragments from New Zealand's Miocene St Bathans Fauna indicate that two taxa of giant flightless moa (one weighing 20–25 kg and another much larger than this) were present in Zealandia 19–16 Ma. Contrary to recent suggestions, we conclude that moa have a long history in Zealandia, almost certainly extending to before the Oligocene “drowning”. This conclusion is consistent with biotic evidence from other sources, which indicates a great antiquity of several Zealandian animals and plants.

TENNYSON, ALAN J.D., TREVOR H. WORTHY, CRAIG M. JONES, R. PAUL SCOFIELD & SUZANNE J. HAND, 2010. Moa's Ark: Miocene fossils reveal the great antiquity of moa (Aves: Dinornithiformes) in Zealandia. In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 105–114.

Moa (Dinornithiformes) have been central to the debate around the antiquity of the terrestrial New Zealand biota—so much so that their presumed Gondwanan origins have seen the country sometimes dubbed “Moa's Ark” (Brewster, 1987; Bellamy *et al.*, 1990). Although numerous taxa have generally been considered to have dispersed over-water to Zealandia, the biota has long been assumed to include Gondwanan vicariant ancestors of some plants (e.g., southern beech *Nothofagus*), many invertebrates (e.g., velvet worms *Peripatus* and hyriid freshwater mussels), New Zealand

frogs (leiopelmatids), tuatara (sphenodontids) and moa (e.g., Fleming, 1979).

The order Dinornithiformes (superorder Palaeognathae) includes nine Recent species of moa, all of which became extinct about 600 years ago as a result of human hunting (Tennyson & Martinson, 2007; Bunce *et al.*, 2009). Their remains are numerous in Late Pleistocene-Holocene fossil deposits (Worthy & Holdaway, 2002; Tennyson & Martinson, 2007). Moa were very large flightless birds, varying in weight from 9–242 kg (Worthy & Holdaway, 2002; Tennyson

* author for correspondence

& Martinson, 2007). Worthy *et al.* (1991) summarized knowledge of Pliocene-Pleistocene moa fossils (then the oldest moa known) but these were morphologically similar to Recent taxa and not particularly informative with respect to the origins of moa. No older moa material was described until our research of the late Early Miocene St Bathans Fauna began in 2001, the first remains recovered being eggshell only (Worthy *et al.*, 2002, 2007; Pole *et al.*, 2003).

The history of New Zealand as a separate landmass began when the continental fragment called Zealandia split away from the Australis section of East Gondwana (see Gibbs, 2006). This rifting occurred between the Late Cretaceous and Early Eocene 83–52 Ma (Gaina *et al.*, 1998). According to the current paradigm, the continent of Zealandia slowly sunk and land area reached its minimum extent in the Oligocene, when it was reduced to perhaps 18% of its current area, before rising again to its present level (Cooper & Cooper, 1995).

Pole (1994) reignited a longstanding debate about the origins of New Zealand's flora and fauna by postulating that the entire forest flora, and perhaps the whole terrestrial biota, arrived by long-distance dispersal. This theory has been built on by others (e.g., Campbell & Landis, 2001; Waters & Craw, 2006; Campbell & Hutching, 2007; Trewick *et al.*, 2007; Campbell *et al.*, 2008) and comprehensively presented by Landis *et al.* (2008), who suggested that the marine drowning of Zealandia at the Oligocene-Miocene boundary (25–22 Ma) was complete, based primarily on geological evidence of Tertiary wave cut platforms and extensive Oligocene marine limestone deposits (and a concurrent absence of terrestrial deposits). In addition, some genetic studies have indicated the relatively recent arrival of the ancestors of supposedly Gondwanan modern-day taxa and post-Oligocene radiations, notably for one classic example: *Nothofagus* beech (e.g., Cooper & Cooper, 1995; Cook & Crisp, 2005; Knapp *et al.*, 2005; Goldberg *et al.*, 2008; but see Heads, 2006). An increasingly popular assertion is that there is no vicariant Gondwanan biota represented by descendants in the Recent New Zealand biota and that all terrestrial taxa, including the ancestors of moa, arrived via dispersal.

A long-standing but controversial theory is that the Recent palaeognaths (tinamou Tinamidae, moa, kiwi Apterygidae, cassowary and emu Casuariidae, ostrich Struthionidae, rhea Rheidae, elephant bird Aepyornithidae) attained their present distributions through vicariance as the southern super-continent Gondwana broke apart (e.g., Cracraft, 2001; Grellet-Tinner, 2006). Although details of these events and the relationships between palaeognaths are hotly debated (e.g., Harshman *et al.*, 2008; Phillips *et al.*, 2010), there is much continued support for a Cretaceous origin of palaeognaths (e.g., Cooper & Penny, 1997; Phillips *et al.*, 2010) and the great antiquity of moa in Zealandia (e.g., Haddrath & Baker, 2001).

If the ancestors of moa arrived in Zealandia after the Oligocene, they presumably arrived by flying (Pole, 1994; Waters & Craw, 2006), since during the Oligocene and ever since, emergent Zealandia has been 1,850 km from the nearest Australian land (Stevens, 1980). Some proponents of the post-Oligocene arrival theory have stated recently that the oldest known moa fossils are only 1.5 Ma (Landis *et al.*, 2008), with Goldberg *et al.* (2008) declaring that “there is as yet no direct evidence... that their pre-Pleistocene ancestors were giants”, contrary to information in Worthy *et al.* (2007) and preceding abstracts in the geological literature (e.g.,

Jones *et al.*, 2002; Worthy *et al.*, 2002). Campbell & Landis (2008) concluded that “The giant extinct flightless bird, the moa, may be an evolutionary phenomenon of the past 23 million years”.

Here, we challenge these assertions by presenting evidence of the presence of large, flightless moa in Zealandia during the late Early Miocene.

New Zealand has an extensive Late Pleistocene-Holocene terrestrial vertebrate fossil record younger than 25,000 years but, until recently, the Tertiary (65–2.6 Ma) avifauna record was restricted to marine birds (Worthy & Holdaway, 2002). However, the late Early Miocene (19–16 Ma) St Bathans Fauna of Central Otago, South Island, has now revealed a diverse vertebrate fauna dating from just after the Late Oligocene “drowning” event (Worthy *et al.*, 2006, 2007, 2008, 2009; Jones *et al.*, 2009). Thousands of bird bones have been recovered from at least 30 taxa, as well as hundreds of pieces of bird eggshell.

Methods

The St Bathans Fauna has been recovered from three main fossil sites near St Bathans: 1, Manuherikia River = various “HH” sites; 2, Mata Creek, which includes the “Croc Site”; 3, Vinegar Hill (for detailed information on localities see Worthy *et al.*, 2007). The terrestrial vertebrate remains are found mainly in sandy layers and were deposited in a large paleo-lake. Owing to reworking and transport resulting from water movement at the lake edge, there is no articulation of specimens and all fossils are less than 15 cm long. Our excavations were carried out between the years 2001–2009, using an excavator to remove alluvial over-burden, followed by hand-excavation of thin sandy layers, wet sieving of sediment using 1–4 mm mesh, drying and subsequent sorting under magnification in labs.

We studied the fossil record of moa from the St Bathans Fauna to determine how it contributes to the debate on the “drowning” of Zealandia, specifically looking at the size of these moa and how this information contributes to our understanding of the time of their arrival in Zealandia. We re-examined purported moa eggshell from the deposits (Worthy *et al.*, 2007) and also studied newly discovered material, including some large bone fragments. All measurements were taken with vernier callipers.

The structure of eggshell collected in 2001–2007 was examined and its thickness measured. Excavations in 2008–2009 have recovered many more pieces of eggshell but these remain to be fully sorted and studied in detail. Initially we divided the eggshell into two groups based on thickness. Measurements were taken at the least damaged point on the edge of each fragment but, because of wear, some measurements may be under-estimates. We then examined the structure of some of the thicker specimens. In order to obtain fresh surfaces exposing the internal crystalline structure of the eggshell for examination by scanning electron microscopy (SEM), specimens were washed and air dried and small portions were carefully broken off with tweezers. These broken fragments were mounted securely on aluminium SEM stubs with carbon tape and carbon coated. All specimens were examined using the LEO 440 SEM at the Institute of Geological & Nuclear Sciences. Specimens from the same collection location could be from the same egg but generally it was not possible to associate fragments

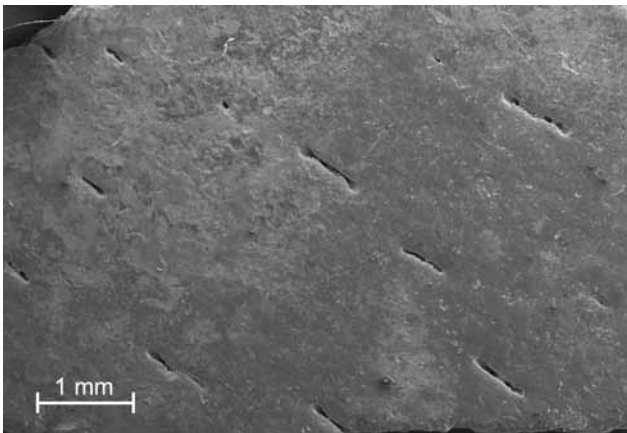


Figure 1. SEM of the external surface of “thick” Miocene fossil eggshell from the St Bathans deposits (NMNZ S.44766) showing the characteristic elongate pore-depressions, smooth surface and lack of ornamentation.

and they are treated here as independent specimens unless noted in Appendix 1.

Bone fragments large enough to be potentially from moa were compared with Pleistocene and Recent avian material in the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ).

Results

We list 154 pieces of eggshell (Appendix 1) and six bone fragments (Table 3) that we consider likely to be from moa. These eggshell remains were recovered from about 10 m³ of deposit excavated in 2001–2007, giving an average rate of occurrence of about 15 pieces per m³.

Eggshell

Comparison of palaeognath eggshell structure. In cross-section, the Miocene St Bathans eggshell shows distinct layers that identify it as avian and rule out testudines and crocodylians (Williams & Vickers-Rich, 1991; Mikhailov, 1992, 1997; Grellet-Tinner, 2006); crocodylians are also represented in the fauna by fossil bones (Molnar & Pole, 1997; Worthy *et al.*, 2009).

The most common thin eggshell found in the St Bathans deposits has tiny circular surface pore-depressions spaced about 1 mm apart and three internal layers in cross-section, with the inner mammillae wider than high. These structures are found in most neognaths, so this fossil eggshell is presumed to be mainly from the abundant anatids found in this fauna (Jones *et al.*, 2002; Worthy *et al.*, 2007). Our analysis focuses on the rarer thicker eggshell found in the St Bathans deposits.

The “thick” fossil eggshell has a smoothly homogeneous surface structure and sometimes slit-like surface pore-depressions (see Fig. 1), as found in moa, rhea and elephant bird eggs (e.g., Hutton, 1872; Gill, 2007; also see Appendix 2). The pore-depressions can be up to 1.1 mm long and sometimes densely-spaced (e.g., 0.5 mm apart) but the pores on other fragments have more oval surface depressions and occur at a lower density.

Scanning electron microscopy of a piece of the “thick” fossil eggshell (see Fig. 2, also Worthy *et al.*, 2007, fig.

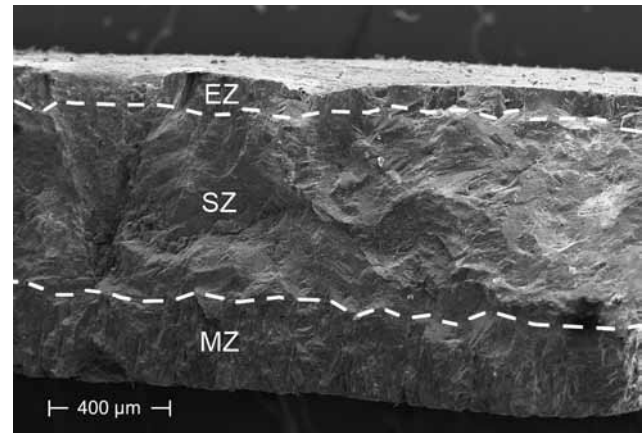


Figure 2. SEM image of a broken cross-section of “thick” Miocene fossil eggshell from the St Bathans deposits (NMNZ S.40938.9) showing the structure. The upper surface is the external layer of the shell. EZ = external zone, SZ = squamous “spongy” zone, MZ = mammillary zone. Features consistent with moa eggshell include (a) the mammillae consisting of tabular wedges; (b) the mammillae being higher than wide; (c) the vesiculation in the MZ being weak or absent; (d) the absence of a resistant zone between the SZ and EZ; (e) the EZ being blocky (see Appendix 2).

18E, which is a thin section of the same piece of eggshell) facilitates examination of its internal structure. It has three layers and thus is similar in structure to most palaeognath eggshell (Mikhailov, 1997; Zelenitsky & Modesto, 2003; Grellet-Tinner, 2006): (1) a thick innermost lower mammillary zone (MZ) with mammillae higher than wide (unlike neognaths); (2) a thick squamous “spongy” zone (SZ) outside the MZ; and (3) a thin external zone (EZ) (see Fig. 2). Tyler (1957) and Mikhailov (1992, 1997) failed to detect the EZ layer in moa eggshell but subsequent studies have detected it (e.g., Grellet-Tinner, 2006). Contrary to our earlier finding (Jones *et al.*, 2002), the “thick” St Bathans Miocene eggshell also has an EZ.

The combination of structural features identified in the “thick” fossil eggshell is unique to that of moa eggshell (see Appendix 2).

Internal layers of the “thick” Miocene eggshell have the following thickness percentages: MZ 26.7, SZ 63.7, EZ 9.7 and ratios of SZ/MZ of 2.40 and EZ/SZ of 0.15 (calculated from cross-section of NMNZ S.40938.9). Moa have a SZ about twice as thick as the MZ (Hutton 1872, Tyler, 1957), although some individual pieces of moa eggshell measured by Tyler (1957) and Mikhailov (1997) had a SZ/MZ ratio of about 2.5—similar to the ratio observed in the St Bathans Miocene fossil. These authors did not detect the EZ, however, and their samples may have been eroded. The ratio of SZ/MZ in other palaeognaths examined (tinamou, kiwi, cassowary, emu, ostrich, rhea, elephant bird) can vary from about 1–3.5 (Tyler & Simkiss, 1960; Mikhailov, 1997; Grellet-Tinner, 2006 and figs in Williams, 1981; Silyn-Roberts & Sharp, 1985; Zelenitsky & Modesto, 2003; also see Appendix 2 and discussion of Grellet-Tinner’s [2006] character 14). Thus the “thick” Miocene eggshell has a SZ/MZ ratio consistent with palaeognaths, including moa. Moa have an EZ/SZ ratio of about 0.14–0.19 (Grellet-Tinner, 2006 and estimated from Mikhailov, 1997, fig. 1E and Zelenitsky & Modesto, 2003, fig. 2A). The ratio of the “thick” St Bathans Miocene eggshell of 0.15 falls within this range but is lower than the EZ/SZ

Table 1. Comparative thickness of Recent palaeognath and St Bathans Miocene fossil eggshell, listed from thickest to thinnest (data from Tyler & Simkiss, 1960; Silyn-Roberts & Sharp, 1985; Zelenitsky & Modesto, 2003; Gill, 2000, 2007). SB = St Bathans.

taxon	eggshell thickness (mm)
Elephant bird	3.47–3.51
Ostrich	1.74–2.23
Moa (all species)	0.54–1.89
SB Miocene fossils (“thick”)	0.58–1.68
Rhea	0.86–1.25
Emu	0.86–1.25
Cassowary	0.75–1.09
SB Miocene fossils (common “thin”)	< 0.5 mm
Kiwi	0.34–0.50
Tinamou	0.18–0.25

ratio in emus, cassowaries, kiwi and tinamou (Grellet-Tinner, 2006; also see Appendix 2 character I).

It is worth noting that the other group of giant terrestrial birds occurring in Australasia—the extinct Australian dromornithids (order Anseriformes)—also had very thick eggshell (1.0–4.1 mm) but they are not palaeognaths, so their eggshell differs from the “thick” St Bathans eggshell in structure (Williams, 1981; Williams & Vickers-Rich, 1991; Grellet-Tinner, 2006). One key difference is that they lack the EZ layer found in all palaeognaths.

Comparison of palaeognath eggshell thickness. The common fossil eggshell at St Bathans is thin (< 0.5 mm, Table 1) and presumed to be mainly from anatids (Jones *et al.*, 2002; Worthy *et al.*, 2007). The rarer, thicker fossil eggshell (0.58–1.68 mm) is consistent in thickness with that laid by medium-sized to large ratites and is within the range of that of moa (Table 1). Additionally, there appear to be two classes of “thick” eggshell (see Fig. 4). The most common “thick” eggshell has an average thickness of 0.94 mm (± 0.12 s.d., range 0.58–1.19 mm, $n = 153$) (Appendix 1). The specimens measured in this study include all those measured by Worthy *et al.* (2007), with the larger sample size here exhibiting a unimodal distribution range and a slightly lower average thickness. Some eggshell at the thinner end of this range (up to about 0.7 mm thick) could belong to species other than moa (see Gill, 2010) because the internal structure of every piece was not examined. Eggshell thickness appears to be thicker when derived from larger moa species and the most common “thick” Miocene eggshell has a thickness consistent with that from a small moa (Gill, 2007; Worthy *et al.*, 2007). The thickness of the Miocene eggshell is similar to that of eggshell attributed primarily to the Holocene coastal moa (*Euryapteryx curtus*) in Northland by Gill (2000, 2010).

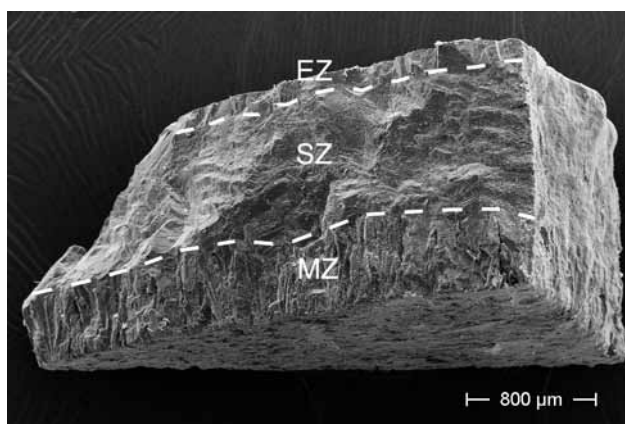


Figure 3. SEM image of a broken cross-section of the thickest piece of Miocene eggshell from the St Bathans deposits (NMNZ S.40937.2) showing the structure. The lower surface is the internal layer of the shell. EZ = external zone, SZ = squamous “spongy” zone, MZ = mammillary zone.

Coastal moa were the smallest moa and the Northland birds weighed 12–34 kg (Worthy & Holdaway, 2002: 146–147). Therefore the most common thick Miocene eggshell in the St Bathans deposits probably represents birds in that size range, perhaps averaging about 25 kg.

A uniquely thick piece of St Bathans Miocene eggshell (NMNZ S.40937.2), at 1.68 mm, is well above the thickness range of other St Bathans fossil eggshell (see Fig. 4). Preliminary sorting of our 2008–2009 collections has not produced additional pieces of eggshell this thick. NMNZ S.40937.2 is consistent in thickness with eggshell from a bird the size of a heavy-footed (*Pachyornis elephantopus*) or giant moa (*Dinornis* spp.) (see Gill, 2007, 2010). These species are the largest moa, weighing 34–242 kg (Tennyson & Martinson, 2007). Although we earlier considered that this piece of eggshell may have been altered through diagenesis (see Worthy *et al.*, 2007), there is no evidence of such alteration (see Fig. 3) and it suggests that at least two taxa, including a very large species, are represented by the “thick” eggshell from St Bathans.

Variation in frequency of occurrence of “thick” fossil eggshell between sites. The frequency of occurrence of “thick” eggshell varied considerably among the main layers at the St Bathans fossil sites (Table 2). The Manuhirikia site layers HH1b (“riverbank” and “trench”) and HH1d and the Vinegar Hill site were far richer in “thick” eggshell than other sites examined. Possible explanations for these differences are that “thick” eggshell may occur in sites that had either a higher energy input or a higher terrestrial (and less lacustrine) input at the time of deposition. It is notable that the HH1b

Table 2. Frequency of occurrence of “thick” Miocene eggshell in the St Bathans deposits from different layers, arranged from highest to lowest frequency.

layer	no. of “thick” eggshell specimens (A)	volume of sediment excavated 2001–2007 (B)	number of “thick” eggshell fragments per m ³ (A/B)
HH1b “riverbank”	45	ca. 0.15 m ³	300
Vinegar Hill (all sites)	31	ca. 0.2 m ³	155
HH1b “trench”	36	0.3 m ³	120
HH1d	4	ca. 0.1 m ³	40
HH1a	32	7.16 m ³	4.5
Croc site, layer 1	3	1.96 m ³	1.5

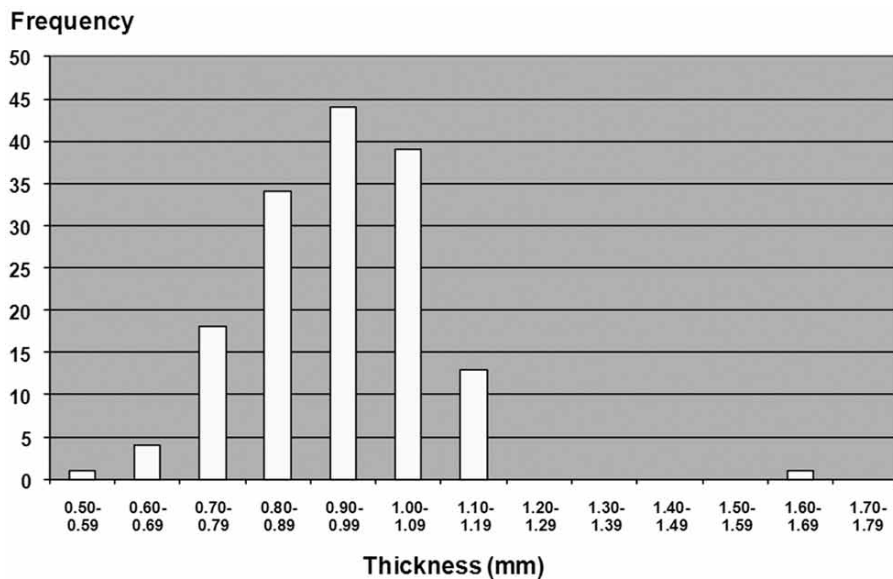


Figure 4. Distribution of thickness in a sample of 154 eggshell fragments from the Miocene St Bathans deposits (based on data in Appendix 1).

sites contain a relatively high number of quartz pebbles and heavily eroded bone, which may indicate a higher energy depositional environment. It is also notable that at least one significant terrestrial specimen has been found at Vinegar Hill (Jones *et al.*, 2009) despite the comparatively low volume of sediment excavated at this site (Table 2). Further analysis is required to understand these possible preservational trends.

Large bone fragments. Several bone fragments from the St Bathans deposits represent birds the size of moa. New Zealand's other Recent giant flightless land birds that could have had giant Miocene ancestors (adzebills *Aptornis* and geese *Cnemiornis*) have limb bones that, in parts, have a cortex thickness sometimes 5 mm or greater, so only the very thickest examples (> 4 mm) of limb bone fragments from the St Bathans deposits are noted in this study. As was found for the distribution of "thick" eggshell, the varied localities for the large bone fragments show that these remains are found at all three of the main St Bathans sites but at higher densities in the Manuherikia site layers HH1b ("riverbank" and "trench") and the Vinegar Hill site (compare Tables 2 and 3).

The most useful fragment for identifying the probable presence of large cursorial birds that might be ratites is NMNZ S.44691, which matches part of the proximal shaft of a right tibiotarsus. The shape and thickness matches the right tibiotarsus of a small moa (see Fig. 5). The position of the fibular crest relative to the ridge from the outer cnemial crest is similar to that in several palaeognaths, including tinamou,

kiwi, cassowary, emu and elephant bird, but very different from that in ostrich and rhea. The size of the fragment indicates a bird of similar size to NMNZ S.447.1, which is a relatively small Holocene specimen of the moa *Megalapteryx didinus*. This species varies in weight from 14–63 kg (Tennyson & Martinson, 2007). Body mass can be calculated based on NMNZ S.447.1 having a minimum tibiotarsus shaft circumference of 67 mm. An algorithm (where mass in grams = $a \cdot x^b$ and $a = 0.076$, x = minimum tibiotarsus circumference, and $b = 2.424$; Campbell & Marcus, 1992, table 2) gives a mass of 20.3 kg.

Apart from moa, the only other known New Zealand land birds that approach this size are extinct flightless adzebills and giant geese (Tennyson & Martinson, 2007).

Both have the fibula and outer cnemial crests further apart than in the Miocene fossil and the geese have two ridges emanating from the outer cnemial crest. Probable ancestors of the giant geese have been described from the St Bathans Fauna previously (Worthy *et al.*, 2008). As these were considered to be volant, it is highly unlikely that they had a tibiotarsus as large as one represented by NMNZ S.44691.

Discussion

Before work began on the Miocene St Bathans Fauna, the oldest known moa fossils were 1.8–2.5 million years old (Worthy *et al.*, 1991; Worthy & Holdaway, 2002: 8–10). This is slightly older than the 1.5 million years noted by some Oligocene "drowning" proponents (Landis *et al.*, 2008). However, fossils indicate that the moa genera *Anomalopteryx* and *Euryapteryx* separated more than 2.5 million years ago (Worthy *et al.*, 1991) and the fossils in the St Bathans deposits now strongly suggest that moa were present in Zealandia at least 19–16 Ma. Additionally, it is worth noting that a fossil toe bone of Late Cretaceous age (80–65 Ma) from Hawkes Bay, New Zealand, may be from a very large bird (Scarlett & Molnar, 1984).

The most common "thick" eggshell (which has a structure consistent only with moa) and the large tibia fragment from the St Bathans deposits suggest that in the late Early Miocene some moa weighed about 20–25 kg, not as large as the largest

Table 3. Likely moa bone fragments from the Miocene St Bathans deposits (long bone shaft fragments are listed if their cortex thickness is > 4 mm).

NMNZ S.	site	description
40968.1	HH1b "riverbank"	long bone shaft (maximum cortical thickness 4.3 mm)
42812	Croc Site, layer 1	?distal right tibiotarsus shaft (maximum cortical thickness 4.4 mm); preserves what appears to be a fossa for an unfused ascending process of the astragalus, so represents an immature bird
44691	Vinegar Hill, site 2	proximal right tibiotarsus shaft (maximum cortical thickness 7.9 mm)
50271	HH1a	long bone shaft (maximum cortical thickness 4.7 mm)
51323	HH1b "trench"	skull element; ?left nasal; 35 x 12 mm; its poor state of preservation does not allow us to identify this element with certainty

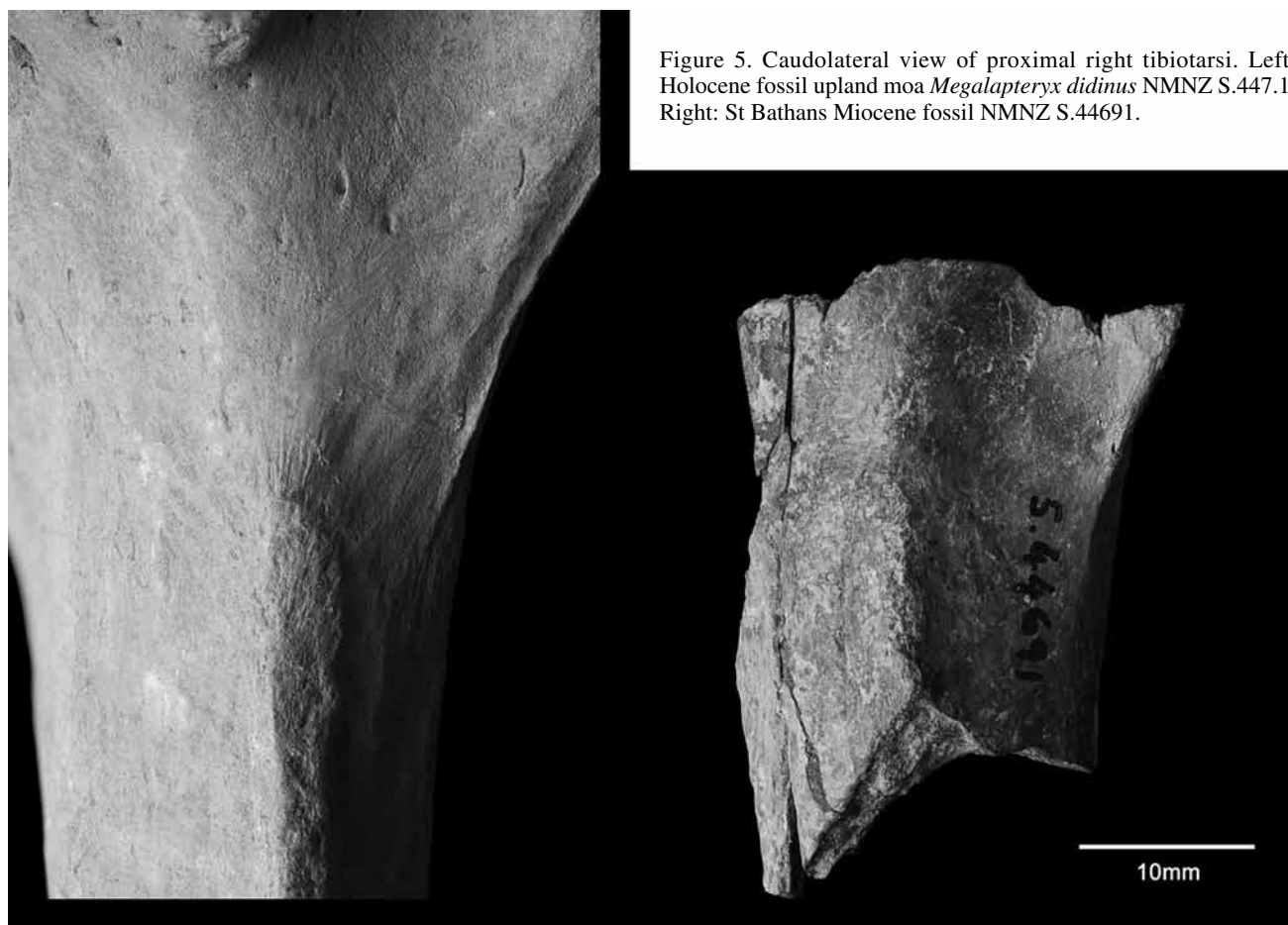


Figure 5. Caudolateral view of proximal right tibiotarsi. Left: Holocene fossil upland moa *Megalapteryx didinus* NMNZ S.447.1. Right: St Bathans Miocene fossil NMNZ S.44691.

Recent species but still sizable birds. Tantalisingly, there is one much thicker piece of fossil eggshell that presumably came from a moa weighing considerably more. Some moa were already enormous by the beginning of the Pleistocene 1.8 Ma (e.g., a giant moa *Dinornis*, represented by a femur NMNZ S.450; Marshall, 1919; Worthy *et al.*, 1991). Large giant moa with femora of comparable size to this femur weighed 76–242 kg (Bunce *et al.*, 2003). An algorithm for birds, based on NMNZ S.450 having a minimum femur shaft circumference of 198 mm (where mass in grams = $a \cdot x^b$ and $a = -0.065$, x = minimum femur circumference, and $b = 2.411$; Campbell & Marcus, 1992, table 2), gives a mass of 224.0 kg for this animal. We therefore feel confident in debunking the stance of Goldberg *et al.* (2008) that “there is as yet no direct evidence... that their pre-Pleistocene ancestors were giants”.

The large size of moa in the late Early Miocene (weighing somewhere between 20 and 242 kg) makes it likely that they were flightless, although proof of this is lacking. All Recent New Zealand bird taxa about 20 kg or larger were flightless (see Tennyson & Martinson, 2007).

If the ancestors of moa arrived in Zealandia after the Oligocene “drowning” 25–22 Ma by flying (Pole, 1994; Waters & Craw, 2006), then the new Miocene fossil finds reduce the time available for the colonization and the evolution of giant flightless forms to as little as three million years. Birds can become large and flightless within three million years (e.g., Trewick, 1997; Slikas *et al.*, 2002) and, by itself, the St Bathans fossil evidence is insufficient to prove that moa had a pre-“drowning” origin in Zealandia. However, we have demonstrated that there is a much shorter time interval for this evolution to have occurred than previously

known. The fact that moa are the only birds worldwide without even vestigial wing bones (Worthy & Holdaway, 2002) also suggests a very long history of flightlessness.

Although moa seem to have gone through a genetic bottleneck during the Oligocene marine transgression (Cooper & Cooper, 1995) and Recent lineages may have arisen only since the Late Miocene (Bunce *et al.*, 2009), nearly all independent evidence indicates that moa diverged from their nearest relatives in the Paleocene or Cretaceous (at least 60 Ma) (e.g., Cooper *et al.*, 2001; Cracraft, 2001; Haddrath & Baker, 2001; Grellet-Tinner, 2006; Phillips *et al.*, 2010)—well before the Oligocene (34–24 Ma).

Another intriguing find of relevance to this debate is the presence of a probable divaricating plant in Early Miocene fossil lake sediments of central Otago (Campbell *et al.*, 2000). This growth form is considered to have evolved as protection against moa feeding, with Lee *et al.* (2008) concluding that “New Zealand plants have been protecting themselves against moa browsing for at least the past 20 million years”.

The St Bathans Fauna has provided the first glimpse of the land animals that were living in Zealandia after the Oligocene-Miocene submergence. Many characteristic Recent New Zealand taxa were present in the late Early Miocene 19–16 Ma but substantial changes have occurred subsequently resulting from both extinctions and colonizations (Worthy *et al.*, 2009). Evidence of other “Gondwanan” vertebrate taxa in the St Bathans Fauna makes the total “drowning” theory even less likely: ancestors of New Zealand frogs, geckos (diplodactylines), tuatara, New Zealand wrens (Acanthisittidae) and the unusual ground-

dwelling mammal would all have needed to colonize since the “drowning” (Jones *et al.*, 2009; Lee *et al.*, 2009; Worthy *et al.*, 2009, 2010) ... and where would they have come from when there are no known Neogene source populations? In short, almost all archetypical Gondwanan terrestrial vertebrate taxa known from New Zealand’s Recent fauna are now known to have had ancestors present in Zealandia in the late Early Miocene. If Zealandia was completely submerged, as Landis *et al.* (2008) and others contend, then all such taxa would need to have dispersed to Zealandia in as little as three million years and no such taxa would have arrived in the last 16 million years.

In addition to terrestrial vertebrates, numerous invertebrates, including hyriid freshwater mussels (Graf & Foighil, 2000), pettalid harvestmen (Boyer & Giribet, 2009), micropterigid moths, weta (Orthoptera) and freshwater crayfish (*Paranephrops* spp.) (Gibbs, 2006), and some plants (e.g., kauri *Agathis*; Stöckler *et al.*, 2002; Knapp *et al.*, 2007), also appear to be Gondwanan vicariants.

In summary, the traditional theory of some vicariant Gondwanan taxa surviving in the Recent fauna of New Zealand is supported by moa and other late Early Miocene (19–16 Ma) St Bathans fossils. Although the Zealandian continent was largely submerged from the Late Oligocene to the Early Miocene (about 25–22 Ma), there is increasing biotic evidence that some land must have remained. Moa appear to be an evolutionary phenomenon of much greater antiquity than “the past 23 million years” (contra Campbell & Landis, 2008) and “Moa’s Ark” remains an appropriate epithet for New Zealand.

ACKNOWLEDGMENTS. We thank Ann and Euan Johnstone and Jack Enright for access to their land; the many people who helped in the excavations and sorting over the years; for photography we are indebted to Te Papa staff: Jean-Claude Stahl and Raymond Coory; Raymond also helped prepare Figs 1–4 for publication; Jane Cherry provided essential library resources; Brian Gill and Gerald Grellet-Tinner provided helpful comments on the manuscript. The excavations were funded primarily by Australian Research Council DP0770660, with significant contributions from Te Papa, the Canterbury Museum, the Universities of New South Wales and Adelaide, and the South Australian Museum.

References

- Bellamy, D., B. Springett, & P. Hayden, 1990. *Moa’s Ark: The Voyage of New Zealand*. New York: Viking.
- Boyer, S.L., & G. Giribet, 2009. Welcome back New Zealand: regional biogeography and Gondwanan origin of three endemic genera of mite harvestmen (Arachnida, Opiliones, Cyphophthalmi). *Journal of Biogeography* 36: 1084–1099. <http://dx.doi.org/10.1111/j.1365-2699.2009.02092.x>
- Brewster, B., 1987. *Te moa—the life and death of New Zealand’s unique bird*. Nelson: Nikau Press.
- Bunce, M., T.H. Worthy, T. Ford, W. Hoppitt, E. Willerslev, A. Drummond, & A. Cooper, 2003. Extreme reversed sexual size dimorphism in the extinct New Zealand moa *Dinornis*. *Nature* 425: 172–175. <http://dx.doi.org/10.1038/nature01871>
- Bunce, M., T.H. Worthy, M.J. Phillips, R.N. Holdaway, E. Willerslev, J. Haile, B. Shaprio, R.P. Scofield, A. Drummond, P.J.J. Kamp, & A. Cooper, 2009. The evolutionary history of the extinct ratite moa and New Zealand Neogene paleogeography. *Proceedings of the National Academy of Sciences of the United States of America* 106: 20646–20651. <http://dx.doi.org/10.1073/pnas.0906660106>
- Campbell, H., & G. Hutching, 2007. *In Search of Ancient New Zealand*. Auckland: Penguin and GNS Science.
- Campbell, H., & C. Landis, 2001. New Zealand awash. *New Zealand Geographic* 51: 6–7.
- Campbell, H., & C. Landis, 2008. That Sinking Feeling. In *A continent on the move—New Zealand geoscience into the 21st century*, ed. I.J. Graham, pp. 134–135. Wellington: Geological Society of New Zealand in association with GNS Science.
- Campbell, H.J., C.J. Adams, & N. Mortimer, 2008. Exploring the Australian geological heritage of Zealandia and New Zealand. *Proceedings of the Royal Society of Victoria* 120: 38–50.
- Campbell, J.D., D.E. Lee, & W.G. Lee, 2000. A woody shrub from the Miocene Nevis Oil Shale, Otago, New Zealand—a possible fossil divaricate? *Journal of the Royal Society of New Zealand* 30: 147–153.
- Campbell, K.E., & L. Marcus, 1992. The relationship of hindlimb bone dimensions to body weight in birds. In *Papers in Avian Paleontology Honoring Pierce Brodkorb*, ed. K.E. Campbell, pp. 395–412. Los Angeles: Natural History Museum of Los Angeles County Science Series No.36.
- Cook, L.G., & M.D. Crisp, 2005. Not so ancient: the extant crown group of *Nothofagus* represents a post-Gondwanan radiation. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 272: 2535–2544. <http://dx.doi.org/10.1098/rspb.2005.3219>
- Cooper, A., & R.A. Cooper, 1995. The Oligocene bottleneck and New Zealand biota: genetic record of a past environmental crisis. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 261: 293–302. <http://dx.doi.org/10.1098/rspb.1995.0150>
- Cooper, A., & D. Penny, 1997. Mass survival of birds across the Cretaceous-Tertiary boundary: molecular evidence. *Science* 275: 1109–1113. <http://dx.doi.org/10.1126/science.275.5303.1109>
- Cooper, A., C. Lalueza-Fox, S. Anderson, A. Rambaut, J. Austin, & R. Ward, 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* 409: 704–707. <http://dx.doi.org/10.1038/35055536>
- Craft, J., 2001. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 268: 459–469. <http://dx.doi.org/10.1098/rspb.2000.1368>
- Fleming, C.A., 1979. *The geological history of New Zealand and its life*. Auckland: Auckland University Press.
- Gaina, C., R.D. Müller, W.R. Roest, & P. Symonds, 1998. The opening of the Tasman Sea: a gravity anomaly animation. *American Meteorological Society, AMS Journals OnLine* 2: 1–23.
- Gibbs, G., 2006. *Ghosts of Gondwana—The History of Life in New Zealand*. Nelson, New Zealand: Craig Potton Publishing.
- Gill, B.J., 2000. Morphometrics of moa eggshell fragments (Aves: Dinornithiformes) from Late Holocene dune-sands of the Karikari Peninsula, New Zealand. *Journal of the Royal Society of New Zealand* 30: 131–145.
- Gill, B.J., 2007. Eggshell characteristics of moa eggs (Aves: Dinornithiformes). *Journal of the Royal Society of New Zealand* 37: 139–150.
- Gill, B.J., 2010. Regional comparisons of the thickness of moa eggshell fragments (Aves: Dinornithiformes). In *Proceedings of the VII International Meeting of the Society of Avian Paleontology and Evolution*, ed. W.E. Boles and T.H. Worthy. *Records of the Australian Museum* 62(1): 115–122. [This volume] <http://dx.doi.org/10.3853/j.0067-1975.62.2010.1535>
- Goldberg, J., S.A. Trewick, & A.M. Paterson, 2008. Evolution of New Zealand’s terrestrial fauna: a review of molecular evidence. *Philosophical Transactions of the Royal Society of London B* 363: 3319–3334.

- <http://dx.doi.org/10.1098/rstb.2008.0114>
- Graf, D.L., & D.Ó. Foighil, 2000. Molecular phylogenetic analysis of 28S rDNA supports a Gondwanan origin for Australasian Hyriidae (Mollusca: Bivalvia: Unionoidea). *Vie et Milieu* 50: 245–254.
- Grellet-Tinner, G., 2006. Phylogenetic interpretation of eggs and eggshells: implications for phylogeny and Palaeognathae. *Alcheringa* 30: 141–182.
<http://dx.doi.org/10.1080/03115510608619350>
- Haddrath, O., & A.J. Baker, 2001. Complete mitochondrial DNA genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 268: 939–945.
<http://dx.doi.org/10.1098/rspb.2001.1587>
- Harshman, J., E.L. Braun, M.J. Braun, C.J. Huddleston, R.C.K. Bowie, J.L. Chojnowski, S.J. Hackett, K.-L. Han, R.T. Kimball, B.D. Marks, K.J. Miglia, W.S. Moore, S. Reddy, F.H. Sheldon, D.W. Steadman, S.J. Stepan, C.C. Witt, & T. Yuri, 2008. Phylogenomic evidence for multiple losses of flight in ratite birds. *Proceedings of the National Academy of Sciences of the United States of America* 105: 13462–13467.
<http://dx.doi.org/10.1073/pnas.0803242105>
- Heads, M., 2006. Panbiogeography of *Nothofagus* (Nothofagaceae): analysis of the main species massings. *Journal of Biogeography* 33: 1066–1075.
<http://dx.doi.org/10.1111/j.1365-2699.2006.01479.x>
- Hutton, F.W., 1872. On the microscopical structure of the egg-shell of the moa. *Transactions and Proceedings of the New Zealand Institute* 4: 166–167.
- Jones, C.M., J.A. McNamara, A.J.D. Tennyson, & T.H. Worthy, 2002. Ratite eggshell from Early-Middle Miocene age microvertebrate sites, Manuherikia Valley, Central Otago, New Zealand. In *Programme & abstracts, Geological Society of New Zealand annual conference 2nd–5th December, Whangarei, Northland 2002*, ed. H.R. Grenfell, p. 31. Wellington: Geological Society of NZ Miscellaneous Publication 112A.
- Jones, M.E.H., A.J.D. Tennyson, J.P. Worthy, S.E. Evans, & T.H. Worthy, 2009. A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (*Sphenodon*). *Proceedings of the Royal Society of London, Series B, Biological Sciences* 276: 1385–1390.
<http://dx.doi.org/10.1098/rspb.2008.1785>
- Knapp, M., R. Mudaliar, D. Havell, S.J. Wagstaff, & P.J. Lockhart, 2007. The drowning of New Zealand and the Problem of *Agathis*. *Systematic Biology* 56: 862–870.
<http://dx.doi.org/10.1080/10635150701636412>
- Knapp, M., K. Stöckler, D. Havell, F. Delsuc, F. Sebastiani, & P.J. Lockhart, 2005. Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (southern beech). *PLoS Biology* 3: 38–43.
<http://dx.doi.org/10.1371/journal.pbio.0030014>
- Landis, C.A., H.J. Campbell, J.G. Begg, D.C. Mildenhall, A.M. Paterson, & S.A. Trewick, 2008. The Waipounamu Erosion Surface: questioning the antiquity of the New Zealand land surface and terrestrial fauna and flora. *Geological Magazine* 145: 173–197.
<http://dx.doi.org/10.1017/S0016756807004268>
- Lee, D., L. Kennedy, J. Bannister, & J. Wood, 2008. Paleo-gardens. In *A continent on the move—New Zealand geoscience into the 21st century*, ed. I.J. Graham, pp. 240–243. Wellington: Geological Society of New Zealand in association with GNS Science.
- Lee, M.S.Y., M.N. Hutchinson, T.H. Worthy, M. Archer, A.J.D. Tennyson, J.P. Worthy, & R.P. Scofield, 2009. Miocene skinks and geckos reveal long-term conservatism of New Zealand's lizard fauna. *Biology Letters* 5: 833–837.
<http://dx.doi.org/10.1098/rsbl.2009.0440>
- Marshall, P., 1919. Occurrence of fossil moa-bones in the lower Wanganui strata. *Transactions and Proceedings of the New Zealand Institute* 51: 250–253.
- Mikhailov, K.E., 1992. The microstructure of avian and dinosaurian eggshell: phylogenetic implications. In *Papers in Avian Paleontology Honoring Pierce Brodkorb*, ed. K.E. Campbell, pp. 361–373. Los Angeles: Natural History Museum of Los Angeles County Science Series No.36.
- Mikhailov, K.E., 1997. *Avian eggshells: an atlas of scanning electron micrographs*. Tring: British Ornithologists' Club Occasional Publications No.3.
- Molnar, R.E., & M. Pole, 1997. A Miocene crocodylian from New Zealand. *Alcheringa* 21: 65–70.
<http://dx.doi.org/10.1080/03115519708619185>
- Phillips, M.J., G.C. Gibb, E.A. Crimp, & D. Penny, 2010. Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. *Systematic Biology* 59: 90–107.
<http://dx.doi.org/10.1093/sysbio/syp079>
- Pole, M., 1994. The New Zealand flora—entirely long-distance dispersal? *Journal of Biogeography* 21: 625–635.
<http://dx.doi.org/10.2307/2846036>
- Pole, M., B. Douglas, & G. Mason, 2003. The terrestrial Miocene biota of southern New Zealand. *Journal of the Royal Society of New Zealand* 33: 415–426.
- Scarlett, R.J., & R.E. Molnar, 1984. Terrestrial bird or dinosaur phalanx from the New Zealand Cretaceous. *New Zealand Journal of Zoology* 11: 271–275.
- Silyn-Roberts, H., & R.M. Sharp, 1985. Preferred orientation of calcite in the ratite and tinamou eggshells. *Journal of Zoology London A* 205: 39–52.
- Slikas, B., S.L. Olson, & R.C. Fleischer, 2002. Rapid, independent evolution of flightlessness in four species of Pacific Island rails (Rallidae): an analysis based on mitochondrial sequence data. *Journal of Avian Biology* 33: 5–14.
<http://dx.doi.org/10.1034/j.1600-048X.2002.330103.x>
- Stevens, G.R., 1980. *New Zealand Adrift: The Theory of Continental Drift in a New Zealand Setting*. Wellington, New Zealand: A.H. & A.W. Reed.
- Stöckler, K., I.L. Daniel, & P.J. Lockhart, 2002. New Zealand kauri (*Agathis australis* (D. Don) Lindl., Araucariaceae) survives Oligocene drowning. *Systematic Biology* 51: 827–832.
<http://dx.doi.org/10.1080/10635150290102474>
- Tennyson, A.J.D., & P. Martinson, 2007. *Extinct birds of New Zealand*. Wellington: Te Papa Press.
- Trewick, S.A., 1997. Flightlessness and phylogeny amongst endemic rails (Aves: Rallidae) of the New Zealand region. *Philosophical Transactions of the Royal Society of London B* 352: 429–446.
<http://dx.doi.org/10.1098/rstb.1997.0031>
- Trewick, S.A., A.M. Paterson, & H.J. Campbell, 2007. Hello New Zealand. *Journal of Biogeography* 34: 1–6.
<http://dx.doi.org/10.1111/j.1365-2699.2006.01643.x>
- Tyler, C., 1957. Some chemical, physical and structural properties of moa egg shells. *Journal of the Polynesian Society* 66: 110–130.
- Tyler, C., & K. Simkiss, 1960. A study of the egg shells of ratite birds. *Proceedings of the Zoological Society of London* 133: 201–243.
- Waters, J.M., & D. Craw, 2006. Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology* 55: 351–356.
<http://dx.doi.org/10.1080/10635150600681659>
- Williams, D.L.G., 1981. *Genyornis* eggshell (Dromornithidae; Aves) from the Late Pleistocene of South Australia. *Alcheringa* 5: 133–140.
<http://dx.doi.org/10.1080/03115518108565426>
- Williams, D.L.G., & P. Vickers-Rich, 1991. Fossil eggs from the Tertiary and Quaternary of Australia. In *Vertebrate palaeontology of Australasia*, ed. P. Vickers-Rich, J.M. Monaghan, R.F. Baird, and T.H. Rich, pp. 871–892. Melbourne: Pioneer Design Studio & Monash University Publications Committee.
- Worthy, T.H., A.R. Edwards, & P.R. Millener, 1991. The fossil record of moas (Aves: Dinornithiformes) older than the Otira

- (last) Glaciation. *Journal of the Royal Society of New Zealand* 21: 101–118.
- Worthy, T.H., S.J. Hand, M.S.Y. Lee, M. Hutchinson, A.J.D. Tennyson, R.P. Scofield, B. Marshall, J.P. Worthy, J.M.T. Nguyen, W.E. Boles, & M. Archer, 2009. New Zealand's St Bathans Fauna: an update on its composition and relationships. In *Geology & Genes IV*, ed. S. Trewick, N. Hillier [sic], and R. Cooper, pp. 40–43. Wellington: Geological Society of New Zealand Miscellaneous Publication No. 126.
- Worthy, T.H., S.J. Hand, J.M.T. Nguyen, A.J.D. Tennyson, J.P. Worthy, R.P. Scofield, W.E. Boles, & M. Archer, 2010. Biogeographical and phylogenetic implications of an Early Miocene wren (Aves: Passeriformes: Acanthisittidae) from New Zealand. *Journal of Vertebrate Paleontology* 30: 479–498.
- Worthy, T.H., & R.N. Holdaway, 2002. *The Lost World of the Moa*. Christchurch: Canterbury University Press.
- Worthy, T.H., A.J.D. Tennyson, M. Archer, A.M. Musser, S.J. Hand, C. Jones, B.J. Douglas, J.A. McNamara, & R.M.D. Beck, 2006. Miocene mammal reveals a Mesozoic ghost lineage on insular New Zealand, southwest Pacific. *Proceedings of the National Academy of Sciences of the United States of America* 103: 19419–19423.
<http://dx.doi.org/10.1073/pnas.0605684103>
- Worthy, T.H., A.J.D. Tennyson, S.J. Hand, & R.P. Scofield, 2008. A new species of the diving duck *Manuherikia* and evidence for geese (Aves: Anatidae: Anserinae) in the St Bathans Fauna (Early Miocene), New Zealand. *Journal of the Royal Society of New Zealand* 38: 97–114.
- Worthy, T.H., A.J.D. Tennyson, C. Jones, & J.A. McNamara, 2002. A diverse Early-Miocene (15–20 Ma) terrestrial fauna from New Zealand reveals snakes and mammals. *IPC2002, Geological Society of Australia, Abstracts* 68: 174–175.
- Worthy, T.H., A.J.D. Tennyson, C. Jones, J.A. McNamara, & B.J. Douglas, 2007. Miocene waterfowl and other birds from Central Otago, New Zealand. *Journal of Systematic Palaeontology* 5: 1–39.
<http://dx.doi.org/10.1017/S1477201906001957>
- Zelenitsky, D.K., & S.P. Modesto, 2003. New information on the eggshell of ratites (Aves) and its phylogenetic implications. *Canadian Journal of Zoology* 81: 962–970.
<http://dx.doi.org/10.1139/z03-076>

Appendix 1

Thickness of “thick” Miocene eggshell from the St Bathans deposits (combined data from Worthy *et al.*, 2007 and new data).

NMNZ S.	site	no. of pieces	thickness (mm)
40935	Croc Site, layer 1	1	0.95
40936	Vinegar Hill	8	0.90 × 2, 1.00, 1.06, 1.10 × 4
40937.1	HH1b “riverbank”	1	0.86
40937.2	HH1b “riverbank”	1	1.68
40938.1–3	HH1b “riverbank”	1 (3 parts)	1.02
40938.4	HH1b “riverbank”	1	0.76
40938.5–8	HH1b “riverbank”	1 (4 parts)	1.08
40938.9	HH1b “riverbank”	1	1.02
40939	HH1b “riverbank”	1	1.12
42469	Croc Site, layer 1	1	0.91
42726	HH1a	1 (2 parts)	1.03
42822	HH1d	1	0.74
42936	Croc Site, layer 1	1	0.97
43159	HH1a	1	0.88
43210	HH2b/c	1 (2 parts)	0.90
44312	HH1b “riverbank”	37	0.68, 0.69 × 2, 0.70, 0.77 × 2, 0.79 × 2, 0.80 × 2, 0.82 × 2, 0.83, 0.84 × 2, 0.85, 0.86, 0.88 × 5, 0.89 × 3, 0.90 × 4, 0.91 × 2, 0.94 × 2, 0.96, 0.98, 1.01, 1.03
44343	HH1d	1 (4 parts)	1.14
44346	HH1d	1	1.04
44347	Between HH1a & HH1d	1 (4 parts)	1.13
44695	Vinegar Hill surface	1	0.91
44701	HH1a	1	1.00
44713	HH2	1	1.16
44766	HH1b “riverbank”	1	1.09
50292	HH1a	1	0.89
50181	HH1b “trench”	36	0.58, 0.71, 0.74 × 2, 0.77, 0.79, 0.84, 0.85, 0.86, 0.87, 0.88, 0.89 × 2, 0.90, 0.91, 0.92, 0.94 × 2, 0.95 × 2, 0.96 × 5, 0.97 × 5, 1.04, 1.07 × 2, 1.08 × 2, 1.19
50497	other side of valley from the main Vinegar Hill sites	1	1.00
50793	HH1d	1 (3 parts)	0.60
50687	Vinegar Hill, site 2	21	0.77, 0.79 × 2, 0.80, 0.84, 0.88, 0.91, 0.94, 0.95 × 2, 0.97, 1.02, 1.03 × 2, 1.04, 1.07, 1.08 × 2, 1.09, 1.10, 1.12
50820	HH1a	28	0.76, 0.77, 0.78, 0.85, 0.87, 0.88, 0.89, 0.90, 0.92, 0.95, 0.96 × 2, 1.02, 1.03, 1.04 × 5, 1.05, 1.07, 1.08 × 3, 1.09 × 2, 1.14, 1.15
		total = 154	mean thickness of 0.94 (±0.12 s.d.) mm (n = 153, excluding S. 40937.2)

Appendix 2

Data matrix of character-state distributions for eggshell characters of Recent palaeognaths.

List of characters based on Zelenitsky & Modesto (2003) and Grellet-Tinner (2006), including the character numbers used by them in brackets. Some of Grellet-Tinner's (2006) characters were not used for the following reasons: they could not be applied to eggshell fragments (characters 1 & 2); they were the same in all taxa scored here (characters 8, 11 & 12); or, after considering descriptions and figures in Tyler (1957), Tyler & Simkiss (1960), Silyn-Roberts & Sharp (1985), Mikhailov (1997) and Zelenitsky & Modesto (2003), seemed too variable to be useful (character 14). The data for elephant birds are based on Tyler & Simkiss (1960), Mikhailov (1997) and Grellet-Tinner (2006):

- A (Zelenitsky & Modesto 59, Grellet-Tinner 10). EZ morphology:
 0 fine/porous, or
 1 blocky crystals.
- B (Zelenitsky & Modesto 60). Composition of mammillae:
 0 poorly defined acicular wedges, or
 1 well-defined tabular wedges.
- C (Zelenitsky & Modesto 61, Grellet-Tinner ?7). Mammillae proportions:
 0 wider than high, or
 1 higher than wide.
- D (Zelenitsky & Modesto 62, Grellet-Tinner 5). Pore canals:
 0 unbranched, or
 1 branched/forked.
- E (Zelenitsky & Modesto 63, Grellet-Tinner 3 and 4). Surficial ornamentation:
 0 present, or
 1 absent.
- F (Zelenitsky & Modesto 65, Grellet-Tinner 9 and 13). Resistant zone (RZ) between the SZ and EZ:
 0 absent, or
 1 present.
- G (Zelenitsky & Modesto 67). Vesiculation in MZ:
 0 present (strong), or
 1 absent (weak).
- H (Grellet-Tinner 6). Surficial pore-depression:
 0 round, or
 1 slit-like.
- I (Grellet-Tinner 15—we modified this character as descriptions and figures in Tyler (1957), Tyler & Simkiss (1960), Silyn-Roberts & Sharp (1985), Mikhailov (1997) and Zelenitsky & Modesto (2003) show that it is more variable than Grellet-Tinner (2006) presented). Ratio of EZ/SZ:
 0 greater than 0.2, or
 1 less than 0.2.

taxon	A	B	C	D	E	F	G	H	I
Tinamou	0–1	0	0	0	1	0	0	0	0 ^a
Moa	1	1	1	1 ^b	1	0	1	0–1 ^c	1
Miocene fossils (thick)	1	1	1	1	1	0	1	0–1	1
Kiwi	1	0	1	0	1 ^d	0	0	0	0
Cassowary	0	1	1	1	0	1	1	0	0
Emu	0	1	1	1	0	1	1	0	0
Ostrich	0	1	1	1	1	0	1	0	0–1
Rhea	0	1	1	1 ^b	1	0	1	0–1 ^c	1
Elephant bird	0	1	1	1 ^b	0–1	0	1	1	1

^a Grellet-Tinner (2006) considered tinamou to have an EZ/SZ ratio of 0.067 but Mikhailov (1997) and estimates from Grellet-Tinner (2006, fig. 21A) and Zelenitsky & Modesto (2003, fig. 1A) give a ratio > 0.2.

^b Grellet-Tinner (2006) considered moa, rheas and elephant birds to have unbranched pore canals but clear branched/forked canals were detected by other workers (Tyler & Simkiss, 1960; Mikhailov, 1997; Zelenitsky & Modesto, 2003) in these taxa.

^c Grellet-Tinner (2006) scored character H as 0 for rheas and 1 for moa but this varies within these groups (Gill, 2007, pers. obs.).

^d We follow Zelenitsky & Modesto (2003) in considering kiwi to have an absence of surficial ornamentation (contrary to Grellet-Tinner, 2006).