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Morphometrics of moa eggshell fragments (Aves: Dinornithiformes) from Late Holocene dune-sands of the Karikari Peninsula, New Zealand

B. J. Gill*

Moa eggshell fragments were examined from Late Holocene coastal dunes at Tokerau Beach and Matai Bay, Karikari Peninsula, Northland The Tokerau eggshell fragments, 0 56–1 69 mm thick, were produced by up to six species of moas recorded from the area A sample of 1042 fragments was bimodally distributed by thickness, with 19% of fragments classed as "thick" (≥1 12 mm thick) and 81% as "thin" (≤1 10 mm) The thin eggshells were probably produced mainly by the small moa *Euryapteryx curtus*, which dominates local bone assemblages The small *Pachyornis mappini*, rare in local bone assemblages, may have produced some of the thin eggshells Thick eggshell could have been produced by *E geranoides* or one or more of the three species of *Dinornis* In a sample of 51 eggshell fragments from Matai Bay, all except one fragment were thin Thickness distributions of thin shell from Matai Bay and Tokerau Beach differed, but the Matai Bay sample may have been too small for reliability Measurements of the curvature of 237 larger fragments from Tokerau Beach suggested that thick eggshell belonged to eggs 161–216 mm long by 116–155 mm wide, while thin eggshell was associated with eggs 138–179 mm × 99–129 mm, all within the size range of known whole moa eggs

Keywords moa, Emeidae, Dinornithidae, eggshell, fossil, Holocene, thickness, curvature, egg size

INTRODUCTION

Eleven species of moas (families Emeidae and Dinornithidae, order Dinornithiformes), unique to New Zealand, died out during the last 1000 years following the arrival of Polynesian settlers Moas are known primarily from their bones, recovered from natural sites (sand-dune deposits, caves and layers of alkaline mud in swamp deposits) and from many archaeological sites

Moa eggs are known from fewer than 20 whole, or substantially intact, eggs (Table 1), 120–240 mm long and 91–178 mm wide They are also represented by fragments of broken eggshell that are especially common in some Late Holocene coastal dunefields. Archey (1931) attributed the smallest known whole moa egg (Table 1, egg r) to *Cela curtus* (= *Euryapteryx curtus*), which was the smallest moa Similarly, Oliver (1930) attributed the largest egg (Table 1, egg a) to the largest species, *Dinornis maximus* (= *D giganteus*), but Archey (1931) and Dell & Falla (1972) argued that it could have belonged to other large moas In general, bigger moas presumably produced bigger eggs with thicker eggshells Egg size and shell thickness are said to be poorly correlated among extinct and living ostriches

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(*Struthio*; Sauer 1968), but the correlation is likely to be stronger in moas with their extreme size range.

In this study I examined moa eggshell fragments from sand-dunes at Tokerau Beach and Matai Bay, Karikari Peninsula, Northland (Fig. 1). I chose a restricted geographical area, with a correspondingly limited moa fauna (six of 11 known species), to attempt to relate different size-classes of fragments to different groups of moas. The main measurements taken were of eggshell thickness. The distribution of thicknesses ought to reflect the relative abundances of the large and small moas that laid the eggs. I compared the thickness profile for Tokerau eggshells with that for Matai Bay. The large Tokerau sample should provide a reference against which other researchers can compare the thickness of fragments from elsewhere. Curvature of the larger fragments was measured to attempt to estimate the size of the eggs involved.

Previous studies of the thickness of moa eggshell fragments

Wilhelm von Nathusius described the fine structure of moa eggshells in two papers (1870, 1871; see translations by Tyler 1964). He found similarities with the eggshells of other ratites, especially rheas. Nathusius noted both thick and thin moa eggshell fragments, but gave only 1.71 mm as a thickness measurement for moas. Hutton (1872) briefly described moa eggshell fragments from an undisclosed location that were "about 0.07 of an inch" (= 1.78 mm) thick. Notes by Hutton appended to a paper by White (1876) described moa eggshell fragments from a cave near Lake Wakatipu. They were "pale sea-green" in colour, reminiscent of the cassowary's egg (*Casuarius*), and 0.04 inches (= 1.02 mm) thick. Owen

Table 1 Summary of the 18 known moa eggs intact enough for measurement of length and width (mm), in order of decreasing length. Year is the year of collection. The four smallest are from the North Island; all others from the South Island. L/W is egg elongation (ratio of length to width). Data from Archey (1941), Oliver (1949) and Simpson (1955); see Dell & Falla (1972) for correct size of egg a. Few can be identified to species with confidence: egg b is *Pachyornis* on the strength of embryonic bones contained within (T. Worthy pers. comm. 1999); egg m was associated with an *Emeus* skeleton (Archey 1941).

	Length	Width	L/W	Locality	Year
a	240	178	1.35	Kaikoura, Marlborough	1850s
b	226	155	1.46	Cromwell, Otago	1866
c	221	150	1.47	Shag River, Otago	1941
d	215	146	1.47	Wairau River, Marlborough	1942
e	207	145	1.43	Wairau River, Marlborough	1942
f	207	139	1.49	Wairau River, Marlborough	1942
g	205	158	1.30	Wairau River, Marlborough	1942
h	201	138	1.46	Clutha River, Otago	c.1900
i	200	138	1.45	Ettrick, Otago	1911
j	195	135	1.44	Clutha River, Otago	c.1900
k	194	139	1.40	Wairau River, Marlborough	1939
l	192	152	1.26	Awamoa, Otago	1852
m	179	134	1.34	Pyramid Valley, Canterbury	1939
n	160	108	1.48	Chatto Creek, Otago	1953
o	159	114	1.39	Kaiiwi, Wanganui	1931
p	152	121	1.26	Tukituki River, Hawkes Bay	1936
q	121	97	1.25	Tokerau Beach, Northland	1900
r	120	91	1.32	Tokerau Beach, Northland	1900

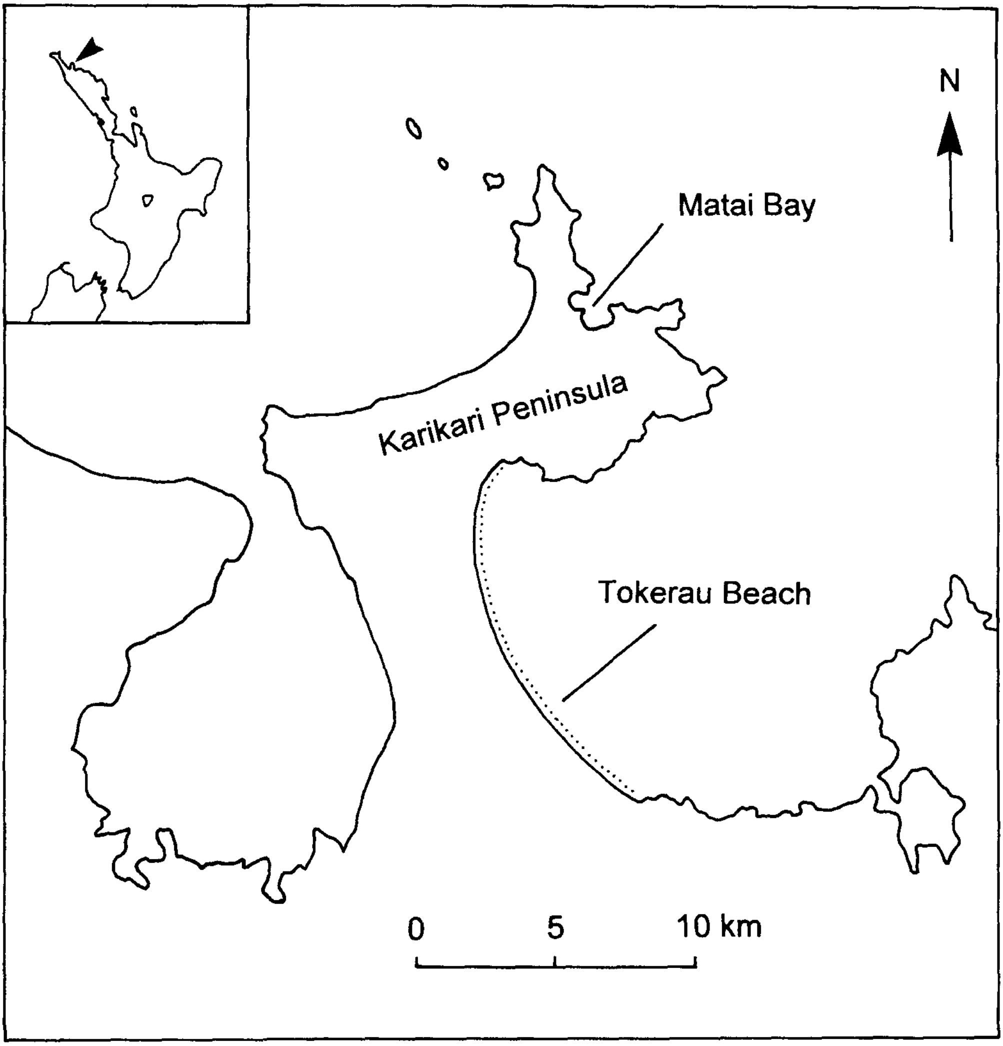

Fig. 1 Locality map showing Tokerau Beach and Matai Bay on the Karikari Peninsula, Northland.

(1879) noted that moa eggshell was both absolutely and relatively thinner than the Ostrich's (*Struthio*). He gave only one measure of thickness—one twelfth of an inch (= 2.1 mm)—for what is now the largest moa egg known (Table 1, egg a).

Archey (1931) reported that eggshell fragments from the southern end of Tokerau Beach fell into two groups: those 0.5–1.0 mm thick and those 1.3–1.7 mm thick. The "surface pitting" of the thinner fragments was "finer, comprising minute punctures and short fine slits". The thicker fragments had "coarser pittings, which show as distinct slits ... never as minute circular punctures". There were about 50 pores/cm^2 on the thin fragments and about 35 pores/cm^2 on the thick. The degree of curvature (judged by eye, presumably) and the pattern of surface pores of the thin fragments seemed to match the condition of two intact eggs from the same area (Table 1, eggs q and r) thought to belong to *Cela curtus* (= *Euryapteryx curtus*). The bones of only two other moas were known from the area at the time, *Cela geranoides* (= *E. geranoides*) and *Dinornis ingens* (= *D. novaezealandiae*). Archey attributed the thicker fragments to the former.

Oliver (1949) stated that the thickest eggshell he measured was 2 mm thick. Fragments studied by Tyler (1957) from five sites in Otago were 1.08–1.46 mm thick (excluding a badly eroded sample). Schönwetter (1960) cited eggshell thicknesses for moas of 0.8–3.7 mm. Most of his thicknesses were calculated from other dimensions rather than measured directly, but values of 3.0–3.7 mm were taken from re-examination of thin sections made by von Nathusius. Schönwetter stated that there was no confusion with *Aepyornis*, but such extreme thicknesses for moas must remain doubtful unless confirmed from other sources. McCulloch (1992) reported dark olive-green eggshell fragments from Rakaia Gorge that were 1.16 mm thick.

In summary, the thinnest moa eggshell appears to be about 0.5 mm thick, as reported by Archey (1931). At the other extreme, the "one twelfth of an inch" (2.1 mm) noted by Owen (1879), and 2 mm by Oliver (1949), may be crude measures. This leaves "about 0.07 of an inch" (1.78 mm) (Hutton 1872) as candidate for the thickest moa eggshell.

Moa fauna of the Karikari Peninsula

Millener (1981) recorded bones of three species of moas from six sites he investigated along Tokerau Beach. Previous museum collections from this beach confirmed the presence of another three species (Millener 1981). In total, there were remains of at least 182 individual moas, the minimum numbers of individuals being: *Euryapteryx curtus* (157 individuals, 87%), *Pachyornis mappini* (15, 8%), *E. geranoides* (2, 1%), *Dinornis struthoides* (4, 2%), *D. novaezealandiae* (2, 1%) and *D. giganteus* (2, 1%). It is reasonable to suppose that all these moas were breeding in the area, and that their eggshells were represented in the large sample of Tokerau Beach fragments examined for this study. Millener found only one moa (*E. curtus*) at his single Matai Bay site.

The relative sizes of these moas, in decreasing size order, using weight estimates (kg) by Cooper et al. (1993), is as follows: *Dinornis giganteus* 180–270, *D. novaezealandiae* 110–200, *Euryapteryx geranoides* 30–150, *D. struthoides* 50–115, *Pachyornis mappini* 15–60 and *E. curtus* 15–50. Some species are thought to have varied widely in size. For example, *P. mappini* and *E. curtus* were sexually dimorphic (Worthy 1987), *P. mappini* was larger on average in the Otiran than in the Holocene (Worthy 1987), and the species of *Dinornis* were larger towards the south (Worthy 1988) following Bergmann's Rule. Moas from the Karikari Peninsula, being Holocene populations in the far north of the country, may not have attained some of the maximum weights given above. Fig. 2 represents graphically the relative size and abundance of the moas of the Tokerau Beach area.

MATERIALS AND METHODS

Study area

The Karikari Peninsula, north-east of Kaitaia, Northland (Fig. 1), comprises a peninsula proper with a coastline of rocky headlands linked by sandy beaches. Matai Bay is a cluster of three small beaches at the north-east of the peninsula, some 6 km from the northern end of Tokerau Beach. The peninsula proper is joined to the mainland by a sand tombolo of which Tokerau Beach (14 km long) forms the eastern margin.

Dunefields behind the beaches incorporate dune units of Pleistocene to Holocene age (Isaac 1996). The dunefields are presently sparsely vegetated and mobile, but palaeontological evidence suggests that they were forest- or scrub-covered until Polynesian settlement about 1000 years ago (Millener 1981; Brook 1999). Before human settlement, the entire Karikari

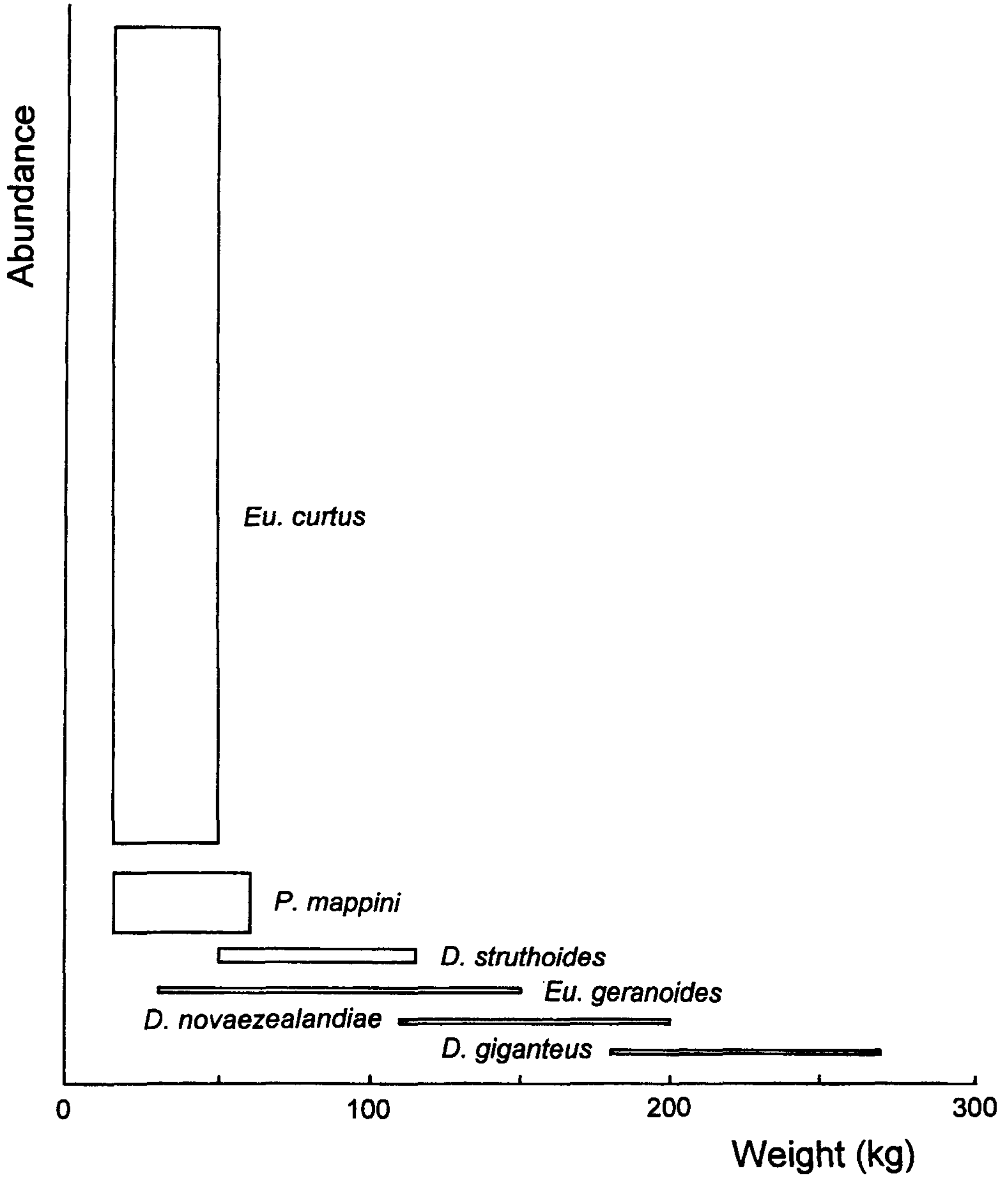

Fig. 2 Graphical representation of relative abundance (y-axis) and size range (weight, kg) of the six species of moas reported from Tokerau Beach by Millener (1981; see text). The y-axis has no scale because the *areas* of the rectangles are proportional to abundance.

Peninsula would have been forested or scrub-covered except for cliffs, foredunes and patches of wetland.

Moa eggshell fragments and fossil bird bones found *in situ*, and on deflation surfaces in the dunes, derive from birds that lived in the forest, scrub and vegetational margins once covering the sites. The fossils accumulated over about 6000 years (see discussion and references in Atkinson & Millener 1991: 164) and are periodically exposed now that the dunes are mobile. The oldest dated vertebrate remains from Tokerau Beach have an age of 3720 ± 77 years B.P. (Millener 1981).

Material examined

I examined 105 samples of eggshell fragments (Appendix 1), a sample being a collection of one or more fragments obtained from a particular locality at a given time. The samples were held at Auckland Museum, Auckland (AIM, n = 32); at the Geology Department, Auckland University, Auckland (AU, n = 61); at the Museum of New Zealand, Wellington (NMNZ, n = 2); and in the private collections of Trevor Worthy, Nelson (n = 9); and Brian Reeve, Upper Hutt (n = 1).

With most samples, all fragments in satisfactory condition were measured. However, with the largest samples, a subsample—usually the largest and soundest pieces—was selected from among the unworn fragments. Between 1 and 57 fragments were used from each sample (Appendix 1).

Nearly all samples (97; from which a total of 1042 fragments were examined) were from dunes behind Tokerau Beach; another eight samples (51 fragments examined) were from Matai Bay. The samples were collected between 1931 and 1998, and the main collectors were G. Archey, F. J. Brook, E. T. Frost, B. J. Gill, L. T. Griffin, L. J. & G. Matthews, P. R. Millener, B. Reeve and T. H. Worthy.

Moa eggshell fragments from dunes are often in remarkably good condition, having been protected by a covering of sand until shortly before collection. In this study, fragments with badly weathered or eroded surfaces were rejected from consideration of thickness. Some with meandering surface markings that suggested rasping by land snails were acceptable since thickness was not affected over the entire fragment.

Eggshell fragments in the dunes are sometimes found in isolation, but more often in concentrations. These concentrations of fragments presumably represent one or more eggs of a clutch, or two or more eggs from two or more clutches. Fragments of very different thickness may occur together proving that separate clutches can mix. Concentrations are rarely discrete and often appear to coalesce over large areas. The relationship between museum samples, and any scatterings that were perceived in the field, is seldom recorded, so no account of these concentrations was made in this study and initially all fragments were treated as belonging to a single sample.

The total number of eggs involved in the study is not known, but is presumed to be large since the fossiliferous dune sites at Tokerau Beach extend geographically for about 10 km. There were many groups of fragments in the samples that would have belonged to the same eggs. It is also probable that particular eggs were sampled successively by collections of fragments made at different times. Tens of eggs would be involved at the very least and the maximum possible would be about 1000. In reality the sample probably represented hundreds of eggs.

Thickness

Vernier calipers were used to measure thickness (to the nearest 0.01 mm) at an undamaged point on the edge of the fragment for a total of 1093 fragments.

Curvature

The curvature of fragments was measured with a surface gauge (Teclock TM–110, Teclock Corp., Japan) modified by the addition of two fixed probes, one each side of the measuring probe, as described by Williams (1981). The assembly was zeroed by pressing it against a glass microscope slide. The fixed probes were 12 mm apart, so measurable fragments had to include a roughly circular area at least 14 mm in diameter Curvature was measured on the inner surface of the eggshell A pair of curvatures, maximum and minimum, was obtained for a given point Most fragments were too small to permit readings at more than one point, but on large fragments I obtained two pairs of readings—the maximum curvature (with its associated minimum curvature at that point) and minimum curvature (with associated maximum) For Tokerau Beach a total of 248 curvature measurements was obtained from 237 fragments Curvature was not assessed for Matai Bay fragments, as only one was large enough for a curvature reading

I calibrated the gauge by measuring the internal curvature of 16 cylinders of known diameter to obtain the following regression equation

$$\text{Diameter (mm)} = 42\ 26 \times (\text{Dial reading})^{0\ 9056}$$

This equation was used to convert each curvature reading to a diameter

If the maximum and minimum curvatures of a fragment are the same, it is from one of the egg's poles (Sauer 1968, Williams 1981, Williams & Vickers-Rich 1991) Where the curvatures differ, the fragment is from a position away from the poles, those with the greatest differences being nearest the egg's equator A fragment's maximum curvature is the curvature in the egg's transverse plane, expressed as the diameter D_W, which indicates egg width at that point, since eggs have a circular outline in transverse section The fragment's minimum reading, or longitudinal curvature, yields the diameter D_L This has no direct physical meaning, because eggs are elliptical in longitudinal section, but it orientates the fragment on the egg's long axis The results are graphed as D_L as a function of D_W

RESULTS

General description of the fragments

Moa eggshell fragments from the Karikari Peninsula were typically white or cream-coloured, which may or may not represent the original colour The cream coloration may have developed by subsequent staining, from leaching by percolating ground-water, or some other factor

In the hand, most fragments were readily identifiable by feel as either "thick" or "thin" As noted by Archey (1931), the thick shells tended to have slit-like pores on the outer surface, each slit up to about 1 3 mm long and running in the direction of the egg's long axis (see Pl 16 fig 3 of Archey 1931) Many of the thin fragments had dot-like pores, with little or no indication of the orientation of the fragment with respect to the egg (see Pl 16 fig 2 of Archey 1931) Some thin fragments had no pores discernible to the naked eye

Most fragments were small Only 23% of those chosen for thickness measurement were large enough for curvature measurement, i e , at least 14 mm across *in all directions* For a more precise indication of size, I measured the greatest length of each fragment in a subsample of 193 from the AU collection This was 10–41 mm with a mean of 21 0 mm (s d = 5 65) The lower figure is not meaningful since in most samples there would have been a bias against the collector finding, or bothering to collect, the smallest fragments only a few millimetres across The upper figure is a little misleading Many fragments were elongate or triangular If squarish or rounded, most had indentations Thus size in the longest direction did not reflect the smaller size in other directions

There was no strong correlation between the greatest lengths of fragments and their thicknesses (correlation co-efficient = 0 299, n = 193), and a plot of thickness as a function of greatest length showed a broad scatter Thus the largest fragments were not all thick and the smallest were not all thin Most moa eggshell samples are biased in favour of larger fragments because these will tend to be noticed first against the sand surface, and selectively retained by the collector However the thickness of a shell fragment is not apparent until it is

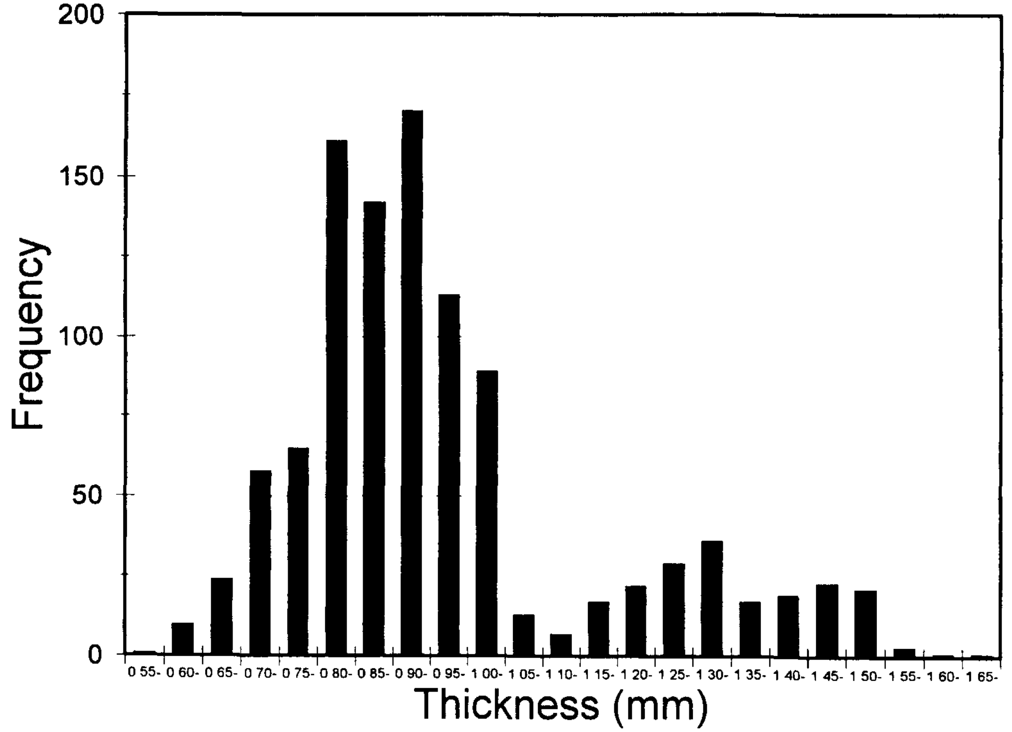

Fig. 3 Distribution of thicknesses in a sample of 1042 eggshell fragments from Tokerau Beach.

picked up, so the samples will be unbiased as to thickness, however biased they may be as to size.

About 1.4% of fragments showed signs of deformity. In some, part of the shell was undulating in cross-section, rather than smoothly curved. In others, areas of the shell's outer surface were raised into clusters of smooth, round tubercles.

Eggshell thickness

The thinnest fragment in the study was 0.56 mm thick, and the next thinnest two fragments of 0.60 mm. The thickest fragment was 1.69 mm, followed by fragments of 1.62 mm and 1.57 mm thick.

Fig. 3 shows the distribution of thicknesses for the large Tokerau Beach sample. The distribution is broadly bimodal, reflecting the division between thick and thin eggshells that is subjectively apparent from handling. The histogram shows a separation between thick and

Table 2 Summary statistics for the thickness (mm) of samples of thick and thin eggshell fragments from Tokerau Beach, and thin fragments from Matai Bay.

	Tokerau thick	Tokerau thin	Matai thin
mean	1.346	0.8740	0.814
n	193	849	50
s.d.	0.119	0 0970	0.0964
range	1.12–1.69	0.56–1.10	0.58–1.02

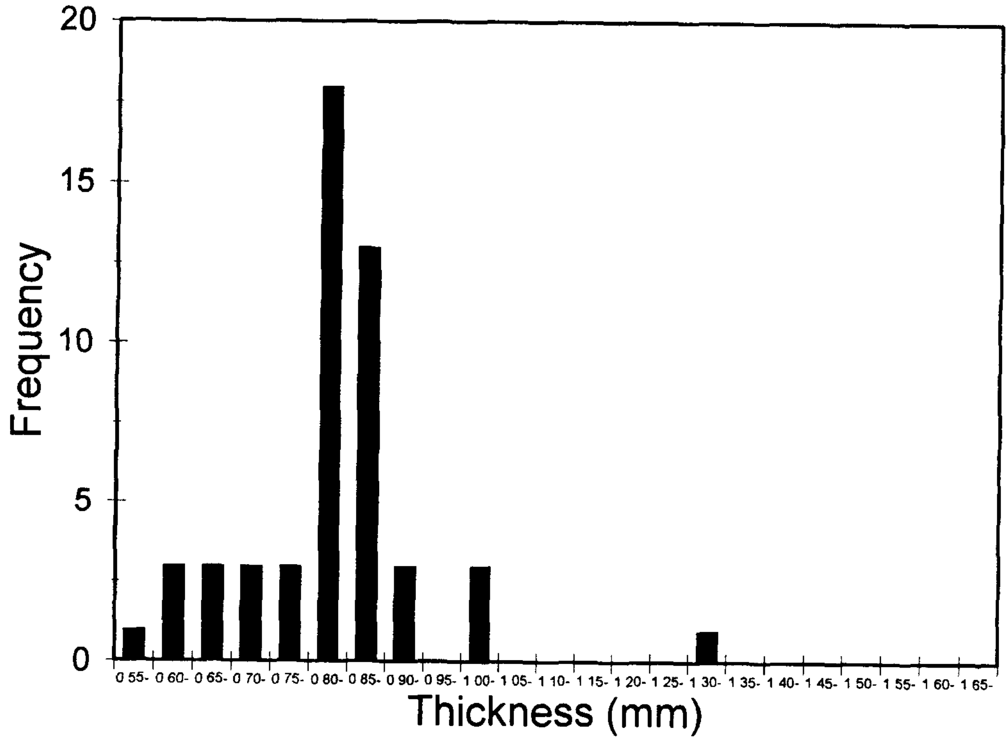

Fig. 4 Distribution of thicknesses in a sample of 51 eggshell fragments from Matai Bay.

thin shells in the region of 1.10–1.14 mm. The seven shells in this group had the following thicknesses: 1.10 mm (3), 1.12 mm, 1.13 mm, 1.14 mm (2). For subsequent analysis I therefore arbitrarily defined thin shells as being ≤1.10 mm and thick shells as being ≥1.12 mm. If eggshell thicknesses for each moa species are normally distributed then there will be overlap of thick and thin shells in the range 1.05–1.19 mm, perhaps beyond. However, the dearth of fragments in the 1.10–1.14 mm range indicates that overlap is slight. Table 2 shows the summary statistics for thick and thin shells at Tokerau Beach.

In the Tokerau sample, 81% of fragments (849) were thin, presumably reflecting the great abundance of small moas in the area as indicated by bones (Fig. 2). Thin eggshell at Tokerau was probably produced mostly by *Euryapteryx curtus*—by far the most abundant moa—and to a lesser extent by *Pachyornis mappini*, the other small species. Similarly, the four larger moas (*Dinornis* spp. and *E. geranoides*) were probably responsible for most of the thick shell fragments, which were 19% of the shell sample. The four large moas made up 5.5% (10 out of 182) of the individuals represented by bones.

Fig. 4 and Table 2 summarise eggshell thicknesses from the small Matai Bay sample. All fragments were thin except for one measuring 1.30 mm (excluded from the sample in Table 2). The mode at 0.80–0.84 mm for Matai Bay matches a peak at the same thickness for Tokerau Beach, but abundant shells of 0.90–1.04 mm in the Tokerau sample are lacking at Matai Bay. The difference between the means for the Matai Bay sample and the thin sample from Tokerau Beach was highly significant ($t = -4.266$, d.f. $= 897$, $P < 0.0001$). The Matai Bay fragments presumably belonged predominantly to *E. curtus*, the only moa known from bones at the site, and the main species at nearby Tokerau Beach.

Eggshell curvature and egg width

Table 3 summarises statistics for the diameters (D_W and D_L) calculated from measurements of the curvature of eggshell fragments. The thick and thin eggshell samples were significantly different for both D_W ($t = -5.83$, df = 246, $P < 0.0001$) and D_L ($t = -4.02$, df = 92, $P < 0.0001$). Fig. 5 and 6 show D_L plotted as a function of D_W for thick and thin samples respectively.

In the graphs, points representing an elliptical egg would give a J-shaped scatter meeting the line $D_L = D_W$ (the locus of spheres) at the lower left (Williams 1981). Fig. 5 and 6 show scatterings with a somewhat J-shaped tendency. The points are broadly spread presumably because the thick and thin samples each represent the eggs of many individuals of more than one species. Points closest to the line $D_L = D_W$ represent fragments from polar regions of the egg; points furthest from the origin represent equatorial regions.

In a large sample of fragments the maximum D_W will be an equatorial diameter – 160 mm for thick shell from Tokerau Beach and 134 mm for thin. It is advisable to reduce the observed maximum by 5% to approximate the average of the cluster of maximum values scattered below the extreme value (Williams & Vickers-Rich 1991). It is also necessary to add 2.7 mm to the thick estimate, and 1.8 mm to the thin—twice the eggshell thickness (means in Table 2)—to give the external width of the egg. Doing this suggests that the largest thick-shelled egg at Tokerau Beach was 155 mm wide, and the largest thin-shelled egg was 129 mm.

In mixed-species samples the maximum D_W indicates the maximum egg width of only the largest species. In Fig. 5 and 6, outlying points towards the tops of the graphs (arrowed) may represent equatorial diameters of smaller eggs within the samples. Reducing these diameters by 5% and adding the shell thickness (see above), we have 116 mm, 122 mm, 134 mm and 139 mm for thick fragments and 99 mm, 105 mm, 118 mm and 122 mm for thin. In summary, the values of D_W suggest widths of 116–155 mm (mean = 133 mm, s.d. = 15.3, n = 5) for thick-shelled eggs at Tokerau Beach, and 99–129 mm (mean = 115 mm, s.d. = 12.3, n = 5) for thin-shelled eggs.

Egg elongation and egg length

Egg elongation—the ratio of length to width—is given in Table 1 for all known moa eggs sufficiently intact for measurement. The average egg elongation is 1.39 (s.d. = 0.0846, n = 18, range = 1.25–1.49). Length can be estimated from width using this factor. The widths calculated from the curvatures for thick eggshell fragments (116–155 mm) correspond to estimated lengths of 161–216 mm. Thin fragments, which yielded estimates for width of 99–129 mm, had corresponding lengths of 138–179 mm. All these dimensions are within the size ranges known for moa eggs (Table 1).

Table 3 Summary statistics for the diameters D_W and D_L (mm) for thick and thin eggshell fragments from Tokerau Beach.

	D_W thick	D_W thin	D_L thick	D_L thin
mean	122.9	111.7	289.6	203.2
n	87	161	87	161
s.d.	14.93	14.11	197.19	50.79
min.	75.1	67.1	115.3	85.4
max.	159.9	133.8	1460.6	374.1

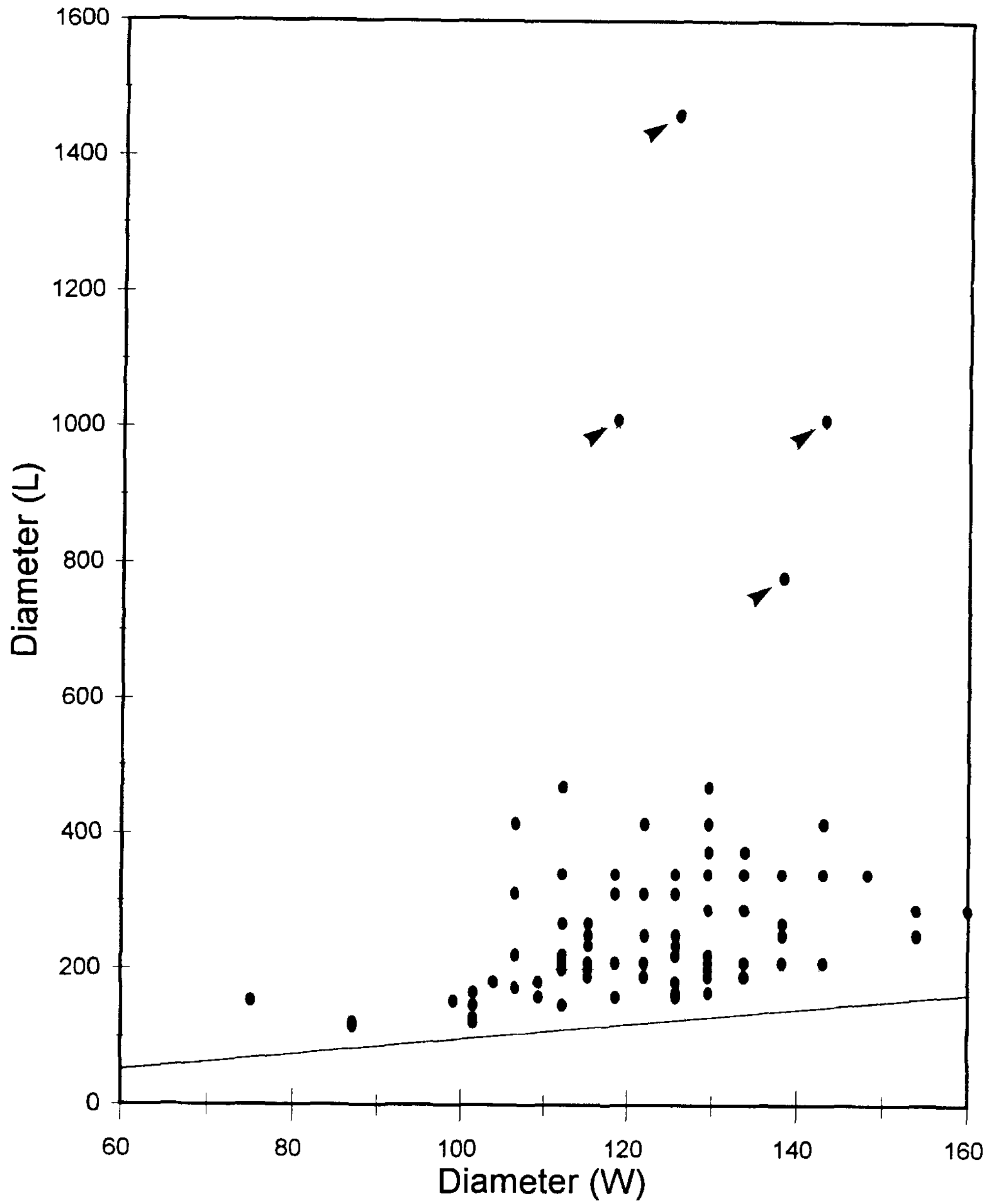

Fig. 5 Curvature of thick eggshell fragments (≥1.12 mm thick) from Tokerau Beach. Plot of diameters (D_L and D_W, in mm) calculated from the minimum and maximum curvature readings (respectively) taken at points on the inside of eggshell fragments. D_l has no direct physical meaning (see text). The line below the data points is $D_L = D_W$. Multiple records of the same data point do not show: the graph shows 72 data points, based on a total sample of 87. Arrowed points are mentioned in the text.

Eggshell weight

I weighed egg r in Table 1 (AIM B4003) at 67.0 g, a slight underestimate of original weight as it has a small perforation and part of the egg surface is worn. (Egg q cannot provide a useful weight because a large section is missing.) Egg q (Table 1; AIM B4005) has a shell

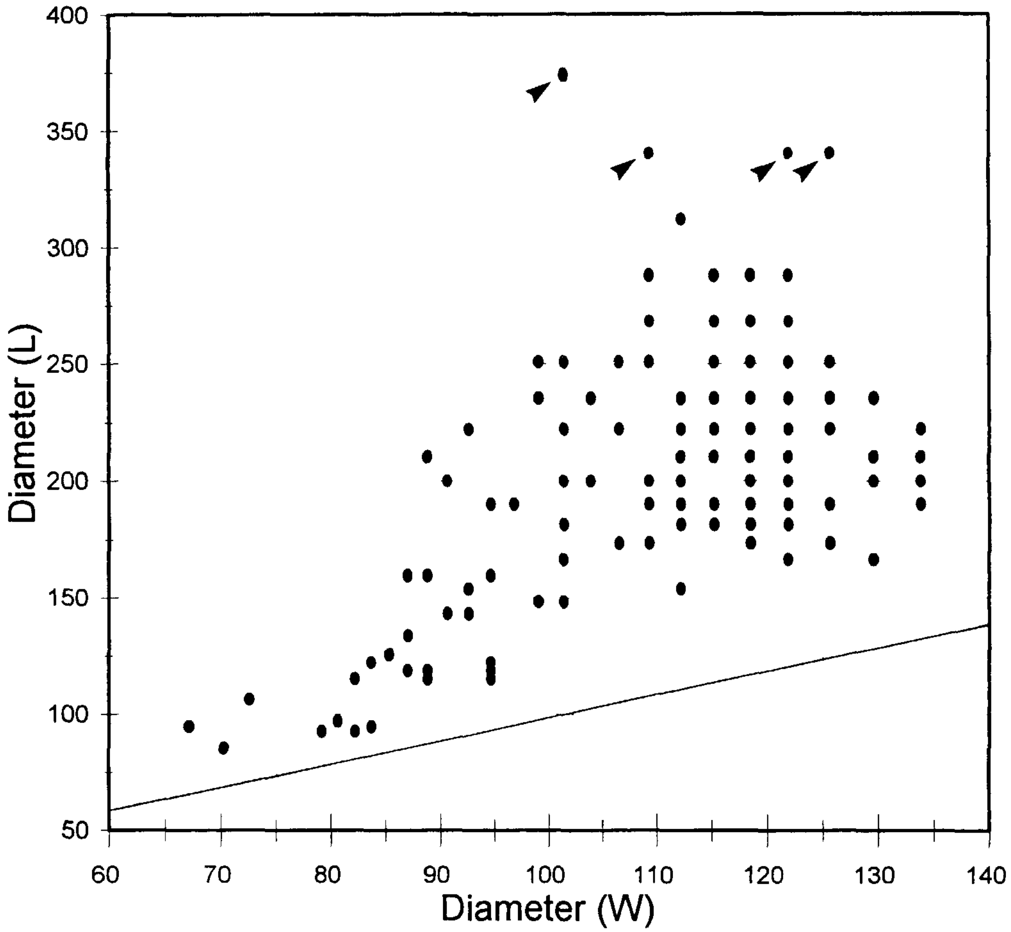

Fig. 6 Curvature of thin eggshell fragments (≤1.10 mm thick) from Tokerau Beach. Plot of diameters (D_L and D_W, in mm) calculated from the minimum and maximum curvature readings (respectively) taken at points on the inside of eggshell fragments. D_L has no direct physical meaning (see text). The line below the data points is $D_L = D_W$. Multiple records of the same data point do not show: the graph shows 101 data points, based on a total sample of 161. Arrowed points are mentioned in the text.

thickness of 0.9 mm (Archey 1931). (The thickness of egg r has not been measured because its perforation is too small to admit an instrument.) Both are thought to have belonged to *Euryapteryx curtus*.

In December 1996, Trevor Worthy found and sieved a discrete group of eggshell fragments scattered over less than 2 m^2 of dune surface at Tokerau Beach. The collection contained several thousand fragments, mostly small. The shell was thin (mean of a sample of 13 fragments = 0.88 mm, s.d. = 0.055, range = 0.78–0.96) with dot-like pores, and probably belonged to *E. curtus* (or perhaps *Pachyornis mappini*). I obtained a total weight for the fragments of 361 g, which is enough shell for 5–6 eggs of *E. curtus*.

DISCUSSION

The thınnest eggshell fragments ın thıs study (0 56–0 69 mm) mıght have belonged to large bırds other than moas, but Mıllener (1981) recorded few large specıes from the fossıl sıtes ın questıon *Cygnus sumnerensıs* was rare (one ındıvıdual), though the eggshells of Cygnınae may reach 0 7 mm thıck (Mıkhaılov 1997) The only other large bırds reported from the sıtes were *Apteryx australıs, Pelecanus novaezealandıae* (rare, one ındıvıdual), *Phalacrocorax carbo, Tadorna varıegata, Porphyrıo mantellı* and *Strıgops habroptılus* Probably none of these produced shells above 0 5 mm thıck Eggshell of *Apteryx* ıs 0 34–0 50 mm thıck (Tyler & Sımkıss 1960, Sılyn-Roberts & Sharp 1985) Eggshell thıckness ın the Pelecanıformes ıs 0 15–0 40 mm (Mıkhaılov 1997) It therefore seems safe to assume that vırtually all eggshells examıned ın thıs study belonged to moas

The maxımum eggshell thıckness at Tokerau Beach (1 69 mm) ıs short of the maxımum relıably recorded for moas (1 78 mm, see Introductıon) Sımılarly, the greatest egg length (216 mm) and egg wıdth (155 mm) estımated from the curvature of Tokerau Beach fragments were short of the dımensıons of the largest known moa egg (Table 1, egg a) However, the largest moa eggs would not be expected ın the far north of New Zealand because the *Dınornıs* moas ıncreased ın average sıze southwards (Worthy 1988) followıng Bergmann's Rule

An alternatıve to the conclusıon that *Euryapteryx curtus* and *Pachyornıs mappını* together produced the thın shell at Tokerau Beach (Fıg 3) ıs that *E curtus* produced the thın shell, *P mappını* the thıck, and that the other moas were too rare to be represented ın the eggshell sample Thıs can be ruled out, sınce the thıck Tokerau fragments approach the thıckest recorded ın New Zealand, and must therefore have been produced by some of the largest moas, not *P mappını*, whıch was a small specıes

The small moa *Euryapteryx curtus* accounted for 87% of the ındıvıduals represented by bones from Tokerau Beach Thıs agrees wıth thın eggshell from the sıte makıng up 81% of the sample, and encourages the hope that a frequency hıstogram of eggshell thıcknesses from a localıty may gıve a good ındıcatıon of the relatıve abundance of the large and small moas that once bred there Comparıng thıckness dıstrıbutıons from dıfferent sıtes may suggest dıfferences ın the moa faunas, and the hıstogram for Tokerau Beach eggshell fragments (Fıg 3) ıs a reference agaınst whıch other samples may be compared

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APPENDIX 1

Registration numbers of the 105 samples from which moa eggshell fragments were selected for study. The number of fragments measured for thickness in each sample is shown in brackets.

TOKERAU BEACH (97 samples, 1,042 fragments)

Auckland Museum, Auckland, AIM, 29 samples (452 fragments):

B323 (33), B3679 (17), B3686 (10), B4009 (4), B6671 (4), B6672 (30), B6673 (28), B6674 (40), B6675 (16), B6677 (9), B6703 (1), B6704 (4), B6708 (15), B6716 (21), B6742 (2), B6743 (1), B6755 (14), B6779 (15), B6780 (57), B6781 (17), B6782 (9), B6783 (7), B7471 (48), B7473 (9), B8054 (14), B8292 (10), B8293 (6), B8443 (2), B8928 (9)

Geology Department, Auckland University, Auckland, AU, 56 samples (390 fragments):

4625.A (3), 4626.A (12), 4655.B (4), 4658.12–3 (2), 4661.A (49), 4667.D (5), 4668.3 (1), 4696.17–8 (2), 4703.2–3 (2), 4706.23–4 (2), 4757.A (4), 4833.37 (1), 4834.A&E (18), 4835.A (6), 4870.G (15), 4879.B (19), 4951.A (5), 4952.D (5), 4954.16 (1), 4955.C (5), 4957.12 (1), 5802.16 (1), 5805.B (20), 5806.A (8), 5850.110–4 (5), 5854.A (5), 5856.6 (1), 5857.11–2 (2), 5858.B (4), 5871.B (9), 5872.B (3), 5873.C (2), 5874.15 (1), 5875.46–9 (4), 6118.C (3), 6119.A (6), 6121.D (8), 6125.A (3), 6126.B (11),

6127 C (22), 6130 A (4), 6131 A (5), 6132 A (28), 6203 A (4), 6206 2 (1), 6751 A (10), 6754 17 (1), 6757 C (3), 6762 D (4), 6765 A-B (20), 6766 A (3), 6804 C (8), 6805 A (1), 6806 E (7), 6807 G (7), 6808 G (4)
Museum of New Zealand, Wellington, NMNZ, 2 samples (9 fragments)
Unregistered (2, 7)
Private collection of Trevor Worthy, Nelson, 9 samples (139 fragments)
Unregistered (4, 7, 10, 13, 15, 20, 22, 22, 26)
Private collection of Brian Reeve, Upper Hutt, 1 sample
111/1–1269 (52)

MATAI BAY (8 samples, 51 fragments)
Auckland Museum, 3 samples (42 fragments)
B6777 (16), B6778 (7), B7472 (19)
Geology Department, Auckland University, 5 samples (9 fragments)
5812 10 (1), 5849 10 (1), 6141 15 (1), 6142 A (4), 6809 E (2)