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DINORNIS –

AN INSULAR ODDITY, A TAXONOMIC CONUNDRUM REVIEWED.

Trevor H. WORTHY, Michael BUNCE, Alan COOPER & Paul SCOFIELD

Resum

Es revisa la història taxonòmica del gènere extingit de moa *Dinornis* (Aves: Dinornithiformes). Fins fa poc, les dimensions dels ossos i l'illa d'origen (Nord o Sud) eren els factors primordials per a la determinació específica dintre del gènere *Dinornis,* ja que es podia esperar que ocells avoladors evolucionats sobre diferents territoris aïllats podrien no pertànyer a la mateixa espècie. Anàlisis recents de DNA mitocondrial i nuclear han comportat una nova explicació de la variació de talla a *Dinornis*. En aquest treball establim una nova hipòtesi, derivada de la genètica, d'una espècie per illa, en la qual la variació de mida registrada a partir de les dades morfomètriques es deu a dimorfisme sexual revertit. Les dades de llargària dels principals ossos llargs s'analitzen per regió o per localitat i es demostra una bimodalitat clara en la qual les mitjanes per a les formes masculines i femenines varien entre regions/localitats, però pugen o baixen en paral·lel. Les bases de dades regionals demostren que a l'Holocè mitjà – superior els ocells més petits es trobaven a les zones subalpines i als boscos de muntanya i els més grans a les baixes altituds i a les regions pluvials baixes, tals com Canterbury (a l'est de l'Illa del Sud) i a la costa d'Horowhenua, al nord de Wellington, al sud de l'illa del Nord.
Paraules clau: *Dinornis,* Nova Zelanda, DNA fòssil

Abstract

The taxonomic history of the extinct moa genus *Dinornis* (Aves: Dinornithiformes) is reviewed. Until recently limb bone dimensions and island of origin (North or South) were the pre-eminent factors in species determination within the genus *Dinornis* due to the expectation that flightless birds on distinct landmasses could not be the same species. Recent morphological analyses applying modern concepts of biological variation reduced the number of acceptable taxa, but size remained of paramount importance in defining species boundaries. Recent analyses of mitochondrial and nuclear DNA have resulted in a radical new explanation of the size variation in *Dinornis*. Here we assess the new genetics-derived hypothesis of one species per island where the size variation seen in the morphometric data is due to reversed sexual dimorphism. Length data from main limb bones is analysed by region or site and demonstrates clear bimodality where averages for the male and female forms vary between regions/sites but move up or down in parallel. The regional datasets demonstrate that in the mid-late Holocene, birds were smallest in subalpine zones and montane forests and largest in low altitude and low rainfall regions such as Canterbury (in eastern South Island) and the Horowhenua coast north of Wellington in southern North Island.
Keywords: *Dinornis,* New Zealand, Ancient DNA

INTRODUCTION

The moas (Aves: Dinornithiformes) of New Zealand have excited palaeontologists and evolutionary biologists ever since their discovery by the scientific world in 1839 (Owen, 1840; 1842). Following the initial announcement that there had existed in New Zealand a struthious bird about the size of an ostrich, a wealth of bones were sent to England resulting in many species being described over the next few decades notably by Richard Owen, Julius von Haast, Richard Lydekker, and Frederick Hutton , as fully reviewed in Worthy & Holdaway (2002).

From the outset with Owen's early papers, size as measured by length and widths (proximal, shaft, and distal) of the leg bones (femora, tibiotarsi, tarsometatarsi)

were the main criteria for separating and diagnosing species of moa. Shape characters such as might be used in modern cladistic studies were not identified until Hutton's work in the 1890s. However, even for Hutton, size was of paramount significance, and he "allowed" only a certain amount of size variation within a species. For example, after not accepting the distinctiveness of *Palapteryx plenus* Hutton, 1891 and *Dinornis altus* Owen, 1879, Hutton (1892) distinguished the true dinornithids with length ranges for tibiotarsi as shown in Table 1.

After just a few years Hutton abandoned the method of separating moa species by absolute length and started to use a 'method of averages' where he plotted length and width onto cluster diagrams. Using such diagrams, he identified three 'clusters' in the data from the large South Island assemblages from Kapua and Enfield, causing

him to accept just *D. maximus*, *D. robustus* and *D. torosus* from these sites (Hutton, 1896a,b) and also from Glenmark (Hutton, 1897a). These analyses have influenced the subsequent taxonomic treatment of *Dinornis* and for first half of the twentieth century, three species in each of the North and South islands were generally accepted, e.g., Archey (1941). Oliver (1949) also basically accepted this arrangement but erected two new taxa for outliers in the size ranges in the North Island: *D. gazella* for a very small form and *D. hercules* for a very stout large form.

Authors supporting the distinctiveness of the North and South Island forms presented no data or only compared a very few bones. They did state, however, that the South Island forms attained greater size and had leg bones tending more robust than those in the North Island (e.g., Owen, 1846; Lydekker, 1891; Hutton, 1897b; Archey, 1941).

Like most palaeontological taxonomy in the 19th century the taxonomic decisions were influenced by the principles of Uniformitarianism formulated by Hutton and Lyell, which dictated that moas were giant flightless birds and were on separate island landmasses and thus had always been so. Until the acceptance of plate tectonics in the 1960s, the fixity of the present geography was generally assumed and certainly the rapidity with which tectonic activity can result in significant modifications to the geography was not appreciated. However, Archey (1941) noted that Cook Strait cannot have been a consistent barrier as he perceived one taxon with a New Zealand wide distribution, and that the several North-South taxon pairs varied in the amount of difference exhibited between the members of a pair, and that the Strait was geologically young – 'Late Pliocene'. He placed more significance on mountain barriers, but we now know that the axial ranges about Wellington for example are less than 2Ma old and the Southern Alps, less than 5-10Ma (Suggate, 1978). However, many of the terrestrial

birds found in the North and the South islands constitute North-South pairs of various antiquity. In the first catalogue of the birds of New Zealand (Hutton, 1871), only one flightless species was recorded as found on both islands: all others were restricted to one island. Among volant taxa, well distinguished North-South species pairs were recognised then, and continue to be now e.g., within the genera *Turnagra, Philesturnus, Callaeas, Petroica*, and *Mohoua* (Holdaway *et al.*, 2001, Worthy & Holdaway, 2002). Observations of the modern fauna undoubtedly swayed the interpretation of the osseous fragments.

MODERN MORPHOLOGICAL STUDIES

A modern biological approach to moa classification was introduced by Cracraft (1976a, b, c) when he applied acceptable ranges of size variation as ascertained from extant taxa to intrageneric populations of moa bones. Size variation was assessed by coefficients of variation (CV) and CVs of 10-12 were considered acceptable values in sexually dimorphic species, in contrast to species that lacked sexual size dimorphism where values of 3-5 were considered usual. This philosophy combined with a multivariate analysis of length and width measurements led Cracraft to accept just three species in *Dinornis*: *D. struthoides*, *D. novaezealandiae*, and *D. giganteus* ranging over both North and South islands, and provisionally *D. torosus* in the South Island.

One of the problems with assessing size variation in *Dinornis* is that members of this genus are generally uncommon in fossil sites and usually only a few individuals are represented in contrast to relatively much more abundant emeids. Therefore the data from the very large sites such as Kapua, Enfield and Glenmark that was available to Hutton was very significant. Due to judicious exchanges by Hutton and others a majority of these assemblages is now spread through many institutions around the world, making measurements of the original large samples impractical. Lumping data from individuals from many sites is less desirable as this introduces temporal and geographic variation which is known to be significant in other moa (Worthy & Holdaway, 2002). The remarkable assemblage from Makirikiri near Wanganui is the largest from a single site still accessible in a single collection. Worthy (1989) presented a simple length frequency analysis of the *Dinornis* femora, tibiotarsi and tarsometatarsi overlaid with joined lines for bones from individual skeletons. For each element there was a distinct group of small individuals that were referred to *Dinornis struthoides*. As the size range of larger bones spanned the range for *D. novaezealandiae* and *D. giganteus*, as given by Archey (1941) and Oliver (1949), Worthy (1989) considered that both taxa must be represented. Detecting a break in the distribution of tibiotarsi near 750 mm and using the linked lines of known individuals, *D. giganteus* was defined as having femora longer than 320 mm, tibiotarsi longer than 750 mm, and tarsometatarsi longer than 440 mm. These values are near the boundaries given by Archey (1941) and Oliver (1949) and so the three species arrangement seemed to be confirmed.

North Island:	Length	Metric conversion
D. excelsus	37.5-38 inches	952-965 mm
D. giganteus	34.2-36.0 inches	869-914 mm
D. firmus	30.0-33.0 inches	762-838 mm
D. ingens	27.0-29.5 inches	686-749 mm
D. gracilis	25.0-26.5 inches	635-673 mm
D. struthoides	22.0-23.5 inches	559-597 mm
South Island:		
D. maximus	39.0-39.2 inches	991-996 mm
D. validus	34.0-35.5 inches	864-902 mm
D. robustus	30.0-32.7 inches	762-831 mm
D. potens	27.0-29.5 inches	686-749 mm
D. torosus	24.0-25.3 inches	610-643 mm

Table 1. The length ranges in inches advocated by Hutton (1892) for tibiotarsi of *Dinornis* species.

Taula 1. *Intervals de llargària, en polçades, esmentats per Hutton (1892) per als tibiotarsos de les espècies de* Dinornis.

Having been able to distinguish other moa taxa on sets of characters for most leg bones and other major elements (Worthy, 1988), the inability to do likewise for *Dinornis* species was problematic. In an attempt to redress this situation, Worthy (1994) reassessed the taxonomy of *Dinornis* using cranial characters and multivariate analysis of leg bone measurements and accepted just three species with *D. torosus* in the synonymy of *D. novaezealandiae* following Worthy (1989). Taxa were separated on cranial features and then measurements of the associated leg bones from individual skeletons analysed. Crania were separated into three forms with the large and small size classes essentially identical, and the median size class separated from them by less well developed postorbital processes, not so prominent occipital tuberosities, and poorly developed mamillar tuberosities.

The analysis was hampered by small sample sizes and that as the groups of leg bones were predefined by crania that primarily differed in size, then they too necessarily were separated primarily by length. Multivariate analysis indicated that the middle sized class had slightly stouter bones. The three forms were accepted as species, and this taxonomic arrangement seemed to corroborate the trimodal structure Hutton (1896a,b; 1897b) had detected and which also seemed to be present in the large sample from Makirikiri in the North Island (Worthy, 1989). Moreover, as an earlier analysis of the distribution of moas had shown that while *D. struthoides* appeared to have a widespread distribution, *D. novaezealandiae* and *D. giganteus* had largely non-overlapping distributions (Worthy, 1990), the acceptance of three taxa made sense.

However, a recent reanalysis of the large Pyramid Valley *Dinornis* assemblage revealed that lengths for all individuals except one contributed to an essentially normal and unimodal size distribution. For example, excluding the smallest individual, tibiotarsi had a mean of 838 mm, ranged from 681-992 mm, and had a CV of 9.65. As a result all were referred to *D. giganteus*, except the small one, which was referred to *D. struthoides*. Elsewhere in New Zealand there are few faunas with sufficient numbers of *Dinornis* to analyze for the presence of distinct size clusters among individuals that may be presumed to represent natural groups, but the surviving bones in New Zealand collections from Te Aute constitute one. The 107 leg bones of *Dinornis* had a bimodal size distribution with the grouping of larger individuals having a size distribution near double the absolute range of that of the smaller individuals. As a result, two species *D. struthoides* and *D. giganteus* were accepted (Worthy, 2000).

Thus throughout the taxonomic history of the genus *Dinornis*, size has been of paramount importance in defining the taxa and no fewer than 17 species have been erected for dinornithids. There has been in essence an unwritten paradigm that only a certain amount of size variation is acceptable within a species. The degree of acceptable variation has increased through time so that recently Worthy & Holdaway (2002) indicated that lengths of tibiotarsi of *D. struthoides* ranged 27% less than the maximum length of 620 mm, *D. novaezealandiae* 23% less than 740 mm, and *D. giganteus* 31% less than of 992 mm.

This summary of the history of dinornithids essentially mirrors that for the moa group as a whole. Some 64 species have been erected (Worthy & Holdaway, 2002), but the most recent morphological analysis only accepted 11 species, two families, and six genera (Worthy & Holdaway 2002, Fig. 4.34 p. 130). In that study, based on 82 morphological characters, a consensus parsimony analysis provided strong support for the distinction of *Dinornis* from other moa, but was unable to resolve the branching order of *Anomalopteryx*, *Pachyornis*, *Emeus*+ *Euryapteryx*, and *Dinornis*.

ANCIENT DNA INVESTIGATIONS OF DINORNITHIDS

DNA degrades rapidly post-mortem; however given the right preservation conditions (cold and constant temperatures) DNA can persist in the environment for thousands of years. The extraction and amplification of "old" DNA, primarily from bones, is referred to as ancient DNA (aDNA). New Zealand is fortunate to have a suitable climate and an extensive Quaternary fossil record, a combination which makes it an ideal locality for aDNA studies.

The first aDNA investigations of moa were based on 12S mitochondrial DNA (mtDNA) and were designed to test the relationship between moas and other ratites (Cooper *et al.*, 1992). These early analyses were expanded and resulted in the complete mitochondrial genome for two moas being sequenced, revealing much about ratite phylogeny as well as plate tectonics following the break-up of Gondwana (Cooper *et al.*, 2001; Haddrath & Baker, 2001). MtDNA genes that mutate rapidly also provided valuable insights into the internal phylogenetic structure of Dinornithiformes (Cooper, 1997).

Initial analysis of sequence results from *Dinornis* somewhat surprisingly showed that phylogenetic trees bore no relationship to accepted morphological based taxonomy. Continued investigations into the *Dinornis* phylogeny using an enlarged data set and both mitochondrial and nuclear DNA have supported initial findings and reveal that all *Dinornis* individuals analysed, irrespective of referred taxon, form two genetically distinct allopatric populations dependant on the island of origin (Bunce *et al.*, 2003; Huynen *et al.*, 2003). Furthermore, there was no support for the association of individuals into taxa such as *D. struthoides* or *D. giganteus* within each island clade (Fig. 1). Even in the largest analysis that included several mitochondrial genes (in total about 2000 base pairs) and 32 individuals, no associations were evident that made sense relative to the current morphological taxonomy (Bunce *et al.*, 2003).

Good DNA preservation in some specimens has also allowed extraction and analyses of nuclear DNA, and so the sex-specific KW1 gene, first identified for ratites by Huynen *et al.* (2002), became the key to sexing moa. Many of the individuals could be sexed and the conclusion that *D. struthoides* were male birds and all larger individuals of *Dinornis* were female was reached more or less simultaneously by two research teams using an overlapping but not identical set of specimens (Bunce *et al.*, 2003; Huynen *et al.*, 2003). As a result, Bunce *et al.* (2003) advocated that *Dinornis* fossils can henceforth be

referred to *D. novaezealandiae* in the North Island and *D. robustus* in the South Island. Morphologically there is little to separate these two allopatric populations, but the deep genetic split may reflect a mid-Pleistocene divergence of the clades (Bunce *et al.*, 2003).

The data show that *Dinornis* had unprecedented (amongst birds) reversed sexual size dimorphism (RSD) with the largest females some 280% the weight and 150% the height of the largest sympatric males. Individual mass ranged 76-242 kg for females and 34-85 kg for males. Support for a single species of *Dinornis* is provided by data from sites and regional faunal assemblages that indicate average sex ratios, assuming *D. struthoides* were males and others female, of 1 male to 1.44 females, which is within the normal range for extant ratites (Bunce *et al.*, 2003).

This taxonomic arrangement serves to resolve several problems. For instance, Worthy (1994) noted that the type of *Dinornis giganteus* was not very representative of bones usually referred to that species, being rather small and therefore not overly good to distinguish the larger taxon from *D. novaezealandiae*. In addition, recent collections of *Dinornis* specimens have included several skulls in the size range of *D. novaezealandiae* yet with well-developed post-orbital processes, and prominent occipital and mamillar tuberosities (e.g., MNZ S32677), so it now appears that the development of these features has no taxonomic significance. As each feature is associated with the attachment site for ligaments, it is more probable that the prominence or otherwise of these features is individually variable and may be related to age of
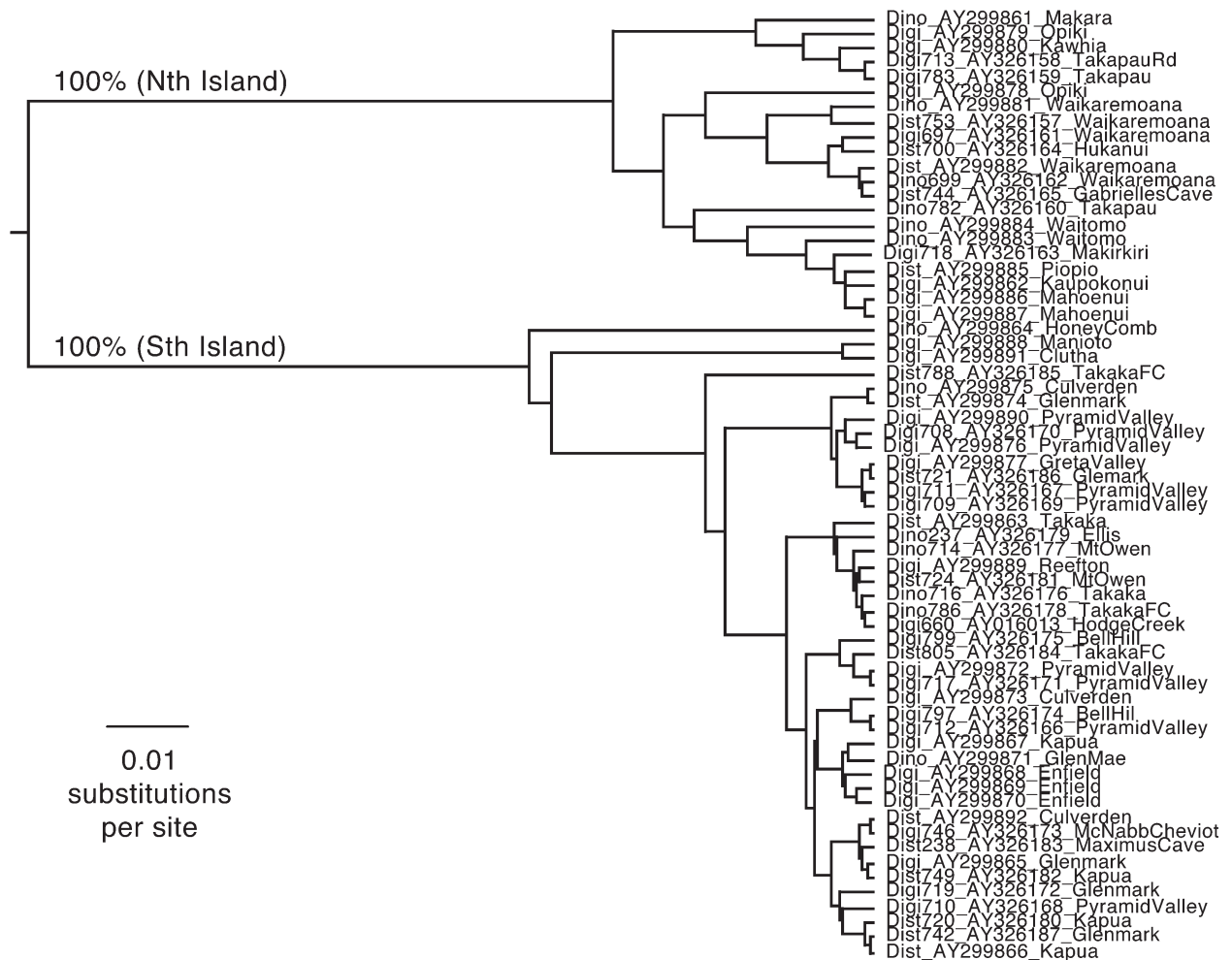

Fig. 1. The maximum *a posteriori* tree of *Dinornis* mitochondrial control region DNA sequences generated from the posterior distribution using Metropolis–Hastings MCMC (Drummond *et al.*, 2002). The sequences of between 243 and 375 base pairs in length are a combined dataset of Bunce *et al.* (2003) and Huynen *et al.* (2003). The associated tags indicate original species designation, GenBank accession number and sample location respectively (*D. giganteus* = Digi, *D. novaezealandiae* = Dino and *D. struthoides* = Dist). The split between the islands has a posterior probability of 100%, and based on other avian molecular rates, is estimated to be mid-Pleistocene in origin. Support for other nodes on the tree are not shown. Bayesian analysis was performed using BEAST (http://evolve.zoo.ox.ac.uk/beast/) using an HKY + G + I substitution model for 5000000 generations (Drummond *et al.*, 2002; Drummond & Rambaut, 2003).

Fig. 1. L'arbre a posteriori màxim de les seqüències de DNA de la regió control mitocondrial generada a partir de la distribució posterior fent servir MCMC Metropolis-Hastings (Drummond et al.*, 2002). Les seqüències d'entre 243 i 375 parells de bases són una base de dades combinada de Bunce* et al. *(2003) i Huynen* et al. *(2003). Les etiquetes associades indiquen respectivament les designacions específiques originals, els nombres d'accés al GenBank i la localització de la mostra (*D. giganteus = Digi, *D. novaezealandiae = Dino i *D. struthoides = Dist). La separació entre les illes té una probabilitat posterior del 100%, es basa en altres taxes moleculars ornítiques i s'estima que es va originar al Pleistocè mitjà. No es mostra el suport per a altres nodes de l'arbre. Es va dissenyar un anàlisi Bayesià emprant BEAST (http://evolve.zoo.ox.ac.uk/beast/) fent servir un model de substitució HKY + G + I per a 5000000 generacions (Drummond* et al.*, 2002; Drummond & Rambaut, 2003).*

the bird at death. The post-orbital processes do not consist of a specific bone identifiable in the juvenile bird such as the lacrymal, which contributes to the prefrontal process. Rather, post-orbital processes are just outgrowths of the frontals and expand through ontogeny (Worthy & Holdaway; 2002: 79-83) so mature birds might be expected to have better developed ones than younger yet also adult birds, as assessed by nasal fusion (last element in skull to fuse to rest of skull).

REGIONAL AND TEMPORAL VARIATION COMPLICATES MATTERS

How is this new hypothesis of small males and larger females to be resolved with the apparently disjunct distributions of *D. novaezealandiae* and *D. giganteus* described by Worthy (1990)? Hutton was the first to document regional and or temporal variation in a moa when he noted that specimens of *Meionornis* [now *Emeus*] were on average bigger in the presumed younger deposit

Fig. 2. Map of New Zealand showing study regions and sites from which samples of *Dinornis* bones were analysed. The 1000 m contour lines are shown and the margins show the New Zealand map series 260, 1:50000 metric grid.

Fig. 2. *Mapa de Nova Zelanda que mostra les regions d'estudi i les localitats a partir de les quals s'han analitzat les mostres d'ossos de* Dinornis. *Es mostren les línies de contorn de 1000 m i els marges, mapa de Nova Zelanda sèrie 260, xarxa mètrica 1:50000.*

of Enfield compared to those in Glenmark (Hutton, 1897a). And more recently Worthy (1987) and Worthy & Holdaway (1995; 2002) have demonstrated that there is significant regional size variation in some taxa, and equivalent or greater variation in mean individual size over time. That some moa exhibit geographical size variation does not seem to explain why females might change in size yet apparently the males did not across a landscape, which is what the differential distribution of *D. novaezealandiae* and *D. giganteus* necessitates.

This issue was resolved by Bunce *et al.* (2003) who presented some data to show that mean individual size in different populations of *Dinornis* assumed to be of similar Holocene age did vary significantly with habitat. They suggested that both sexes varied in size across a geographic gradient, but that as the size increase was small in absolute terms in the smaller sex (*D. struthoides*), it was not so obvious and the total size variation for the small sex was able to be encompassed in the one taxon. In contrast, for the larger sex, a 20% increase in size, essentially moved some individuals out of the acceptable range for one species (*D. novaezealandiae*), so that they were necessarily referred to *D. giganteus*.

Our aim here is to enlarge the datasets used by Bunce *et al.* (2003) and assuming *D. struthoides* to be male and larger *Dinornis* to be female, assemble comparative data for various fossil localities or regions to assess geographic variation in limb bone sizes and whether it is in fact consistent for each sex.

METHODS

The database provided by Bunce *et al.* (2003) was taken as a starting point and expanded by THW. Data was collected for *Dinornis* from selected study regions and sites as follows (Fig. 2). Total lengths of adult *Dinornis* bones were measured for specimens as per the methods of Worthy (1987). For the North Island, the data from disassociated bones used in the Makirikiri analysis (Worthy, 1989) and Te Aute (Worthy, 2000) were augmented by measurements of individuals from the Takapau Road site, whose fauna was described by Worthy (1989), and a combination of individual skeletons from numerous cave sites located within lowland closed forest habitat in the Waitomo and Waikaremoana areas in the central North Island. The Makirikiri fauna is of late Holocene in age (Huynen *et al.*, 2003), Te Aute dates to the Late Glacial (Worthy, 2000), and Takapau is of late Holocene age (authors unpublished data). The individuals from the Waitomo and Waikaremoana areas are assumed to be mainly of Holocene age as all were surface collected specimens and all Waikaremoana specimens are from sites within the rockfall that formed the lake 2200 yrs BP (Newnham *et al.*, 1998).

For the South Island, only Pyramid Valley provides a large assemblage that is now easily accessed, the material from others like Kapua, Enfield and Glenmark is now either destroyed or dispersed to dozens of museums around the world where often its locality data is now lost. The Pyramid Valley site has a unique taphonomy
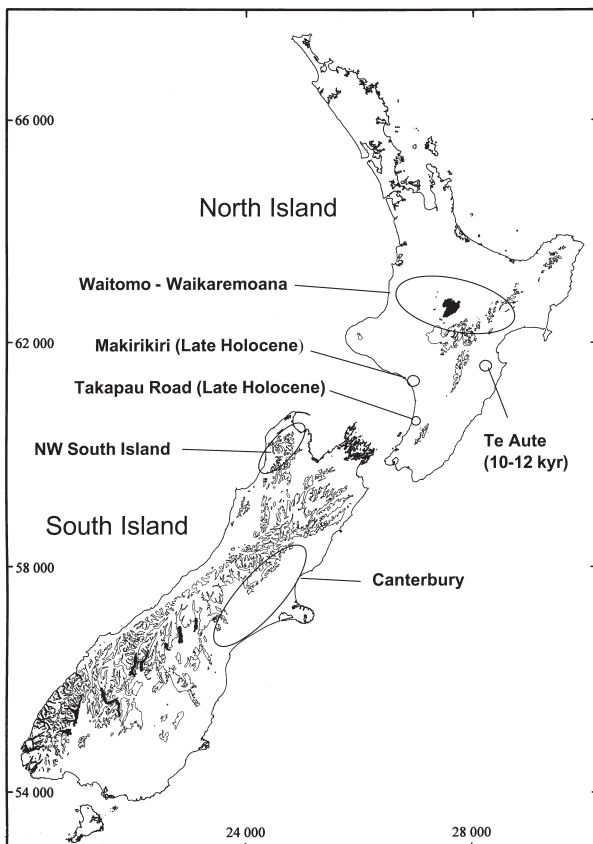
(Holdaway & Worthy, 1997) and females dominate the *Dinornis* assemblage. Therefore, variation in the Canterbury region was assessed by making regional compilations of data from disassociated material from late Holocene sites. Data were taken from bones from Pyramid Valley, Glenmark, Bell Hill Vineyard, Cheviot Swamp, Kapua, and Enfield (Worthy & Holdaway, 1996; Worthy 1997; 1998).

Data from the north-western South Island region for sites under 600 m altitude were compiled from individuals from the Punakaiki karst region (Worthy & Holdaway, 1993), Honeycomb Hill Cave System in the Oparara River (Worthy, 1993), and from karst in the Buller River. All these individuals were found on cave floors and most are assumed to be of Holocene age. An upland assemblage of fossils from this same region but from sites above 600 m was compiled from individual skeletons from caves on Mt Owen, Mt Arthur and Takaka Hill. Those on Mt Owen

and Mt Arthur are assumed to be of Holocene age as these regions were ice-covered during the late Pleistocene. Those from Takaka Hill are assumed or known to be mostly of Holocene age (Worthy & Holdaway, 1994; Worthy & Roscoe, 2003).

Sex was assessed by plotting the lengths of all bones from the site or assemblage as histograms which revealed clear bimodal size distributions. Boundaries between the two size distributions were determined as described in Appendix 1. Thus femora shorter than 290 mm in the Waitomo-Waikaremoana area were classed as males, those longer as female. For assemblages based on individuals, the summary statistics of the lengths of the associated tibiotarsi and tarsometatarsi were then calculated for each femur-determined sex. For the assemblages based on disassociated individuals the intermediate point

Fig. 3a. Length frequency histograms for named elements of *Dinornis* from Canterbury sites, specimens listed in Appendix 2.

Fig. 3a. Histogrames de freqüència de llargàries per als elements indicats de Dinornis *de les localitats de Canterbury, exemplars llistats a l'apèndix 2.*

Fig. 3b. Length frequency histograms for named elements of *Dinornis* from Makirikiri, North Island, data from Worthy (1989).

Fig. 3b. Histogrames de freqüència de llargàries per als elements indicats de Dinornis *de Makirikiri, Illa del Nord, dades de Worthy (1989).*

between each mode for each element was used to delimit putative sex boundaries. Femur lengths of each sex only overlapped in the Northwest Nelson >600 m assemblage, but here the males were noticeably more slender than females. Eight of the 15 individuals were sexed genetically including all in the overlap zone (Appendix 2).

Height of the birds was assessed as the sum of the lengths of the femur, tibiotarsus and tarsometatarsus. It is acknowledged that the femur is usually held at about
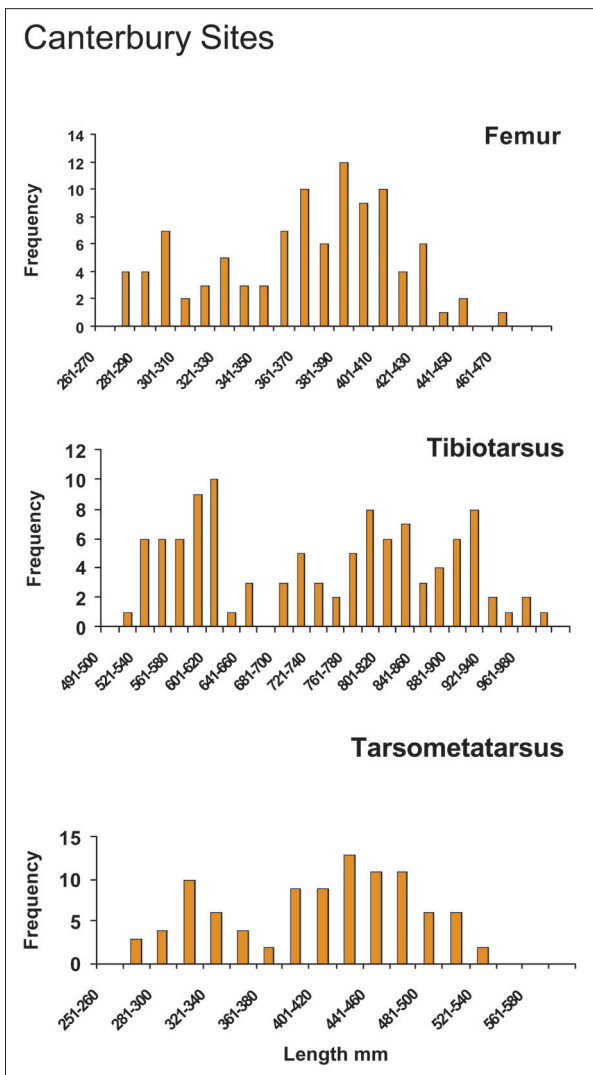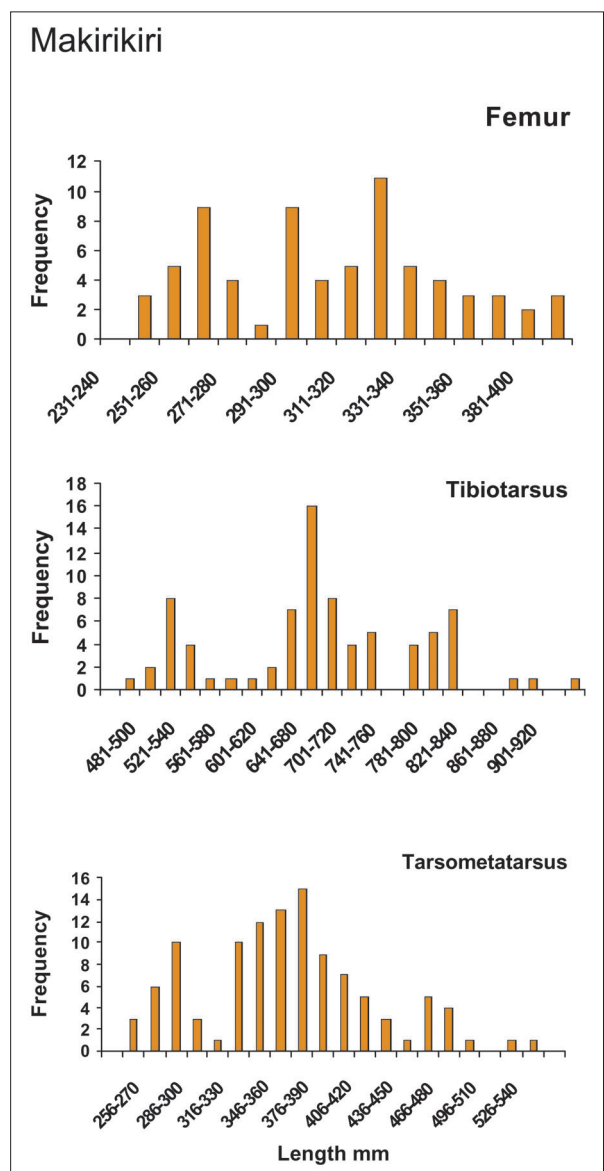

Fig. 3c. Length frequency histograms for femora of *Dinornis* from combined South Canterbury sites, specimens listed in Appendix 2.

Fig. 3c. Histogrames de freqüència de llargàries per a fèmurs de Dinornis *de les localitats combinades de Canterbury, exemplars llistats a l'apèndix 2.*

Fig. 3d. Length frequency histograms for femora of *Dinornis* from sites less than 600 m altitude in northwest South Island, specimens listed in Appendix 2.

Fig. 3d. Histogrames de freqüència de llargàries per a fèmurs de Dinornis *de localitats de menys de 600 m d'altitud al nord-oest de l'Illa del Sud, exemplars llistats a l'apèndix 2.*

30-45 degrees below horizontal (Worthy & Holdaway, 2002) and so only about half of its length contributes to the bird's height, but the tibiotarsus and tarsometatarsus are usually oriented near enough to vertical in life. However, the height above the femur in the pelvis and overlying tissues roughly equates to half a femur length so the sum of lengths of the three bones roughly approximates the height of the bird at its back. While this may be inexact, the method gives a consistent comparative height for the back among individuals. Comparative estimates of mass were generated with an algorithm based on femur length (Prang *et al.*, 1979).

RESULTS

Summary data for lengths of femora, tibiotarsi, and tarsometatarsi, and for height and mass by site or region, as defined above, is presented in Appendix 1. Exemplary length frequency histograms of this data are shown in Fig. 3. Summary statistics of mass data derived from femur length are plotted graphically in Fig. 4.

The length data shows that North Island populations of *Dinornis* from the Late Glacial deposits at Te Aute, and from Holocene assemblages from closed forest habitats in the Waitomo – Waikaremoana region and Makirikiri, each have similar mean values for males and females. However, the population from Takapau Road, which is in a lowland dune-swale shrubland forest mosaic area, had mean values for both females and males considerably larger than for the other North Island populations despite also being of late Holocene age.

The absolute size range was usually greater for females than males and larger samples had greater variation. The assemblage of individual skeletons from Waitomo-Waikaremoana had more females than males, but the CVs were broadly similar between the sexes indicating a similar relative size range for each sex. In contrast, the large collection from Makirikiri had over twice as many females as males and variation within females was 2-3 times that shown by males (CVs females 9.22-12.55 *vs.* 3.4-5.17 for males). The small number of males in Takapau Road precludes meaningful comparisons of absolute size range with the females, but the size variation of females was similar to that in the Makirikiri sample.

The South Island populations had some differences from those in the North Island. The size distributions of the sexes were essentially abutting in the South Island samples, whereas they were more widely separated in the North Island. Secondly, the South Island exhibits more inter-population variation. While females in the higher rainfall zones of northwest South Island from less than 600 m altitude were of similar size to females from the Waitomo – Waikaremoana region, the males were larger, and not as differentiated in size from the females as in the North Island populations. For individuals from altitudes above 600 m in the northwest South Island (mainly Takaka Hill, Mt Owen, and Mt Arthur), females had smaller mean masses than those at lower altitude and the size of males overlapped that of females. In these instances sex was determined genetically. Males had
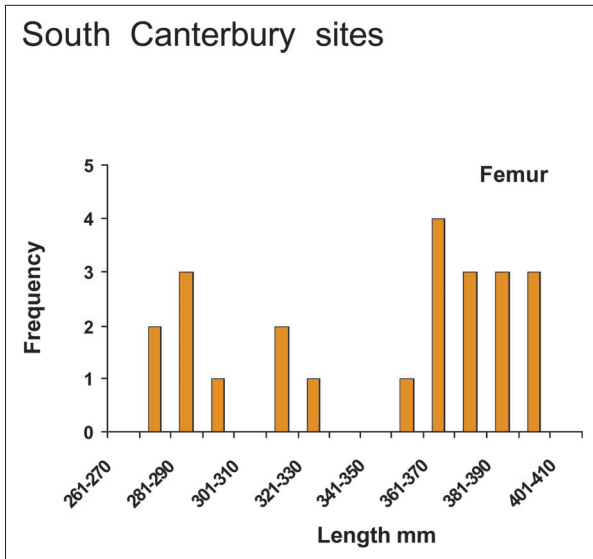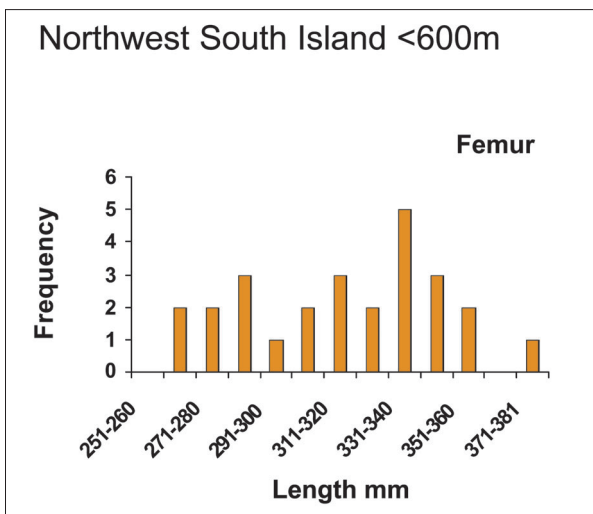
more slender leg bones than females but, as the range of femur lengths overlapped and as mass is here based on femur length, the ranges of calculated body mass necessarily overlap. But the more slender elements of the males suggest the algorithm may over-estimate mass of males in these cases. The size variation for each sex in Northwest South Island birds, in areas both above and below 600 m altitude, was similar, as indicated by CV values, mirroring the situation for North Island birds in the Waitomo – Waikaremoana region. Both the males and females in eastern South Island were larger than their equivalents in northwest South Island, thus paralleling the trend seen in the North Island between the wetter climate regions with closed forests and the drier climate experienced around the Takapau Road site. The size variation observed in each sex for the Eastern South Island sample was also very similar, that is each had similar CV values, in marked contrast to the situation for Makirikiri. This suggests that a collecting and or preservation bias may have resulted in fewer of the smaller bones of males being recovered in the Makirikiri sample: imperfect bones are noticeably under-represented in this collection.

Basically populations with the largest samples have the greatest absolute size ranges, e.g., Makirikiri and Eastern South island, but the average mass for Makirikiri is similar to that of the Waitomo – Waikaremoana sample which is from a similar habitat.

DISCUSSION

The existence of clear bimodal size distributions for *Dinornis* within discrete geographic areas supports the hypothesis that only a single species with strong sexual dimorphism is present in each island, as advocated by Bunce *et al.* (2003) based on genetic evidence. North Island birds are referred to *D. novaezealandiae* and South island birds to *D. robustus*. The data clearly show that the mean size of males and females moves in unison across the landscape. It also reveals considerable size variation between geographic regions of each of North and South islands. The size distributions of North Island males and females characteristically have a greater separation than do their South Island counterparts where size distributions of each sex more or less abut or even overlap (as measured by femur length) in one region.

Across the central North Island, the size of individuals appears to have remained remarkably similar over time, if the late Glacial Te Aute sample is representative of older faunas. However, birds in the Waitomo – Waikaremoana and Makirikiri populations were markedly smaller than those in the contemporary Takapau Road deposit. The former populations lived in a closed-canopy lowland podocarp forest (McGlone, 1988) whereas the Takapau Road site is in a coastal dune – swale area where scrub-forest mosaic vegetation was likely. These vegetation differences reflect a combination of average rainfall, propensity for summer drought and soils. In the Waitomo – Waikaremoana region rainfall is presently 1500-2000 mm whereas at Makirikiri rainfall is about 900 mm, but summer drought is rare and a closed-canopy forest prevailed during the Holocene. In contrast, on the Horowhenua Coast about Takapau Road rainfall is 750-1000 mm (NIWA data 1971-2000), but summer drought is common, which combined with well-drained sand substrates and wet interdune swamps would have resulted in a variety of vegetation types.

The northwest South Island below 600 m originally had similar vegetation and climate characteristics (wet, > 2000 mm rainfall, closed-canopy podocarp forest) to that in the central North Island, and the birds were of similar
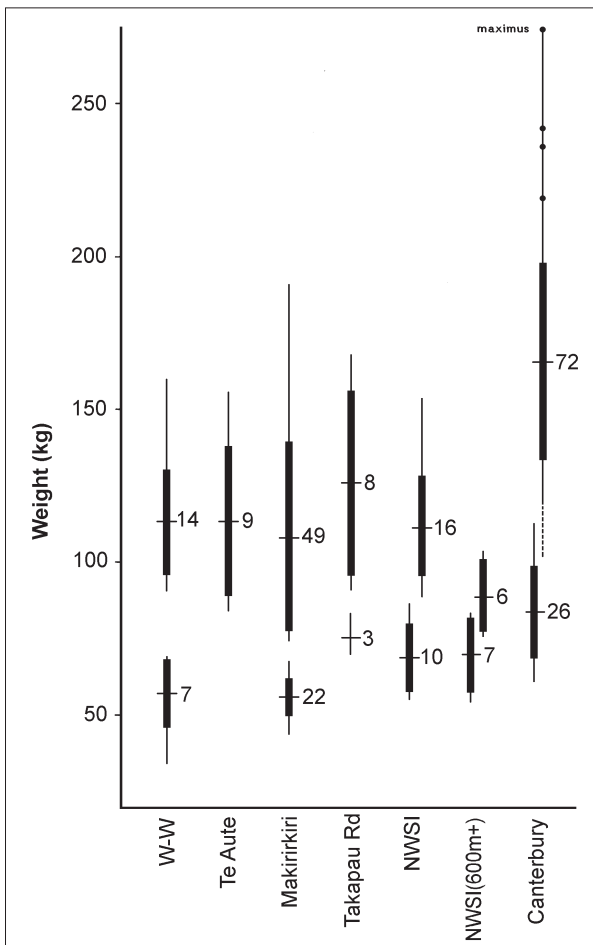
Fig. 4. A plot of weight data derived from femur length for named sites and regions. Each plot shows mean (small horizontal bar), standard deviation (filled box), range (line), and *n*. Males (smaller) are plotted separately to females, data derived from Appendix 1. W-W is Waitomo-Waikaremoana region, NWSI is northwest South Island. The dots adjacent to the plot for NWSI (600m+) represent data points for known sexed individuals determined genetically. The plot for females from Canterbury includes the data for the four largest individuals (dots on the range line) showing how much of the extreme in range is accounted for by few individuals. The largest individual ever documented is the type of *Dinornis maximus*.

Fig. 4. *Diagrama de dades de pes derivat de les llargàries de fèmurs per a les localitats i regions esmentades. Cada diagrama mostra la mitjana (petita barra horitzontal), la desviació típica (rectangle ple) l'interval (línia) i n. Els mascles (més petits) es presenten separats de les femelles. Dades obtingudes a partir de l'apèndix 1. W-W és la regió Waitomo-Waikaremoana, NWSI és el noroest de l'Illa del Sud. El diagrama per a les femelles de Canterbury inclou les dades dels 4 individus més grans (punts a la línia d'interval) i mostra com gran part dels extrems de l'interval es deu a pocs individus. L'individu més gran mai documentat és el tipus de* Dinornis maximus.

size to birds from that region. But at higher altitudes, it is as if *Dinornis* encountered a maximum size limit and so mean female size was reduced markedly compared to lowland equivalents, but males were only marginally smaller. In direct contrast, in lowland eastern regions, it is as if size limiting factors were relaxed and so while both males and females were both larger than western counterparts, females exhibited a greater size increase. Individual females from this region achieve the largest size for the species *D. robustus*. In these eastern lowlands rainfall is typically 500-750 mm (NIWA data 1971-2000) and a grassland - scrub – forest mosaic existed in the late Holocene.

Therefore size variation in *Dinornis* appears strongly correlated with palaeo-vegetation characteristics. At this stage we can only speculate that the drier regions with grass-scrub-forest mosaics provided an on average more nutritious browse than wet closed-canopy forests. Conversely, the upland montane forests of *Nothofagus* and their bounding subalpine zones provided the least nutritious food. Perhaps now that we can perceive *Dinornis* as a highly variable species, the causes of this variation may be able to be traced with interpretations of diet by isotope analyses.

Moreover, now that the sexes are able to be recognised perhaps the sex composition in different sites may reveal something of the behaviour of these birds. Surely the extent of this reversed sexual dimorphism will have necessitated complex mating behaviour at the least. Such behaviour did not involve violence as no part of the skeleton appears adapted towards combat, unlike in a cassowary, which has a lengthened ungual spur on digit 2, which provides an effective weapon in defence. However, does this RSD also suggest differential resource partitioning among the sexes. For example, male cassowary not only incubates the eggs but look after the young while they grow in the absence of the females (Marchant & Higgins, 1990).

Perhaps this RSD is integral to understanding the distribution of *Dinornis* fossils in Pyramid Valley swamp. Most assemblages or sites, e.g., Bell Hill Vineyard, where collector bias was eliminated, have a male to female ratio of about 1:1, but in Pyramid Valley there were only five males (femur length < 340 mm) and the other 47 adult birds were female. Pyramid Valley differs from other swamp entrapment sites in another vital way: it was a shallow lake wherein birds only became trapped in drought conditions (summer) when water levels receded and birds were able to walk out over the lake sediments and break through a crust of peat into the gyttja below (Holdaway & Worthy, 1997). The apparent absence of males is not explained by the site somehow not trapping smaller moas as the much smaller *Emeus crassus* is abundant. Moreover, there is a parallel paucity of juvenile *Dinornis* in the deposit, only 9 of 63 birds in total (Holdaway & Worthy, 1997), yet all other typical spring-hole type swamps, where entrapment is essentially random throughout the year, have roughly equal proportions of males and females and a high number of juveniles. For example, Bell Hill Vineyard is only a couple kilometres from Pyramid Valley but has roughly equal proportions of sexes (unpubl. data). The highly seasonal frequency of entrapment in Pyramid Valley and the near absence of males suggests that males and females were segregated over summer. Perhaps there is a parallel with cassowary in that females are separated from the males and young for part of the year, and if so it suggests that the larger females controlled prime habitat around water in times of stress such as summer.

CONCLUSION

On islands, paradigms constructed from data taken from continental situations may be inappropriate. Here we have demonstrated that intraspecific size variation in the genus *Dinornis* is greater than that for any other bird. Such variation is due to extreme reversed sexual dimorphism and significant geographic variation. It is not surprising that in the "land of birds", New Zealand has produced another insular extreme, with not only the tallest bird, but one with the greatest degree of reversed sexual dimorphism known in the avian world.

ACKNOWLEDGEMENTS

REFERENCES

Archey, G. 1941. The moa: a study of the Dinornithiformes. *Bulletin of the Auckland Institute and Museum, no. 1.* 145 p.

Bunce, M., Worthy, T.H., Ford, T., Hoppitt, W., Willerslev, E., Drummond, A. & Cooper, A. 2003. Extreme reversed sexual size dimorphism in the extinct New Zealand moa *Dinornis*. *Nature*, *425*: 172-175.

Cooper, A. 1997. Ancient DNA and avian systematics: From Jurassic Park to modern island extinctions. *In* Mindell, D. (ed.), *Avian Molecular Evolution and Molecular Systematics*: 345-373. Academic Press.

Cooper, A., Lalueza-Fox, C., Anderson, S., Rambaut, A., Austin, J. & Ward, R. 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature*, 409: 704-707.

Cooper, A., Mourer-Chauvire, C., Chambers, G.K., Haeseler, A., Wilson, A.C. & Pääbo, S. 1992. Independent origins of New Zealand moas and kiwis. *Proceedings of the National Academy of Sciences, USA*, 89: 8741-8744.

Cracraft, J. 1976a. Covariation patterns in the post-cranial skeleton of the moas (Aves, Dinornithidae): a factor analytic study. *Paleobiology*, 2: 166-173.

Cracraft, J. 1976b. The hindlimb elements of the moas (Aves, Dinornithidae): a multivariate assessment of size and shape. *Journal of Morphology*, 150: 495-526.

Cracraft, J. 1976c. The species of moas (Aves: Dinornithidae). *Smithsonian Contributions to Paleobiology*, 27: 189-205.

Drummond, A.J. & Rambaut, A. 2003. BEAST v1.0, Available from http://evolve.zoo.ox.ac.uk/beast/.

Drummond, A.J., Nicholls, G. K., Rodrigo, A. G. & Solomon, W. 2002. Estimating mutation parameters, population history and genealogy simultaneously from temporally spaced sequence data. *Genetics*, 161: 1307-1320.

Haddrath, O. & Baker, A.J. 2001. Complete mitochondrial DNA genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proceedings of the Royal Society London Series B*, 268: 939-945.

Holdaway, R.N. & Worthy, T.H. 1997. A reappraisal of the Late Quaternary fossil vertebrates of Pyramid Valley Swamp, North Canterbury, New Zealand. *New Zealand Journal of Zoology*, 24: 69-121.

Holdaway, R.N., Worthy, T.H. & Tennyson, A.J.D. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology*, 28(2): 119-187.

Hutton, F.W. 1871. *Catalogue of the birds of New Zealand with diagnoses of species*. Geological Survey of New Zealand, James Hughes, Printer, Ix. Wellington. 85 pp.

Hutton, F.W. 1892. The moas of New Zealand. *Transactions and proceedings of the New Zealand Institute*, 24: 93-172.

Hutton, F.W. 1896a. On a deposit of moa-bones at Kapua. *Transactions and proceedings of the New Zealand Institute*, 28: 627-644.

Hutton, F.W. 1896b. On the moa bones from Enfield. *Transactions and proceedings of the New Zealand Institute*, 28: 645-650.

Hutton, F.W. 1897a. On the leg bones of *Meionornis* from Glenmark. *Transactions and proceedings of the New Zealand Institute*, 29: 558-560.

Hutton, F.W. 1897b. The moas of the North Island of New Zealand. *Transactions and proceedings of the New Zealand Institute*, 29: 541-557.

Huynen, L., Millar, C.D. & Lambert, D.M. 2002. A DNA test to sex ratite birds. *Molecular Ecology*, 11: 851-856.

Huynen, L., Millar, C.D., Scofield, R.P. & Lambert, D.M. 2003. Nuclear DNA sequences detect species limits in ancient moa. *Nature*, 425: 175-178.

Lydekker, R. 1891. *Catalogue of fossil birds in the British Museum (Natural History)*. British Museum (Natural History). London. 368 pp.

McGlone, M.S. 1988. New Zealand. *In* Huntley, B. & Webb, T. III, (eds.), *Handbook of vegetation science, Volume 7: Vegetation history*: 557-599. Kluwer Scientific Publishers. Dordrecht, Netherlands.

Marchant, S. & Higgins, P.J. (coords.) 1990. *Handbook of Australian, New Zealand & Antarctic birds, vol. 1 - Ratites to Ducks*. Oxford University Press, Melbourne.

Newnham, R.M., Lowe, D.J. & Matthews, B.W. 1998. A late Holocene and prehistoric record of environmental change from Lake Waikaremoana, New Zealand. *The Holocene*, 8: 443-454.

Oliver, W.R.B. 1949. The moas of New Zealand and Australia. *Dominion Museum Bulletin*, 15. 206 p.

Owen, R. 1840 [March]. [untitled: On the bone of an unknown struthious bird from New Zealand, read meeting of November 12, 1839] *Proceedings of the Zoological Society London* for 1839, VII, No, lxxxiii,: 169-171.

Owen, R. 1842. Notice of a fragment of femur of a gigantic bird of New Zealand. *Transactions of the Zoological Society of London*, III(1): 29-33.

Owen, R. 1846 [July]. [Proceedings of a meeting: Owen read his second memoir on *Dinornis* remains]. *Proceedings of the Zoological Society, London for 1846.* XIV, No. clx: 46-49.

Prang, H.D., Anderson, J. F. & Rahn, H. 1979. Scaling of skeletal mass to body mass in birds and mammals. *American naturalist*, 113 (1): 103-122.

Suggate, R.P. 1978. *The geology of New Zealand*. Government Printer. Wellington, New Zealand.

Worthy, T.H. 1987. Sexual dimorphism and temporal variation in the North Island moa species *Euryapteryx curtus* (Owen) and *Pachyornis mappini* Archey. *National Museum of New Zealand Records*, 3 (6): 59-70.

Worthy, T.H. 1988. An illustrated key to the main leg bones of moas (Aves: Dinornithiformes). *National Museum of New Zealand Misc. Publ. Series*, 17. 37pp.

Worthy, T.H. 1989. An analysis of moa bones (Aves: Dinornithiformes) from three lowland North Island swamp sites: Makirikiri, Riverlands and Takapau Road. *Journal of the Royal Society of New Zealand*, 19: 419-432.

Worthy, T.H. 1990. An analysis of the distribution and relative abundance of moa species (Aves: Dinornithiformes). *New Zealand Journal of Zoology*, 17: 213- 241.

Worthy, T.H. 1993b. *Fossils of Honeycomb Hill*. Museum of New Zealand Te Papa Tongarewa. 56 p.

Worthy, T.H. 1994. Reappraisal of *Dinornis* (Aves: Dinornithiformes) species - a morphometric analysis. *New Zealand Journal of Zoology*, 21: 113-134.

Worthy, T.H. 1997. Quaternary fossil fauna of South Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 27 (1): 67-162.

Worthy, T.H. 1998. Quaternary fossil faunas of Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 28 (3): 421-521.

Worthy, T.H. & Holdaway, R.N. 1993. Quaternary fossil faunas from caves in the Punakaiki area, West Coast, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 23 (3): 147-254.

Worthy, T.H. & Holdaway, R.N. 1994. Quaternary fossil faunas from caves in Takaka valley and on Takaka Hill, northwest Nelson, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 24 (3): 297-391.

Worthy, T.H. & Holdaway, R.N. 1995. Quaternary fossil faunas from caves on Mt Cookson, North Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 25 (3): 333-370.

Worthy, T.H. & Holdaway, R.N. 1996. Quaternary fossil faunas, overlapping taphonomies, and palaeofaunal reconstruction in North Canterbury, South Island, New Zealand. *Journal of the Royal Society of New Zealand*, 26 (3): 275-361.

Worthy, T.H. & Holdaway, R.N. 2002. *The lost world of the moa: Prehistoric life of New Zealand*. Indiana University Press, Indiana. Xxxiii + 718 pp.

Worthy, T.H. & Roscoe, D. 2003. Takaka Fossil Cave – a stratified Late Glacial to Late Holocene deposit from Takaka Hill, New Zealand. *Tuhinga*, 14: 41-60.

Appendix 1. Summary statistics for bone lengths mm (Fem, femora; Tib, Tibiotarsi; Tmt, tarsometatarsi). Height as sum of leg bone lengths provides an estimate of height of the back, and weights based on femur length (Prang *et al.*, 1979). Height is only computed from lengths from constituent bones of individual skeletons. Sexes were defined by gaps in bimodal distribution of data for each region. Cut-off length values (mm) are given in the row by the sex.

Apèndix 1. Resum estadístic per a les llargàries dels ossos, en mm (Fem, fèmurs; Tib, tibiotars; Tmt, tarsometatarsos). L'alçària, com a la suma de les llargàries dels ossos del membre, que subministra una estima de l'alçària al dors, i el pes està basat en la llargària del fèmur (Prang et al.*, 1979). L'alçària només es computa a partir de les llargàries d'ossos que formen part d'esquelets individualitzats. Els sexes es defineixen a partir dels buits a la distribució bimodal de les dades per a cada regió. A les fileres es donen els valors límits per sexe.*

Waitomo – Waikaremoana region

	FemL	TibL	TmtL	Height	Weight
Females	>290	>570	>310		
Mean	339.9	709.8	371.9	1413.8	113.5
Standard Error	4.44	11.24	7.79	26.11	4.31
Standard Deviation	16.61	42.06	24.62	82.55	16.14
Minimum	315	660	328	1324	91
Maximum	385	810	421	1616	160
Count	14	14	10	10	14
CV	4.89	5.93	6.62	5.84	14.22
Males					
Mean	264.3	504.1	276.3	1052.6	56.6
Standard Error	7.65	10.89	7.63	30.39	4.14
Standard Deviation	20.23	32.66	20.18	67.95	10.96
Minimum	222	462	247	934	34
Maximum	285	541	301	1103	69
Count	7	9	7	5	7
CV	7.65	6.48	7.30	6.46	19.34

Makirikiri. Data previously figured by Worthy (1989).

	Fem L	Tib L	Tmt L	Weight	
Females	>290	>570	>310		
Mean	333.3	713.3	381.7	109.1	
Standard Error	4.39	9.65	5.11	4.24	
Standard Deviation	30.72	76.58	47.92	29.66	
Minimum	292	580	312	74	
Maximum	411	940	530	191	
Count	49	63	88	49	
CV	9.22	10.74	12.55	27.19	
Males					
Mean	263.6	512.9	271.9	55.8	
Standard Error	2.19	4.35	3.00	1.28	
Standard Deviation	10.28	17.41	14.07	6.02	
Minimum	242	480	242	44	
Maximum	284	545	298	68	
Count	22	16	22	22	
CV	3.90	3.40	5.17	10.79	

Te Aute (Late Glacial), unpublished length data (Worthy, 2000).

	Fem L	Tib L	Tmt L	Weight	
Females	>290	>570	>310		
Mean	338.2	780.8	434.2	112.8	
Standard Error	8.83	21.19	8.79	8.24	
Standard Deviation	26.48	51.89	44.83	24.72	
Minimum	306	680	342	84	
Maximum	382	832	507	156	
Count	9	6	26	9	
CV	7.83	6.65	10.32	21.92	
Males					
Mean	229.5	460.2	260.7	37.8	
Standard Error	1.50	1.78	3.56	0.69	
Standard Deviation	2.12	4.36	16.30	0.97	
Minimum	228	455	227	37	
Maximum	231	466	295	38	
Count	2	6	21	2	
CV	0.92	0.95	6.25	2.57	

Takapau Road (Late Holocene) authors' unpublished data.

	FemL	TibL	TmtL	Height	Weight
Females	>310	>640	>330		
Mean	352	734	405	1516	126
Standard Error	10.74	28.78	14.46	90.60	10.65
Standard Deviation	30.39	81.40	43.37	181.19	30.14
Minimum	315	650	351	1321	91
Maximum	392	855	472	1719	168
Count	8	8	9	4	8
CV	8.63	11.09	10.72	11.96	23.89
Males					
Mean	294	545	295	1129	75
Standard Error	5.78	5.07	7.50	7.00	4.18
Standard Deviation	10.02	10.13	10.61	9.90	7.24
Minimum	286	530	287	1122	70
Maximum	305	552	302	1136	83
Count	3	4	2	2	3
CV	3.41	1.86	3.60	0.88	9.62

Northwest South Island (<600m asl)

	FemL	TibL	TmtL	Height	Weight
Females	>305	>645	>330		
Mean	337	695	369	1429	111
Standard Error	4.33	12.18	6.04	33.62	4.10
Standard Deviation	17.34	45.57	21.77	88.96	16.41
Minimum	312	650	341	1348	89
Maximum	380	786	403	1567	154
Count	16	14	13	7	16
CV	5.14	6.55	5.91	6.22	14.76
Males					
Mean	285	563	283	1140	70
Standard Error	5.01	11.99	6.89	31.36	3.40
Standard Deviation	15.84	41.53	24.85	89.83	10.77
Minimum	262	505	248	1031	55
Maximum	310	642	325	1267	87
Count	10	12	13	8	10
CV	5.56	7.37	8.77	7.88	15.48

Northwest South Island (>600m asl): (Takaka Hill, Mt Arthur, Mt Owen). Specimens sexed by DNA (Appendix 2) and relative stoutness as bone lengths overlap.

	FemL	TibL	TmtL	Height	Weight
Females					
Mean	311	645	336	1278	89
Standard Error	6.09	16.48	10.28	26.82	4.85
Standard Deviation	14.91	43.61	25.19	65.69	11.89
Minimum	295	605	304	1205	76
Maximum	331	725	370	1356	105
Count	6	7	6	6	6
CV	4.79	6.76	7.51	5.14	13.41
Males					
Mean	285	543	278	1113	70
Standard Error	6.66	14.94	9.15	32.74	4.54
Standard Deviation	17.63	42.27	25.87	86.62	12.01
Minimum	263	506	254	1040	55
Maximum	307	609	319	1229	85
Count	7	8	8	7	7
CV	6.18	7.78	9.32	7.79	17.17

Canterbury (Pyramid Valley, Bell Hill, Glenmark, Cheviot, Kapua, Enfield). Lengths separating the sexes are as shown except for a single 'female' with a femur of length 328 mm (CM Av9532), which is shorter than expected for the associated tibiotarsi and tarsometatarsi. The femur may be abnormally short or the 'skeleton' a composite of more than one individual, which is likely for a Glenmark specimen.

	FemL	TibL	TmtL	Height	Weight
Females	>341*	>700	>365		
Mean	389	844	449	1688	166
Standard Error	3.17	8.92	4.95	19.01	3.85
Standard Deviation	26.94	67.92	39.32	124.63	32.63
Minimum	328	718	372	1419	102
Maximum	468	992	538	1888	275
Count	72	58	63	43	72
CV	6.93	8.05	8.75	7.38	19.64
Males					
Mean	304	589	313	1250	84
Standard Error	3.85	6.46	4.80	73.24	2.99
Standard Deviation	20.02	43.32	25.38	179.40	15.27
Minimum	273	510	264	935	61
Maximum	340	693	363	1391	113
Count	27	45	28	6	26
CV	6.58	7.36	8.11	14.35	

Appendix 2. Specimens used in the analysis, indicating morphological species attribution used here, collection locality, and sex determined from DNA either by Bunce *et al.* (2003) or Huynen *et al.* (2003).

Apèndix 2. Espècimens emprats a l'anàlisi, indicant l'atribució específica morfològica que hem fet servir, la localitat de recol·lecció i el sexe determinat pel DNA a partir de Bunce et al. *(2003) o* Huynen et al. *(2003).*

Waitomo-Waikaremoana area

Cat No	Species	Sex Bunce	Sex Huynen	Collection locality
AIM B6316	*D. struthoides*		M	Waikaremoana
AIM B6349	*D. struthoides*			Waikaremoana
AIM B6353	*D. struthoides*			Mangaotaki
AIM B6828	*D. novaezealandiae*			Waikaremoana
AIM B6829	*D. novaezealandiae*			Waikaremoana
AIM B6833	*D. novaezealandiae*			Waikaremoana
AIM B6839	*D. novaezealandiae*			Waikaremoana
AIM B6920.1	*D. novaezealandiae*			Mangaotaki
AIM B6952	*D. novaezealandiae*			Mangaotaki
AIM B7037.8	*D. novaezealandiae*		F	Mangaotaki
AIM B7168	*D. struthoides*			Waikaremoana
AU6393.18	*D. giganteus*			Cave, Murchies Farm, Waitomo
B. Reeve colln	*D. struthoides*	M		Waikaremoana
MNZ S240	*D. struthoides*			Cave, Tahora
MNZ S25761	*D. giganteus*	F		Waikaremoana
MNZ S299	*D. novaezealandiae*	F		Waikaremoana
MNZ S37874	*D. struthoides*	M		Gabrielle's cave
MNZ S37875	*D. struthoides*	M		Gabrielle's cave
MNZ S421a	*D. novaezealandiae*			Waikaremoana
MNZ S421b	*D. novaezealandiae*	F		Waikaremoana
MNZ S422	*D. struthoides*			Waikaremoana
MNZ S422	*D. struthoides*			Waikaremoana
Turangi	*D. giganteus*			Cave, Turangi, Lake Taupo
WO30.41	*D. novaezealandiae*			Briars Cave, Waitomo

Te Aute
Dinornis struthoides: MNZ S108, MNZ S24342, S110, S158, S158, S108, S109, S158, S35084, CM Av8512, CM Av8777, CM Av8817, CM Av8846, CM Av32693, OM Av4004.
Dinornis giganteus: MNZ S109, S111, S112, S113, S115, S24385, S24386, S24461, S24585, S35091, S35093, S35094, S35095, S35096, S35097, S35098, S35100, S35103, S35104, S35105, CM Av8770, CM Av8771, CM Av8778, CM Av8785, CM Av8786, CM Av8920, CM Av8980.

Makirikiri
Data previously summarized and figured by Worthy (1989) based on specimens in the Wanganui Museum and MNZ S145. Data previous attributed to *Dinornis novaezealandiae* and *D. giganteus* were combined for females in this study.

Takapau Rd
D. giganteus MNZ S1013, S1014 M?, S1015, S24377.
D. novaezealandiae MNZ S1016, S1017, S1018, S1019, S1019a, S1023, S1022, S24365.
D. struthoides MNZ S1025, S24363, S24364.

Northwest South Island, less than 600m

Cat No	Species	Bunce sex	Site
CM Av12589	*D. giganteus*		Cave, Paturau, West Coast
CM Av29320	*D. giganteus*		Unique Wonder cave, West Coast
Hochstetter' specimen, Wien	*D. novaezealandiae*		Cave, Aorere Valley
In situ	*D. struthoides*		Moonsilver Cave
MNZ S23526	*D. struthoides*		Honeycomb Hill Cave
MNZ S23654	*D. struthoides*		Honeycomb Hill Cave
MNZ S24338	*D. struthoides*		Buller area cave
MNZ S24339	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24350	*D. struthoides*		Buller area cave
MNZ S24462	*D. struthoides*		Honeycomb Hill Cave
MNZ S25765	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S25766	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S25768	*D. novaezealandiae*		Honeycomb Hill Cave
MNZ S27135	*D. struthoides*		Moonsilver Cave
MNZ S27136	*D. novaezealandiae*		Moonsilver Cave
MNZ S27137	*D. novaezealandiae*		Moonsilver Cave
MNZ S28075	*D. struthoides*		Madonna Cave, West Coast
MNZ S28088	*D. struthoides*		Madonna Cave, West Coast
MNZ S28114	*D. giganteus*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave, West Coast
MNZ S28115	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28116	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28119	*D. novaezealandiae*		Madonna Cave West Coast
MNZ S28225	*D. struthoides*	M	Maximus Cave
MNZ S28381	*D. struthoides*		Metro Cave, West Coast
MNZ S32677	*D. novaezealandiae*		Moonsilver Cave
MNZ S32678	*D. novaezealandiae*		Moonsilver Cave
MNZ S33517	*D. struthoides*		Commentary Cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave
MNZS24351	*D. novaezealandiae*		Buller area cave

Northwest South Island, greater than 600m

Cat No	Species	Bunce sex	Site
MNZ S34095	D. giganteus	F	Cave, Hodge Ck, Mt Arthur
AIM B723	D. novaezealandiae		Cave, Takaka Hill
MNZ S211	D. novaezealandiae	F	Cave, Takaka Hill
MNZ S23342	D. novaezealandiae	F	Cave, Mt Owen
MNZ S32667	D. novaezealandiae	F	Cave, Ellis Basin, Mt Arthur
MNZ S38981	D. novaezealandiae		Takaka Fossil Cave
MNZ S38988	D. novaezealandiae	F	Takaka Fossil Cave
MNZ S23570	D. struthoides	M	Mt Owen
MNZ S27891	D. struthoides		Cave, Paynes Ford, Takaka Valley
MNZ S32715	D. struthoides		Struthoides Cave, Takaka Hill
MNZ S32716	D. struthoides		Struthoides Cave, Takaka Hill
MNZ S33517	D. struthoides		Hodge Ck cave system, Mt Arthur
MNZ S38990	D. struthoides		Takaka Fossil Cave
MNZ S39003	D. struthoides	M	Takaka Fossil Cave
MNZ S39004	D. struthoides	M	Takaka Fossil Cave

Canterbury Region.

Cat No	Species	Sex Bunce	Sex Huynen	Site
AMNH7301	D. struthoides			Pyramid Valley
AMNH7303	D. giganteus			Pyramid Valley
CM Av13778	D. giganteus			Pyramid Valley
CM Av13779	D. giganteus	F		Pyramid Valley
CM Av14448	D. giganteus		F	Pyramid Valley
CM Av14449	D. giganteus	F		Pyramid Valley
CM Av14451	D. giganteus			Pyramid Valley
CM Av14549	D. giganteus			Pyramid Valley
CM Av15024	D. giganteus			Pyramid Valley
CM Av15025	D. giganteus			Pyramid Valley
CM Av15026	D. giganteus			Pyramid Valley
CM Av15028	D. struthoides			Pyramid Valley
CM Av20118	D. giganteus			Pyramid Valley
CM Av20123	D. giganteus			Pyramid Valley
CM Av20124	D. giganteus			Pyramid Valley
CM Av23466	D. giganteus	F		Pyramid Valley?
CM Av8415	D. struthoides			Pyramid Valley
CM Av8416	D. giganteus			Pyramid Valley
CM Av8417	D. giganteus		F	Pyramid Valley
CM Av8418	D. giganteus	undet (tmt)	F	Pyramid Valley
CM Av8419	D. giganteus			Pyramid Valley
CM Av8420	D. giganteus			Pyramid Valley
CM Av8421	D. giganteus	F		Pyramid Valley
CM Av8422	D. giganteus			Pyramid Valley
CM Av8423	D. giganteus			Pyramid Valley
CM Av8436	D. giganteus			Pyramid Valley
CM Av8464	D. giganteus			Pyramid Valley
CM Av8466	D. giganteus			Pyramid Valley
CM Av8467	D. giganteus			Pyramid Valley
CM Av8468	D. giganteus		F	Pyramid Valley
CM Av8469	D. giganteus			Pyramid Valley
CM Av8470	D. giganteus			Pyramid Valley
CM Av8471	D. giganteus			Pyramid Valley
CM Av8473	D. giganteus			Pyramid Valley
CM Av8475	D. struthoides			Pyramid Valley
CM Av8476	D. giganteus			Pyramid Valley
CM Av8477	D. giganteus			Pyramid Valley
CM Av8478	D. giganteus			Pyramid Valley
CM Av8479	D. giganteus			Pyramid Valley
CM Av8480	D. giganteus			Pyramid Valley
CM Av8484	D. giganteus			Pyramid Valley
CM Av8486	D. giganteus			Pyramid Valley
CM Av8487	D. giganteus			Pyramid Valley
CM Av8488	D. giganteus			Pyramid Valley
CM Av8489	D. giganteus			Pyramid Valley
CM Av8490	D. giganteus			Pyramid Valley
CM Av8491	D. giganteus			Pyramid Valley
CM Av8492	D. giganteus		F	Pyramid Valley
CM Av8493	D. giganteus			Pyramid Valley
CM Av8494	D. giganteus			Pyramid Valley
CM Av8495	D. struthoides			Pyramid Valley
CM Av8547	D. giganteus			Pyramid Valley
CM Av8756	D. struthoides			Enfield
CM Av8757	D. struthoides			Enfield
CM Av8758	D. struthoides			Kapua
CM Av8759	D. struthoides			Glenmark
CM Av8760	D. struthoides			Enfield
CM Av8761	D. struthoides			Kapua
CM Av8762	D. struthoides			Kapua
CM Av8763	D. struthoides	M		Kapua
CM Av8764	D. giganteus			Kapua
CM Av8766	D. struthoides	M		Kapua
CM Av8767	D. struthoides			Glenmark
CM Av8768	D. struthoides			Kapua
CM Av8773	D. struthoides			Glenmark
CM Av8774	D. struthoides			Kapua
CM Av8781	D. struthoides			Kapua
CM Av8787	D. struthoides			Glenmark
CM Av8788	D. giganteus			Glenmark
CM Av8790	D. giganteus			Kapua
CM Av8791	D. giganteus			Kapua
CM Av8804	D. giganteus			Kapua
CM Av8805	D. struthoides			Kapua
CM Av8806	D. struthoides			Kapua
CM Av8807	D. struthoides			Enfield
CM Av8809	D. struthoides			Enfield
CM Av8811	D. struthoides			Glenmark
CM Av8821	D. struthoides			Glenmark
CM Av8823	D. struthoides			Kapua
CM Av8824	D. struthoides			Kapua
CM Av8871	D. struthoides			Kapua
CM Av8872	D. struthoides		M	Glenmark
CM Av8976	D. struthoides			Glenmark
CM Av8978	D. giganteus			Kapua
CM Av8979	D. giganteus			Glenmark
CM Av8983	D. novaezealandiae			Kapua
CM Av8984	D. giganteus			Glenmark
CM Av8985	D. giganteus			Enfield
CM Av8986	D. struthoides			Kapua
CM Av8987	D. struthoides			Glenmark
CM Av8988	D. struthoides			Glenmark
CM Av8990	D. giganteus			Enfield
CM Av8992	D. giganteus			Kapua

CM Av8993	D. struthoides			Kapua
CM Av8994	D. giganteus			Enfield
CM Av8995	D. struthoides			Kapua
CM Av8997	D. struthoides			Glenmark
CM Av8998	D. struthoides			Enfield
CM Av8999	D. giganteus			Enfield
CM Av9001	D. giganteus			Glenmark
CM Av9003	D. giganteus			Enfield
CM Av9005	D. giganteus			Enfield
CM Av9006	D. giganteus			Enfield
CM Av9007	D. struthoides			Enfield
CM Av9008	D. giganteus			Kapua
CM Av9009	D. giganteus			Kapua
CM Av9010	D. giganteus			Kapua
CM Av9011	D. giganteus			Kapua
CM Av9012	D. giganteus		F	Enfield
CM Av9013	D. giganteus			Kapua
CM Av9015	D. giganteus		F	Kapua
CM Av9016	D. giganteus		F	Glenmark
CM Av9017	D. giganteus			Enfield
CM Av9018	D. struthoides			Enfield
CM Av9019	D. struthoides			Glenmark
CM Av9020	D. struthoides			Enfield
CM Av9021	D. struthoides			Enfield
CM Av9022	D. giganteus			Enfield
CM Av9023	D. giganteus		F	Enfield
CM Av9024	D. giganteus			Kapua
CM Av9025	D. giganteus			Kapua
CM Av9026	D. struthoides			Kapua
CM Av9031	D. struthoides			Enfield
CM Av9032	D. giganteus		F	Enfield
CM Av9034	D. giganteus			Enfield
CM Av9035	D. giganteus			Enfield
CM Av9036	D. giganteus			Kapua
CM Av9037	D. struthoides		M	Kapua
CM Av9040	D. struthoides			Kapua
CM Av9041	D. struthoides			Enfield
CM Av9042	D. struthoides			Enfield
CM Av9043	D. struthoides			Kapua
CM Av9044	D. struthoides			Enfield
CM Av9083	D. struthoides			Glenmark
CM Av9436	D. struthoides	undet		Glenmark?
CM Av9440	D. struthoides	undet		Glenmark?
CM Av9434	D. struthoides			Glenmark?
CM Av9435	D. struthoides			Glenmark?
CM Av9437	D. struthoides			Glenmark?
CM Av9438	D. struthoides			Glenmark?
CM Av9439	D. struthoides			Glenmark?
CM Av9441	D. struthoides			Glenmark?
CM Av9442	D. struthoides			Glenmark?
CM Av9443	D. struthoides			Glenmark?
CM Av9444	D. struthoides			Glenmark?

CM Av9511	D. giganteus		F	Glenmark
CM Av9529	D. giganteus			Glenmark
CM Av9531	D. giganteus			Glenmark
CM Av9532	D. giganteus	undet		Glenmark
CM Av9535	D. struthoides			Glenmark
CM Av9543	D. struthoides		M	Glenmark?
CM SB47	D. giganteus	F		Cheviot
CM SB 51	D. giganteus			Cheviot
CM SB54	D. giganteus			Cheviot
CM SB53	D. giganteus			Cheviot
CM SB50	D. giganteus			Cheviot
CM SB 50	D. giganteus			Cheviot
CM SB47	D. giganteus			Cheviot
CM SB214	D. giganteus			Cheviot
CM SB49	D. giganteus			Cheviot
CM SB51	D. giganteus			Cheviot
CM SB49	D. giganteus			Cheviot
CM SB48	D. giganteus			Cheviot
CM SB47	D. giganteus			Cheviot
CM SB48	D. giganteus			Cheviot
CM SB52	D. giganteus			Cheviot
MNZ S34088	D. giganteus	undet		Pyramid Valley
MNZ S39875	D. giganteus	F		Bell Hill Vineyard
MNZ S39946.1	D. struthoides			Bell Hill Vineyard
MNZ S39946.2	D. struthoides			Bell Hill Vineyard
MNZ S39946.3	D. struthoides			Bell Hill Vineyard
MNZ S39946.4	D. struthoides			Bell Hill Vineyard
MNZ S39445	D. giganteus			Bell Hill Vineyard
MNZ S39954	D. giganteus			Bell Hill Vineyard
MNZ S39959	D. giganteus			Bell Hill Vineyard
MNZ S39960	D. giganteus			Bell Hill Vineyard
MNZ S39961	D. giganteus			Bell Hill Vineyard
MNZ S39962	D. giganteus			Bell Hill Vineyard
MNZ S40074	D. struthoides			Bell Hill Vineyard
MNZ S40075	D. struthoides			Bell Hill Vineyard
MNZ S40076	D. struthoides			Bell Hill Vineyard
MNZ S40077	D. struthoides			Bell Hill Vineyard
MNZ S40078	D. struthoides			Bell Hill Vineyard
MNZ S40124	D. giganteus			Bell Hill Vineyard
MNZ S40136	D. struthoides			Bell Hill Vineyard
MNZ S40137	D. struthoides			Bell Hill Vineyard
MNZ S40187	D. struthoides			Bell Hill Vineyard
MNZ S40189	D. giganteus			Bell Hill Vineyard
MNZ S40232	D. struthoides			Bell Hill Vineyard
MNZ S40333	D. struthoides			Bell Hill Vineyard
MNZ S40335	D. struthoides			Bell Hill Vineyard
MNZ S40336	D. struthoides			Bell Hill Vineyard
MNZ S40337	D. struthoides			Bell Hill Vineyard
MNZ S40338	D. struthoides			Bell Hill Vineyard
MNZ S40339	D. struthoides			Bell Hill Vineyard
MNZ S40341	D. struthoides			Bell Hill Vineyard
MNZ S40342	D. struthoides			Bell Hill Vineyard