

when both nested under erratic boulders in the forest remnants of the headlands. Then the Kea got its flea. And already the Kea was a separate species from the Kaka, which has no flea.

THANKS

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EXTERNAL FEATURES OF THE TONGUES OF NEW ZEALAND PSITTACIFORMES

By CHARLES McCANN

INTRODUCTION

The structure of the tongue of birds frequently gives some clue to the principal diet and manner of feeding of the species. Its character has a bearing on evolutionary trends and relationships. Salvadori (1891) placed *Nestor* in a separate family, Nestoridae; *Strigops* he also placed in a separate family, Strigopidae, and *Cyanoramphus* in the family Psittacidae, subfamily, Platycercinae. Mudge (1902) classified the order Psittaciformes on the lingual myology and osteology. In his classification Mudge (1902) followed Salvadori (1891) in placing *Nestor* in a separate family, Nestoridae, but, *Strigops* and *Cyanoramphus* he placed in the family Psittacidae, subfamily, Cacatuinae. The *Check-list of New Zealand Birds* (1953) included all the New Zealand Psittaciformes in the one family, Psittacidae. Oliver (1955) placed *Nestor* and *Strigops* in separate families, Nestoridae and Strigopidae, respectively, and *Cyanoramphus* he retained in the family Psittacidae.

In view of the marked anatomical and biotic differences between the three groups of indigenous Psittaciformes of New Zealand, the retention of the three separate families, Nestoridae, Strigopidae and Psittacidae is, perhaps, desirable and a more meaningful classification.

As the main theme of this paper is based on the external morphology of the tongue, it necessarily hinges largely on the food of these birds and the means of obtaining it, the bill. In most authoritative works the food of the various species is described in fairly general terms. They are said to be phytophagous, frugivorous or melivorous, for lack of specific observations in the field and the laboratory. One of the great difficulties of analysing the crop or stomach contents of parrot-like birds is that the food is generally reduced to fine particles, before it is swallowed or in the case of fibrous foods, it is masticated and the fibrous material rejected, the juice alone being swallowed. Under such circumstances the determination of the food sources is often next to impossible. Nevertheless, the great differences in the

structure of the tongue and bill have an important bearing on the diet of each species and the niche it occupies in the economy of Nature.

Only once has the Kakapo (*Strigops habroptilus*) been known to have eaten lizards, *vide* Huegel (1875). The Kea (*Nestor notabilis*) has often been reported and known to eat the flesh of sheep, and has thus earned for itself a bad name, as a wanton carnivore. This 'habit' has been amply authenticated, but the charge of flesh-eating is not general; it has been fortuitously acquired by some individuals only. The impudence and curiosity of the Kea are well-known to most 'trampers' in the mountains of their habitat and it is probably the satiation of these two characteristics which has triggered off the flesh-eating 'habit' in some individuals. At first, the birds may have been attracted by the colour of open wounds (red or purple — the colour of some fruits), tasted the flesh and then subsequently acquired a taste for raw flesh. Be this as it may, the remarkable differences in the structure of tongues and bills between the two species, are undoubtedly significant and bespeak a difference in diet under natural conditions. The diets may overlap, in part, in some materials, but this does not negative the fact that the predominant food is of a particular nature and that each species is adapted to it.

In the course of years it has been my wont to salvage bits and pieces from the taxidermy department for study. In this way I was fortunate in obtaining the fresh tongues of *Strigops*, *Nestor notabilis* and *Cyanoramphus* spp. I was greatly struck by the disparity the tongues of these birds displayed in external features and in the shape of the bill, for which I have tried to find some plausible explanation. At first, it was my intention to contrast these structures of the Kakapo and the Kea only, but as I had the material for two species of *Cyanoramphus*, I have included them also. The accompanying drawings, with one exception (*C. unicolor*), were made from fresh material (before fixation) and show the remarkable differences between the species.

If this brief article, in spite of its short-comings, serves to create an interest in this fascinating aspect of bird study, it will have served its purpose in stimulating others.

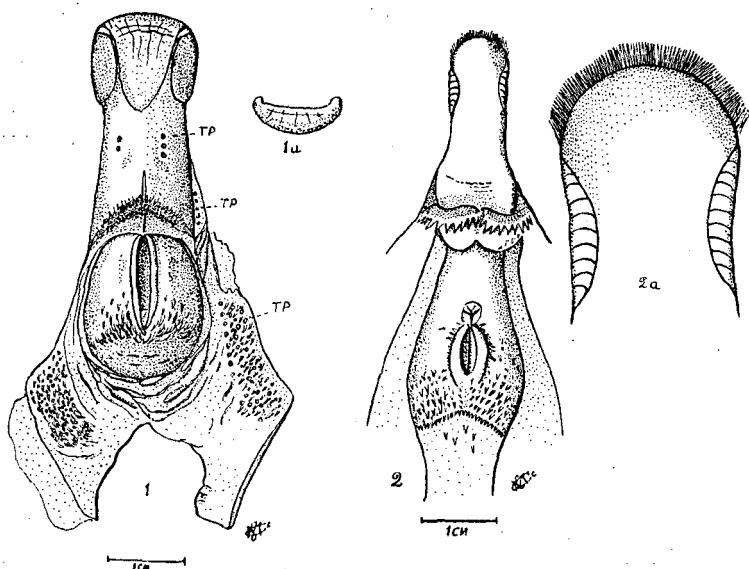
Tongue of *Strigops* — Figures 1, 1a

The apex of the tongue of *Strigops* is almost abruptly truncated (fig. 1a). Viewed dorsally, the anterior extremity is covered by a horny 'lobe,' somewhat ovoid posteriorly; on either side of this 'lobe' there is a horny 'flap,' the termination of the horny 'collar' embracing the ventral aspect of the tongue. The lateral margins are almost parallel but diverge slightly, posteriorly. The posterior margin or base of the tongue is bordered by an open, inverted V-shaped row of raised denticles or papillae, separated mesially by a short sulcus. On either side of the longitudinal mid-line of the tongue, there are some large pits (2 on the left and 3 on the right of this specimen) which appear as taste-pits (*papillae vallatae*).

The mucous membrane between the tongue and the rami is beset with several pits similar to those on the dorsum of the tongue.

Behind the tongue is the large (in comparison with that of the Kea) laryngeal 'pad' containing the glottis. The margins of the glottis are devoid of spicules. Posteriorly, on either side of the 'pad,' there are numerous large, horny denticles. Above the glottis, the buccal

membrane (divided in drawing) is beset with numerous denticles, with large taste pits interspersed between them.



Tongue of *Nestor notabilis* — Figures 2, 2a

The apex of the tongue of the Kea is rounded; its extremity is fringed with minute 'hairs' giving it a brush-like appearance; the lateral walls are slightly concaved towards the middle. Behind the fringe of 'hair,' the 'flaps' of the sub-lingual horny 'collar' appear dorsally, as in the Kakapo. The posterior margin or base of the tongue is bordered by two, somewhat lunate flaps of large, horny denticles.

A short distance behind the tongue is the laryngeal 'pad' with the glottis; the glottis is irregularly margined with large denticles and posteriorly of the 'pad' is beset with similar denticles interspersed with smaller ones between. This patch of denticles terminates in a broad inverted V-shaped row of denticles; behind the V there are a few irregularly scattered spicules.

In the Kea no denticles were observed in the buccal cavity, above the laryngeal 'pad,' as in the Kakapo, nor any large taste-pits.

DISCUSSION

The great disparity in the tongues of *Strigops* and *Nestor* clearly indicates that the food of these two birds, although it may overlap, in part, cannot be described in generalised terms, because both are Psittaciformes. This theoretical conclusion, although I have not had the opportunity of observing the birds in the field, appears to be supported by the differences in structure, habit and habitat.

The nocturnal or crepuscular habit of *Strigops*, coupled with its more terrestrial mode of life and progression, has called forth a greater need for tactility. This need is, perhaps, best expressed in the development of the long hair-like feathers surrounding the bill and, to a lesser extent, in the gular region. Although, similar 'hairs' are present

around the bill of *Nestor*, they are comparatively short. Likewise, there is a great need for the development of the senses of smell and taste; this, too, appears to be expressed in the large nostrils and the presence of taste pits on the tongue and in the buccal cavity. Similar large taste pits are apparently absent in *Nestor* (cf figures). In *Cyanoramphus*, a few taste-pits appear in each of the two species examined and will be referred to below. The greater development of the three senses, referred to above, is linked with a possible reduction in vision and, adaptation to feeble light, or, perhaps, even partial myopia. The eye of *Strigops* is relatively small for the size of the bird.

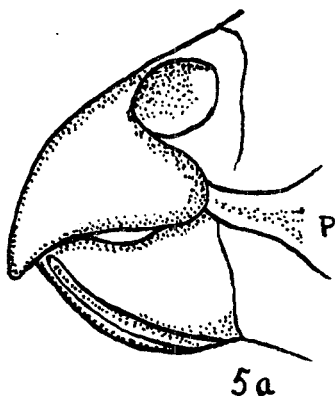
The more terrestrial and nocturnal habit of *Strigops*, in contrast to the canopy-frequenting *Nestor*, itself suggests a difference in feeding habit and menu. I have not referred to the sense of hearing, for, I believe, that most birds have a well-developed sense of hearing and, in the case of the birds discussed it has little bearing on the feeding habits.

Parrot-like birds, as is well-known, are, generally speaking, destructive feeders, for they destroy and displace more than they can comfortably eat. What they do swallow is normally so finely reduced that accurate determination of the food substances is often most difficult, if not an impossible task. Accordingly, *Nestor* and other diurnal canopy feeders drop much food on the forest floor (so do nocturnal canopy feeders also). Thus, the forest floor is often strewn with fruits or leaves, entire or partially eaten, which contribute to part of the diet of the terrestrial feeders, whether diurnal or nocturnal. (This knowledge was often used by me with considerable success when collecting specimens on various expeditions). It is, perhaps, common knowledge that the surplus from the 'tables' of diurnal, arboreal species constitutes the repast of many of the terrestrial feeders. Under the circumstances there is a probable overlap in the menu of *Strigops* and *Nestor*; the former feeding on the discards from the 'table' of the latter. This residual supply provided by the diurnal species is often supplemented by the nocturnal species with other substances, both vegetable and animal.

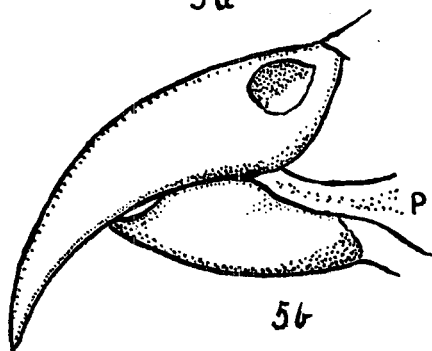
The bill of *Strigops* (fig. 5a), in contrast to that of *Nestor* is shorter, broader and thicker. The upward curve of the mandible of *Strigops* is markedly more vertical than in *Nestor*. A remarkable feature of the lower mandible of *Strigops* is that its horny sheath is longitudinally fluted (five ridges) whereas in *Nestor* the mandible is smooth. The fluting of the mandible obviously gives it additional mechanical strength. On the interior of the upper section of the bill, there is a large 'anvil' upon which the lower mandible operates. A similar 'anvil' is present in *Nestor* but it is far less developed. In short, the bill of *Strigops* is a veritable 'nut-cracker' or crusher, suitably adapted, mechanically, for dealing with hard food material, such as hard seeds and nuts, to obtain the kernel.

The bill of *Nestor* (fig. 5b) is not so admirably adapted as a nut-cracker. The upward sweep of the mandible is far more gentle and is not fluted to give it additional strength; it is mechanically weaker and obviously suited for another form of diet. The greatly elongated culmen is apparently more suited to excavation or removal of obstructions when in search of food. The shape of the bill suggests that the Kea feeds on softer foods, the pulp of fruits and soft-bodied animal foods. Likewise, the bill suggests that the hard stones of fruit are rejected.

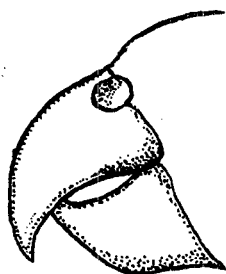
Without delving deeply into the cranial anatomy of the two



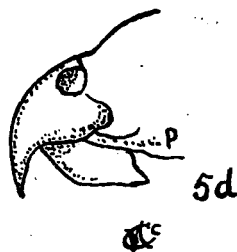
5a



5b



5c



5d

species under consideration, it will be observed that the mandible in *Strigops* is much heavier than in *Nestor* and that the palatines are larger and deeper in the former than in the latter — their points of contact with the bill also vary in the two birds (*cf* figures) and accordingly tend to greater strength.

Together with the truncated, leathery tongue, the bill of *Strigops* is more efficiently equipped to deal with hard food materials. As the seeds are dealt with in the mouth, the eyes play little or no part in the selection of the material actually swallowed. Discrimination by

taste to such "blind" feeders is of greater importance, hence the provision of large taste pits in *Strigops*. In *Nestor*, the selection of the food is apparently more visual, the food being selected by shape and size, and, perhaps, more important, by colour. As already indicated, *Nestor* apparently has no large taste-pits, for none was observed in any part of the mouth. Accordingly, it would appear that *Strigops* is predominantly nucivorous and *Nestor* frugivorous, feeding on the softer parts of the fruits alone.

Both *Strigops* and *Nestor* are stated to be, at least in part, melivorous or nectarivorous. There can be no doubt that both birds will take or accept honey or nectar when readily available, but this part of the diet is probably supplementary. Likewise, they will also feed on sap and gummy exudations from the trunks and branches of trees and shrubs which are palatable to them. However, if one may draw any conclusions from the structure of the tongue and terrestrial habit of *Strigops*, it is far less suited to a nectarivorous habit than *Nestor* with its fringed lingual extremity and canopy-haunting habits. The fringe of 'hairs' possibly assists the collection of the juice of the succulent fruits it feeds on. In any case, it seems more likely that the birds would destroy the flowers, with their 'crude instruments' in the quest for nectar, and not serve the role of pollinators. Their attention to the flowers would be largely detrimental to seed production.

That *Strigops* is in part graminivorous, feeding on portions of Snow Grass (*Danthonia* spp.) and other fibrous materials is well established. (It is believed to feed on mosses and tender shoots of plants also.) However, fibrous materials are apparently well-chewed, the juice extracted and the residual fibrous tissue rejected in the shape of 'pellets.' The stout bill and tough tongue can efficiently deal with fibrous materials; conversely, the bill and tongue of *Nestor* are adapted for a more succulent diet.

In passing, a point worthy of comment at this stage, although it is not directly connected with the subject in hand, is the comparatively large size of the laryngeal 'pad' (see figure) observed in *Strigops*. It is well-known that the Kakapo, in addition to a number of varied vocal sounds, from 'screeches' to 'grunts,' is also capable of producing a loud 'booming' or 'drumming' sound, audible over a considerable distance. This 'booming' is believed to be indulged in during the breeding season. This large laryngeal 'pad' and the gular air-sacs, possessed by the males alone, are undoubtedly linked in the production of the 'booming' sound. Henry (1903) described the air-sac as being almost as large as the bird itself, when fully inflated. The position of sacs is clearly visible when sought for, even on museum specimens; they are marked by patches of skin, devoid of feathers, on the side of the neck. However, Williams (1956) evidently doubted Henry's statement and overlooked the presence of the sacs himself, for, he wrote: "As we shall see later in the section on calls, there is some reason to accept this air sac-drumming hypothesis with reserve" (p. 40); and again on page 42: "Any one must be chary of challenging Henry's unrivalled observations, but his claim that this genus of the *Psittacidae* possesses an inflatable air sac as part of the vocal equipment should be treated with some scepticism at present, for such an organ is, to the best of my knowledge, unknown among the rest of the parrots." The Kakapo is such an aberrant member of the *Psittaciformes* and it has deviated so much in various directions from the rest of the order

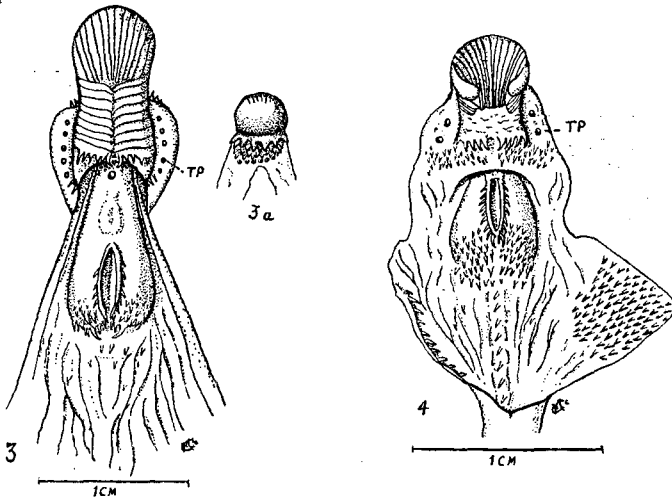
that we may expect to find some other departures from the more 'normal' Psittaciformes when the species becomes better known.

The inflation of the air-sacs to function as resonators in the Kakapo is somewhat homologous to use of the air-sacs in the Prairie-Hen (*Tympanuchus*). They may serve a similar role during courtship and sexual display.

Tongue of *Cyanoramphus unicolor* — Figures 3, 3a

The apex of the tongue is rounded; there is no fringe of 'hairs' as in the Kea. The lateral margins are slightly concaved. Dorsally, the anterior portion is marked by radiating 'sulci,' behind which other 'sulci' run transversely from the mid-line to the margins. The posterior margin is bordered by two groups of large denticles, separated from each other by a shallow median sulcus. Ventrally, five rows of denticles (fig. 3a) decreasing in size from the anterior to the posterior row, are present (see figure). Such denticles do not appear in either *Strigops* or *Nestor notabilis*. The mucous membranes between the tongue and the rami have five taste-pits on either side. In addition to these pits, a single large pit is found behind the tongue which apparently serves the same function.

The laryngeal 'pad' is somewhat elongate. Its posterior is echinate with denticles of varying size. The glottis is margined with a few denticles on either side. A few irregularly disposed denticles are present on the mucous membrane behind the laryngeal 'pad.' No denticles were observed in the buccal cavity above nor were any large taste-pits.



Tongue of *Cyanoramphus auriceps* — Figure 4

The apex of the tongue is rounded without a fringe of 'hairs' as in the Kea. Laterally, two horny 'flaps' of the ventral 'collar' appear dorsally. Dorsally, the anterior portion of the tongue (almost half) is sulcated somewhat fan-wise; behind the horny 'flaps' there are a few oblique 'sulci' also. Laterally, the margins are slightly concaved towards the middle. Posteriorly, the tongue is margined by two series of large denticles, separate at the centre. On either side, between the

tongue and the rami there are two large taste-pits. Numerous small denticles form an angular band between the tongue and the glottis.

The laryngeal 'pad' is somewhat similar to that of *C. unicolor*, but it is less elongated and more denticulate. The glottis is margined with largish denticles. A median row of largish denticles extends into the gullet. The buccal cavity has a considerable patch of denticles above. No taste-pits were observed other than those already mentioned. Beneath the free portion of the tongue similar transverse rows of denticles are present in this species, as in *C. unicolor* (fig. 3a).

DISCUSSION

In the genus *Cyanoramphus* the tongues appear to differ specifically. So far, I have been able to obtain the tongues of two species only — *C. unicolor* and *C. auriceps*. The consensus of opinion is that the food of *Cyanoramphus* spp. consists largely of seeds and soft fruits. That they are largely dependent on small hard seeds and grain is, perhaps, supported by the mechanical structure of the mandibles (figs. 5c., 5d) for the lower mandible, like that of *Strigops* rises abruptly to meet the culmen, and the bill, as a whole, appears as an efficient 'crusher.' In this respect *Cyanoramphus* differs from *Nestor*.

Of the two species illustrated and discussed, the Yellow-fronted Parakeet (*C. auriceps*) is an inhabitant of the forests, frequenting the lower and upper tiers of foliage, feeding on the berries of various plants. As many of the fruits are small seeded, it is likely that the seeds are also crushed and swallowed. As most of the fruits eaten are highly coloured when ripe, it is, perhaps, safe to assume that the birds are guided visually. The eye plays the more important role in food getting as in the case of the Kea (*Nestor*). When seeds are eaten, need for verification as to their edibility arises, and for this the requisite taste-pits are necessary. These we find on either side of the tongue (see, figure).

In contrast to *C. auriceps*, the Antipodes Island Green Parakeet (*C. unicolor*) is of necessity a ground feeder and nester, as the vegetation of the island is very stunted or composed of tussock. Under the circumstances, the birds appear to be largely dependent on seeds or other material washed up between the rocks of their habitat, for subsistence. The seeds are sampled in the mouth for their edible qualities, which necessitates the possession of a sense of taste. This requirement is fulfilled by the presence of five large taste pits on either side of the tongue, between it and the rami. In addition there is the large pit behind the tongue already referred to.

A remarkable feature in the construction of the bill of *C. unicolor* is that the posterior edge of the culmen, near the gape, is flexed slightly inwards, apparently making it a more efficient cutting edge to deal with graminaceous food. In common with the Kakapo, *C. unicolor* appears to be a "blind" feeder, depending more on the sense of taste than on sight for discriminating between its food substances.

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