FIRST NORTH ISLAND FOSSIL RECORD OF KEA, AND MORPHOLOGICAL AND MORPHOMETRIC COMPARISON OF KEA AND KAKA

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ABSTRACT

A Kea (*Nestor notabilis*) is recorded as a fossil from the late Pleistocene of the North Island of New Zealand. Morphological and morphometric differences in osteology between the Kea and the Kaka (*Nestor meridionalis*) are described and discussed. Fossil and recent osteological specimens of the Kea and South Island Kaka have been confused in the past, resulting in Kea being identified as Kaka in collections and published lists. A fossil recorded as *Nestor* n. sp. in the Canterbury Museum is shown to be a South Island Kaka.

INTRODUCTION

The Kea (*Nestor notabilis*, Psittacidae) is restricted to the South Island of New Zealand (Bull *et al.* 1985, Turbott 1990). For the first few decades after its discovery in 1856 (Gould 1856), it was recorded from only the southern South Island, as far north as Arthur's Pass (O'Donnell & Dilks 1986). According to Oliver (1955), it was not found north of the Hurunui River before 1870. He also recorded specimens from Riwaka and Appleby, near Nelson, taken in 1904, and suggested that Kea had increased in numbers after 1870 and that, driven by population pressure, they "overflowed from their mountain habitat and came down to the lowlands on both sides of the Alps. They also spread north and by 1904 had reached the north coast of Nelson." These comments were repeated by Falla *et al.* (1979). Kea were first noted near the Nelson lakes (Rotoroa and Rotoiti) in 1903 (Marriner 1908).

Kea are unlikely to have increased in numbers as much as was generally accepted at the time (Marriner 1908, Oliver 1955). It is more likely that, as Marriner noted, the number of records increased as the number of observers increased in the alpine areas and elsewhere. The bounties offered for Kea suspected of sheep-killing certainly stimulated reports of them near sheep stations and provided a means of recording abundances, lacking before 1870.

The Kea was almost certainly in the northwest Nelson area before the 1870s. In the Nelson high country there were no sheep and so observers were fewer than in the sheep country of the Alps, and Kea were of little interest to prospectors, who were the major explorers of the area. We agree with Marriner (1908) that the lack of a record "being found further north than the Lochinvar Station [in North Canterbury] until 1882 ... is very likely due to the fact that no scientific man explored the country. If one did, he left no available records." We consider that the lack of records near Nelson before 1904 does not prove a lack of Kea.

The Kea mainly inhabits the subalpine zone and adjacent montane forest, but occasionally it descends to less than 100 m on the West Coast (O'Donnell & Dilks 1986) and in Northwest Nelson and Marlborough (pers. obs.).

Fossil records near Punakaiki (Worthy & Holdaway 1993) and at Honeycomb Hill Cave, near Karamea (Worthy & Mildenhall 1989), show that the Kea was widespread in lowland areas west of the Main Divide. At Punakaiki, fossils are apparently of both Holocene and Otiran (last glacial) age, but the abundant material from Honeycomb Hill Cave is all of Otiran age (> 10 000 years old). Fossils of possible Holocene age (< 10 000 years old) from Takaka Hill and Takaka Valley (authors' unpublished data) show that if the Kea did expand recently into Northwest Nelson (Falla *et al.* 1979), it was recolonising its former range.

Although a few vagrants have been recorded in the North Island (Oliver 1955, Cunningham 1974), a lack of historical or published fossil evidence suggests that the Kea has not been a permanent resident there in historical times.

While examining fossil *Nestor* material in the Canterbury Museum, we discovered a Kea (AV 18389) collected from a cave in the Waitomo area in the west-central North Island that had been incorrectly identified as a Kaka (*Nestor meridionalis*). Here we present evidence that the bird is indeed a Kea and suggest that it may indicate a former resident population of Kea in the North Island.

We compiled comparative morphological and morphometric data on the two living *Nestor* species and present it as a basis for future identifications. In doing so, we show that the undescribed small Kaka from the South Island (Dawson 1952) does not exist, as the analysis was based on mis-identified specimens.

MATERIAL

Comparative material (Kea and Kaka) (complete, or almost complete, skeletons) : Kea – Canterbury Museum specimens, AV 5161 ♂; AV 5224 (previously misidentified as Kaka); AV 5549; AV 16188; AV 16418; AV 16590 ♀; AV 22397; AV 29330-3; AV 29335; AV 36592 ♀; unnumbered Landcare NZ collection, Nelson (Roaring Lion River, 27 Nov 1989). *South Island Kaka* – AV 9956 ♂ (Peel Forest, South Canterbury); AV 12315 (coracoid, scapula, femur); Landcare NZ collection, Nelson, NMNZ band no. L-24706 (right leg), L-24717 (left leg) ♀; L-24710. OMNZ 2232. *North Island Kaka* – AIM 1526 ♀; AIM 1572 ♀; AIM 1584 ♂. NMNZ 854; NMNZ 18923; NMNZ 22936; NMNZ 23712 ♀; NMNZ 23721 ♀; NMNZ 23918 ♀; NMNZ 24148; NMNZ 24165 ♀; NMNZ 24418 ♀; NMNZ 24419; NMNZ 24509.

Fossil North Island Kea (AV 18389): The fossil was collected by John Hobson in April 1962 from Haggas Hole, a cave near Waitomo Caves, in the west-central North Island. J. Hobson (pers. comm. to THW, September 1992) recalled that the skeleton was found with other bird fossils near a former entrance, now blocked by rockfall debris. *Material*: An almost complete skeleton, comprising (L, left, R, right) cranium; premaxilla; mandible; LR

palatines; LR posteropterygoids; L (broken) and R quadrates; the entoglossal and one basibranchial bones of the hyoid; 19 presacral vertebrae (including atlas and axis), two caudal vertebrae; sternum; pelvis; LR coracoid; LR scapula; LR humerus; LR ulna; LR radius; LR ulnare; LR radiale; LR carpometacarpus; LR phalanx I/1 of wing; L (broken) and R phalanx II/1 of wing; one phalanx II/2 and one phalanx III/1 of wing; LR femur; LR tibiotarsus; LR fibula; LR tarsometatarsus; one first metatarsal; 27 pedal phalanges (missing one ungual phalanx); ribs and fragments of ribs.

Collection site and associated fauna: The Kea skeleton was collected from a passage leading from the blocked entrance about 100 m northwest of the present entrance of Haggas Hole cave (Crossley 1988), NZMS 260 R16 891250. The following fossil taxa were collected from the same site (minimum number of individuals, MNI, in parentheses): *Cnemiornis gracilis* Extinct Goose (1 – AV18035 and material held at Waitomo Caves Museum [Wo]); *Porphyrio mantelli* Takahe (9 – AV 18826-31, 19143, 18230, 28205 and material at Wo, more material left in cave); *Apteryx* cf. *australis* Brown Kiwi (1 – AV 18832); *Euryapteryx geranoides* Stout-legged Moa (1 – AV 18833-4 plus material at Wo); *Euryapteryx curtus* Coastal Moa (1 – AV 18335, 19149); *Gallirallus australis* Weka (3 – AV 19144-6); *Fulica chathamensis* Extinct Coot (1 – AV 19148, 30690, and material at Wo); *Prosthemadera novaeseelandiae* Tui (1 – AV 19231); *Strigops habroptilus* Kakapo (1 – AV 28370).

Fossil South Island Kaka (AV 16711): 17 elements of one skeleton [cranium, premaxilla, mandible, LR palatines, R quadrate, furcula, pelvis, L coracoid, LR humerus, L radius, LR femur, L tibiotarsus, LR tarsometatarsus]. 'Holotype' on label and box, but with no nomenclatural status. Collected from Pothole 3 cave, Canaan, Takaka [= Takaka Hill, Nelson], by Owen R. Wilkes, Jan 1960. Age probably Holocene.

Abbreviations: Institutions holding material used in this study are as follows: AIM, Auckland Institute and Museum, Auckland; CMNZ, Canterbury Museum, Christchurch; Landcare NZ, Landcare Research New Zealand, Nelson; NMNZ, Museum of New Zealand, Wellington; OMNZ, Otago Museum, Dunedin.

METHODS

We compared the morphology of major bones of the specimen with those of recent reference specimens of 5 South Island, 14 North Island Kaka, and 14 Kea. We also measured the length, width, and depth of the cranium, the length and depth of the premaxilla and mandible, and the length of the scapula, the coracoid, and the four major wing and three major leg bones. The measurement datum points are shown in Figure 1. Measurements were made with vernier or dial calipers to 0.01 mm.

Differences between mean dimensions were tested by Student's *t*-tests, adjusted for equal or unequal variances as necessary.

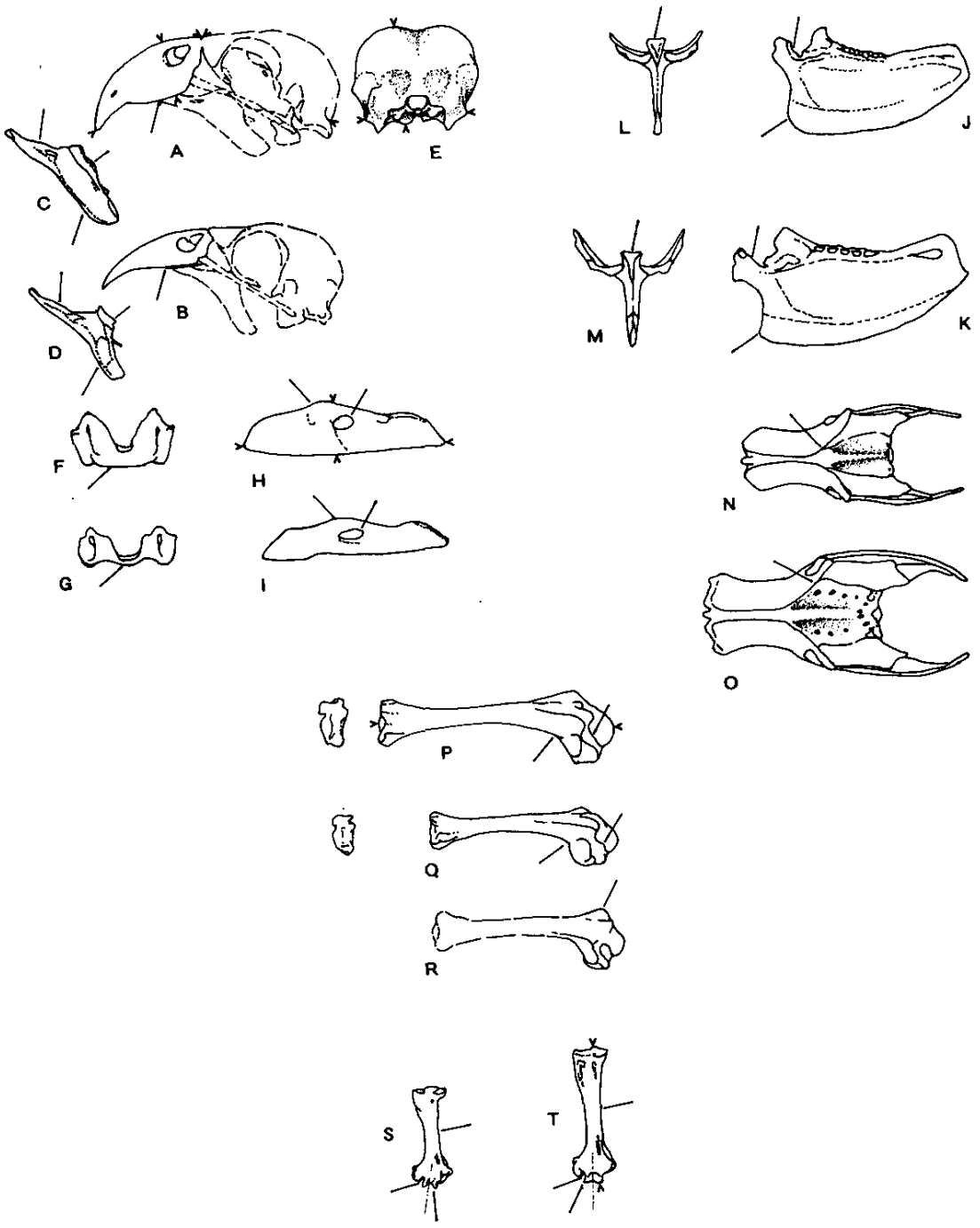

FIGURE 1 —Principal morphological characters of skeleton useful in separating Kaka *Nestor meridionalis* (A, C, E, F, H, J, L, N, Q, S) from Kea *Nestor notabilis* (B, D, G, I, K, M, O, P, T). Humerus of New Zealand Pigeon (*Hemiphaga novaeseelandiae*), which has also been misidentified as Kea or Kaka, is shown for comparison (R). Characters mentioned in text are indicated by solid lines. Measurement landmarks are indicated by open arrowheads (>). (A, B) Left lateral view of premaxilla and cranium; (C,D) left lateral view of palatine; (E) caudal view of cranium; (E,G) left lateral view and (H,I) rostral views of mandible; (J,K) left lateral and (L,M) cranial views of sternum; (N,O) dorsal view of pelvis; (P, Q, R) anconal view of humerus; (S, T) cranial view of tarsometatarsus. Specimens: *Nestor meridionalis* CMNZ AV 9956; *Nestor notabilis* CMNZ AV 22397, AV 5224 (cranium), AV 5284 (mandible); *Hemiphaga novaeseelandiae* CMNZ AV 22438.

RESULTS

Morphometrics and morphology of Kaka and Kea

Morphometrics: Summary statistics for lengths of major skeletal elements of North and South Island Kaka and Kea are given in Table 1A. Lengths of measurable elements from AV 18389 and of a fossil *Nestor* from Takaka Hill in the northwestern South Island are also given in Table 1A, for comparison. The results of Student's *t*-tests for equality of mean lengths of each element for each pair of taxa are presented in Table 1B.

TABLE 1A — Measurements (mm) of crania, premaxillae, mandibles, coracoids, scapulae, and major limb bones in samples of recent Kea and Kaka. Haggas Hole (HH) Kea and Takaka Hill (TH) Kaka included for comparison. Mean (*n*, SD)/Range, CV(%); -, no value.

Element/dimension	North Island Kaka	South Island Kaka	TH Kaka AV16711	HH Kea AV18389	Kea
Cranium length	48.29 (11, 2.198) 44.88-50.80, 4.55%	52.16 (3, 0.431) 51.90-52.66, 0.83%	-	-	52.00 (11, 2.156) 49.38, 4.15%
Cranium depth	28.96 (11, 1.431) 26.92-31.15, 4.94%	29.42 (1, -) -, -	-	-	32.23 (11, 7.735) 29.49-34.02, 5.38%
Squamosal width	36.01 (11, 2.285) 32.54-38.91, 6.34%	38.87 (3, 0.686) 38.17-39.54, 1.76%	-	-	39.2 (11, 2.015) 35.4-42.64, 5.23%
Premaxilla length	45.01 (11, 3.902) 39.70-51.04, 8.67%	49.24 (3, 1.797) 47.3-50.85, 3.65%	-	-	46.05 (8, 6.579) 42.29-51.45, 7.77%
Premaxilla depth	16.65 (11, 1.493) 13.97-18.70, 8.97%	17.94 (3, 0.302) 17.60-18.17, 1.69%	-	13.1	12.68 (8, 0.546) 11.62-13.34, 4.30%
Mandible length	60.64 (12, 4.618) 52.42-66.12, 7.62%	66.86 (2, 0.340) 66.62-67.1, 0.51%	55.94	-	65.79 (14, 3.254) 60.26-70.72, 4.96%
Mandible depth	14.89 (12, 1.482) 12.58-16.72, 9.95%	16.88 (3, 0.156) 17.06-16.80, 0.93%	13.0	11.1	11.06 (14, 0.780) 10.05-12.16, 7.05%
Coracoid	35.88 (14, 1.476) 33.15-38.00, 4.11%	39.63 (5, 0.785) 38.50-40.69, 1.98%	38.08	45.47	46.75 (14, 2.059) 42.92-49.14, 4.40%
Scapula	42.57 (14, 1.956) 39.37-45.40, 4.59%	45.89 (3, 2.152) 43.80-48.10, 4.69%	-	-	55.16 (12, 2.096) 52.86-58.60, 3.80%
Humerus	58.60 (14, 1.665) 54.81-61.72, 2.84%	64.49 (4, 0.865) 63.24-65.20, 1.34%	61.26	73.24	78.00 (14, 2.527) 73.44-81.21, 3.24%
Ulna	66.13 (11, 1.673) 63.28-68.60, 2.57%	72.40 (4, 1.223) 70.78-73.62, 1.69%	-	78.73	84.95 (14, 2.859) 79.96-88.34, 3.37%
Radius	60.78 (14, 1.563) 58.10-63.20, 2.57%	66.38 (4, 1.486) 64.46-67.80, 2.24%	64.24	73.14	78.07 (14, 2.656) 73.46-81.7, 3.40%
Carpometacarpus	43.47 (11, 1.358) 41.90-45.40, 3.12%	47.58 (4, 1.105) 46.56-49.15, 2.32%	-	51.71	56.86 (13, 1.891) 53.66-60.00, 3.33%
Femur	49.18 (14, 1.480) 46.55-51.42, 3.01%	53.97 (5, 0.938) 52.85-55.27, 1.74%	51.11	65.17	64.96 (14, 2.473) 61.24-68.15, 3.81%
Tibiotarsus	80.50 (10, 1.617) 77.40-82.54, 2.01%	86.75 (4, 0.964) 86.04-88.16, 1.11%	85.06	96.49	100.80 (14, 2.698) 96.29-105.1, 2.68%
Tarsometatarsus	34.26 (11, 1.050) 32.45-65.42, 3.06%	36.52 (4, 0.832) 35.60-37.50, 2.28%	34.48	42.01	45.13 (12, 1.102) 43.23-46.69, 2.44%

Few individuals in the comparative series had been sexed by dissection, but the coefficients of variation (CVs) were consistent with some sexual size dimorphism (Holdaway 1990), males being larger (P. Wilson, pers. comm.). The premaxilla and mandible dimensions had especially large CVs (8-10%), suggesting more dimorphism in the bill than in other body dimensions (CVs 2-5%). Size frequency histograms for femur length, an indicator of body

TABLE 1B — Student's-*t* values for comparisons of means of measurements of crania, premaxillae, mandibles, coracoids, scapulae, and major limb bones in samples of recent Kea and Kaka. Levels of significance indicated as: n.s., not significant ($P > 0.05$); *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values for equal or unequal variances as tested by *F* test; degrees of freedom in parenthesis.

Element/dimension	NI Kaka - SI Kaka	NI Kaka - Kea	SI Kaka - Kea
Cranium length	2.950** (12)	3.996*** (20)	0.124 n.s. (12)
Cranium depth		4.821*** (19)	
Squamosal width	2.087* (12)	3.473** (20)	0.272 n.s. (12)
Premaxilla length	1.786 n.s. (12)	0.593 n.s. (17)	1.442 n.s. (9)
Premaxilla depth	1.447 n.s. (12)	8.106*** (13)	15.479*** (9)
Mandible length	1.842* (12)	3.324** (24)	0.451 n.s. (14)
Mandible depth	4.552*** (12)	8.048*** (16)	12.555*** (15)
Coracoid	5.349*** (17)	16.054*** (26)	7.425*** (17)
Scapula	2.631* (15)	15.832*** (24)	6.822*** (13)
Humerus	6.715*** (16)	23.987*** (26)	10.324*** (16)
Ulna	6.794*** (13)	19.332*** (26)	8.413*** (16)
Radius	6.379*** (16)	20.921*** (26)	8.275*** (16)
Carpometacarpus	5.400*** (13)	19.573*** (22)	9.210*** (15)
Femur	6.700*** (17)	20.483*** (26)	9.544*** (17)
Tibiotarsus	7.135*** (12)	21.154*** (22)	10.042*** (16)
Tarsometatarsus	3.857*** (13)	24.170*** (21)	14.204*** (14)

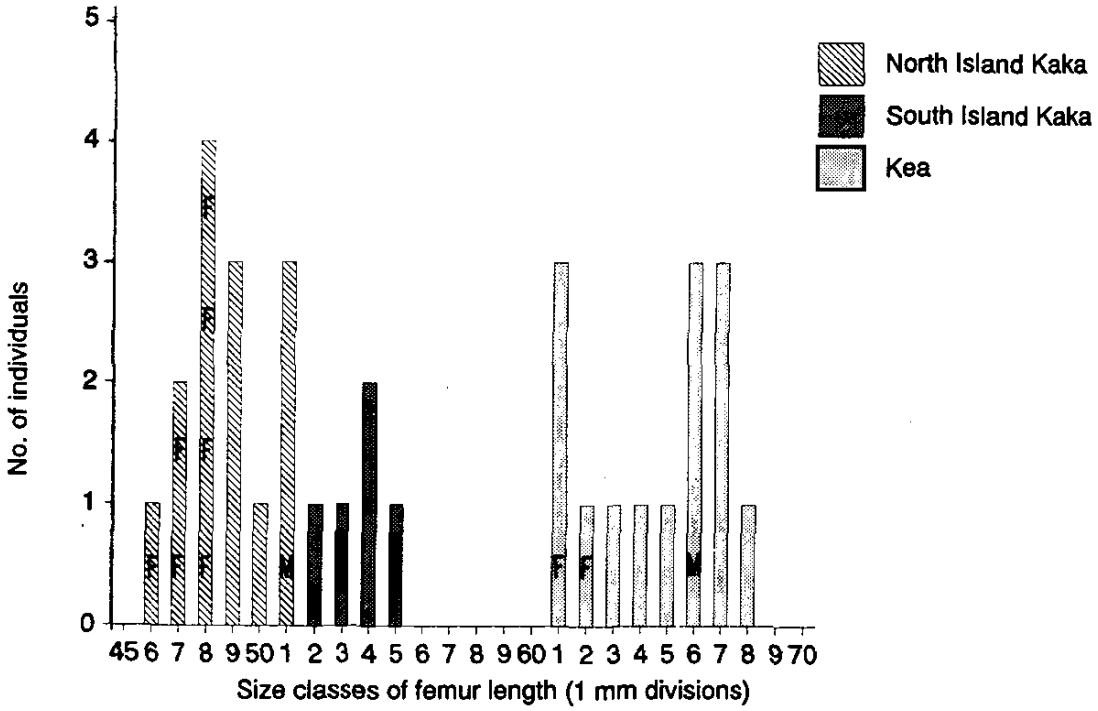

FIGURE 2A — Histogram showing distribution of femur lengths for samples of North and South Island Kaka and of Kea. M, male; F, female.

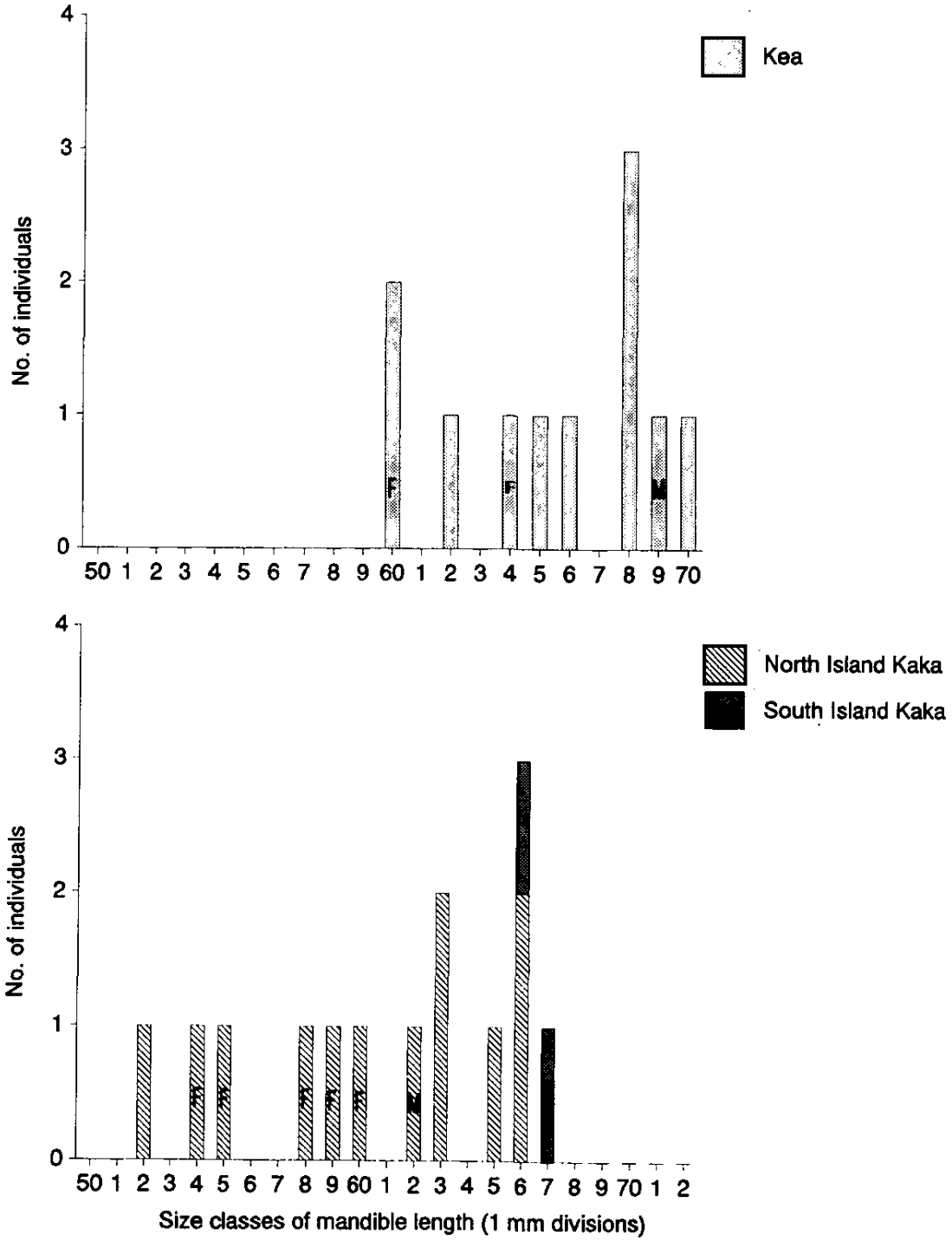

FIGURE 2B — Histogram showing distribution of mandible lengths for samples of North and South Island Kaka and of Kea. M, male; F, female.

size (Alexander 1983), and mandible length supported this interpretation (Figures 2A, 2B), although there was much overlap, and many individuals were of unknown sex. In contrast, the CVs for the small sample of South Island Kaka were generally low (Table 1A), suggesting that most or all of the sample was of one sex, which the distributions in Figure 2 suggested were males.

The small sample of South Island Kaka included only one possible female. The full range of size variation in the South Island Kaka was therefore not available. Comparing only the larger males of the South Island Kaka with both sexes of the North Island Kaka accentuated any size differences between the two forms, but the differences were large enough (and statistically significant at a high enough level) for us to be confident that the two forms would still differ in size even if female South Island Kaka were included.

Cranium: South Island Kaka and Kea did not differ significantly in cranial length or squamosal width. North Island Kaka, however, had significantly shorter ($P<0.01$, 12df) and narrower ($P<0.05$, 12df) crania than South Island birds.

Beak: Kea and Kaka did not differ significantly in premaxilla length, but the premaxilla was much deeper in Kaka than in Kea ($P<0.001$, df 17, 19). Mandible length was similar in Kea and South Island Kaka, but South Island Kaka had slightly longer mandibles than North Island birds ($P<0.05$, 13df).

In both races of Kaka the mandible was significantly deeper than in the Kea ($P<0.001$, df 24, 15). The South Island Kaka had the deeper mandible ($P<0.05$, 13df), although the inclusion of further South Island females may have reduced the magnitude of the difference.

Body size and limb length: All limb bones, and the scapula and coracoid, were shortest in the North Island Kaka and longest in the Kea, the South Island Kaka being intermediate. Differences between each pair were all highly significant ($P< 0.001$), except for the tarsometatarsus of North and South Island Kaka ($P<0.01$).

The slenderness ratio of the proximal tarsometatarsus (proximal width/length) can be used as a guide to the identification of isolated elements of South Island Kaka and Kea (Table 2A). Midshaft slenderness was not significantly different between Kaka samples or between the South Island Kaka and the Kea (Table 2B). Indeed, the North and South Island Kaka had very similar tarsometatarsi (Table 2), especially given the disparity in their body sizes (Table 1).

The heads and beaks of the Kaka were proportionately larger with respect to limb bone lengths than those of the Kea. Measurements of the fossil North Island cranium indicated that the bird had a relatively small head with respect to its body size (Table 1A). The other measurements mostly fell just below corresponding measurements for living Kea. The measurements therefore support the identification of AV 18389 as a Kea, made on a comparison of morphological traits.

Morphology: Kea and Kaka clearly differ in both cranial and post-cranial features of their skeletal morphology. The major morphological differences are summarised in Figure 1 and Table 3. No constant morphological

TABLE 2A — Ratios of proximal, shaft, and distal widths of the tarsometatarsus for Kea, Kaka, and the Haggas Hole fossil (AV 18389). Mean (*n*, SD)/Range, CV (%).

Tarsometatarsus Ratio	North Island Kaka	South Island Kaka	HH Kea AV 18389	Kea
Proximal width : length	0.2897 (11, 0.020) 0.278-0.314, 4.13%	0.293 (3, 0.0154) 0.28-0.31, 5.25%	0.28	0.267 (11, 0.007349) 0.258-0.281, 2.75%
Shaft width : length	0.117 (11,0.006) 0.107-0.128, 5.00%	0.117 (3, 0.009) 0.107-0.125, 7.92%	0.12	0.111 (11, .008022) 0.098-0.126, 7.22%
Distal width : length	0.352 (11, 0.027) 0.278-0.382, 7.77%	0.376 (3, 0.041) 0.371-0.420, 10.96%	0.33	0.320 (12, 0.02083) 0.261-0.348, 6.51%

TABLE 2B — Student's-*t* for differences between means for ratios of proximal, shaft, and distal widths of tarsometatarsus for Kea, and North and South Island Kaka. Conventions and details as in table 1B.

Tarsometatarsus Ratio	NI - SI Kaka	NI Kaka - Kea	SI Kaka - Kea
Proximal width : length	0.268 n.s. (12)	3.613** (12)	4.343*** (12)
Shaft width : length	0 n.s. (12)	2.002* (20)	1.117 n.s. (12)
Distal width : length	1.224 n.s. (12)	3.176** (21)	3.456** (13)

differences were found between North and South Island Kaka: the races are separated osteologically purely on morphometrics.

North Island Kea

Identification: Specimen AV 18389 was identified as a Kea by the following combination of morphological characters (see Figure 1 and Tables 1, 2, and 3): **premaxilla** shallow (13.1 mm deep at anterior end of external nares) with no ventral notch [Kea 12.68 mm, NI Kaka 16.65 mm, SI 17.94 mm]; **mandible** shallow (maximum depth 11.1 m at anterior end of mandibular fenestra), mandibular fenestra elongate (12.54 x 3.66 mm), ventral margin of mandible concave in lateral view [Kea 11.06 mm, 10.70 x 4.55 mm, NI Kaka 14.89 mm, SI Kaka 16.88 mm, 6.3 x 4.72 mm]; **palatines** latero-ventral margin concave, rostral and caudal processes narrow, articulation with basiparasphenoidal rostrum and pterygoid short; **cranium** tall dorsoventrally as in Kea; **wing** and **leg** bones much longer than in Kaka (see Table 1); **tarsometatarsus** shaft elongate in proportion to width of extremities as in Kea (Table 2); trochlea 3 broad, ± in line with shaft axis.

The main morphological characters differentiating Kea from Kaka are illustrated in Figure 1.

Geological age: Although the skeleton has not been dated directly, the associated fauna suggests that it was of Otiran age (> 10 000 years Before Present). Taxa such as the Takahe, Stout-legged Moa, Extinct Goose, and Extinct Coot, in association, are unusual in faunas in the central North Island. Similar assemblages are not found in deposits of Holocene age at Waitomo (Millener 1981, Worthy 1984a) but are similar to others presumed to be of Otiran age because of stratigraphic evidence (Worthy 1984b) and the presence of Otiran size morphs of *Pachyornis mappini* and *Euryanas finschi* (Worthy, unpublished data).

TABLE 3 — Principal morphological features separating skeletons of Kea and Kaka. See also Figure 1.

Element	Feature	Kea	Kaka
Premaxilla	Dorso-ventral depth	Shallow	Deep
	Ventral notch	Absent	Present
Mandible	Dorso-ventral depth	Shallow	Deep
	Mandibular fenestra	Elongate	Rounded
	Ventral outline in lateral view	Concave	Straight
	Floor of symphysis in rostral view	Curved	Flat
Palatine	Latero-ventral margin	Concave	Straight
	Rostral and caudal process	Narrow	Wide
	Articulation with basiparasphenoidal rostrum and pterygoid	Short	Long
Cranium	Dorso-ventral height	High	Compressed
Sternum	Angle between cranial and ventral margins of carina	Sharply angled	Rounded
	Axis of rostrum	Antero-posterior	c 45° to body axis
Pelvis	Junction of ilial crest with caudal iliac plate	Lateral	Medial
	Lateral margin of caudal sacral plate	Broader cranially	Broader caudally
Humerus	Bicipital crest at shaft	Meets gradually	Sharp angle
	Proximal margin of Incisura capitis	Straight	Notched
Tarsometatarsus	Shaft	Elongated	Short
	Width of extremities in proportion to shaft	Narrower	Broader
	Groove in Trochlea 3	Shallow	Deep
	Axis of Trochlea 3	± on shaft axis	Directed medially
	Notch between Trochleae 3 and 4	Narrowing proximally	Squared proximally

The situation of the deposit also supports an Otiran age for the fauna, including the Kea. The entrance through which the birds presumably came is an abandoned stream submergence that pre-dates that of the main entrance. We infer that the fossils accumulated after the stream had abandoned the passage but before it was blocked by the rockfall which now seals the site from direct contact with the surface. During the period of deposition, a stream may have flowed in the valley below the entrance, as it does now. If the fossils were deposited during the Otiran, the vegetation was probably low forest and shrubland (McGlone 1988).

***"Nestor* n.sp."**: Lengths of measurable elements of the specimen labelled as the "holotype" of an undescribed species of *Nestor*, CMNZ AV 16711, are given in Table 1A. They are at the low end of, or slightly below, the range for each element for South Island birds in the recent sample. They are, correspondingly, at or above the top end of the range for North Island birds. Its intermediate size and the lack of morphological differences suggest that AV 16711 is a female South Island Kaka (*Nestor m. meridionalis*) and does not represent a new taxon.

DISCUSSION

Shufeldt (1918) described and illustrated the skeleton of *Nestor notabilis*, the Kea. There are, to our knowledge, no comparable descriptions of the skeleton of the Kaka (*N. meridionalis*) or comparisons of the morphology or morphometrics of the two species.

Oliver (1955) noted sexual dimorphism in bill length and curvature in the Kea, as well as a slight colour dimorphism (the female being paler). He did not record size or plumage dimorphism in either North or South Island Kaka (Oliver 1955), but P. Wilson (pers. comm.) and C. O'Donnell (pers. comm.) confirm that both races of Kaka are size dimorphic.

Previous studies of fossil *Nestor* material seem to have assumed that there were no consistent morphological differences between the species, and that species discrimination of bones and skeletons had to be made on the basis of their size (Dawson 1952).

The results presented here show that Kea and Kaka differ substantially in the morphology of many of their major bones, as well as in the lengths of all major skeletal elements except the cranium. Although their bones do not differ morphologically, North and South Island Kaka are as distinct in measurements as they are in plumage (Oliver 1955, Falla *et al.* 1979) and constitute good subspecies on osteological grounds.

All three taxa are sexually dimorphic in standard dimensions, and some dimensions of female South Island Kaka and male North Island birds probably overlap. The most obvious dimorphism is in the bill (Marriner 1908, Oliver 1955, Falla *et al.* 1979).

North Island Kea

The specimen from Haggas Hole is clearly a Kea and so is the first record of the species as a fossil from the North Island. As noted above, the morphological characters used to differentiate Kea from Kaka skeletons are clearcut for most elements. The determination therefore was not based simply on mensural characters, although these also distinguish clearly between populations of the two species.

Although all dimensions of the Haggas Hole Kea are substantially greater than those of either Kaka, all its limb and girdle element lengths (apart from coracoid length, one of the more variable elements, see CVs in Table 1A) lie below the range for living Kea. Parrots are rather variable in size within a species, but the magnitude of the differences shown here suggest that Kea in the North Island during the Otiran could have been smaller than South Island birds.

The Haggas Hole specimen seems to have been included in the series of measurements given by Scarlett (1972: 17) for the North Island Kaka. The upper limit of the ranges of lengths for the femur, tibiotarsus, tarsometatarsus, humerus, ulna, and radius all coincide with those of the Haggas Hole specimen. This resulted in an erroneously large size range for the North Island Kaka, and contributed to the confusion over the identity of South Island *Nestor* material (Worthy & Holdaway, in prep.).

Even individuals of species occurring abundantly near cave entrances are rarely preserved in cave deposits (Worthy & Holdaway, in press), and so it is extremely unlikely that the fossil represents a vagrant individual. It is therefore almost certain that the bird was 'sampled' from a resident population.

The presence of a Kea in an Otiran age deposit in the North Island is not surprising, as the presumed environment in the central North Island at that time was similar to that of many areas where the species occurs today (McGlone *et al.* 1984). The landbridge connection between the North and South Islands was severed by rising sea levels at the end of the Otiran glaciation about 10 000 years ago. Starting about 14 000 years ago, the vegetation of the North Island rapidly took on its modern aspect of tall, wet forest (McGlone 1988). The North Island was left with limited areas of the subalpine habitat that presumably formed an important part of the Kea's range.

Although Kea were rare in Holocene fossil deposits of the West Coast (Worthy and Mildenhall 1989, Worthy & Holdaway, in press), they were common at Pyramid Valley in the east, in the mid-Holocene (authors' unpublished data). The drier climate and structurally more diverse vegetation in the eastern South Island (Burrows 1989) may have provided a more favourable habitat for Kea than the tall rainforests of Westland and the North Island Holocene.

Evidence for a small South Island, "*Nestor* n. sp."

References to a South Island Kaka smaller than the present form date from Hutton (1896), and the subject was discussed extensively by Dawson (1952). Dawson accepted one rather variable North Island species, and accepted two forms in the South Island, separated by size. The larger form was based solely on the dimensions of AV 5224, which he accepted as being the normal green South Island Kaka. He did not mention any morphological characters of the bones.

If, as Dawson thought, the South Island Kaka was as large as AV 5224, the remaining much smaller *Nestor* material could not belong in *N. meridionalis*. On this basis, a new, unnamed species was recognised on labels in the Canterbury Museum collections and in various faunal lists. A complete skeleton from Pothole 3, a cave on Takaka Hill (AV 16711), was labelled as the holotype, but the unpublished name has no standing in nomenclature – ICZN 1985: Article 9 (9).

Dawson's (1952) analysis was flawed as his single reference specimen of 'South Island Kaka' (AV 5224) is actually a Kea (morphological characters and morphometric evidence presented above, and Table 1, Figure 1). Dawson (1952) suggested that the only small, recent South Island Kaka (AV 9956) seen by him was probably an escaped North Island cage bird. It is a Kaka and there is no reason to doubt, as Dawson did, that it came from Peel Forest, South Canterbury. Indeed, on the label there is a note stating that it was a "Typical white-headed S.I. bird". There is, as Dawson showed, no significant difference in size between the small fossil Kaka and recent North Island specimens.

In summary, the main factor involved in the recognition of a supposedly smaller Kaka in the South Island was the misidentification of the larger AV 5224 (a Kea) as a Kaka of the South Island green form (*Nestor m. meridionalis*). The only recent Kaka skeleton in the Canterbury Museum collection was dismissed as being "a North Island bird which has escaped from captivity" and not considered further.

The identification of the Kea as a South Island Kaka reinforced the general preconception that the green South Island Kaka was much larger than the brown North Island bird (*N. m. septentrionalis*). The smaller South Island birds had, according to this scheme, to be a different species. The South Island Kaka is, indeed, larger than birds from the North Island, but the differences are much smaller than those between the Kea and either race of Kaka (Table 1). Another consequence of the confusion between South Island Kaka and Kea was the illustration of Kea bones in mistake for 'Kaka' bones in Scarlett (1972). In fact, no fossil *N. notabilis* was ever recognised by Scarlett.

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