

ANATOMY OF THE MANDIBLES, TONGUE AND ALIMENTARY TRACT OF KAKAPO, WITH SOME COMPARATIVE INFORMATION FROM KEA AND KAKA

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ABSTRACT

Preserved material from two Kakapo (*Strigops habroptilus*), two Kea (*Nestor notabilis*) and two Kaka (*Nestor meridionalis*) was dissected. A fledgling Kakapo had short, stout mandibles, a wide, thick tongue and a thick pharyngeal pad. The lower mandible closed against both the rostral end of the hard palate and the underside of the free end of the tongue. The crop was well defined. In the fledgling and in the headless body of an adult Kakapo a fusiform proventriculus was followed immediately by an approximately spherical, uniformly muscular gizzard. There were five main intestinal loops and no evidence of a vitelline diverticulum or of caeca. In Kea and Kaka the upper mandible was longer, the tongue (especially in Kaka) was narrower and fimbriated, and the crop was similar to that of the Kakapo. The mandibles, tongue and palate of the Kakapo appear to be particularly well adapted for the grinding of fibrous plant tissues to extract soft portions and juices.

INTRODUCTION

The Kakapo (*Strigops habroptilus*), an endemic New Zealand parrot, has a combination of biological features not shared by any other bird; it is nocturnal, flightless, and lek-breeding. About 1000 years ago Kakapo were widespread and abundant over the three main islands (Williams 1956, Millener 1981), but the species is now critically endangered, principally as a combined result of forest clearance and of predation and competition by introduced mammals (Powlesland 1989). Approximately 50 birds remain, of which only about 16 are females. Various conservation activities are under way to try and ensure the survival of the Kakapo (Powlesland 1989).

The aim of the work reported here was to describe in detail the beak, tongue and alimentary tract of the Kakapo and to compare them with those of Kea and Kaka. A better knowledge of the anatomy of the Kakapo's digestive tract could show features which may produce dietary restraints and thereby benefit both the supplementary feeding programme on Little Barrier Island (Powlesland & Lloyd 1992) and any captive maintenance programme. The Kakapo's beak, tongue and adjacent tissues have been described by Mudge (1902) and McCann (1962). Apart from comments that the crop is quite ventrally placed (Portmann 1950) and large (McClelland 1979) and that the oesophagus is large (Ziswiler & Farner 1972) and its thoracic portion short and straight with no crop-like expansions (Böker 1929 cited in McLelland 1979), the alimentary tract of the Kakapo has not been described previously so far as we are aware.

MATERIALS

The bodies of two Kakapo from Stewart Island were available for dissection; one, found on 7 June 1985, was the cadaver of a fledgling male which appeared to have died of starvation; the other, found on 17 April 1983, was the headless body of an adult male that had probably been killed by a feral cat (*Felis catus*). Unfortunately, both birds had been dead for two to four days before their bodies were found and preserved in alcohol, and so, as confirmed by histological examinations, considerable autolysis of tissues had occurred. The present observations are therefore limited to details of gross anatomy. The preserved head and neck regions of two adult Kea (*Nestor notabilis*) and two adult Kaka (*Nestor meridionalis*) were used in comparisons: most of the more caudal parts of the digestive tracts of these birds had been removed in other dissections and were not available.

TABLE 1 — Dimensions of mandibles (mm)

	Kakapo	Kea	Kea	Kaka	Kaka
<i>Upper mandible</i>					
Direct length of culmen	30.5	54.3	*	49.1	47.3
Width at base	20.0	13.1	13.4	13.8	12.5
Height at base	18.6	14.8	14.0	19.9	18.3
Width:height ratio	1.08	0.89	0.96	0.69	0.68
<i>Lower mandible</i>					
Width at base	19.9	14.5	15.1	15.7	*
Depth at base	15.9	12.6	12.5	13.2	*
Width:depth ratio	1.25	1.15	1.21	1.19	*

* In one Kea the tip of the upper mandible was missing, and in one Kaka the lower mandible was damaged.

RESULTS

Mandibles

The mandibles of Kakapo, Kea and Kaka are shown in Figure 1, and their dimensions are listed in Table 1.

The mandibles of the fledgling Kakapo were comparatively short and stout, and together formed an approximate equilateral triangle when viewed from the side, except that the upper mandible extended 6.5 mm past the lower mandible. On each side, the nostril, at the base of the upper mandible, was prominent, the opening being 4.5 mm long.

When the mouth of the Kakapo was closed, the basal halves of the occlusal borders of the lower mandible were in direct contact with the upper mandible, and the palate could not be seen. The central portions of these borders were concave (1.5 mm deep), and the margins of the lower mandible lay within those of the upper mandible for 35 mm, so that when the mouth was fully closed, the concavity was completely covered by the upper mandible. The borders of the upper mandible were not notched by the lower mandible.

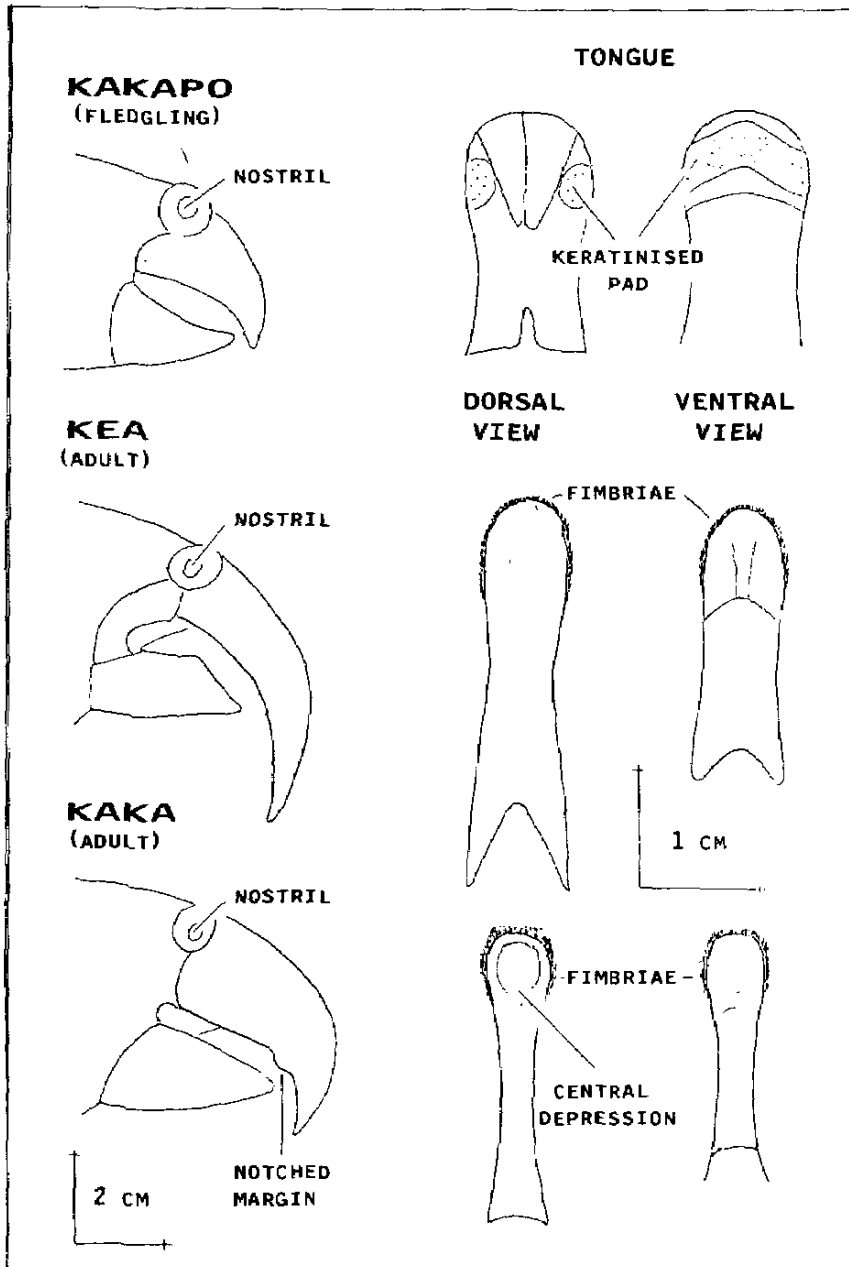


FIGURE 1 — Mandibles and tongues of Kakapo, Kea and Kaka, drawn from preserved material

The inner surface of the upper mandible of the Kakapo bore 14 small transverse ridges, spaced approximately 1 mm apart; the distal nine being smaller than the other five. When the beak was wet, a black spot was seen at each end of each ridge, within the margins of the mandible. The ventral border of the lower mandible was straight and the mandibular symphysis extensive (19 mm long in the midline). On the ventral surface of the lower mandible, five longitudinal ridges approximately 2 mm wide and 1 mm high extended evenly from the tip to the caudal border of its symphysis. The central ridge lay in the midline, and the outermost ridge on each side formed the lateral boundaries of the undersurface of the mandible. The mandible had a slight median concavity in its tip, and its occlusal surface was distinctly

concave longitudinally. It fitted neatly against a ridged front pad at the front of the hard palate in the 12 mm wide crescent-shaped space between the sides of the upper mandible.

The upper mandible of each Kea was longer and narrower (Table 1) and more strongly curved (Figure 1) than that of the Kakapo, and its borders were evenly curved. Laterally, part of the front portion of the palate was still visible between the mandibles when the mouth was closed. The broad occlusal surface of the lower mandible was concave longitudinally (to a maximum depth of 0.5 mm) and the terminal 17-18 mm of its length could be apposed evenly against the inner portions of the upper mandible, without touching its edges. Correspondingly, the ventral side of the upper mandible, between its margins and for 17-18 mm in front of the palate, appeared as a smooth shallow depression that complemented the evenly rounded free end of the tongue, and over which the occlusal surface of the lower mandible fitted exactly. In both Kea, the mandibular symphysis extended for 28.5 mm in the midline, and the front end of the mandible was rounded.

The upper mandibles of the Kaka were even more curved, and the widths of their bases were slightly greater than those of Kea but narrower than those of the Kakapo (Table 1). The lateral rim of each upper mandible was distinctly notched (2 mm deep) to receive the end of the oblique surface of the lower mandible. This surface fitted against the basal 23-25 mm of the underside of the upper mandible, 11.5 mm of this distance extending in front of the palate in each bird. The undersurface of the upper mandible was markedly concave at the level of the tip of the opposing mandible. Viewed from below, each lower mandible tapered evenly to a squared-off free end (6 mm - 6.5 mm wide), and the mandibular symphyses extended for 31 - 32 mm in the midline.

Palate

In the Kakapo, the largest portion of the palate (about 15 mm in diameter) was concave, with the rostral edge raised above the adjacent parts. Beyond this rostral edge the palate sloped abruptly upwards for 4 mm and then merged with the underside of the upper mandible. This rostral portion of the palate bore two curved transverse ridges, and the end of the lower mandible could be fitted neatly against them.

The palates of the Kea lacked a central circular depression but were deeply arched transversely. In contrast, the rostral portion of the palate in each Kaka projected downwards as a small convex mass of tissue, behind which was the rostral end of the choanal opening.

Tongue

The tongue of the Kakapo was relatively short and wide (Figure 1) and also quite thick: its unattached rostral part was 12 mm wide, 11 mm long and up to 6 mm deep. Keratinised "pads" at each side of the blunt tip were continuous with an approximately 5 mm wide keratinised band across the undersurface of the tongue. Caudal to the low, wide dorsal elevations, numerous small pits were present in the surface of the organ. In the dead bird, the slightly convex upper surface of the front of the tongue fitted neatly

against the adjacent concavity of the palate, so that the margins of the tongue and the concavity of the palate matched precisely. In addition, the slope of the keratinised undersurface of the tongue continued the slope of the front portion of the palate. When the tongue was moved to touch the palate, a band of keratinised tissue which extended 10 mm longitudinally was formed, against which the lower mandible fitted neatly.

The tongue of the Kea was also fleshy, but narrower (6.5 mm) than that of the Kakapo. The Kea's tongue had an almost smooth dorsal surface, the front 6 mm of which was angled at 45 degrees to the axis of the tongue and matched the underside of the upper mandible. The lateral and rostral margins of the 10 mm long free end carried conspicuous fimbriae (0.4 mm long at the tip of the tongue, progressively shorter along the sides).

The tongue of each Kaka was comparatively long and narrow. Viewed from above, its free end was 1 cm long and approximately rectangular, with small lateral elevations caudally. The rostral fimbriae were 2 mm long laterally and 1 mm long in the midline, giving a somewhat "squared" appearance to the tip of the tongue. The organ was also characterised by a conspicuous hollow (of 2.5 mm, 3 mm diameter) in the dorsal surface of its free end. The "spooned" shape of each tongue was enhanced by the narrowness of the more caudal portions of the organ. Viewed from the side, the free end of each tongue sloped evenly downwards at an angle of approximately 30 degrees, producing an oblique surface which fitted neatly against the front portion of the palate. Immediately behind the free end, the tongue was 3 mm wide, caudal to which it widened evenly to a width of 4.5 mm.

Pharyngeal region

In the Kakapo, the floor of the pharyngeal region of the tongue contained a relatively large fibrous elevation, immediately caudal to the laryngeal opening. This fibrous elevation was much smaller in the Kea and Kaka.

All three species had a single row of transverse papillae at the base of the tongue. In the Kakapo individual papillae were up to 1 mm long: in the Kea and Kaka the papillae were much smaller. In the Kakapo, additional, smaller papillae were grouped on the side walls of the pharynx. In all of the birds small papillae guarded the choanal and laryngeal openings.

Alimentary tract

Crop: In the Kakapo, the portion of the oesophagus between the pharynx and the crop appeared to be a regular, muscular tube (Figure 2). The crop was readily distinguished at the base of the neck, on the right side, as a discrete enlargement (34 x 31 mm) of the oesophagus and was firmly bound by connective tissue to the overlying skin. Externally, a 2 mm deep notch was present in the centre of the greater curvature of the crop. The 1.5 mm thick wall of the crop was uniformly muscular, had a greater thickness than that of the oesophagus, and the lining mucosa was raised in numerous convoluted folds approximately 1 mm high. Caudal to the crop, the oesophagus merged into the proventriculus without any evidence of further dilations.

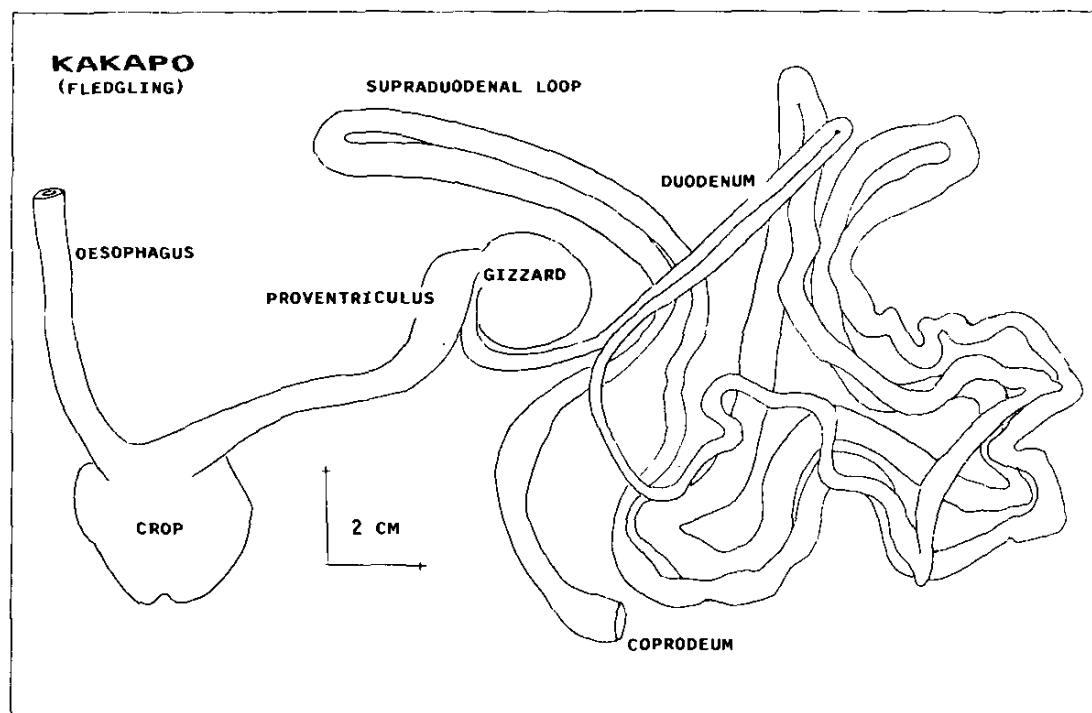


FIGURE 2 — Alimentary tract of fledgling Kakapo, drawn from preserved material

In each Kea the crop was a simple enlargement of the oesophagus, approximately 30 mm in length and reaching 20 mm in width. The lining of each crop presented 25-26 conspicuous (1 mm high) longitudinal folds. The crop in one Kaka was intermediate between those of the Kakapo and Kea in shape and size, with a slight central constriction visible externally. The crop of the second Kaka was not available.

Proventriculus and gizzard: Dorsal to the sternum, the digestive tract of the Kakapo was in the midline of the body. The proventriculus began as a fusiform expansion of the digestive tract and ended at the entrance to the gizzard (Figure 2). It was approximately 35 mm long, its muscular wall was 1.0 - 1.5 mm thick and its lining mucosa was raised in longitudinal folds. The approximately spherical gizzard (25 mm external diameter) lay ventrally on the left side, partly between the two lobes of the liver (which lacked a gallbladder). The gizzards in the adult and juvenile Kakapo were similar in size and shape and had evenly muscled, 1 - 2 mm thick walls, which were thus only slightly thicker than those of the crop. The gizzard was lined by a 0.6 mm layer of what appeared to be koilin material (Hofmann & Pregl 1907 cited by Eglitis & Knouff 1962). This was moulded to, but separate from, the low coarse folds of the underlying muscle of the wall.

The proventriculus in Kea and Kaka was also fusiform, with the mucosa raised in longitudinal folds, and, again, the gizzard lay partially between the two lobes of the liver. No distinct lining was evident in the gizzards of these two species.

Intestine: The abdominal viscera of the Kakapo were displaced to the left of the abdominal cavity by the right abdominal airsac (which was larger than the corresponding left sac) but this might have been a post mortem effect. The duodenum, which began close to the junction between proventriculus and gizzard, lay within the full length of the duodenal loop of the intestine.

The intestinal tract was folded into a further four large loops (Figure 2). The ends of these loops were independent (i.e., not formed in a regular spiral) and the proximal portions of the loops were linked by the mesentery which supported the cranial mesenteric artery and its branches. No evidence of a vitelline diverticulum was seen, either on the presumptive axial loop or on any of the other loops, and no traces of caeca were seen either. The intestinal tracts of the Kea and Kaka were quite similar to that of the Kakapo, and also lacked caeca. In all three species, a distinct coprodeum formed the initial part of the cloaca.

DISCUSSION

The features of the mandibles and tongue of the Kakapo observed in the present study are in accord with those described by Mudge (1902) and McCann (1962), and those of the crop are consistent with the reports by Boker (1929) and Portmann (1950). Notably, the short, stout upper mandible is suited to the grasping of fibrous food (Smith 1975), and the lower mandible seems equally well adapted for this purpose. The smooth curve of the upper mandible of the Kea contrasts with the notched borders of the upper mandible of the Kaka: a species difference which we have also observed in captive live birds and in the field.

The size and shape of the tongue differed considerably among the three species. Nevertheless, in all specimens the dorsal surface of the free end of the tongue fitted neatly against the palate, and the lower mandible, in turn, fitted closely against the underside of the tongue. This confirms the idea (Smith 1971) that, in parrots, the tongue is used to hold food against the rather broad, ribbed tip of the upper mandible and the lower mandible provides the main cutting force. Specifically, the slender tongue of the Kaka appears well suited for a diet in which nectar and honeydew are prominent (Beggs & Wilson 1988), and we suggest that the distinct "spoon" might serve to collect each "bolus" of juice. Kea ingest a wide range of food materials (Clark 1970) and the relatively unspecialised tongue of the Kea, with its curved brush-border, is consistent with this diversity. The tongue of the Kakapo, with the cornified lobes near the tip, the close match to the concavity in the palate and the prominent pharyngeal pad, seems well suited to assist in the grinding and squeezing of juices from vegetable matter against the ridged upper palate. Although the Kakapo takes nectar (Henry 1903), its tongue seems much less suitable than the fimbriae-tipped tongues of Kaka and Kea for the ingestion of fluid.

In the wild, Kakapo produce "chews" of discarded plant material that are characteristic of the species (Powlesland, 1989). We speculate that the birds produce these "chews" by means of an additional mechanism, in which the concavity in the upper surface of the lower mandible is used to hold

plant material between the mandibles while the basal part of the lower mandible squeezes the material against the keratinised undersurface of the front of the tongue and against the adjacent front-most portion of the palate. This would mean that Kakapo, in effect, use their comparatively thick tongue in a two-stage break down of food: gross material first being squeezed between the lower mandible and the underside of the front of the tongue, and finer material then being squeezed between the upper surface of the tongue and the concavity in the central part of the palate.

Whether the last suggestion is valid or not, the prominent glossal processes of the hyoid apparatus (Mivart 1895), and the relatively discrete thyroglossus muscle and the separate, accessory parts to the thyrohyoideus muscles (Mudge 1902) that are found in Kakapo probably add to the mechanical strength of the tongue.

In each species the crop was a circumscribed dilation of the oesophagus, and its wall was of the same general thickness as that of the adjacent portions of the oesophagus. The external notch suggests that the organ might be basically bilobed, a bilobed crop being present in galliform and columbiform species (Ziswiler & Farner 1972). The obvious crop of the Kakapo, together with the fact that the gizzard is larger than the proventriculus, is consistent with the observation that the Kakapo ingests and excretes much fibrous plant material. Even accepting that the sizes of the crops could have been affected by the preserving fluids, the size of the crop in the Kea and Kaka (i.e., almost as long as that of the fledgling Kakapo, and approximately two-thirds its width) was consistent with these birds having diets which are generalised (Jackson 1962, Holyoak 1973, Falla *et al.* 1979) but less bulky than that of the Kakapo.

The closeness of the openings of the proventriculus and the duodenum into the gizzard seems to be a general avian feature which permits food not requiring further grinding to all but bypass the gizzard (Evans 1982). Because of the autolysis of the tissues, it was not possible to be sure that the gizzard of the Kakapo had had a specialised lining. However, the limited muscular development in the gizzard of the Kakapo, as compared with the gizzard of the domesticated fowl (*Gallus gallus*), suggests that the Kakapo relies on its specialised tongue and palate and vigorous chewing to break coarse plant material into small fragments suitable for digestion. The presence of five main intestinal loops is a feature typical of parrots (Gadow 1889 cited in McLelland 1979, Beddard 1911, Evans 1982). The absence of caeca also seems consistent with observations that Kakapo do not swallow long strands of cellulose material, reducing food to small particles before swallowing it (Henry 1903, McCann 1962). On the other hand, field observations that Kakapo produce a large faecal volume are consistent with the notion that digestion might be more complete had caeca been present. Caecectomized Japanese Quail (*Coturnix coturnix*) both ingested and excreted more food material than did intact birds (Thompson & Boag 1975). Lability of visceral dimensions with changes in diet has also been reported (Drobney 1984).

CONCLUSIONS

The specialised features of the beak, tongue and palate enable the Kakapo to chew coarse plant material such as foliage and rhizomes, ingest the juices and soft portions, and then spit out much of the indigestible fibrous residue.

The features of the Kakapo's alimentary tract are typical of parrots, even though a more muscular gizzard might be expected for the species' bulky and fibrous diet.

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LITERATURE CITED

- BEDDARD, F.E. 1911. On the alimentary tract of certain birds and on the mesenteric relations of the intestinal loops. *Proc. Zool. Soc. Lond.* 20: 47-93.
- BEGGS, J.R.; WILSON, P.R. 1988. Feeding energetics of Kaka in South Island beech forest. *NZ J. Ecol.* 11: 129-130.
- BENHAM, W.B. 1898. Notes on certain of the viscera of Notornis. *Trans. Proc. NZ Institute* 31: 151-156.
- BÖKER, H. 1929. Flugvermögen und Kopf bei *Opisthocomus cristatus* und *Stringops habroptilus*. *Morph. Jb.* 63: 152-207. Cited by McLelland (1979).
- CLARK, C.M.H. 1970. Observations on population, movements and food of the Kea, *Nestor notabilis*. *Notornis* 17: 105-114.
- DROBNEY, R.D. 1984. Effect of diet on visceral morphology of breeding Wood Ducks. *Auk* 101: 93-98.
- EGLITIS, I.; KNOUFF, R.A. 1962. An histological and histochemical analysis of the inner lining and glandular epithelium of the chicken gizzard. *Amer. J. Anat.* 111: 49-59.
- EVANS, H.E. 1982. Anatomy of the Budgerigar. Pages 111-187 in *Diseases of Cage and Aviary Birds* 2nd Edition, Petrak, M.L. (ed.), Philadelphia: Lea & Febiger.
- FALLA, R.A.; SIBSON, R.B.; TURBOTT, E.G. 1979. *The New Guide to the Birds of New Zealand and Outlying Islands*. Auckland: Collins.
- GADOW, H. 1889. On the taxonomic value of the intestinal convolutions in birds. *Proc. Zool. Soc. Lond.* 1889: 303-316. Cited by McLelland (1979).
- HENRY, R. 1903. *The Habits of Flightless Birds of New Zealand: with Notes on Other New Zealand Birds*. Wellington: Government Printer.
- HOFMANN, K.B.; PREGL, F. 1907. ber Koilin. *Hoppe Seyler's Zeitschr. f. Physiol. Chemie.* 52: 448-471. Cited by Eglitis & Knouff (1962).
- HOLYOAK, D.T. 1973. Comments on taxonomy and relationships in the parrot subfamilies Nestorinae, Loriinae and Platycercinae. *Emu* 73: 157-176.
- JACKSON, J.R. 1962. Keas at Arthurs Pass. *Notornis* 9: 39-58.
- MCCANN, C. 1962. External features of the tongues of New Zealand psittaciformes. *Notornis* 10: 326-345.
- MCCLELLAND, J. 1979. Digestive System. In: *Form and Function in Birds*. Vol. 1. London: Academic Press.
- MILLENER, P.R. 1981. The Quaternary Avifauna of New Zealand. Unpubl. PhD thesis, University of Auckland, Auckland.
- MIVART, St G. 1895. On the hyoid bone of certain parrots. *Proc. Zool. Soc. Lond.* 19: 162-174.
- MUDGE, G.P. 1902. On the myology of the tongue of parrots, with a classification of the order based on the structure of the tongue. *Trans. Zool. Soc. Lond.* 16: 211-278.
- PORTMANN, A. 1950. Le Tube Digestif. In *Traité de Zoologie*, Vol 15. Paris; Libraires de l'Académie de Médecine.
- POWLESLAND, R.G. 1989. Kakapo Recovery Plan 1989-1994. Wellington: Department of Conservation, Wellington.
- POWLESLAND, R.G., LLOYD, B.D. 1992. Supplementary feeding of Kakapo on Little Barrier Island, May 1990 - June 1991. Science & Research Internal Report No. 122. Wellington: Department of Conservation.
- SMITH, G.A. 1971. The use of the foot in feeding, with special reference to parrots. *Avic. Mag.* 77: 93-100.
- SMITH, G.A. 1975. Systematics of parrots. *Ibis* 117: 18-68.
- THOMPSON, D.C.; BOAG, D.A. 1975. Role of the ceca in Japanese Quail energetics. *Canad. J. Zool.* 53: 166-170.
- WILLIAMS, G.R. (1956). The Kakapo (*Stringops habroptilus*, Gray). A review and re-appraisal of a near-extinct species. *Notornis* 7: 29-56.
- ZISWILER, V.; FARNER, D.S. 1972. Digestion and the digestive system. In: *Avian Biology* Vol. 2, Farner, D.S.; King, J.R. (eds). New York: Academic Press.

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