

## TONGUES OF THE ZOSTEROPIDAE (WHITE-EYES)

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### INTRODUCTION

The *Zosteropidae* are a family of small passerine birds, with breeding ranges that between them extend from Senegal and the Cape to Ussuri-land, Japan, Samoa and New Zealand, including numerous oceanic islands. The family consists of about 82 species, 59 of them in the genus *Zosterops*. There are perhaps only 3 of these (including one very highly polytypic) in Africa <sup>1</sup>), 7 in the islands of the Indian Ocean, and 49 from India eastwards (as listed by MEES 1957); but the uniformity within the genus *Zosterops* is such as gravely to complicate taxonomic treatment. The remaining 23 species of the family fall into 11 small genera, one in the Gulf of Guinea area and the others all from the Philippines eastwards. In the great majority of the Zosteropids the beak is short, sharply pointed and slightly curved, the eye is surrounded by a ring of tiny white feathers, which has given the family its popular name, and the tongue is specialized.

In literature the references to the tongues of the *Zosteropidae* have been contradictory and misleading to an extent that is extraordinary in the full meaning of the word. The first contribution to the subject appears to have been that of GADOW (1883), who figured the tongue of *Z. lateralis* (of Australia) as simply and smoothly bifid. As will be shown below there was misapprehension here; we have ample evidence that the tongue of *Z. lateralis* is heavily fimbriated (Fig. 1). However, shortly afterwards, GADOW (1884) characterized the *Meliphagidae*, in which he included the *Zosteropinae* without noting them as exceptional, as having the tongue "bifid, each half broken up into stiff horny fibres, so as to form a 'brush'". Nevertheless, when SHARPE (1891) — following A. NEWTON in the *Encyclopaedia Britannica*, 9th edition (1888) — formally raised the white-eyes to family rank, he remarked that "an examination of the tongue of *Zosterops* [which species?] shows that it resembles the tongue of a Tit and has no similarity to the 'brush' tongue of a Honey-eater". Meanwhile BEDDARD (1891) had examined tongues of "*Z. simplex*" = *Z. japonica simplex* (of southeastern Asia). He noted that the upper surface of one was nearly flat, in another more rolled, and he commented that the tendency for the edges of the tongue to roll into tubes depended on whether it was dry. He stated that each half of the bifid tongue was "frayed out into two or three brush-like processes" (but his figure shows six projections at the tip of each half of the tongue).

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<sup>1</sup>) *Z. virens* is now regarded as conspecific with *Z. pallida* (CLANCEY 1967).

In 1919 WETMORE & TOWNSEND described the tongue of a specimen from Kusaie = Ualan in the eastern Caroline Islands, *Z. cinerea cinerea*, as having the tip "divided into a number of filaments, all fine, but varying in size, that tend to turn somewhat in slow spirals". This clear evidence of fimbriation seems to have been overlooked by subsequent writers on the *Zosteropidae*. So also has the fact that *Woodfordia superciliosa* of Rennell Island (off the Solomons), described in 1906 as a Meliphagid, but transferred to the *Zosteropidae* by SHARPE (1909) on the grounds of its "absence of tenth primary", has a tongue that is "deeply grooved down the centre, bifid and brush-like at the tip" (NORTH *cit.* WOODFORD 1916).

GARDNER (1925) in a general review of avian tongues figured 200 species. He commented that, while slight fraying and forking at the tip are of widespread occurrence in passerine birds, a high development of both characters is found only in the *Meliphagidae* (Honeyeaters). He regarded (p. 11) as "a most difficult problem . . . the explanation of variations in closely related birds where presumably the diet is very similar" and cited as an example "the genus *Zosterops*, with a forked and smooth tongue in *Z. lateralis*, while it is much curled and frayed in *Z. simplex* and *Z. japonica*" (now regarded as conspecific). Here GARDNER was presumably basing himself on GADOW's (1883) erroneous description and on BEDDARD's work. Later in the same paper (p. 26) he emphasized the "elaborate curled, split and fimbriated tongues" of *japonica*, thus actually exaggerating the fimbriation demonstrated by BEDDARD and at the same time discounting that author's suggestion that the curling might be an artefact. GARDNER's personal contribution to knowledge of Zosteropid tongues was to figure *Z. atrifrons*, a species that ranges from Celebes to the Solomons, and to comment that that of *Z. sarasinorum* = *Z. m. montana* (MEES 1957), also of Celebes, is similar. GARDNER's version of the *atrifrons* tongue is an intermediate type, deeply slit, with "some fraying of the margins", but no terminal brush (and no tubulation). In a subsequent review (GARDNER 1927), while reiterating the (erroneous) contrast between *Z. lateralis* and *Z. japonica*, he referred to the *Zosteropidae* as a "group in which a semi-tubular arrangement is found".

PORSCH (1929), in his paper on flower-frequenting by birds, thought it "hardly correct to put forward the possession of pronounced brush-tongues (*ausgesprochenen Bürstenzungen*) as an essential (*durchgreifende*) character of the *Zosteropidae*". MOLLER (1931), in a discussion of the bill- and tongue-mechanisms of flower-frequenting birds, seems to have been the first to consider an African Zosteropid. He had sectioned the bifid tongue of *Z. annulosa* = *Z. pallida capensis* of the Cape Province, and he figured copious terminal "brushes", but no fimbriation on the edges. He discounted the tendency to rolling-up by noting that it is favoured both by drying and by preservation in alcohol. Nevertheless, STRESEMANN (1934) in his encyclopaedic treatment of the *Aves* mentioned the tongue of *Zosterops* only to cite it as an example in which the edges curve upwards so that a channel is formed, and he made no allusion to a brush effect.

Then BERLIOZ (in GRASSÉ 1950) made a generalization for the *Zosteropidae*, that is startling in view of what had been published before: "langue rappelant celle des Nectariniidés, protractile et bifide, mais ni lasciniée ni penicillée",

thus both implying a double tubular structure and ruling out any subsidiary splitting or brush effect. MAYR & AMADON (1951), in the notes on their classification of birds, wrote of the *Zosteropidae* merely that "some of them are somewhat specialized for feeding on nectar", without indicating whether they had a tubular or a brush tongue-mechanism in mind.

BEECHER (1953) diagnosed the *Zosteropidae* as having "tongue unspecialized, but that of *Z. virens* whipped-out into quadrifid tip and tubular" (though his accompanying figure shows the tongue as bifid); and in his discussion he referred to "the sometimes specialized tongue" in this family. Subsequently BEECHER (*in litt.*) commented that if he had seen more tongues at the time he wrote the paper cited he "probably would not have written 'tongue unspecialized' ". He added that he had since found the tongues of "*Z. polioaster*, *Z. senegalensis* and *Z. winifredae*", all African and regarded as probably conspecific (*senegalensis*) by MOREAU (1957), as well as of the Asiatic *Z. japonica* and *Z. palpebrosa* subsp., to have "specialized", "whipped-out" tongues; but he had also examined *Z. lateralis* and [unaccountably to us] agreed with GADOW (1883) that it had a simple tongue. BANNERMAN (1953) mentioned the "brush-like appendages at the tip" of the tongue of the African *Zosteropidae*, but VAN TYNE & BERGER (1959) made no reference to the tongue in their diagnosis of the family. By contrast, the impression of AUSTIN (1961) is that the *Zosteropidae* "show their closest affinities to the honey-eaters, for their tongues are brush-tipped instead of tubular as in the sunbirds and the flower-peckers".

From all the foregoing it will be seen that past statements, both specific and general, regarding the tongues of the *Zosteropidae* have some of them affirmed and some of them denied the prevalence of brush-tongues and have to a varying degree accepted the existence of tubulation, which some workers have thought to be an artefact. It cannot, however, be too strongly stressed on how extremely limited a basis all that has been written on the subject in the past appears to rest. There is nothing to show that more than the eight species named above had been examined—and not all of these satisfactorily; in fact only seven out of about sixty species of *Zosterops* and one out of the 23 species that make up the 11 aberrant genera.

Interest in the subject was originally aroused in one of us when he thought it might be possible to use the structure of the tongue as an ancillary character in the classification of the African *Zosterops*, especially in the difficult problems of their specific limits (MOREAU 1957). The idea was not pursued at the time, partly because it seemed likely to be unrewarding for the immediate purpose and partly because it would clearly be necessary to widen the scope of the enquiry beyond the few African representatives of the family. This has now to a small extent been done and, since circumstances make it impossible to pursue this admittedly preliminary and very partial study further, the results are

given in their present form. We think that we have been able to advance knowledge in this field, but only at a late stage in our investigation have we realized how much we have been handicapped by the nature of our material. The low-power microscopical examination has been largely done by **M.P.**, the high-power all by **J.T.H.**

Recently F. B. GILL (*in litt.*), working in Réunion, has detected in *Z. borbonica* and *Z. olivacea* "a delicate epithelium which overlies the dorsal tongue surface" which adheres and becomes unrecognizable within "a couple of minutes exposure to the air". This explains two anomalous appearances in our material, which had baffled us.

For material we have to thank chiefly the American Museum of Natural History, the British Museum (Natural History), the Rijksmuseum van Natuurlijke Historie, Leiden, and Dr. J. KIKKAWA. We are under exceptional obligations to Dr. FRANK B. GILL for keeping us informed of his progress on Réunion and allowing us to quote from his unpublished work. We are also indebted to CLAUDE AUSTIN, C. W. BENSON, Dr. G. M. DUNNETT, A. FORBES-WATSON, Dr. H. FRITH, C. J. O. HARRISON, Professor A. KEAST, ALLAN R. McEVEY, Professor B. J. MARPLES, Dr. IAN NEWTON, Mrs. R. G. RITCHIE, Dr. W. SERLE, K. D. SMITH, JOHN TRUSCOTT and Dr. J. VINSON. In the early stages of the investigation we owe much to the interest of Dr. A. J. CAIN. Latterly we have benefited greatly by discussion with Dr. G. F. MEES and also with Dr. A. BEECHER, Dr. R. LIVERSIDGE and Dr. FINN SALOMONSEN. Miss J. COLDREY has been of considerable help with the literature and the figures have been drawn by Miss C. COURT. For reading this manuscript in draft we are indebted to Dr. G. F. MEES and Dr. D. LACK.

#### MATERIAL EXAMINED

A large proportion of the tongues examined have been extracted from study skins in which collectors had accidentally left them. Others were obtained from specimens that had been preserved entire, usually in alcohol. Both these types of material were obtained by gently prising open the beak and cutting at the base of the tongue with a scalpel. Considering the small size of the tongues — usually around 10 mm. in length — and the delicacy of much of their terminal structure, they were often extracted with surprisingly little damage. Some other tongues have come to us that have been cut out soon after the birds' death and kept in non-hardening fluid. In the result, the tongues we have seen that have been in good enough condition to provide information are as listed below. Unfortunately, at the beginning of the investigation it was decided to fix each tongue as a microscope slide, which has been done with all but the latest acquisitions; but experience has shown that lateral viewing may disclose structural features missed when the tongue is looked at dorsally or ventrally. The use of the asterisk\* in the list will be explained later.

#### ADULTS

<i>Chlorocharis *emiliae</i> subsp., Borneo	2	<i>melanocephala</i> , Cameroon Mt.	4
<i>Lophozosterops goodfellowi</i> , Mindanao	1	<i>Woodfordia *superciliosa</i> , Rennel Is.	3
<i>javânica</i> , Java	1	<i>Zosterops *abyssinica abyssinica</i> , N. E.	
<i>Speirops leucophaea</i> , Principe Is.	1	Africa	5
* <i>lugubris</i> , São Tomé Is.	4	* <i>abyssinica flavilateralis</i> , E. Africa	2

* <i>abyssinica socotrana</i> , Socotra Is.	2	* <i>lateralis tepbropleura</i> , Lord Howe Is.	1
<i>albogularis</i> , Norfolk Is.	1	* <i>lutea</i> , N. Australia	7
<i>atrifrons delicatula</i> , New Guinea	1	* <i>maderaspatana</i> , Madagascar	5
* <i>borbonica borbonica</i> , Réunion	1	* <i>mayottensis</i> , Mayotte Is.	1
<i>borbonica mauritiana</i> , Mauritius	2	* <i>montana montana</i> , Malaysia	2
* <i>cinerea finschii</i> , Palau Is.	1	<i>olivacea chloronothos</i> , Mauritius	1
* <i>chloris maxi</i> , islets off Java	3	<i>olivacea olivacea</i> , Réunion	2
* <i>everetti basilanica</i> , Mindanao	1	<i>pallida</i> (including <i>virens</i> ), South Africa	8
* <i>ficedulina ficedulina</i> , Principe Is.	2	* <i>palpebroso palpebroso</i> , India	3
* <i>flavifrons flavifrons</i> , Tanna Is., New Hebrides	6	<i>palpebroso</i> subsp., captivity	2
<i>griseotincta rennelliana</i> , Rennell Is.	2	* <i>senegalensis</i> , five lowland African intergrading subsp.	14
* <i>griseovirescens</i> , Annobon Is.	5	* <i>eurycricotus</i> , * <i>jacksoni</i> , * <i>mbuluensis</i> , * <i>poliogastra</i> , four isolated montane subsp.	7
* <i>japonica alani</i> , Bonin Is.	2	* <i>stresemanni</i> , Malaita Is.	1
* <i>japonica simplex</i> , China	2	<i>vaughani</i> , Pemba Is.	3
<i>lateralis flaviceps</i> , Fiji	1		
* <i>lateralis gouldi</i> , W. Australia	2		
* <i>lateralis lateralis</i> , S. E. Australia	47		
<i>lateralis macmillani</i> , Tanna Is., New Hebrides	2		
			163

It will be seen that the 163 tongues we have examined come from representatives of 23 species of *Zosterops* and seven species belonging to aberrant genera, *Chlorocharis* (1), *Lophozosterops* (2), *Speirops* (3) and *Woodfordia* (1) — in all, 30 out of the 82 species that comprise the *Zosteropidae*. As a basis for generalization we can add *Rukia longirostra*, mentioned above. The geographical distribution admittedly leaves much to be desired, since 57 of our tongues come from Africa and the adjacent islands and 56 from Australia (including Tasmania), while numerous species inhabiting Malaysia and islands further east are not represented. No doubt this deficiency could have been to some extent remedied if access to all existing museum material had been sought, but circumstances at present preclude this. Also, even on what we have, it will be possible for us to advance the subject somewhat and to clear up certain misapprehensions.

#### NESTLINGS

- Z. flavifrons flavifrons* 2 unfeathered  
*Z. lateralis flaviceps* 2 unfeathered  
*Z. lateralis lateralis* 4, namely:  
 1 5 days old, teste CLAUDE AUSTIN  
 1 estimated 6 days old  
 1 7 days old, teste Mrs. B. RITCHIE  
 1 estimated 9 days old  
*Z. pallida capensis*, 3 half feathered, estimated 7 days old

#### DESCRIPTION OF ADULT TONGUES: GROSS ANATOMY

All the adult tongues examined conform more or less in main features to that of *Z. lateralis*, as depicted in Figure 1. We have, however, repeatedly encountered individual differences that have so baffled us as almost to lead us to drop the study in despair; and A. KEAST (*in litt.*) has stressed the individual variation he found in a small sample of *Z.*

*l. lateralis* from near Sydney, N.S.W. On the other hand, of 26 tongues of Tasmanian birds, which have usually been ascribed to the same subspecies, only one differs appreciably from that in Figure 1. Incidentally, this fine series, derived from sexed specimens, shows that, as might have been expected, male and female tongues do not differ. Eventually we have come to the conclusion that the differences that have troubled us may be due in part to wear, but chiefly to postmortem changes, varying greatly with the method of preservation and also with the time elapsing before this took effect.

The main features of the tongues examined are as follows: —

(1) At the base a number of strong pointed processes at the back of the tongue, which arise from the hind edge and adjacent sides and are directed backwards — a feature about which no comment is necessary, except that the adaptation is presumably for feeding on insects.

(2) A central cleft in the terminal part of the tongue, supplemented in most tongues by a much smaller cleft on each side, so that towards the tip each tongue is quadrifid.

(3) Fimbriation (fringing), both terminal and lateral, arising from the outer edges of the tongue, but not from the edges of the clefts.

(4) Various degrees of curvature, ranging from almost total absence to extensive tubulation.

It may be added that in a fresh tongue of *Z. senegalensis stierlingi* sketched and reported on by Mrs. F. M. BENSON the basal third was dull reddish and the remainder dull yellowish, except for an oval dark-grey area on either side, just forward of the reddish area. So far these data stand by themselves. It may be suspected that they point to anatomical features not disclosed by our study material.

#### THE CLEFTS

In every specimen examined the central cleft is very obvious, extending as a rule for about one third of the entire organ, as measured from the centre of the hind edge. The longest clefts, approximating to one half, are prevalent in *Z. olivacea* of Réunion Island and Mauritius, a species that has proportionately the most elongated beak and tongue in the entire family. The shortest clefts we have seen, not more than one quarter of the tongue-length, are in *Speirops* spp. — one *leucophaea*, two *melanocephala* and one out of three *lugubris* — and in two neighbouring but very different birds of northeastern Africa, *Z. s. poliogastra* of the highlands of Abyssinia and Eritrea, and *Z. a. abyssinica* of the surrounding lowlands. It may be noted parenthetically that individual variation in

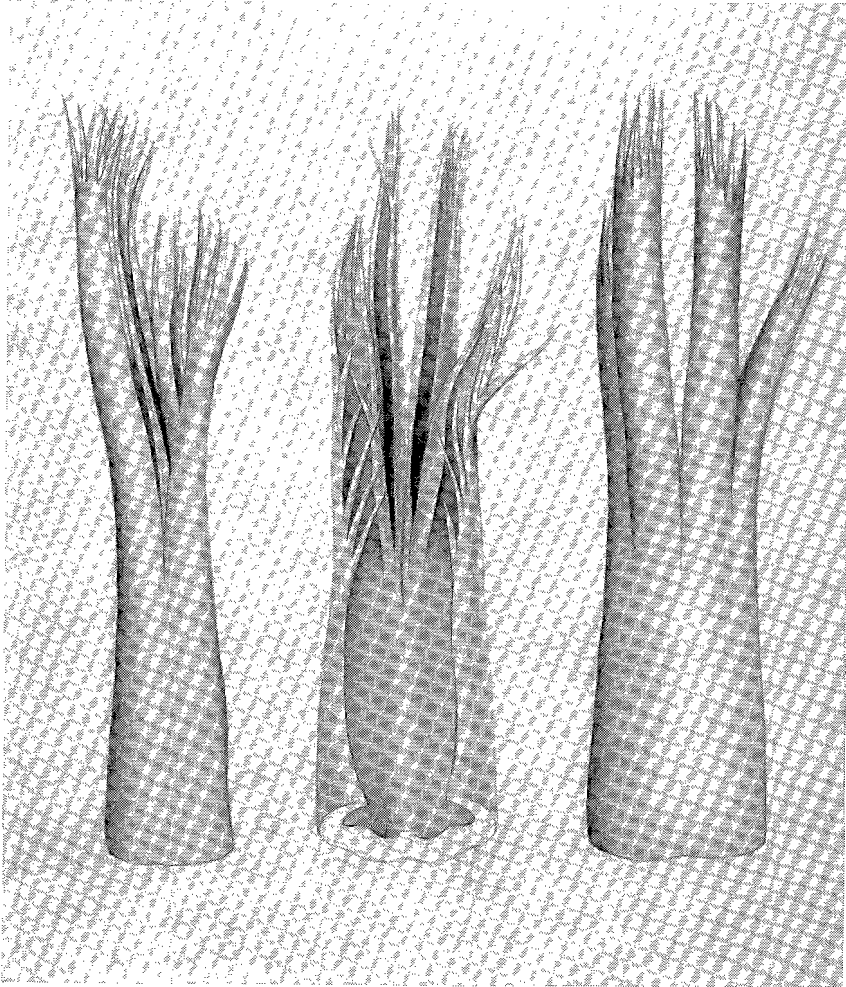
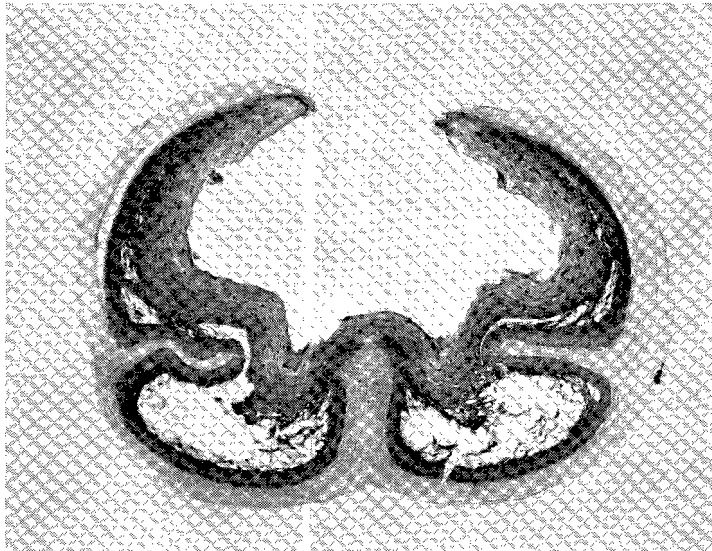


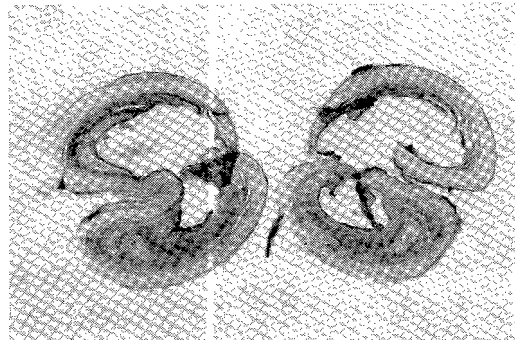
FIGURE 1. Drawings of distal part of *Zosterops lateralis lateralis* tongue showing, from left to right, lateral, dorsal and ventral views.  $\times$  circa 20.



(a) Near the base, undivided.



(b) Soon after the beginning of the central cleft.



(c) Nearer the tip of the tongue, subdivision begun.

FIGURE 2. Transverse sections of tongue of *Zosterops lateralis lateralis*.  $\times 60$ .



total length of tongue is marked, for example, from about 7 mm to 9 mm in the little *Z. a. abyssinica*, 13.6 to 15.6 in the long-billed *Z. olivacea* of Réunion (F. B. GILL *in litt.*), but data are insufficient to show what correlation may exist between length of tongue and length of wing, either within a population or between species.

Far less obvious is a subsidiary cleft on either side of the main one and usually extending to less than half its depth. These small clefts are extremely easy to miss in preserved tongues and indeed in the collecting experience of F. B. GILL (*in litt.*) they tend to close up after a few minutes exposure to air. Nevertheless, these features have been detected by us in all those birds which are distinguished by an asterisk\* in the list of material in the foregoing section. We are also fairly sure that these clefts exist in our imperfect specimen of *Lophozosterops javanica*. A negative by no means can be taken as good evidence that the subsidiary clefts are absent. As an example, they are not detectable in our dried material of *Z. pallida* (including "*virens*") but both BEECHER (1953) and LIVERSIDGE have described the tongue of *Z. capensis* (now regarded as conspecific with *pallida*) as quadrifid. Moreover, LIVERSIDGE (*in litt.*) has found the subsidiary clefts "constant for all" the specimens he has examined and he has shown them in his figure of a *Zosterops* tongue (presumably derived from this bird) in SKEAD (1967: 28). Incidentally it may be noted that he depicts it as less tapering and with a broader, flatter, end than in the *Zosteropid* tongues we have examined.

We have been much puzzled by what appear to be struts, a thickening and presumably strengthening on each side of the central cleft, which appears sporadically in a few of our specimens, most noticeably in *Z. albogularis*. We have come to the conclusion that these "struts" must be artefacts produced by the overlap of drying tissue, perhaps connected with the secondary clefts. On the whole it seems probable that at least the great majority of the *Zosteropidae* have tongues that are primarily bifid and secondarily quadrifid. In this respect, then, they agree with those of the *Meliphagidae* (honeyeaters), which have however a specific and generic variety (SCHARNKE 1931, DORST 1952) altogether greater than is found in the *Zosteropidae*.

#### FIMBRIATION

In all the tongues examined both terminal and lateral fimbriation can be discerned, but the extent is variable, individually and perhaps also as between species. As a rule the terminal fimbriation is strong and dense, with a marked tendency in some species, e.g. *Speirops melanocephala*, for

the individual fimbriae, especially those nearest to the central cleft, to be flattened and pointed.

The lateral fimbriae are easy to miss in a few tongues in which the sides have rolled inwards but in our experience they are always present. Again much variation is shown; even in the same population they may be few and short or numerous and long. They may spring from the edges of almost the whole terminal half of the tongue, that is, from further back than the base of the central cleft, or occupy only half that distance. These lateral fimbriae appear as a rule to be hair-like, not flattened. Again, individual variation is found; for example, in 26 Tasmanian *Z. l. lateralis* some have the individual fimbriae distinctly wider than others.

We think that much of the variation can be attributed to wear of the fimbriae and also to the extent to which they form by splitting from the main tissue of the tongue.

#### LATERAL CURVATURE AND TUBULATION

At an early stage of this investigation we were struck by the fact that these features appeared irregularly and even within a species or subspecies to an extremely variable degree. One tongue would be practically flat or slightly curved in cross-section; in another each edge had curved upwards and inwards so far as to form two tubes. As a rule any tendency to tubulation extended forward to beyond the base of the central cleft in the tongue, but about the terminal fifth as well as the distal fifth of the organ was unaffected.

We have come to the conclusion that in material such as ours, on which, in the past, comment on Zosteropid tongues has of necessity been based, is an artefact, induced most often by desiccation — which can take place quickly — and also by preservation in alcohol, as suspected by BEDDARD (1898) and by MOLLER (1931). Apart from the fact that such a postulate is demanded by the sporadic incidence of rolling in preserved tongues, this view is supported by many specific examples, of which the following may be cited.

*Z. senegalensis poliogastra*. Two examined just after collecting by K. D. SMITH (*in litt.*) were flat.

*Z. senegalensis anderssoni*. A tongue, examined by C. W. BENSON (*in litt.*) within two hours of being collected, was flat.

*Z. lateralis lateralis*. 26 tongues, preserved apparently in Bouin's fluid, were all flat or slightly curved in cross-section. Another sample of nine, received dry, had the edges rolled into almost complete tubes, except for one which was nearly flat. One tongue that was nearly flat when it was examined and sketched in 1964 has subsequently dried out and formed two tubes.

*Z. lutea*. Seven tongues show every variation from flat to almost completely tubular.

*Z. chloris maxi*. Of three tongues one shows practically complete tubulation, the other two no more than slight up-curving at the edges.

*Z. olivacea*. Of four tongues put into Bouin's fluid within a couple of minutes of being collected three were some weeks later "still moist and flat and non-tubular"; the fourth has dried up and is tubular (F.B. GILL *in litt.*).

*Z. borbonica*. Of 14 preserved specimens three were subsequently found to be "definitely curled, forming an incomplete tube", the others are "without conspicuously curved edges" (F. B. GILL *in litt.*).

We infer that any statement implying that in nature the tongues of the *Zosteropidae* show tubulation or more than very slight lateral curvature is unwarranted.

#### DESCRIPTION OF ADULT TONGUES: INTERNAL ANATOMY

Two adult tongues of *Z. l. lateralis* were prepared, the distal parts being embedded together and cut serially. These serial sections were mounted five to a slide and were stained alternately by haematoxylin and eosin and haematoxylin and Van Gieson. The mounted sections were numbered from 1—80 and after 80 only the debris of the tip of the tongue could be recognized. 800 sections were examined in all.

In the sections numbered from 1—15 the tongue appeared in one piece and without any of the cleavages that later appeared. In section 8 (x 100), taken as an example, it will be seen that the structure in transverse section is that of a partially opened tube (Fig. 2a). The inside of this is formed by squamous epithelium which has the complex contour seen in the diagram.

An unexplained feature is the presence of vesicles, which appear white in Figure 2a. Keratin is applied to the squamous epithelium on all its sides but is most conspicuous on the outer aspect, forming a hard outer coat.

The first division of the tongue took place at about section 16 and Figure 2b is taken from section 23. It will be seen that, as the tip of the tongue is approached, the partial tube divides into two similar structures by a thinning of the tube opposite the open part. We now have two mirror-image structures each rather resembling the original before division. The anatomical arrangement is the same, with squamous epithelium having a complicated contour on the inside and an outer layer of keratin. The remains of the vesicles in the centre of the squamous epithelium are still to be seen.

At some point after section 26, each of the two primary divisions subdivided. At this stage of the anatomy the squamous epithelium has become very slight and the main bulk of the tongue consists of keratin. This subdivision now results in two unequal halves, one containing more squamous epithelium than the other (Fig. 2c). With reference to the naked-eye appearance of the tongue it will be seen that the portions having only keratin are probably shorter bristles than the main tip of the tongue, which is probably longer.

The sections forward of No. 30 consist only of keratin and have no cellular structure. Thus the tip of the tongue consists only of bristles of keratin given off from the more proximal squamous epithelium.

It is interesting to speculate from this anatomical arrangement the manner in which this tongue grows and divides. It will be seen that

there is a primary subdivision into two equal and mirror-image halves and then secondary subdivisions, which are however not into equal parts but result in the bristles seen macroscopically. It is apparent that abrasion of the end of the tongue will result in shortening of the keratin bristles which would be replaced by continuous growth from their parent squamous epithelium. These remarks apply only to the tip of the white-eye tongue which is not apparently muscular at the level at which it divides into these bristles.

#### DESCRIPTIONS OF NESTLING TONGUES

*Z. l. lateralis* (Australia). The useful series of four tongues enables the development to be followed. At 5 days old the tongue is blunt and broad, 2.5 mm at the widest part, against 5 mm in length, and it appears to be enclosed in a kind of sheath. Otherwise it has no features, except that spikes at the base are already well developed. This is in accord with the diet; the stomach of this tiny nestling contained parts of six comparatively large caterpillars up to nearly 5 mm in diameter (also one midge and one large seed that looked like a grape pip).

The tongue of the nestling estimated to be six days old shows the first beginning of the central cleft. In the (definitely) 7-day tongue the cleft is a little deeper but there is no visible line of weakness running backwards from it. By the ninth day the cleft is 1.5 mm long but there is still no fimbriation. The spikes on the base of the tongue are better developed than at five days. This bird also had been fed with caterpillars (about 6 mm. in diameter) and other insects, besides, most astonishingly, a minute snail.

*Z. lateralis macmillani* (Tanna, New Hebrides). The two tongues from naked young, which can hardly be more than five days old, show an unexpected contrast to those of *Z. l. lateralis*, just described. The median cleft is already well begun and its distal extension is adumbrated. Two of what appear to be struts are obvious alongside the central cleft and fimbriated at the tips. Outside the struts there is what appears to be very delicate tissue, extending for more than the terminal half of the tongue and already bearing short fimbriae.

*Z. f. flavifrons*. The two tongues, also from Tanna and also from unfeathered nestlings presumably no more than five days old, show similar features.

*Z. pallida virens* (South Africa). In the three half-feathered nestlings, probably about nine days old, the median cleft is already about 1/6 of the total length of the tongue, and in one of them a subsidiary cleft on each side is just beginning. No fimbriation is discernible but it must develop rapidly, within the next few days, for R. LIVERSIDGE (*in litt.*) found that a fledgling had "much the same tongue as an adult".

All that can be said about the foregoing data, from four different populations, is that in the insular nestlings of two species development of the tongue appears to be more precocious than in the continental (Australian and African) nestlings available. From such scanty material it would of course be premature even to speculate about this apparent difference. It is at least clear that all the nestlings are provided at an early stage with equipment for holding insect food. It may be added that the normal period spent in the nest is probably around 12 days — SKEAD (1967) for *Z. pallida* of South Africa, FALLA *et al.* (1967) for *Z. lateralis*

in New Zealand. But that *lateralis* can fledge in barely 11 days is proved by the observations of Mrs. R. B. RITCHIE (*in litt.*): 15 January, 6 a.m., 3 young and 1 egg, 6 p.m. 4 young; 25 January 6.30 a.m. 4 young, 5 p.m. 2 young; 26 January 6 a.m. 2 young, 9 a.m. none. For the last-hatched young the fledging period was thus 10 days 19½ hours  $\pm$  7½ hours. As especial care was taken to create little disturbance on inspection of the nest, the period thus arrived at can probably be taken as "natural". We have no indication of how long elapses before a fledgling supports itself.

#### THE FEEDING HABITS OF THE ZOSTEROPIDAE

An ultimate aim of any study of this nature should be to relate structure to function; in the present one, to consider any variations in the structure of tongue in relation to the feeding habits of the birds concerned. Among the *Zosteropidae*, however, it is not clear what, if any, significant differences in the gross anatomy of the tongues exist, even in the more aberrant genera and certainly not to the same extent as in the *Meliphagidae* (honeyeaters) — which, indeed, as at present conceived have been doubted to form a natural unit (DORST 1952, RAND 1961). The anatomy of the *Zosteropid* tongues, as described in the foregoing pages, would seem adapted by means of the fimbriae to the taking of nectar, pollen and minute insects, and by means of the backward processes at the base of the tongue to the taking of larger insects. Marked lateral curvature or tubulation, which could facilitate the uptake of liquids, seem to be absent in life.

Although the data are defective and often doubtfully critical, it is clear that the feeding habits of the *Zosteropidae* and of their individual species are exceptionally catholic. Published references to their food are nearly all confined to mention of insects and/or fruit and/or seeds (presumably derived from fruit). The fruit cited is of two kinds, small berries that are swallowed whole and the pulp of more juicy fruits, especially of cultivated, introduced, species. Most of this information comes from stomach examination and so does not necessarily exclude the ingestion of nectar, for this material would not normally be detected in a bird's stomach unless it were particularly sought. As showing the adaptability of the birds, it may be added that *Z. lateralis* has been seen to tear up petals (of *Feijoa*) and swallow the pieces (LAWRENCE 1961). At a bird table the same species eats caster sugar eagerly.

According to KUNKEL (1958), *Z. japonica* takes insects on the wing and by searching foliage or bark and has been seen to investigate the nests

of other birds, presumably for insects. Its technique of examining crevices is interesting. The bird inserts its closed beak, then opens it with frequent protrusion of the tongue, while peering into the crevice. Here, therefore, the fimbriae come into play where there is no possibility of taking up nectar. On the other hand A. FORBES-WATSON tells us that when he was trying to resuscitate a damaged *Z. senegalensis* by offering it honey and water in an eye-dropper "in a minute or two it had learnt to put the tip of the bill into the narrow glass tube, and it apparently sucked the honey with no protrusion of the tongue". In one species, *Woodfordia superciliosa*, apparently alone among the *Zosteropidae*, the beak seems to be adapted for the taking of berries and/or insects. Described by STRESEMANN (1931) as "*grob gezähnel*" (coarsely toothed), it would, on the evidence of specimens in the British Museum, be more accurate to say that one or two notches are present just behind the tip of the upper mandible (Mrs. B. P. HALL *in litt.*). Unfortunately nothing seems to be known of the bird's actual feeding habits, but its tongue conforms closely to the normal, as described above.

For the *Zosteropidae* as a whole even imperfectly critical indications that nectar is taken are astonishingly limited, for when birds have been reported as visiting flowers it cannot always be assumed that they were taking nectar. In the whole of Africa there seems to be no evidence at all except from the southern end. Here STARK (1900) reported that *Z. capensis* (i.e. *pallida*) was "fond of the saccharine juices of many flowers in the municipal gardens in Cape Town . . . notably the Australian 'Bottle Brush' (*Callistemon*)". R. LIVERSIDGE (*in litt.*) has observed the same bird frequenting flowers of *Eucalyptus* (also of course from Australia), MEES has seen it piercing the corollas of (introduced) Azaleas in Natal, and M. B. MARKUS (*in litt.*) has recorded it as taking nectar from (introduced) *Peinsettia* in Pretoria. The only specific evidence connecting white-eyes with native African flowers comes from SKEAD & RANGER (1958) and SKEAD (1967 and *in litt.*). "White-eyes are not the keen nectar-feeders sunbirds are, but they do take it. They go for the less conspicuous flowers such as *Scutia* and *Royena* but they also feed on aloes . . . and pierce the corolla tubes of *Burchellia*, *Tecomaria* and *Watsonia* in order to bring their short bills to bear on the nectar source, otherwise too deep in the tube for the normal approach through the mouth." On the other hand such an experienced observer as J. P. CHAPIN (*in litt.*) had no evidence in the Congo that *Zosterops* took nectar; nor had C. W. BENSON (*in litt.*), although for many years he lived in Malawi, Abyssinia and Zambia, in all of which *Zosterops* are prevalent, and constantly had under

his eyes flowering trees that attracted Sunbirds. On the other hand M. K. ROWAN (*in litt.*) from personal experience believes that nectar-feeding is more common in South Africa than would be inferred from the literature and cites the nipping of a hole in the base of *Watsonia* corollas. It is difficult to know how to interpret the observation that what appeared to be a regularly circulating flock of up to 180 *Z. p. pallida* were seen "clambering about in the flower clusters of eucalyptus in a Johannesburg suburb, which were at that time attractive to the sunbird *Nectarinia amethystina*, while ignoring the flowers of interspersed wattles (introduced Australian acacias)".

On the island of Réunion GILL (*in litt.*) has found a situation that may be unique except perhaps on Mauritius. On Réunion in the absence of *Nectariniidae* the long-billed *Z. olivacea* is a "functional sunbird", defending flowering trees and bushes and feeding primarily on nectar, at least seasonally, while the short-billed *borbonica* concentrates on "a warbler-like gleaning and foraging for small insects, supplemented by fruit, though it has also been seen to puncture flowers at the site of the nectary".

From India eastwards MEES (1957, 1961) has collated evidence on the feeding habits of the *Zosteropidae*. The evidence that nectar is taken is so far limited to *Z. japonica*, *Z. palpebrosa* in Indo-China (pecking holes in *Hibiscus* calyx) and Java, and *Z. montana* also in Java (frequenting the flowers of the introduced sisal *Agave americana*). The importance of nectar-feeding in *Z. palpebrosa* in India is stressed by SALIM ALI (1946) "nectar of flowers forms a substantial part" of the diet, cf. DHAR-MARKUMARSINHJI (n.d.); and in Ceylon HENRY (1955) has mentioned that this species "probes flowers for nectar". MEES (*in litt.*) has personally observed another species, *Z. natalis*, feeding from *Stachytarpheta* on Christmas Island (Indian Ocean) and has directed our attention to two other relevant published statements, namely, by DOCTERS VAN LEEUWEN (1933) regarding *Lophozosterops javanica* on *Vaccinium* in Java and by BAKER (1951) regarding *Rukia sanfordi* = *longirostra* on Ponapé Island in the Carolines. Here the birds were observed "collecting [*sic*] from the flowers" of "a sort of gum-tree" and one bird had "yellowish sap adhering to its bill".

In the Australasian literature most references give the food as insects and fruit (often elaborating on the damage done in orchards), without mentioning nectar. Indeed some of our correspondents, who have specially concerned themselves with *Zosterops* there, have no evidence that they take nectar at all. On the other hand Dr. J. KIKKAWA (*in litt.*)

has seen *Z. lateralis* doing so from *Eucalyptus* spp. in Australia and from a wide variety of both native and introduced species in New Zealand — where indeed FALLA *et al.* (1966) mention that this bird “eagerly takes nectar”. Moreover MEES (*in litt.*) has observed this species dipping into *Erythrina*, *Xanthorrhoea* and *Hakea* flowers in Western Australia and into leguminous flowers on Norfolk Island. MORCOMBE (1967) has recorded white-eyes [presumably *Z. lateralis*] tearing open the long corollas of Kangaroo Paws *Anigozanthos* sp. “to gain access to nectar otherwise denied” to birds with such short beaks. Finally, it may be mentioned that in the experience of KIKKAWA *Zosterops* prefers honey to fruit when both are made available on a bird table.

The foregoing provides evidence that out of over 80 species of *Zosteropidae* nectar is taken by nine but of these perhaps only to *palpebrosa* and *olivacea* is it important.

#### DISCUSSION

Making all allowances for faulty observation, it does seem that nectar must be accepted as no more than a minor element in the diet of the *Zosteropidae* in general <sup>1)</sup>, but the fact that it is not negligible makes it worth while to compare the structure of the Zosteropid tongue with that of other birds to which nectar is of major importance. In the first place, it is now clear that the Zosteropid specialization has nothing in common with that of the sunbirds, which rely entirely on tubulation. It is almost equally unlike that of the sugarbirds (which are best regarded as forming the family *Promeropidae*, not as part of the *Meliphagidae*, cf. SKEAD 1967), which have tongues that are primarily tubular though with slight fimbriation at the tip. In those species of flowerpecker (*Dicaeidae*) which are most dependent on nectar the tongue is deeply cleft, with the edges of “each half curled to form two slender semi-circular tips”, but in the berry-eating species the tongue is simple (SALOMONSEN 1964, amplified *in litt.*). More than anything else the Zosteropid tongue resembles those of the honeyeaters in being quadrifid, highly fimbriate and also non-tubular, but it shows nothing like the same high degree of

<sup>1)</sup> It is amusing to find that the supposed importance of nectar-feeding to the *Zosteropidae* has given the place to these birds in the sequence of Passerine families. “It seems to be mostly convention to place the *Zosteropidae* near the other nectar-feeding birds” (Professor E. MAYR *in litt.*). With the unjustified lack of uniformity that is a current bedevilment of ornithology, the sequence of AMADON (1957) is *Meliphagidae*, *Zosteropidae*, *Dicaeidae*, *Nectariniidae*, while in the “Check-list of birds of the world” vol. 12 (1967), it is *Dicaeidae*, *Nectariniidae*, *Zosteropidae*, *Meliphagidae*. (*Promerops* is included in the *Meliphagidae* in both works but in the Check-list at the end of this family, as “probably” representing a separate one.)



variation within the family. In particular, so far as we know, there is in the white-eyes no species comparable to the Meliphagid *Melipotēs*; this bird, abnormal in its family in being essentially frugivorous, has both furcation and fimbriation of the tongue greatly reduced though its stomach is said to be of nectivorous type (DORST 1952).

However much further field observations may increase the evidence for nectar-feeding by the *Zosteropidae*, it is virtually certain that the present conclusion that these birds obtain most of their food from other sources will not be upset. We are then presented with the paradox that the high specialization of their tongues appears to have been developed for a subsidiary function.

It has been suggested that a parallel to this Zosteropid situation is afforded by the Bullfinch *Pyrrhula pyrrhula*, in that though mainly a seed-eater, its short, rounded bill — peculiar amongst the European *Fringillidae* — is adapted to take buds. However, although buds form only a minor part of the Bullfinch's food as a whole they are seasonally essential: they are "taken in late autumn and spring when seeds are least readily available; and in years when seeds are particularly scarce buds form almost the entire food from January to April" (NEWTON 1967). The difference from the *Zosterops* situation is that the minor food of Bullfinch appears to be essential for survival at a certain season. There is no evidence so far that this applies to *Zosterops* spp. and because they take a wide range of other foods, invertebrates and fruits, it is not easy to envisage a *Zosterops* population, let alone all of them, being regularly reduced to dependence on nectar for survival, whether regularly or not.

The possibility that we are wrong in accepting the specialization of the Zosteropid tongue as an adaptation for nectar cannot, however, be ruled out in view of the tongue-structure of the strictly arboreal *Parmoptila woodhousei*, about the size of a small *Zosterops*, which ranges from Ghana to the Congo basin and Angola. This monotypic genus is placed among the estrildine weavers but its tongue appears to be unique in the family. As depicted for us by A. FORBES-WATSON, its tip is narrowly cleft to about one third of the length of the tongue and both the edges and the two tips are thickly set with short fimbriae. There is no evidence that this bird eats anything but insects. For example, the stomachs of *P. w. jamesoni* examined by CHAPIN (1954) contained only insects, many of them ants. The *P. w. rubrifrons* recently collected by FORBES-WATSON (*in litt.*) on Mount Nimba had been eating ants. Here then is evidence

both for the power of convergent tongue-specialization in birds of different families and also for specialization for a long way in the direction of the Zosteropid tongue with no reason whatever to believe that the evolution in *Parmoptila* has anything to do with nectar-feeding. For the taking of small insects the efficiency of the brush tongue could be greatly increased if it were sticky, which we do not know.

The Zosteropid tongue is of course not merely bifid but quadrifid. By analogy with the honeyeaters, this strengthens the view that its specialization is for nectar-feeding. In any case, the resemblances of the tongues of the two families raise four possibilities. One is that both the white-eyes and the honeyeaters are derived from the same immediate ancestral stock, which already had a quadrifid and fimbriate tongue. If so, this feature has persisted, with little change throughout the *Zosteropidae*, but with wide variation among the *Meliphagidae*, while the two families diverged much in other respects. The second possibility is that the *Zosteropidae* derive from a Meliphagid; if so, while developing strong family characters and evolving a number of genera, their tongues show unaccountable uniformity — in *Woodfordia superciliosa* in face of the fact that the bill shows adaptation to the taking of food other than nectar. The third possibility is that the *Meliphagidae* have been derived from the *Zosteropidae*; but if so, the birds of the younger family have developed a much greater variety of tongue-structure and of other features than has the older. The fourth possibility is that the resemblance between the Zosteropid and the Meliphagid tongues is due purely to convergence. This calls for an explanation of why the Zosteropids developed so elaborate a mechanism for what is now a subsidiary feature of their lives. Was their original stock far more dependent on nectar than are the present populations? If so, why has there been a change? And why has there been no conspicuous obsolescence in tongue specialization, comparable to that in some of the *Meliphagidae* (and perhaps also in the *Dicaeidae*), in step with the preponderance of other food in the diet? A very nice evolutionary problem.

#### SUMMARY

Published statements regarding the tongues of the *Zosteropidae*, based on uncritical examination of a very small proportion of the described species, are conflicting and otherwise unsatisfactory. Examination of a wider range of material leads to the conclusion that the tongues are quadrifid and are fimbriated both at the sides and at the tip, but that any tendency to tubulation is an artefact.

A survey of feeding habits, which are very imperfectly documented, suggests that in general nectar is by no means a main component of the diet of the *Zosteropidae*. Yet *prima facie* the anatomy of the tongue is adapted to its taking. The evolutionary problem is discussed in relation to other nectivorous families. R. E. MOREAU\*, "Curlews", Sutton, St. Nicholas, Hereford, England. MRS. MARY PERRINS\*, 46 Cumnor Hill, Oxford, England. DR. J. TREVOR HUGHES, Radcliffe Hospital, Oxford, England.

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#### SAMENVATTING

De brilvogels (*Zosteropidae*) vormen een familie van kleine zangvogels, die verspreid is over tropisch en subtropisch Afrika, Azië en het Indo-Australisch gebied. Er zijn ongeveer 82 soorten, waarvan 59 tot het geslacht *Zosterops* behoren terwijl de overige 23 over 11 kleine genera verdeeld worden. Haast alle soorten hebben een ringetje van witte veertjes om het oog, waaraan zij hun Nederlandse zowel als hun wetenschappelijke naam ontleenen. In uiterlijk (vederkleed gewoonlijk geelgroen) en structuur zijn zij zeer eenvormig, en verschillende soorten zijn moeilijk van elkaar te onderscheiden.

Herhaaldelijk zijn tongen van brilvogels in de literatuur beschreven. Zulk onderzoek bleef echter tot dusver steeds incidenteel, beperkt tot slechts één, of hoogstens enkele soorten, terwijl bovendien verschillende beschrijvingen, waarop steeds weer werd teruggegrepen, onjuist zijn.

De auteurs van het hier samengevatte artikel hebben aan de hand van een

materiaal van 30 soorten behorende tot vijf geslachten, de morfologie van de tongen bestudeerd. De voor de familie typische tong (Fig. 1) is dubbel gespleten, en elk der vier slippen heeft een franje-achtig uiteinde. Sterke afwijkingen van dit type, zoals soms beschreven, zijn waarschijnlijk het gevolg van slechte conservering van de tongen, en treden in leven niet op. Ook het opgerolde of althans diep-gootvormige uiterlijk (goed te zien bij de middelste afbeelding van Fig. 1 en aan Fig. 2) is vermoedelijk een gevolg van conservering: in leven is de tong in dwarsdoorsnede vlak.

Tongen zoals beschreven, z.g. penseeltongen, worden op goede gronden geacht gespecialiseerd te zijn op voeding met nectar. Men treft ze ook aan bij de honingeters (*Meliphagidae*) en de bastaard-honingvogels (*Dicaeidae*). Op grond van de morfologie der tongen zou men dus mogen verwachten dat althans in bepaalde jaargetijden nectar een belangrijk deel uitmaakt van het voedsel der brilvogels. Van verschillende soorten brilvogels is inderdaad bekend dat zij nectar uit bloemen zuigen, maar volgens de auteurs vormt nectar toch een te gering element in het menu om de vèrgaande specialisatie van de tong daarmee te verklaren. Zij vragen zich daarom af of de penseeltong der brilvogels misschien niet aan nectaropname, maar aan een andere, nog onbekende, functie is aangepast. Zij speculeren ook over de mogelijkheid dat de penseeltong tegenwoordig geen speciale functie meer heeft, maar verklaarbaar zou zijn uit zijn afstamming van voorouders die zich met nectar voedden, en van welke ook de *Meliphagidae* zouden kunnen zijn afgeleid. (G. F. MEES)