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SHORT NOTE

Extreme female-biased sexual size dimorphism in *Euryapteryx* moa (Aves: Dinornithiformes: Emeidae)

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The major conclusion of the most recent morphometric analyses of the moa genus *Euryapteryx* was that, apart from a north-south cline of increasing size in the North Island, there were no significant size differences between regional populations (Worthy 1987, 1992). As the regions and sites chosen did not include any of the populations west of the South Island's Main Divide (Worthy 1992), I measured leg bone lengths of individuals from the West Coast, Oparara, Takaka Hill, and Takaka Valley to provide a more complete geographic coverage but in the same manner as the original analyses. In particular, I wanted to see if there were any differences in size between birds in the glacial age "Western" and those in the Holocene "Eastern" faunas proposed by Worthy & Holdaway (1993, 2002). For further comparisons outside the regions dealt with in Worthy (1992), I measured bones from the glacial age deposit in Merino Cave (on the Annandale plateau in southern Marlborough), from Holocene sites in South Canterbury, and of an individual from Wakapatu on the Southland coast. The study was not intended to be a comprehensive multidimensional morphometric analysis but rather to extend the coverage of the original papers, and to look for patterns in those data that may have been missed at the time. All specimens and elements measured are listed in Appendix 1. Locations of regions and sites are shown in Figure 1.

To ensure valid comparisons with the values cited in Worthy (1992), I measured the lengths of femora, tibiotarsi, and tarsometatarsi with a steel tape between the same morphological landmarks and rounded measurements to the nearest millimetre. Two contralateral elements of the same or very near the same length from the same site were treated as being from a single individual; only one, usually the left unless the right was less worn, was included in the analyses. In all, the lengths of 30 femora, 5 tibiotarsi, and 24 tarsometatarsi were obtained, representing the seven regions and sites, plus one individual with no locational data. The sample size of complete, adult tibiotarsi was too small for further analysis.

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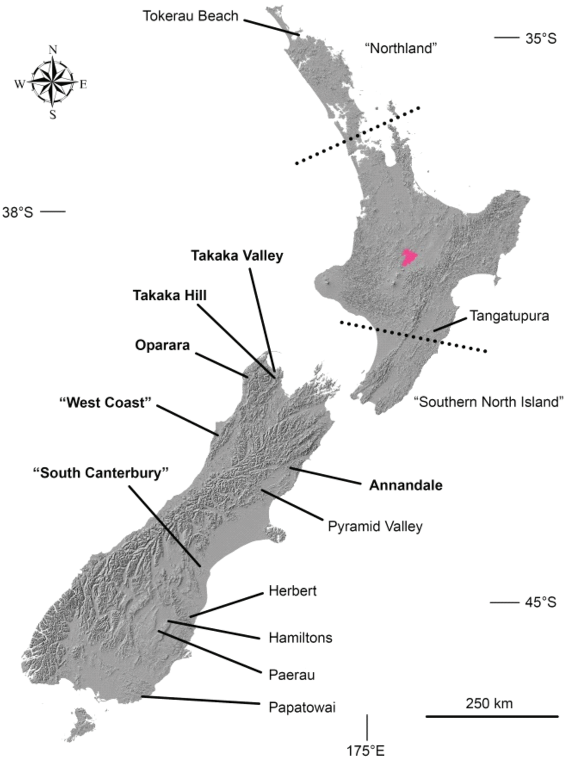

Figure 1. Map of areas and sites (bold) for which new mensural data on *Euryapteryx* were obtained, and of regions and sites for which data are listed in Worthy (1992).

Available radiocarbon ages for the West Coast (Worthy & Holdaway 1993) and Takaka area (Worthy & Holdaway 1994) populations support the view that *Euryapteryx* was present west of the Main Divide only during the late Weichselian-Otiran glacial and the glacial-interglacial transition (17,000 to 11,000 years BP). A new radiocarbon age (UBA43573, 13,455 ± 86 ^{14}C years; 16,156 ± 138 cal BP) for the sole Honeycomb Hill Cave *Euryapteryx* (Worthy 1993) confirmed its glacial-interglacial age. For Merino Cave (Annandale) although only two individuals were listed by Worthy & Holdaway (1995), the S33404 series in the Museum of New Zealand includes three right femora (S33404.4, _4.6, and _4.10) and one left femur (S33404.7) whose length (300 mm) may or may not match that of _4.10 (290+ mm). None of the Merino Cave *Euryapteryx* has been dated but ages on six of the co-occurring *Pachyornis* range from 14,010 ± 110 (NZA4447) to 38,200 ± 980 (NZA3816) ^{14}C years (Worthy & Holdaway 1995). These are equivalent to a calibrated calendar date range of 16,974 ± 181 to 42,442 ± 630 years BP (SHCal20 calibration curve (Hogg *et al.* 2020) in OxCal4.4 software (Bronk Ramsey 1995, 2009).

I calculated summary statistics and performed statistical tests using PAST® Version 3.26b statistical software (Hammer *et al.* 2001). Only basic comparisons were possible with the information in table 1 in Worthy (1992) because that includes only summary statistics (sample size, mean, range, and coefficient of variation): for the *t*-tests I calculated the standard deviations from the means and coefficients of variation.

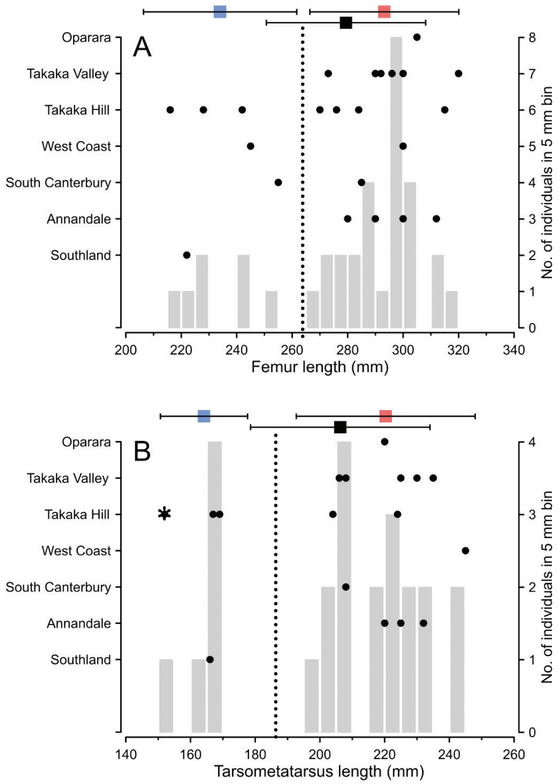

Figure 2. Measurements of leg bones of moa identified (mostly by morphology) as *Euryapteryx* in the collections of Te Papa Tongarewa Museum of New Zealand and Canterbury Museum from sites west of the axial mountain ranges of the South Island, New Zealand, and from the Annandale plateau (southern Marlborough), South Canterbury, and a site (Wakapatu) in Southland. **A**, black circles, femur lengths by site or region; grey bars, 5 mm bin histogram of femur lengths; black square, overall mean, with 1 σ error bars; pink symbol, mean for femora > 260 mm, with 2σ error bars; blue symbol, mean for femora < 260 mm, with 2σ error bars. **B**, black symbols, lengths of tarsometatarsi by site and region; *, holotype tarsometatarsus of *Euryapteryx pygmaeus* Hutton, 1891; other symbols and conventions as in A. In both, vertical dotted lines are centred on the gap between the 2σ error bars for the distributions of larger and smaller elements.

Table 1. Comparisons by Student's *t*-test between mean pooled femur lengths (mm) for *Euryapteryx* populations west of the New Zealand South Island Main Divide (WoMD) with those from east of the Divide (EoMD) and Annandale (Merino Cave) (this study) and measurements in Worthy (1987) and Worthy (1992). Individuals from west of the South Island Main Divide, Annandale, and Tangatupura of Weichselian-Otiran and glacial-interglacial age; remainder of Holocene age. Significant differences in **bold**. See Fig. 1 for locations of sites and regions.

	Site or region	**Mean**	**SD**	*n*	*t*	**df**	*P*
Comparison	WoMD all	281.81	28.05	21	-	-	-
	WoMD "large"	293.35	14.37	17	-	-	-
	WoMD "small"	232.75	13.4	4	-	-	-
WoMD all *versus*	EoMD	279.3	28.37	8	0.2190	27	0.8283
WoMD all *versus*	Annandale	295.5	13.7	4	0.9427	23	0.3557
WoMD all *versus*	Pyramid Valley	288.4	10.38	8	0.6418	27	0.5264
WoMD all *versus*	Herbert	289.7	22.13	20	0.9966	39	0.3251
WoMD all *versus*	Hamilton's	291.5	20.46	16	1.8811	35	0.0683
WoMD all *versus*	O'Malley's, Paerau	300	19.95	21	2.4217	40	**0.0201**
WoMD all *versus*	Papatowai	274.3	14.26	41	1.4031	60	0.1657
WoMD all *versus*	Southern North Island	255.7	19.77	10	2.6374	29	**0.0133**
WoMD all *versus*	Tangatupura	194.4	17.2	88	18.2811	107	**< 0.0001**
WoMD large *versus*	Tangatupura "large"	204.2	9.2	62	31.0534	77	**< 0.0001**
WoMD small *versus*	Tangatupura "small"	171.2	5.4	26	17.0317	28	**< 0.0001**
WoMD all *versus*	Northland	224.7	9.44	7	5.2309	26	**< 0.0001**

It was clear that the pooled distributions for both femur and tarsometatarsus length were bimodal (Fig. 2), with ranges of 216–245 mm for the smaller and 270–320 mm for the larger. There were no differences in femur length between sites for the large birds from western sites (Single factor ANOVA, $F_{3,13} = 0.5366$, $P = 0.6654$), so the site samples were pooled for further analyses. With the pooled samples, the larger birds from west of the South Island Main Divide were the same size as those from east of the Divide (Table 1). This was so both for the (glacial age) contemporary eastern population on the Annandale plateau, and for most of the eastern Holocene sites and regions (Worthy & Holdaway 1995, 1996; Worthy 1997, 1998a, 1998b, 1998c) (Table 1). Only birds in the population preserved at Paerau in eastern Otago were significantly larger than the western birds Table 1).

The birds from the western South Island were, however, much larger than those from the North Island ("Southern North Island", Tangatupura, and "Northland", Table 1). The late glacial aged birds from the Tangatupura site in southern Hawke's Bay were even smaller than those in the sample from Northland measured by Worthy (1992). The Tangatupura birds were much smaller than those from the Holocene of the southern North Island (Table 1), 15,000 years later. If these two populations were of the same taxon, that would be unusual as a temporal application of Bergmann's Rule suggests that birds living in a glacial climate will be larger than those living in warmer climates.

Mean lengths for both femora and tarsometatarsi in individuals in the larger and smaller size classes, taken from either side of the major discontinuity in their distributions were highly significantly different. For femora, the difference between female mean femur length (293.2 mm, 95% confidence interval [CI] 287.41–299.02; $n = 23$) and that of males (234 mm, 95% CI = 221.22–246.78; $n = 7$) was highly significant (Equal variances, $t = 10.151$, $P = 6.9082 \times 10^{-11}$, $P_{\text{Monte Carlo}} = 0.0001$. F test for equal variances, 1.059, P [same var.] = 0.832; Critical F value [$P = 0.05$] = 3.0546; $P_{\text{Monte Carlo}}$ [same var.] = 0.9274). Analysis using single factor ANOVA yielded the same (extremely high) level of significance: $F_{1,28} = 103$, $P = 6.908 \times 10^{-11}$, with homogeneous variances (Levene´s test from means $P = 0.8335$). For the tarsometatarsi, the difference between the size classes (sexes) was also highly significant (Equal variances, $t = 9.4805$, $P = 3.16 \times 10^{-9}$) with means and 95% CIs of females being 220.33 mm and 213.46–227.21 mm, and for males, being 164.17 mm and 157.1–171.24 mm. Variances for the sexes were the same by F test ($F = 4.2114$, $P = 0.1191$). The differences were highly significant by single factor ANOVA ($F_{1,22} = 89.88$, $P = 3.16 \times 10^{-9}$), but the data (just) failed Levene's test for homogeneity of variances ($P = 0.0455$), probably because of the small samples (Welch's F test for unequal variances gave $F_{18.29} = 173.6$, $P = 8.907 \times 10^{-11}$).

The size difference between the sexes in the western South Island birds was as marked as that between the "large" and "small" femora in the

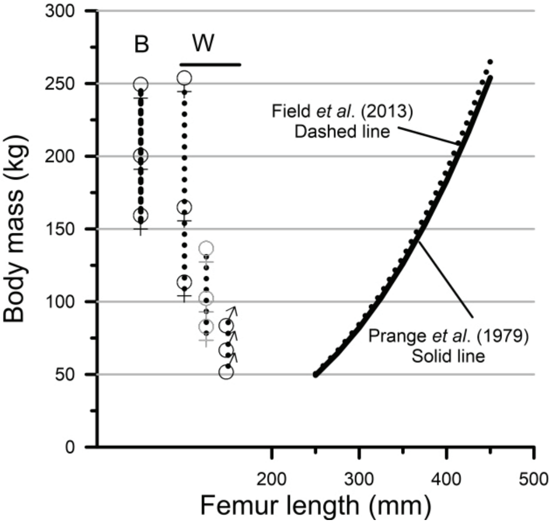

Figure 3. Comparison of body mass estimates between (B) a female *D. robustus* by volumetric analysis (Brassey *et al.* 2013) and two bone length algorithms (black solid line, Prange *et al.* [1979]; dashed, Field *et al.* [2013]). Algorithm estimates from Worthy (1994) (W) using the Prange *et al.* (1979) algorithm for "large" and "mid-sized" and "small" birds now understood to represent (large) females from drier environments, (mid-sized) females from wet forest, and (small) males.

Tangatupura sample (t = 17.0636, df = 86, 2-tailed $P < 0.0001$). These results show that *Euryapteryx* populations were highly sexually size dimorphic, regardless of whether they were from, overall, larger or smaller populations. The degree of size dimorphism (2 to 1 in favour of females) matched that of the South Island giant moa, which is usually considered as having the most extreme difference between the sexes (Allentoft *et al.* 2010).

Predicted body masses

Allometric formulae relating bone dimensions to body mass, e.g. those of Prange *et al.* (1979) and Field *et al.* (2013), derived from measurements on non-ratite birds have nevertheless been much used to estimate body masses for extinct ratites, including moa, e.g. Worthy & Holdaway (2002). These algorithms are now being supplemented, but not yet supplanted, by new techniques involving the generation of digital "envelopes" of body volumes (Brassey *et al.* 2013), which can provide independent estimates of body mass. As body mass is a key factor in the biology and physiology of organisms (Brassey 2016), once femur lengths for the populations and those separately for the males and females were obtained, the next step was to, as it were, put flesh on the bones and estimate the body masses of different populations and for the sexes within those populations.

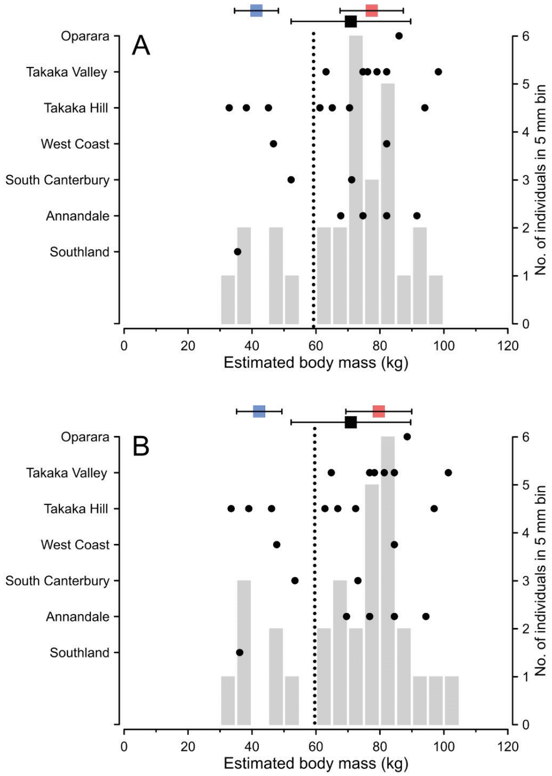

Figure 4. Estimated mean body masses (kg) of moa identified as *Euryapteryx* in the collections of Te Papa Tongarewa Museum of New Zealand and Canterbury Museum. Masses derived from allometric relationships between femur length and mass developed by Prange *et al.* (1979) and Field *et al.* (2013). Individual moa from sites west of the axial mountain ranges of the South Island, New Zealand, and from the Annandale plateau (southern Marlborough), South Canterbury, and a site (Wakapatu) in Southland. **A**, black circles, body mass by site or region according to algorithm in Prange *et al.* (1979); grey bars, 5 kg bin histogram of body mass; black square, overall mean, with 1 σ error bars; pink symbol, mean for birds > 50 kg, with **2σ** error bars; blue symbol, mean for femora < 50 kg, with **2σ** error bars. **B**, black symbols, body mass according to algorithm in Field *et al.* (2013) by site and region; symbols and conventions as in A. In both, vertical dotted lines centred on gap between the 2 σ error bars for the distributions of larger and smaller birds.

The mean (196 kg) for the body mass of a female South Island giant moa (*Dinornis robustus*) estimated by the body volume method (Brassey *et al.* 2013) was much higher than the estimated means (160.48 kg, 166.56 kg; Prange *et al.* 1979, Field *et al.* 2013, respectively) for the large females reported by Worthy (1994) (Fig. 3). The lower limit of the volume-based predicted range (155 kg) was also well above those (109–112 kg) from the algorithms. However, the upper limit of 245 kg agreed well with 254–265 kg – although better with the lower Prange *et al.* (1979) value of 254 kg – from the femur length calculations. It appears that the volumetric method in this instance provided a mass range for large females, but not for the full range of female sizes, and not at all for the males. On this basis, I used the estimates from femur lengths, as being the best available at present, for the comparisons of *Euryapteryx* populations.

The estimated body masses for the South Island *Euryapteryx* populations are summarised in Fig. 4, and the western South Island populations compared with the North Island birds in Table 2. Using the more conservative Prange *et al*. (1979) algorithm, the mean body mass estimated for western South Island *Euryapteryx* females was 11.18% higher than for the pooled sample (Table 2): in contrast, the mean male body mass was only 58.7% of the pooled mean. For the contemporary Tangatupura population in the North Island, the proportions were 14.7% for females and 70.2%, respectively. Hence, the pooled data consistently underestimate the mean body mass of females and overestimate that of males, obscuring the dramatic sexual difference.

Sex ratios

A female-biased sex ratio in giant moa (*Dinornis* spp.) was confirmed by early ancient genetics studies (Bunce *et al.* 2003; Huynen *et al.* 2003). The expectation from a later genetic analysis of four species of moa in North Canterbury (Allentoft *et al.* 2010) was that, if the South Island populations were uniform, a pooled sample from *Euryapteryx* populations would have adult sex ratios close to 2.5:1 in favour of females.

The size distributions of the western South Island birds were numerically skewed, with larger femora outnumbering smaller by 23 to 7, and larger tarsometatarsi outnumbering smaller by 18 to 6. Taking the larger individuals as being females (as they are in taxa where genetic evidence is available (Allentoft *et al.* 2010, 2014), this suggests a sex ratio in the pooled samples of 3.29:1 based on the femora and 3:1 based on tarsometatarsi.

Both the femoral (3.29:1) and tarsometatarsal (3.33:1) sex ratios in the samples from the western South Island were higher than expected from the 2.5:1 of the North Canterbury genetic sample, which was shared by another emeid moa *Pachyornis elephantopus*. In the new data the sex ratio based on the number of femora was statistically significantly different from unity ($\chi^2 = 8.533$, $P = 0.0035$), as it was for the numbers of tarsometatarsi ($\chi^2 = 6.000$, $P = 0.0143$) as well.

The sex ratio in the North Canterbury sample was lower, though, than that for the third emeid there, *Emeus crassus*. Its North Canterbury population was represented in Pyramid Valley and Bell Hill Vineyard by 5.5 females for each male (Allentoft *et al.* 2010). The great difference (19.0:1 *vs* 1:1.5) between the sex ratios of South Island giant moa (*D. robustus*) from adjacent sites was attributed to habitat differences between the sexes (Allentoft *et al.* 2010).

The histograms in Worthy (1987: his figures 5 & 6) suggest that the sex ratios in samples from the late glacial Tangatupura population were, for the femora, nearly a 2:1 ratio in favour of large birds (61 v. 27; 2.26:1), and an even lower dominance at 1.65:1 of females with the tarsometatarsi (38:25, with two indeterminate). The distinction between "large" and "small" was much less clear for the tibiotarsi,

Table 2. Body masses (BM, kg) from femur length (FL, mm) for the western South Island, the contemporary Tangatupura (lower North Island), and Holocene Northland populations of *Euryapteryx*, according to the Prange *et al.* (1979) algorithm (transposed as $\log BM = (\log FL - \log 61.64)/0.359$ and that of Field *et al.* (2013) ($\ln BM = (2.82 \times \ln FL) - 4.74$).

		Body mass estimates (kg)					
		Prange *et al.* (1979)			**Field *et al.* (2013)**		
		Mean	**SD**	**Range**	**Mean**	**SD**	**Range**
Western South Island	All	68.98	17.74	32.88–98.28	70.85	18.43	33.47–101.38
	Males	40.49	6.4	32.88–46.71	41.31	6.61	33.47–47.74
	Females	77.14	10.55	61.22–98.28	79.34	10.99	62.79–101.38
Tangatupura	All	24.52	-	13.52–35.94	24.86	-	13.61–36.62
	Males	17.21	-	13.61–18.88	17.37	-	13.61–19.09
	Females	28.12	-	19.79–35.94	28.56	-	20.01–36.62
"Northland"	All	36.71	-	32.46–46.71	37.41	-	33.03–47.74

but taking the two in the third smallest bin as being "small", the ratio was 2.33:1 (28:12). Worthy (1987) does not comment on the contrast between the Tangatupura ratios and those from Tokerau Beach in the Far North, which did not depart from 1:1. For Tokerau Beach femora, counts from the histogram for the femoral sample are 52 large to 42 small (1:0.81), for the tibiotarsi, 38 large to 36 small (1:0.95), and for the tarsometatarsi, 37 large to 32 small (1:0.86).

Conclusions

Sexual size dimorphism in moa was detected first in leg bone dimensions (Cracraft 1976a, 1976b, 1976c) and explored in several taxa over the next 15 years (Worthy 1987, 1988a, 1988b, 1992), with varying conclusions as to its presence or absence. Female-biased extreme sexual dimorphism is now well established for giant moa (*Dinornis* spp.), based on genetically sexed individuals (Bunce *et al.* 2003; Huynen *et al.* 2003), after being suggested first on the basis of multivariate statistical analyses of leg bone dimensions (Cracraft 1976c). The invocation (Cracraft 1976c) and confirmation (Bunce *et al.* 2003; Huynen *et al.* 2003) of sexual dimorphism allowed the resolution of problems within a previously complex, primarily size-based, species-rich taxonomy which had endured into the 21st century (Worthy & Holdaway 2002). Whether recognition of size dimorphism in *Euryapteryx* foreshadows taxonomic changes is beyond the scope of this study.

This study has showed that birds of different geological ages from east and west of the South Island's Main Divide were generally of equal size. It is the first to show extreme sexual size dimorphism in all populations of *Euryapteryx* moa, with differences of the same magnitude (females near twice the size of males) as in giant moa. In terms of body mass, females ranged from 60–100 kg, with the males at 30–40 kg. These numbers may have some interest for studies of exploitation of *Euryapteryx* moa by early Polynesians, in so far as whether males or females were preferentially included in their diet. That in turn would have to consider the different sex ratios among *Euryapteryx* populations, ranging from two or more to one in most populations to equality in a far northern population. In the pre-human landscape, the body mass per unit area of adult females in most populations of *Euryapteryx* moas was 3–5 times that of males. Females would have consumed a similarly disparate proportion of the available diet.

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Keywords: *Euryapteryx*, moa, Dinornithiformes, sexual size dimorphism, sex ratio

Appendix 1. *Euryapteryx* leg bones measured in Te Papa Tongarewa Museum of New Zealand and Canterbury Museum for this study.

Te Papa Tongarewa Museum of New Zealand - Wren Wrecker Passage, Honeycomb Hill Cave System, Oparara: S25656, Lfem, Ltbt, Ltmt. Tarakohe Lime Works, Takaka: DM 427, fem, tmt. Irvine's Tomo, Payne's Ford, Takaka: S27850, tmt; S27851, tmt; S27854, tmt; S27855, tmt; S27870, Lfem; S27871, Lfem; S27872, Lfem; S27874, Rfem; S27877, Lfem. Payne's Ford, Takaka: S30210, Rfem; S30211, Rfem. Kairuru Cave, Takaka Hill: S27798, tmt; S27895, Rtmt. S39016. Takaka Fossil Cave, Takaka Hill: S39016, fem, RLtbt, tmt (noted by T. Worthy as "very small"; tbt sampled for radiocarbon dating; N. Rawlence sampled fem for DNA); S39017, fem, tbt, tmt; S38942. "Takaka Hill": S24327, Rtmt. "Takaka" (probably Takaka Hill): S24322, LRtmt (Holotype of *Euryapteryx pygmaeus* Hutton, 1891. "Nelson District" (probably Takaka Hill): S24328, Rtmt. "No data": S24343, LRfem (Rfem sampled for DNA by A. Cooper). Locality 13, upper level, Madonna Cave, West Coast: S28083, fem. Madonna-Equinox Cave system, Site 16: S28121, Rfem (intensively sampled), Rtmt. Madonna-Equinox Cave system, S28222, Rfem. Netherton Cave, South Canterbury: S33743, Rfem. Holocene Hole, southern Marlborough: S33370, fem. Merino Cave, Annandale, southern Marlborough: S33404.1, Ltmt; S33404.2, Ltmt; S33404.4, Rfem; S33404.6, Rfem; S33404.7, Lfem; S33404.10, Rfem. Home Creek, Waipara, North Canterbury: S33728, Rtmt. Wakapatu, Southland coast: DM455, Rfem, LRtbt, LRtmt.

Canterbury Museum - Bone Cave, Takaka Hill: Av21330, Lfem. "Takaka Hill, 4 Jan 1945": Av8551, Rfem; Av8555, Rfem; Av21329, Lfem, Ltmt. Av22361, Ltmt. "Charleston District", West Coast: Av29440, LRfem, Ltmt; Av29439, Rfem; Av29450, Rfem. Nettletrench Cave, West Coast: Av31223, Rfem. "Cowan, near Inangahua", West Coast: Av34552, Rtmt. Albury Park, South Canterbury: Av19283, Rtmt; Av19288, Ltmt; Av31328, LRfem, Rtmt.