THE ADAPTIVE MODIFICATIONS AND THE TAXONOMIC VALUE OF THE TONGUE IN BIRDS

By LEON L. GARDNER, Of the United States Army Medical Corps

Since the work of Lucas¹ there has been little systematic investigation on the tongues of birds, and with the exception of an occasional description the subject has been largely neglected. It is in the hope of reopening interest in the subject that this paper is written.

As is well known the tongue is an exceptionally variable organ in the Class Aves, as is to be expected from the fact that it is so intimately related with the birds' most important problem, that of obtaining food. For this function it must serve as a probe or spear (woodpeckers and nuthatches), a sieve (ducks), a capillary tube (sunbirds and hummers), a brush (Trichoglossidae), a rasp (vultures, hawks, and owls), as a barbed organ to hold slippery prey (penguins), as a finger (parrots and sparrows), and perhaps as a tactile organ in long-billed birds, such as sandpipers, herons, and the like.

The material upon which this paper is based is the very extensive alcoholic collection of birds in the United States National Museum. Washington, D. C., for the use of which and for his abundant aid in numberless ways I am very much indebted to Dr. Charles W. Richmond, associate curator of the Division of Birds. To Dr. Alexander Wetmore, assistant secretary in charge of the United States National Museum, I wish to express my thanks for his kind assistance in reviewing the paper and for his help in its preparation.

Part of the material is from my own collection which is now filed with the Museum and which came to me in many ways. Dr. Witmer Stone, director of the Academy of Natural Sciences of Philadelphia, furnished me with much from foreign sources for which I am greatly

¹ Lucas, F. A. The Taxonomic Value of the Tongue in Birds, The Auk, vol. 13, No. 2, April, 1896, pp. 109-115.

Lucas, F. A. The Tongues of Woodpeckers. Bulletin No. 7, U. S. Department of Agriculture, Division of Ornithology and Mammalogy.

Lucas, F. A. (1897). The Tongues of Birds. Report of U. S. National Museum, 1895, pp. 1003-1020.

No. 2591 -- PROCEEDINGS U. S. NATIONAL MUSEUM, VOL. 67. ART, 19. 43316-25----1 . . 1

indebted. J. Eugene Law, Altadena, Calif., provided me with much valuable fresh material, as did also George Willett, Los Angeles, Calif., to both of whom I wish to express my thanks.

Finally I am much indebted to Prof. Charles F. Baker, Los Banos, Philippine Islands, for his assistance, and to my wife for her aid in the preparation of the illustrations.

Before reviewing the variations undergone by the tongue a brief consideration of the histology may be of interest to throw some light on the function.

ANAS PLATYRHYNCHOS

A cross section through the anterior one-third of the tongue reveals the following: The section is very irregular in shape, with a deep groove dorsally. In the center of the tongue is the single cartilaginous and bony mass of the fused ceratohyals. Surrounding this is a complex interlacing of adipose and connective tissue, stratified skeletal muscle, blood vessels, and nerve trunks. Embedded deeply in tissue are found groups of mucous glands, ducts of which here and there can be traced to the dorsal surface of the tongue. Dorsolaterally is seen a double row of cornified spines or hairs, from the base of which strands of cells are scattered deeper into the tongue. Small nerve corpuscles are seen grouped chiefly about the cornified spines. Finally the surface of the tongue is composed of stratified epithelium through which ducts of mucous glands pass.

TYTO PRATINCOLA

The extreme tip of the tongue is composed almost entirely of cornified epithelium. Posterior to this on section the tongue is concave dorsally, the epithelium covering this surface being a relatively thin layer. The center of the tongue is occupied by the bony mass of the ceratohyals surrounded by connective tissue with interlacing fibers of striated muscle. At the mid point between the tip and posterior margin of the tongue mucous glands make their appearance, and from this point posteriorly become abundant.

The glands in this species are quite superficial, being embedded in the layer of stratified epithelium itself and opening to the surface through pores which are visible, with the unaided eye or a small lens, on gross inspection. Nerve corpuscles are either absent in this species or very infrequent.

PICA NUTTALLI

On section the tongue is concavo-convex, with the concavity representing the dorsal surface. The ventral surface is composed of cornified epithelium. The dorsal surface is covered with a deep layer of noncornified stratified epithelium. Glands in this species do not appear except at the extreme posterior portion of the tongue. Nerve corpuscles are infrequent.

CARPODACUS MEXICANUS FRONTALIS

The section is cordiform in shape. The ventral and lateral surfaces are covered with thin cornified epithelium. The dorsal surface is composed of a thick knoblike mass of stratified squamous epithelium through which no glandular ducts were seen to pass. Several large nerve trunks pass through the length of the tongue beneath the branches of the ceratohyals. Nerve corpuscles are found in the posterior end of the tongue.

It is apparent even from such a brief survey that the tongue must serve, in part in some species at least, as an accessory salivary gland. In addition tactile sense must be ascribed to it, if not even that of taste, as Botezat² suggests.

The variations found in bird tongues are very extensive and often complex.

Embryological study shows that this organ in birds is primitively a paired structure arising from the second and third visceral arches. This paired condition reflects itself in the hyoid bones, the two foremost of which, the ceratohyals, being typically unfused and embedded in the flesh of the tongue itself. Posterior to this paired position is a median unpaired tract, the basihyal. Upon this foundation are constructed all the elaborate variations to be found among the tongues of birds. Thus the tongues of woodpeckers, which at first sight seem to be constructed on a wholly different pattern than that of a robin, are, on last analysis, seen to be but an extensive modification of this rather primitive type, the ceratohyals being fused to a small spearlike tip and the basihyal greatly elongated. This is represented superficially by the small barbed sharp tip, the true tongue, while behind this is the fleshy cylindrical extensive basihyal portion often spoken of as the tongue.

As Lucas³ pointed out in his work, the tongue of a robin (fig. 1) serves as a ground pattern for many modifications. In this bird it is a slender, horny, lanceolate organ, wider and fleshier at the base than the tip and narrowing to the tip, which is translucent, cornified, somewhat split and frayed, with a tendency to curl.

Posteriorly the tongue ends in a free edge which is deeply concave, with the concavity looking caudad and armed with many sharp conical spines which are firm in texture but bend readily. Laterally,

² Botezat, E. Die sensiblen Nervenendapparate in den Hornpapillen der Vögel in Zusammenhang mit Studien zur vergleichenden Morphologie und Physiologie der Sinnesorgane, Anat. Anz., vol. 34, 1908.

Botezat, E. Die sensiblen Nervenendapparate und die Geschmacksorgane der Vögel. Vortrag, gehalten auf der 77. Vers. der Naturf. u. Aerzte in Meran 1905. Referat in den Verhandlungen der Gessellschaft.

Botezat, E. Morphologie, Physiologie und phylogenetische Bedeutung der Geschmacksorgane der Vögel. Anatomischer Anzeiger, vol. 36, 1910, pp. 428-461.

⁸ Lucas, F. A. The Tongues of Birds. Rep. U. S. Nat. Mus., 1895, pp. 1003-1020.

the tongue ends in two main branches, tipped with heavy spines many times larger than the marginal spines. In this type of tongue there is a definite line of demarcation between the fleshy body of the tongue and the translucent cornified tip which is frayed.

In studying such a tongue for factors that are constant, one is forced to conclude that beyond the general shape and appearance there is nothing that can be accepted as invariable. The number of posterior spines is inconstant within the species, although they may be counted on to be in a single row (in contradistinction to the multiple rows as seen in owls, for example).

The length depends on the amount of wear. In a series of meadowlark tongues collected in one day in South Dakota the length varies from 16 mm. to 20.5 mm. The birds were feeding almost entirely on grasshoppers that were at that time a serious pest.

The main posterolateral or heaviest spines are not invariable in arrangement; while always present they may be bifid or in birds, as some of the sparrows, where they are normally split into two, there may be three or four subdivisions.

The curling, splitting, and fraying is also variable within the species and shows individual modifications, although, as will be seen later, these characters serve as very important adaptive features and undergo extensive variations in certain families.

Bearing in mind these inconstant factors it is of interest to trace the modifications that may be found of this fundamental pattern.

With slight differences in curling, splitting, length, and arrangement of spines this tongue is to be found in a large number of passerine birds, as the warblers, vireos, thrushes, thrashers, crows, flycatchers, shrikes, wrens, bulbuls, drongos, and the like, with *Glareola* closely simulating it. The divergence from the type, however, is most marked and comes to its greatest development in the flowerfrequenting forms.

The typical tongue has an inherent tendency to curl, split, and fray, and any one or all of these tendencies may be combined to make up the tongues of the flower frequenters.

Thus splitting alone with little tendency to curl and no fraying is exemplified by the tongue of the flowerpeckers or Dicaeidae, which is deeply split, forming very slender long forked tips, two in *Dicaeum* and four in *Prionochilus*.

On the other hand marked curling is seen in the Old World sunbirds (Nectariniidae), where it may be a complete tube for the greater part of its length, without fraying of the margins of the tube and with splitting into two tips either absent or very slight. Whether the tongue be a relatively short one, as in *Hermotimia* (fig. 141), or very long as in *Arachnothera*, this perfect tubular arrangement exists in the anterior two-thirds of each. Splitting is not present in some individuals, or if present is not very deep, although *Anthreptes* is rather deeply cleft, forming two fringeless tubes.

Curling and fraying of the lateral margins is illustrated by the Drepanididae. In *Hemignathus* (fig. 19), *Himatione*, *Chlorodrepanis*, *Vestiaria*, and *Heterorhynchus* it is long and slender, curled into a complete tube, the edges of which are delicately frayed, with the tip ending in a much frayed but not bifid brush.

Finally, beginning with *Dendroica tigrina* (fig. 2), an interesting series of *split* and *frayed* tongues can be demonstrated. In this warbler the maximum of curling in the Mniotiltidae is reached, Baird ⁴ going so far even as to suggest a separate genus for it.

From this it is a near step to the curled tongues of Zosterops simplex and Z. japonica, which are described by Beddard ⁵ as being curled into almost a complete tube with a much frayed tip.

The next step can be traced through the Icteridae, where in Icterus (fig. 3) it is curled, in the anterior one-third to one-half, with elaborately frayed edges and somewhat split to form two semitubular fringed tips. The Coerebidae carry this still further. Glossoptila (Euneornis) makes no advance, with only moderate curling, splitting and fraying at the tip. Chlorophanes (fig. 4) is curled in the anterior one-half and is split and frayed, but the tongue is not yet tubular nor has it reached that stage in *Cyanerpes*. But in Diglossa and Coereba (fig. 5) it is found to have become a complete tube by the overlapping of the upcurled edges and the splitting involves the entire anterior one-half of the tongue, so that, instead of one, we find two complete tubes highly fringed and frayed. Finally this splitting has reached its maximum in the Meliphagidae, so that in Myzomela rubratra (fig. 6) it has become a completely curled tongue in the anterior half, splitting into four tubular frayed tips.

The examples might be unnecessarily multiplied. Suffice it to say that such a study brings to light a most interesting series of elaborately modified tongues, the exact correlation of diet with which offers material for future study.

Returning to the ground pattern we can see a close resemblance between it and the tongues of some of the motmots and todies (see fig. 74), in which birds it is rather flat and the thin horny translucent tip constitutes as much as one-half of the organ.

A curious little variation is seen in the titmice (see fig. 123). In these birds the cartilaginous tips of the ceratohyals project through the tip of the tongue and with two lateral projections form what has been likened to a four-tined pitchfork. The nuthatches (fig.

ART, 19

⁴ Baird, S. F. Review of American Birds, November, 1864, pp. 161-162.

⁵ Beddard, F. E. Ibis, ser. 6, No. 3, 1891, pp. 510-512, Tongue of Zosterops.

121) modify this by having six or seven tangled tips well calculated to collect small insects and spider eggs from the crevices of tree bark.

Such, in brief, is a survey of the modifications of the type pattern seen among birds. There are, however, many tongues that are apparently fashioned on other foundations. Among these are found many of the shore and water birds. Thus the tongue of a gull (fig. 28) (*Larus*) might be selected as a type. In these forms, according to Giebel,⁶ the ceratohyals tend to fuse into one bone. Superficially one sees this manifested by a rather fleshy organ which, while having a median depression or groove running the length of the tongue, still has no tendency to curl and, while often very slightly incised or frayed at the tip, is not split to any degree. Such a tongue, varying in length and breadth, is to be found in a large series of rails, sandpipers, terns, plovers, and the like.

Some interesting adaptations are to be noted especially among the fish feeders. If the tongue is edged laterally with sharp spines for one-half or more its length we would have it as seen in the petrel tribe, fulmars (fig. 25) and shearwaters; loons (fig. 23) modify the pattern by concentrating all the spines in one large sharp patch posteriorly. Finally if this process is continued so that the whole surface of the tongue is covered with retroverted spines we would have the condition as represented by the penguins.

Another ground pattern is seen among the woodpeckers (fig. 13). As has been noted the basihyal has been greatly lengthened in these birds whereas the ceratohyals are fused as a small conical tip. The true tongue then is represented by the sharp horny white tip armed with lateral, backwardly directed spines, while behind this is the long extensile wormlike basihyal portion which, when drawn back into the mouth, inverts and forms a sheath into which the rest of the organ can be retracted. This portion is covered with minute spines scarcely visible to the unaided eye, the apparent function of which is to hold the saliva, which is especially abundant in these birds. This pattern is characteristic of the family Picidae and is seen in no other forms.

An odd pattern is assumed by the Ardeidae (figs. 31-34) in which it is long, fleshy, and cylindrical, the characteristic feature being, however, the absence of sharp spines at the posterior margin of the tongue. Instead is found only a soft, fleshy flap, somewhat serrated in outline, ending laterally in large but flexible tips.

Among the Anatidae (fig. 9) again this organ assumes a characteristic appearance undergoing many interesting variations to be described later.

⁶ Giebel, C. Die Zunge der Vögel und ihr Gerüst, Zeitschr. für die Gesammten Naturwiss., vol. 11, 1858, pp. 19-53.

Hawks, owls, and vultures have powerful rasping tongues, a structure that does not seem to be based primarily on the fundamental pattern. For in most of these birds the ceratohyals, according to Giebel,⁶ are fused the greater part of their length except at about the mid point, where by reason of failure of fusion a hole is left.

Parrots display an individuality of their own. In many of these birds the tongue is broader at the tip than at the base, forming almost a finger, with the anterior margin convex. It may be flat, cupped, grooved, rolled into a tube, or even brush-tipped (figs. 70-73).

Finally, without considering the various rudimentary tongues there are a host of odd types scattered throughout the class Aves, such as the curious feathered tongues of the toucans (fig. 87); that organ as found in the puff-birds (fig. 83), the cuckoos, the flamingoes, and the like. One is constantly impressed with the fact that no reliable guess as to the tongue form can be made by the appearance or function of the bill and that any generalization is a very uncertain procedure.

The color of the tongue is interesting only in passing. Usually flesh colored, it may not be so, however, often taking the color of the bill or assuming a color of its own. Thus it is black in the crow and its allies; has brown spots in some swallows; may be entirely black with white spines in that odd cuckoo, the road-runner (*Geococcyx* californianus), or be almost entirely flesh-colored, mottled with black, in other members of the same species. It is pink in the redbilled Heermann gull (*Larus heermanni*). It is said to be scarlet in the black cockatoo. Still again a light blue is seen. Some of the hawks, as the marsh hawk (*Circus hudsonius*), have the posterior end and the spines this color.

Out of this confusing multiplicity of form it seems possible to make certain groupings as to function and adaptation. And if this is done one finds approximately eight natural groups are formed:

1. An omnivorous diet is productive of a rather generalized pattern. This includes the great majority of tongues found in the Passeriformes, as has been described. The chief adaptive feature lies in the presence of the posterior marginal spines. The tongue is capable of being depressed at the tip and elevated posteriorly. When worked rapidly backward and forward it can be used to force resistant food down the throat. The efficacy of this is most astonishingly manifest if, for instance, a bit of cloth be fed to a nestling. In such an instance it is only with difficulty that the cloth can be withdrawn from the throat without injury to the bird, so eagerly is the tongue with its spines used to resist the effort. In this group falls also the simple fleshy tongues of the gallinaceous birds (fig. 7).

2. Fish eaters, where the tongue is used to hold slippery prey. In these it is found to be plentifully supplied with sharp, stiff retrorse spines. These may be distributed over the whole surface, as in the penguins, edging the lateral margin only as in the fulmars and shearwaters (fig. 8), as a patch of stiff spines situated at the base, as in the loons, or a double row on the surface, as in mergansers (fig. 10). A distinction must be drawn between fish eaters that use the tongue and those in which the food is bolted whole, where it has lost its function and a different condition prevails.

3. A diet of a multiplicity of small things strained from the water is associated with the complex tongues of the Anatidae (fig. 9).

Typically it is roughly rectangular in shape and is thick and fleshy. The tip is composed of a cornified rounded flaplike process. Posterior to this the tongue is broad with a median groove and provided laterally with a double row of heavy hairs, the upper overhanging the lower like a thatched roof. Toward the posterior half the upper row, by a process of agmination of the hairs, becomes converted to a series of large, heavy spines, which vary in number with the different species. Coincidentally the edges of the median groove become cornified with rough, toothlike processes. Lateral to these the surface of the tongue is nodular or papillar and plentifully supplied with openings of ducts of muscous glands. The posterior portion of the tongue is made up of a fleshy eminence heavily armed with strong spines.

The method of use is interesting. The tongue is depressed, allowing water to run along the groove, it is then raised against the palate, the water squirted out from the sides through the hairy edges, straining out and leaving the solids.

Considerable variation is seen, depending on the use of this organ and the width of the bill. Thus in the geese and swans where it is used for tearing up weeds and grasses it has become a very powerful tearing structure. In *Cygnus buccinator*, for example, the edges of the median groove instead of consisting of rather rounded eminences become very sharp, long tearing spines.

A similar purpose is accomplished by *Branta nigricans* by conversion of the entire lateral row of hairs into spines; in other words, all of the lateral hairs have become agglutinated into spines, and this process extends quite to the tip.

On the other hand the red-breasted merganser (fig. 10), having taken to fish fare, has developed sharp dorsal spines and lost one row of marginal hairs, tending to approach in type the fish eaters. 4. Flesh feeders or the birds of prey, including the owls, have developed heavy rasping tongues. The anterior portion is often very rough and hard and in some forms somewhat curled as in eagles and lammergeiers. The posterior spines, which may be in a single or multiple row, are stiff and hard. Opening to the surface are ducts of many mucous glands the function of which is manifest. A curious modification of form is seen in the deep trough-shaped tongues of the vultures and the condor, which are armed with sharp marginal spines (figs. 36-43).

5. Where the food is probed for and consists largely of insects we see the structure as exemplified by woodpeckers. Lucas^{τ} has demonstrated an interesting correlation with diet. Flickers (fig. 14), having made a departure from the regular fare and having taken to an ant diet, are found to possess a blunt-tipped tongue with but two or three reduced barbs, while the extensibility is greatly increased and the whole dorsal tract (basihyal position) plentifully supplied with minute spines to hold mucous. In these birds also the submaxilliary salivary glands reach their maximum development, a combination well adapted to catch ants.

In *Melanerpes* (fig. 15), where the diet has become more generalized, it will be found that the extensibility is reduced and instead of spines at the tip there has been a conversion to vibrissae or hairlike processes.

Finally in the sapsuckers (fig. 16) the extensibility is reduced to a minimum. The dorsal tract is bare of spines except posteriorly, where it is widened into a shieldlike structure bearing papillae. At the tip and along the lateral edges there is a fine brush of hairs which serves well for capillarity but is ill adapted to spearing grubs nor are many of these found in an analysis of stomach contents.

Among this group should be classed the spearing and impaling organs of the titmice, and nuthatches, already described.

6. Seed and nut eaters have fleshy and strong tongues. In this group are to be classed those of the typical parrots (fig. 17) and finches (fig. 18). In parrots it has been described. In finches it is cylindrical or tends toward that form and slopes from base to tip. Since the ability of a bird to project the lower mandible is very limited the rolling of seeds in the act of husking would be difficult. With the inclined surface of the tongue, however, acting as a surface against which seeds may be rolled, this is actually accomplished most dexterously. In many finches for reasons not entirely understood the tongue is often scoop-shaped or even rolled into a semitubular structure, as will be illustrated later.

⁷ Lucas, F. A. The Tongues of Woodpeckers. Bull. No. 7, U. S. Dept. of Agriculture, Div. Ornith. and Mammalogy.

7. Flower frequenters (fig. 19) have most complex tongues. Among these we find the fringed split and tubular tongues of the Drepanididae, the Nectariniidae, Dicaeidae, some of the Icteridae, the Zosteropidae, and the Meliphagidae. In this group also falls the Trochilidae. Finally a most remarkable adaptation is found in the flower frequenting parrots of the family Trichoglossidae (fig. 70), where the tongue is curled at the tip and supplied with a stiff brush of vibrissae.

The correlation of such tongues with a nectar, pollen, insect, diet is easy to see. Of further interest is the fact that members of most of these families possess the ability to very greatly extend the tongue. The hyoid bones are prolonged over the occiput in the same manner as that adopted by the woodpeckers, and like the latter may even extend well down to the base of the bill.

8. Rudimentary. Finally a natural group is formed of tongues that have lost the greater part or all of their function, a condition found among many families. Thus birds that bolt their food whole have this organ often merely a little fleshy cylinder a few millimeters long and no wider. This structure prevails in many of the fish eaters, as the booby, pelican, stork, gannet, darter (fig. 20), man-of-war bird, cormorant, and the like. Again in the huge-billed hornbills we find only a small and unimportant tongue; neither is this organ very large or of much apparent use in their allies, the kingfishers, or again in many of the Caprimulgidae, in which family it is often to be found small and rather simple in structure.

It is apparent in such a review that in a large number of forms tongue structures can be correlated with some special diet and the method of its procurement as might well be expected of an organ so intimately concerned with the function of obtaining food. The exceptions, however, are numerous and present most interesting problems. For example, no special adaptation is to be noted in the tongues of gulls, rails, sandpipers, and the like unless, as it seems not at all improbable, special tactile or even taste sense is located in them. Added to these are certain odd and rather complex tongues the unusual shapes of which are difficult to explain. An instance is this organ in the fruit-eating trogons (fig. 21). It is triangular, thick, heavy, horny tipped, with a central groove bordered by distinct ridges and heavily armed posteriorly with spines. The motmots have a long slender structure, thin and horny and much frayed laterally, somewhat resembling that found in toucans (fig. 87), in which birds, again, a most curious featherlike organ is found with the frayed lateral margins directed anteriorly, the significance of which can not be evaluated at present.

In addition a most difficult problem is the explanation of variations in closely related birds where presumably the diet is very similar. Thus Lucas^{*} called attention to the variation found in the genus *Melospiza*. In *M. fasciata* a much-frayed tip is found, while in *M. lincolni* the tip is only slightly bifid and not frayed. To this may be added 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*. Still again among the warblers of the genus *Dendroica* it varies from a flat and only slightly split organ in *D. petechia* (fig. 155) and *D. fusca* (fig. 158) to a much curled split and frayed one in *D. tigrina* (fig. 2).

The taxonomic value of the tongue in birds is an interesting question which can only be answered by a systematic survey. It is evident that the most useful characters for classification are those founded on strict morphological bases and any structure highly modified in response to external stimuli is of the least value. But no one organ has ever been found that can serve as a complete basis for classification. The history of ornithology evidences many mistakes due to the use of one character alone, as witness the old group Pinnatipedes, including phalaropes, coots, and grebes, through similarity of foot structure. In considering the value of the tongue it must be recognized that it is a highly adapted organ, but this should not rule it out from all taxonomic consideration. If every structure adaptively modified be omitted no part of a bird can be used, since to a greater or less extent this includes the whole organism. Lucas,^s taking note of the adaptive modifications, gives it very little taxonomic value. There is, however, need of a systematic study of this organ in every group, with an evaluation of it in each one. While tongues are adaptively modified it may well be that these changes are constructed on a type pattern distinctive of the group to which the bird belongs and thus indications of affinity be given.

Order COLYMBIFORMES

Loons are distinguished from grebes by the fact that the tongues of the former have a large patch of spinose processes at the base, while the grebes have but a single row posteriorly. Gavia immer (fig. 23) has a relatively large patch, while this is not so prominent in the Pacific loon, Gavia pacifica (fig. 22). Podilymbus podiceps and $\pounds chmophorus$ occidentalis among the grebes have but a weak row of spines, which in the eared grebe Colymbus nigricollis californicus (fig. 24) are prominent but broad and flat.

⁸ Lucas, F. A. The Taxonomic Value of the Tongue in Birds. The Auk, vol. 13, No. 2, April, 1896, pp. 109-115.

Order SPHENISCIFORMES

The penguins so far as known have a characteristic tongue. It is rather long and pointed and the surface is entirely covered with large stiff conical retroverted spines.

Order PROCELLARIIFORMES

In this group there is considerable variation. On the whole it tends to be rather small in comparison to the bill and gape. In Bulweria bulweri it is very small, approaching rudimentary, while in Macronectes and Prion it is larger and more nearly matches the bill in size. In some genera it is well armed with spines, not only posteriorly but along the sides almost to the tip. Thus Fulmarus glacialis glupischa (fig. 25), Pterodroma hypoleuca, and Puffinus cuneatus have lateral spines for the posterior third, while Bulweria bulweri extends this to one-half and Puffinus griseus (fig. 8) and Priofinus cinereus are supplied the whole length of the tongue. This characteristic does not hold good for the entire family Procellariidae, however, since lateral spines are lacking in Halobaena coerulea and Prion desolatus. In the former one finds a rather small, cylindrical, fleshy tongue armed with a single row of very weak spines and tapering to an unsplit tip. The latter has lost most of the posterior row, so that this edge is often a smooth, rounded margin. Occasionally one finds a few inconspicuous spines buried in tissue, the value of which must be negligible.

The Hydrobatidae have very small tongues. Oceanites oceanicus and O. gracilis possess small fleshy cylinders with a weak row of spines.

Order CICONIIFORMES

This is a rather unwieldy group with tongues that vary from minute rudimentary structures to the large fleshy one of the flamingoes.

The Steganopodes are characterized without exception, so far as is known, by rudimentary tongues. In *Phalacrocorax*, *Sula*, *Pelecanus*, and *Anhinga* it is a mere toothpick of flesh. *Anhinga anhinga* (fig. 20) has a curious little tonguelike eminence on the dorsum of the cylindrical rudiment. *Phalacrocorax* has a tongue composed of two plates of cornified tissue meeting in the midline and sloping sharply like a steep roof. *Fregata minor* presents a small triangular structure which has not as yet lost all form and on the surface of which posteriorly are to be found abortive spines.

The Ardeidae have a most characteristic organ already described, the most outstanding feature of which is the soft fleshy posterior flap connected with flexible lateral "horns." So far as has been determined this is a form not approached by any other family of birds and once having been seen is so characteristic that it could not be confused with any other form, most especially with the storks with which herons have often been classed and with which they agree in feeding habits. It is long in Ardea herodias (fig. 32) and shorter in Nycticorax nycticorax naevius (fig. 31) but with the same general structure throughout, including Egretta candidissima, Casmerodius egretta, Botaurus lentiginosus (fig. 33), and Butorides virescens anthonyi (fig. 34).

Of great interest is the fact that in that odd-billed form the boat-billed night heron (*Cochlearius zeledoni*) the same structure is preserved. The tongue is very short but is constructed exactly as in the other herons, much as if the tongue of *Ardea* was cut to the length of an inch or less.

The storks (*Ciconiidae*) have rudimentary tongues, as do the Ibididae (Threskiornithidae). *Ciconia ciconia* (fig. 26) has a flat almost formless structure, while *Plegadis guarauna* has one that is very small but with some semblance of structure, as there are welldefined spines present which, however, are flexible and functionless.

The flamingoes (Phoenicopteridae) are characterized by fleshy tongues supplied on the dorsum with conical spines and posteriorly with a patch of spinose processes. These curl downward, as do the bills. Figure 11 illustrates the tongue of *Phoenicopterus ruber*.

It is interesting to note that the four suborders are readily separated by tongue form. The Steganopodes by rudimentary cylindrical ones (except *Fregata*), Ardeae by their characteristic ones, Ciconiae by flat rudimentary, and Phoenicopteri by large fleshy tongues.

Order ANSERIFORMES

The screamer (*Chauna chavaria*) of the Palamedeidae has a flat tongue with a single row of spines posteriorly not at all like the Anatidae, but resembling more that organ in the gallinaceous birds.

The Anatidae have a characteristic organ which, while modified in response to diet, is readily recognizable as distinct from all others.

Most mergansers have a long slender structure with but one row of lateral hairs, while *Mergus serrator* (fig. 10) has a double row along the entire dorsal surface.

In Branta canadensis and B. nigricans, for tearing purposes, all of the hairs of the two lateral rows have been converted into strong backwardly directed spines, one row on each side, while the dorsal surface is smooth, without the usual gutter. Such an organ is incapable of much if any sifting.

VOL. 67

Chloëphaga leucoptera has a very curious flat tongue. Anteriorly there is a single row of very weak lateral spines or hairs which a little further back develops into three heavy conical tearing "teeth." Posteriorly it ends in a patch of small spines. This is, so far as has been seen, the simplest form found in the family.

The swans have the typical structure found in the family, which is modified, however, by having heavy tearing "teeth" along the edges of the median groove. This is true of *Cygnus gibbus*, *C. buccinator*, and *C. columbianus*.

Coscoroba coscoroba has a very heavy organ, but the edges of the median groove are smooth without corrified processes.

Cereopsis novaehollandiae has a most aberrant form of tongue. Typically there is a very weak row of lateral spines, which may be entirely worn away as in the specimen illustrated (fig. 35). Posteriorly there are various fleshy processes which may be covered with weak spines, absent in the one figured however.

The number of lateral "teeth" vary throughout the family and roughly follows subfamily groups.

Thus the Fuligulinae tend to have from three to five, usually four on each side. While members of the same species may not show a constant number the variation will be found to be within these limits. This is true of *Oidemia*, *Charitonetta*, *Histrionicus*, *Arctonetta*, *Marila*, and *Erismatura jamaicensis* (fig. 29).

On the other hand the Anatinae present from 5 to as high as 12 lateral spines. This is true of *Dendrocygna*, *Anas*, *Dafila*, *Poecilonetta*, *Mareca*, *Nettion*, and *Querquedula cyanoptera* (fig. 9). *Spatula*, being a broad and long tongued form, has as many as 12 on each side.

Aix, Plectropterus, Cairina, and Dendronessa average four to the side, while typically this group is marked by an absence of cornification of the edges of the median groove.

Throughout this group there is a similarity of tongue form that makes each one recognizable as belonging to the family Anatidae. The modifications that exist are all based on a type pattern which is characterized briefly as a fleshy organ with at least one, and usually two, rows of lateral hairlike processes, a few or all of which may be agglutinated to form solid cornified toothlike projections. In these instances it is notable that dissimilarity of diet has not destroyed evidences of relationship. Conversely, similarity of diet as compared with unrelated forms outside the family has not produced similar tongues. As instance witness on the one hand the tongues of several fish eaters—mergansers, loons, and grebes—and on the other the ruddy duck with its diet closely following that of the American coot, and yet without paralleling it in tongue pattern. ART, 19

CONCERNING BIRDS' TONGUES-GARDNER

Within the family there is no reliable basis for separation on tongue form alone. The mergansers are recognizable as a separate group, as are the heavy tearing tongues of the geese and swans, and roughly the Fuligulinae may be distinguished from the Anatinae by the number of lateral "teeth." But with the exception of certain very odd types that mark special genera, as *Chloëphaga* and *Cereopsis*, or a characteristic wide tongue as in *Spatula*, there is often doubt as to what genus and subfamily a single specimen should be referred.

Order FALCONIFORMES

In this group the tongue is a heavy rasping organ. The Cathartidae and the Vulturidae have a deeply curled organ, trough-shaped, with the upcurled margins armed with strong rasping spines. These range in size from the relatively small one of the buzzard, *Cathartes aura septentrionalis* (fig. 38), to the large powerful object of the condor, *Sarcoramphus gryphus* and *Gyps fulvus*, with extreme uniformity of pattern.

In the hawks the posterior border of the tongue may consist of one row of spines or of many, and on this character they may be divided into two natural groups; that is, the Buteonidae, with a single row, and Falconidae, with many spines distributed over the basal portion, as was first suggested by Beddard.⁹

Among the Buteonidae the following genera have been found to present but a single row of spines posteriorly:

Milvus.	Accipiter (cooperi, fig. 43).
Circus (hudsonius, fig. 40).	Astur.
Leucopternis.	Elanus.
Spizaëtus.	Urospiza fasciata.
Archibuteo.	Ictinia.
Dryotriorchis.	Rupornis.
Morphnus.	Buteo.
Asturina.	B. lineatus elegans (fig. 12).
Urubitinga.	B. borealis calurus (fig. 37).
Gypohierax.	B. albicaudatus (fig. 42).

Pandion haliaëtus has a single row, but occupies a family of itself.

The following Falconidae have been found to have many spines distributed over the posterior portion of the tongue:

Tinnunculus alaudarius. Milvago chimango. Hieracidea berigora. Polyborus (plancus, fig. 41). Falco. F. sparverius phalaena (fig. 39).

⁹ Beddard, F. E. On the Modifications of Structure in the Syrinx of the Accipitres, with Remarks Upon Other Points in the Anatomy of That Group. Proc. Zool. Soc. London, 1903, vol. 2, pp. 157-163. The tongue of the lämmergeier *Gypaëtus barbatus* (fig. 36) is very much curled in the anterior third and converted into a scoop or trough-like structure.

In searching for evidences of affinity one is struck by the close similarity of the heavy, rasping, mucous gland bearing, spinose tongues of the owls, which with their multiple rows of spines, resemble the Falconidae. A connecting link to the Buteonidae indeed would seem to be shown through the hawk owl (*Surnia ulula*, fig. 44). Since other evidence does not support this appearance of relationship it is apparent that convergent evolution and similarity of diet have so altered this organ in these divergent types that little dependence may be placed on it outside of limited groups.

The Galliformes, so far as has been determined, all have fleshy tongues, varying with the length of the bill, usually somewhat grooved and provided with a single row of rather prominent posterior spines.

The hoatzin *Opisthocomus cristatus* (fig. 45) has a triangularshaped flat tongue the surface of which is set with small spinules.

Order GRUIFORMES

The Rallidae have simple fleshy tongues varying in length with the length of the bill. They are 'upcurled along the edges to form long, slender, guttered or grooved organs that are usually frayed at the tip and provided posteriorly with short and rather inconspicuous spines. They are long and slender in *Pardirallus r. rytirhynchos*, *Rallus levipes* (fig. 47), *Neocrex erythrops*, and *Hypotaenidia wakensis*, while in the coots (*Fulica americana*, fig. 53) and gallinules (*Gallinula galeata*, fig. 30, and *Ionornis martinica*, fig. 59) they are shorter and broad, and the same holds true for *Porzana carolina*. The Weka rail *Ocydromus earli* has a rather large and heavy one which anteriorly is trough shaped, the edges and tip of which are split to form stiff forwardly directed fimbriations.

Aramidae: Aramus vociferus (fig. 49) has a long slender tongue considerably split at the tip.

Psophiidae: *Psophia leucoptera* has rather prominent posterior spines. The tip is characteristically frayed and the general appearance not at all unlike that seen in rails.

Otididae: Otis tarda has a flat tongue that is heavily armed with powerful spines along the posterior edge and the lateral borders for two-thirds of the distance between base and tip. This is rather suggestive of the tearing organ seen in the geese.

Rhinochetidae: *Rhinochetus jubatus* has a long, slender tongue with weak posterior spines, very slightly grooved and ending in a cornified tip that is somewhat frayed.

Eurypygidae: Eurypyga helias (fig. 52).

Order CHARADRIIFORMES

The tongues of the Limicolae very much resemble those of the rails. They usually are commensurate in length with the bill, although in Numenius, Recurvirostra americana (fig. 50), and Mesoscolopax borealis they lie only in the floor of the mouth and do not extend far toward the tip of the bill. The last-named species has an exceedingly narrow tapering organ that in the anterior portion becomes almost threadlike and does not measure more than one-third the length of the bill. In the rails the tip was found often to be split and frayed while the sandpipers generally have a tip entire. Usually the tongue is guttered or grooved but in the genera mentioned above it tends to be flat. It may be very long as in Catoptrophorus semipalmatus inornatus, and the long-billed dowitcher (Limnodromus griseus scolopaceus, fig. 48) and less so the wandering tattler, (Heteroscelus incanus, fig. 46), while it is very short in the semipalmated plover (Charadrius semipalmatus, fig. 60).

Other variations are seen in Actitis macularia (fig. 54), Oxyechus vociferus (fig. 58), Haematopus palliatus (fig. 61), and Ereunetes pusillus (fig. 57). There is nothing unusual about this organ in Oreophilus ruficollis ruficollis, Pisobia minutilla, Crocethia leucoptera, or Squatarola squatarola. In this group, as in the hawks and owls, due to convergent evolution or to the fact that feeding habits are alike there has developed a very close resemblence to the tongues of rails and an indication of affinity when in fact it is not as real as this organ would lead to believe. So close is the appearance between the groups that given a single tongue one would often be in doubt as to its true connection.

The gulls have a rather broad fleshy tongue that is somewhat grooved and is often forked at the tip, as illustrated by *Larus heer*manni (fig. 27) and *L. occidentalis* (fig. 28). The terns have long, slender, often forked tongues (*Sterna forsteri*, fig. 56) and *S. antillarum*, fig. 55). *Gygis alba kittlitzi* has remarkable fine backwardly directed serrations for the anterior one-half of this organ.

Rynchops nigra (fig 51) has a rather short, wide tongue, somewhat scoop shaped.

Pigeons have flexible tongues that are grooved and posteriorly are supplied with soft spines that are without resistance. These are illustrated in the following figures, Zenaida vinaceorufa (fig. 65), Columba gymnophthalma (fig. 66), Histriophaps histrionica (fig. 63), and Geopelia cuneata (fig. 64), while Nesopelia galapagoensis is very similar.

43316-25----3

Order CUCULIFORMES

In the cuckoos the tongue is rather heavy, long, and well provided with spines. There may be considerable variation in length in the same species, as illustrated by that odd form *Geococcyx californianus* (figs. 67, 68), while the color may be entirely black with white spines or flesh colored with a few black spots. *Saurothera dominicensis* (fig. 69) has much fimbriated edges which are directed forward. *Coccyzus melacoryphus* has a very similar structure. *Carpococcyx radiatus* is well armed posteriorly, but the edges are not split nor is the tip.

Order PSITTACIFORMES

The parrots are characterized by considerable differences in tongue shape. In the common grass parakeet (Melopsittacus undulatus, fig. 72) it is flat and broad, while it is broad but hollowed out in Aprosmictus cyanopygius (fig. 71), Conurus auricapillus (fig. 17), and Poiocephalus senegalensis. It is tightly rolled in Calopsitta novaehollandiae (fig 73), while, as is well known, it is brush tipped in the Trichoglossidae, as illustrated by Psitteuteles chlorolepidota (fig. 70), Glossopsitta, Hypocharmosyna, and Trichoglossus, and in which group the tongue is used as the main taxonomic feature.

Order CORACIIFORMES

Coracias caudata has a lingual structure very similar to that of a robin, with a horny split tip. It is not commensurate in size with the heavy bill, while posteriorly there are very few spines.

Eurystomus. In this large heavy-billed form the tongue is wide and flat, the anterior one-half is horny and frayed, while at the back there are three to four large heavy spines on each side.

The motmots have flat, heavy tongues that are considerably frayed laterally with laciniae that are directed forward. In *Eumomotus* superciliaris this is carried to such a degree that it strongly suggests the feathered structure seen in the toucans. *Momotus caerulei*ceps is not unlike the tongue of *Saurothera* in its general appearance.

The todies have the anterior half thin, horny, and translucent, but the edges are merely roughened and irregular and not deeply incised. *Todus multicolor* (fig. 74) is illustrative.

In kingfishers (Alcedinidae) this organ has become rudimentary. In Ceryle alcyon (fig. 75) it is flat without the posterior row of spines although Ceryle rudis may show a few. The large billed Pelargopsis (Ramphalcyon) has a structure very similar to Ceryle with the exception that the tip is either square or even somewhat indented while the whole organ is quite rudimentary. There is no suggestion of affinity between these forms and the motmots.

The hornbills (Bucerotidae) also have rudimentary tongues, although they are not without form. Thus in *Lophoceros melanoleucus* (fig. 84) it is flat, slender, and square tipped, while in the huge billed *Hydrocorax mindanensis* it is rather triangular, fleshy and supplied with a few small spines, and this is true also for *Dichoceros bicornis*.

Upupidae: The hoopoes have exceptionally small rudimentary tongues which are reduced to a mere triangle of flesh without form or function.

Such a review shows that a wide range of variation is seen in the suborder Coraciae, with few indications of affinity shown and in many forms a rudimentary structure through loss of function.

The suborder Striges have tongues very closely resembling those of hawks, a suggestion of affinity that is misleading.

They are horny tipped and well beset with papillae, while mucous gland pores are abundant, an appearance much like that of the Falconidae and due either to convergent evolution or to the raptorial diet. There is usually a certain degree of curling and the tip is often somewhat incised. As examples are shown *Tyto pratincola* (fig. 78), *Speotyto cunicularia hypugaea* (fig. 76), *Otus asio bendirei* (fig. 79), *Spiloglaux novae zealandiae* (fig. 80), and *Asio wilsonianus* (fig. 77). The hawk owl (*Surnia ulula*, fig. 44) has but one row of spines posteriorly, the reason for which is not apparent. The horned owl (*Bubo virginianus*) has a broad, flat tongue well covered with spines.

Suborder CAPRIMULGI

In this group, Wetmore ¹⁰ finds four main types of tongues. First that of *Nyctibius*, which he describes as "small in proportion to the mouth cavity as in other Caprimulgi. In form it differs considerably from the tongues of related genera. The tip of the tongue in *Nyctibius* is somewhat elongate, with the lateral outlines at first concave. The postero-lateral margins are produced as elongate points that equal the anterior portion in length. The outline of the lateral margin of these is convex. In general the form of the tongue is that of the head of a spear point, with a deeply incised base, spreading posterior angles, and slender point." He finds the lateral margin supplied with spines and a few minute spines on the upper surface.

Podargus is described as having an elongate tongue, being "much larger in proportion to the size of the mouth cavity than in other

¹⁰ Wetmore, A. On the Anatomy of Nyctibius, with Notes on Allied Birds. Proc. U. S. Nat. Mus., vol. 54, pp. 577-586, 1918.

forms examined. The anterior end of the hyoidean apparatus forms a thickened, pointed projection in the tongue base. * * * Anterior to this strong base the tongue is thin and translucent, being not much thicker than a sheet of ordinary writing paper."

Steatornis caripensis shows a "tongue shaped like an arrowhead, with rather elongate, bluntly pointed tip, convex lateral outlines, and spreading, somewhat slender posterior processes that project beyond the hinder border. The margins of these posterior processes are armed with soft, slender, backward projecting papillae, and smaller papillae of the same nature are found on the upper surface of these projections."

The tongue of *Phalaenoptilus nitidus* "is small, measuring 9.5 mm. long by 3 mm. broad. The postero-lateral spinose processes are elongate and pointed. The lateral margins in outline are approximately straight lines. Spinose backward projecting papillae begin at a point anterior to the center and become stronger and heavier toward the base of the tongue. The upper surface of the tongue for its basal two-thirds is thickly set with small horny papillosities all projecting backward. Because of the posterior elongation of the lateral processes, the basal margin appears deeply incised."

This is the general form of the remaining genera of the Caprimulgidae. The tongue of Chordeiles virginianus is described as showing a "slightly different development. This organ in the nighthawk is small in comparison to the size of the mouth opening, but is strong and heavy. It measures approximately 9 mm. long by 4.7 mm. broad at the base, so that it is short and broad in comparison with the lingual appendages of other genera in this family that have been described. * * * In outline the tongue of Chordeiles virginianus is triangular with the lateral margins slightly concave. * * * The lateral margins of the tongue are armed with spinose papillae which are small and weak anteriorly and become strong and heavy toward the base. Stronger processes arm the posterior margin, and the broadened basal third of the tongue has its dorsal surface covered with pointed harsh papillosities all directed toward the pharynx." With this description the tongue of Chordeiles acutipennis texensis (fig. 81) agrees, with the exception that there are no papillosities on the dorsal surface.

The tongues of Nyctidromus albicollis, Caprimulgus europaeus, and Setochalcis vocifera are described by Wetmore as resembling in form that of Phalaenoptilus nitidus, while that of Chordeiles acutipennis is like that of C. virginianus.

It can thus be seen that there are considerable differences manifested in this group not easy of explanation and which do not give any important information as to affinities.

The Cypselidae do not show any striking tongue characters. In some forms there is a close resemblance to tongues of swallows, as Lucas¹¹ pointed out in the case of *Collocalia* (fig. 85, after Lucas) while others have a longer, more slender tongue somewhat curled as in the tree swift *Macropteryx coronata* (fig. 82).

The humming birds (Trochilidae), however, have most characteristic tongues, which are distinct from any others in the class of Birds. The cartilaginous portions of the ceratohyals are divided in the anterior half of the tongue to form separate shafts. These are invested with a membranous covering which is expanded as a lateral flange at the tip, but which inrolls as the base of the tongue is approached to form a rolled membranous tube on each side. (See fig. 86, *Calypte anna*.)

It is not composed of parallel muscular tubes, as has often been described, for the cartilaginous shafts of the tongue are solid; but it is the inrolled fringe of membrane along the lateral margins of these shafts that make up the capillary tubes. This is an entirely different condition than prevails in the passerine flower frequenters where two or more muscular tubes are formed by splitting and curling of the body of the tongue itself.

It is very elastic in the humming birds and capable of great protrusion, the hyoid apparatus also being especially long to permit of this action.

This is a most characteristic organ which readily identifies any bird possessing it as a member of this family, and while markedly modified in response to flower-feeding habits is nevertheless distinctive of the group and hence of taxonomic value.

The trogons have flat, heavy tongues supplied with numerous spines and with a cornified tip. There is a central groove bordered by raised margins, a condition most unusual and not seen elsewhere, except in members of the next group. (*Pyrotrogon neglectus*, fig. 21.)

The puff-birds (Bucconidae) have odd flat tongues that about the center widen to form prominent shoulders, gradually narrowing from this point anteriorly to a blunt tip. The surface is flat except in the anterior third, where a groove is seen, the margins of which are raised forming parallel prominent ridges on the surface. This is well illustrated by *Bucco bicinctus* (fig. 83) and is also seen in *Notharchus dysoni* and *Nystalus maculatus striatipectus*. These are very unusual appearing structures the exact functions of which are not known.

The Ramphastidae are characterized by exceptionally odd feathered tongues which are long and narrow and with deeply incised lateral margins forming anteriorly directed laminae. The fleshy hyoidean portion forms but a small part of the tongue posteriorly while anterior to this it becomes thin, horny, and translucent. This

ART, 19

¹¹ The Auk, vol. 13, pp. 109-115, April, 1896.

change is marked by the dotted line on figure 87, of the tongue of *Pteroglossus frantzii*. This is so striking and characteristic an appearance that it would seem useful for taxonomic purposes.

The Picidae possess a tongue so distinctive of the group, that while modified in response to diet, it could in no way be confused with that of any other family. Even the odd little piculet *Picumnus*, with its rounded tail so unlike that of woodpeckers, has a tongue which, except for its small size, is perfectly typical of the group as exemplified by *Dryobates*. This is the more interesting since the diet of so small a bird must much more nearly approximate that of the creepers, titmice, and nuthatches than of its larger allies and yet the tongue remains in all respects truly that of a woodpecker.

Typically the tongue is very extensile and the tip is armed with six or seven sharp backwardly directed barbs. This is found in Dryobates villosus hyloscopus (fig. 88), Dryobates nuttalli (fig. 89), Picus, Gecinus, Xenopicus albolarvatus (fig. 13), Geocolaptes, Dendrocopus, Centurus, Chryserpes, Micropternus, Dyctiopicus, and Yungipicus. Picoides americanus dorsalis has a rather small tongue for so large a bird, while the barbs at the tip are delicate. Veniliornis cecilii has a small tongue with but a few barbs and the same is true for Nesoctites micromegas. It is also surprising to note that the very large Phloeotomus pileatus, with its large, heavy bill, has an astonishingly small tongue in comparison with the rest of the body. The tip is very short and small and is armed with but four or five barbs.

Colaptes cafer collaris (fig. 14) has the most extensible tongue, but it is not so well accommodated for impaling objects as the tip is not as sharp, nor are the barbs prominent, being reduced to but two or three.

Melanerpes (formicivorus bairdi, fig. 15) has converted the barbs to hairlike processes and Sphyrapicus (thyroideus, fig. 16) has extended this process for the greater part of the length of the tongue, while the ability to project this organ is much reduced.

The wrynecks or Jyngidae are distinguished from the other members of the family by the fact that while the tongue is long, wormlike, and extensile, the sharp tip is not supplied with barbs. In this group they are lost, and the tip while sharp, is smooth.

It is interesting to note that in these birds as in the piculets the tail is soft without spiny shafts, which is misleading from a taxonomic standpoint, and that thus in both of these groups the tongue is a better guide to relationship.

Furthermore the Dendrocolaptinae possess stiff spiny tails which would mislead one in the conclusion that they are allied to woodpeckers when no relationship exists; whereas, in spite of the fact that feeding habits are similar to the latter, the tongues are wholly unlike and therefore yield more reliable evidence.

In this family the tongue fulfils all the requirements for taxonomic use in that differences in feeding habits in related forms have not altered the fundamental pattern in the group, so that the tongue alone is sufficient in all instances to refer its owner to the family and in many instances to the correct subfamily and even genus. Conversely, similar feeding habits in unrelated forms (Dendrocolaptinae) have not produced tongues like these, and this is the more striking since the tail, in response to such habits, has taken on the spiny character so common to that of woodpeckers.

Order PASSERIFORMES

In this heterogeneous group where so much variability is found in all of the anatomy it is not surprising to find the tongue taking part in this diversity in form. A brief survey of this has already been given in an earlier part of this paper; it remains to classify and group such differences.

In many families the thin horny tongue, slightly curled and frayed at the tip, as described for the robin, is found with but slight differences in length and width. Such a tongue has no outstanding character sufficient to identify the particular family to which it belongs and serves to do no more than to indicate a member of the order. As example *Pitta erythrogaster* (fig. 90) is illustrative.

The flycatchers (Tyrannidae) have tongues which are often broadened at the middle, somewhat curled, incised at the tip and often slightly frayed. As examples, are *Myiochanes richardsoni* (fig. 91), *Pyrocephalus rubinus mexicanus* (fig. 92), Sayornis sayus (fig. 93), and S. nigricans (fig. 94), Nuttallornis borealis (fig. 95), Empidonax griseus (fig. 96), Tyrannus verticalis (fig. 97), and Tolmarchus gabbi (fig. 98). The tongue of Culicivora stenura is very similar to these forms as is that of Muscisaxicola maculirostris. See figure 99 which illustrates Myiarchus dominicensis.

There is nothing remarkable about the organ in *Pachyramphus* viridis viridis.

The South American bell bird, *Chasmorhinchus*, has a rather simple flat tongue that is slaty black, matching the gape in color. The postero-lateral branches are long armed with slender spines while the tip is slightly incised and the whole organ is comparatively small in relation to the size of the mouth.

The Dendrocolaptidae are interesting in that the feeding habits of many of them are similar to woodpeckers without developing tongues like the latter. In most of these the anterior two-thirds or more of the tongue is thin, horny, and translucent, and somewhat

ART., 19

frayed, while the whole organ is of good length in proportion to the length of the bill. This is true of *Dendrocolaptes picumnus* and several species of *Picolaptes*. But one specimen of *Drymornis bridgesi* was available and in an excellent state of preservation. In this bird the tongue was exceptionally small, out of all proportion to the huge sickle bill and not at all like the above-mentioned genera. The appearance was much as if the horny anterior end of the tongue was either absent or had been shed. Whether this is an accidental or natural state is not known. Figure 100 illustrates the tongue of *Furnarius agnatus*, which is somewhat fleshier than ordinary and is not supplied with so great a proportion of horny tip. This is true also of *Cinclodes*. Figure 101 illustrates *Sittasomus*, species. (?)

The Formicariidae have thin horny tongues that are frayed somewhat more than the ordinary, extending well back along the sides, as exemplified by that of *Gymnocichla nudiceps* (fig. 102). *Thamnophilus bridgesi* (fig. 103) shows much the same structure.

Figure 104 illustrates the tongue of *Oligura superciliaris*, one of the Timaliidae.

Among the Pycnonotidae, *Pycnonotus* shows a simple flat tongue that is bifid but not frayed, while *Iole philippinensis* has one somewhat curled and both forked and frayed at the tip.

There is little to characterize the Muscicapidae, as the tongues seen are with minor variations much like the standard pattern.

The thrushes and their allies depart from the usual structure by the addition of papillosities on the dorsal surface of the tongue around the basal portion. This is exemplified by *Hylocichla guttata* (fig. 106), *Myadestes townsendi* (fig. 105), *Mimus polyglottos leucopterus* (fig. 107), and *Sialia mexicana* (fig. 108).

Polioptila caerulea obscura (fig. 116) does not have this arrangement, but is supplied with only a single posterior row while the tip is considerably frayed.

Cinclus mexicanus (fig. 110), of the family Cinclidae, has a simple rather fleshy tongue slightly curled and frayed.

The wrens, Troglodytidae, are marked by very thin, horny, translucent, long tongues through which the contained bones are plainly visible. The posterior spines are prominent and needlelike, while the main postero-lateral projections consist of prominent rounded horny spines; an apperance that is quite characteristic, and is not lacking even in that nonwrenlike form *Heleodytes brunneicapillus* couesi. Figures 112 and 111 represent this organ as seen in *Catherpes* mexicanus punctulatus and Thryomanes bewicki charienturus, respectively.

Chamaea fasciata has a trough-shaped square-tipped tongue well supplied with entangling hairlike processes very suggestive of that **ART. 19**

seen in the nuthatches. The tract between the base of the tongue and the glottis has many pores of mucous glands.

Swallows have a simple flat tongue somewhat split at the tip, as illustrated by *Pctrochelidon lunifrons* (fig. 115), and very similar in appearance to Collocalia (fig. 85, after Lucas).

The "cuckoo-shrikes" (Campephagidae) have tongues of the standard pattern, with perhaps more fraying than usual. At least this is true of *Pericrocotus exsul* and *Malindangia maegregori*. *Lalage niger* shows very fine lateral fraying, while *Graucalus* has much the same appearence, the tongue, however, not matching in size the large bill.

In the drongos (Dicruridae) this fraying becomes in some forms very elaborate. Thus, in *Chibia hottentotta*, the tongue is deeply split and the sides are incised. forming long, delieate, forwardpointing hairlike fringes, the delicate strands of which are very uniform in size and length. This is only slightly less marked in *Dicrurus longicaudatus* while in *Bhringa remifer* the processes are very short and delicate. *Dissemurus paradiseus* is much the same, while *Bhuchanga longa* has considerably less fraying.

Some of the Bombycillidae have simple flat tongues (*Bombycilla*), in appearence much like those of swallows, while *Dulus dominicus* (fig. 117) has a much curled tip, which is frayed.

The shrikes are an ill-defined group, Laniidae. There is little characteristic about the tongue. That of *Strepera graculina* is illustrated in figure 133, while *Lanius ludovicianus gambelii* is illustrated in figure 114.

The vireos have simple flat tongues, as represented in figure 119. *Vireo*, species from Tortuga Island, *Lawrencia nana* (fig. 118), and by figure 120, *Vireo belli pusillus*.

The Sittidae as well as the Paridae have impaling organs through the ends of which the cartilaginous tips of the ceratohyals often project. This is illustrated in figure 121, *Sitta carolinesis aculeata*, and figure 122, *Sitta pygmaca*. The titmice and chickadees have four-pronged tongues. See figure 124, *Baeolophus inormatus*, and figure 123. *Penthestes gambeli baileyae*.

The verdin, Auriparus flaviceps (fig. 126), and the bush-tit. *Psaltriparus minimus californicus* (fig. 125), have very irregular lacerated tips, while *Certhia familiaris zelotes* (fig. 113) is not far removed.

The Corvidae have a tongue the anterior third of which is composed of thin, translucent, horny tissue which is often rather deeply incised and is whipped out. The main postero-lateral spines are bifid or double, while over the surface around this region there are many small papillosities. As examples are *Aphelocoma californica* (fig. 128), *Cyanocitta stelleri frontalis* (fig. 130). *Nucifraga colum*-

43316 - 25 - 4

biana (fig. 132), and *Pica nuttalli* (fig. 129). The entire appearance is very characteristic.

The tongues of some of the Sturnidae are of the standard pattern as exemplified by *Scissirostrum dubium* (fig. 131), while *Lamprocorax chalybea* and *L. metallicus* are very similar.

The tongues of the next six families are some of the most elaborate and marvelous throughout the Class of Birds.

The Dicaeidae have small tongues that are flat posteriorly but at about the middle become abruptly narrower and begin to curl into a semitube which is deeply cleft at the tip, the margins of which are smooth, forming two slender semitubular tips. This is found in *Dicaeum cruentatum*, *D. sanguinolentum*, *D. flammeum*, and *D. celebicum*. In *Acmonorhynchus aureolimbatus* the same holds true except that the edges of each tube show a slight notching, with an attempt at the production of four tips, while in *Prionochilus* these notches have deepened to actual splitting with the formation of four semitubular fringeless projections.

The tongue of *Dicaeum trigonostigma* as figured by Gadow¹² shows a complete tubular arrangement by overlapping of the upcurled edges, which are not frayed. The tip is deeply bifurcated, forming two equal tubes, and the tip of each one of these again is cleft, forming a quadruple tongue.

The Zosteropidae.—As to this family some are simple in structure, being rather flat with only a slight tendency to curling, while the tip is deeply slit. Gadow¹³ finds this true of Z. simpler. Z. atrifrons (fig. 135) shows some fraying of the margins, which is true also of Z. sarasinorum. This may be carried to the point where, with curling added to the process, elaborate curled split and fimbriated tongues are found as described of Z. simplex and Z. juponica by Beddard.¹⁴

The Nectariniidae.—In this family curling is the outstanding feature, so that the anterior one-half to two-thirds is a completely rolled tube the upcurled margins of which are overlapped and are not fringed or frayed. In some species there is some forking at the tip to form two tubular projections.

Arachnechthra asiatica has a very long tube for the anterior twothirds, without splitting or fraying. Arachnothera, species (?) has a very long tube slightly frayed at the tip. Cinnyris (Cyrtostomus) pectoralis and C. jugularis woodi have slender tubes, both somewhat forked at the tip. Hermotimia, species (?) (fig. 141) shows the same arrangement.

¹² Gadow, H. Structure of Certain Hawaiian Birds. The Birds of the Sandwich Islands, Wilson and Evans, London, 1890-99, pp. 219-241.

¹³ Gadow, H. Proc. Zool. Soc., London, 1883, p. 63.

¹⁾ Beddard, F. E. Ibis, ser. 6, No. 3, 1891, pp. 510–512.

Cyanomitra verticalis has a long slender tongue, longer than the bill, completely tubular, and somewhat forked, and this is true also for *Chalcomitra fuliginosa* and *Aethopyga boltoni*. In *Anthreptes fraseri*, *malaccensis*, and *wiglesworthi*, the bifurcation is more marked than in any of the others, so that practically a double tongue is formed.

On the other hand the tongue of *Chalcoparia phoenicotis* (fig. 139) is not at all like the above, and this fact together with other evidence has led Oates¹⁵ to separate this species from the family. In view of the fact that there is such a regularity of tongue form in this family the divergence from it as seen in *Chalcoparia* may well have the significance that Oates gives it.

The Drepanididae typically have tubular tongues. These are formed as are all tubular ones by an upcurling of the margins of the horny anterior part which constitutes the major portion of the tongue in these birds. The edges of the dorsally rolled sides meet in the midline and finally overlap. As the tip is approached the edges become broken up and split, forming delicate laciniae. At first one side completely overlaps the other but as these fimbriations become more prominent they interlace in a complex manner finally forming at the tip a whipped-out brush.

This is the fully developed tongue and is well illustrated in the long-billed *Hemignathus procerus* (fig. 19). This same appearance is seen also in *Vestiaria coccinea*. *Chlorodrepanis*, and *Himatione sanguinea*, all of these, however, being shorter than the above. In *Heterorhynchus wilsoni* it is completely tubular only in the anterior third and is bifurcated.

Loxioides bailleui, which Doctor Gadow¹⁶ first classed among the Fringillidae, is described by him as follows. The tongue is

Thick and fleshy, much shorter than the bill, very slightly protractile, tip rounded off and ending in a neat horny scoop, which is formed by the lower horny covering of the tongue projecting a little; the brim of this scoop is slightly frayed out, as is the case in many Fringillidae.

Oreomyza (Oreomystis) bairdi he describes as:

A little shorter than the bill, thin and horny but at first sight apparently different from that of the Drepanid'dae. However, the lateral horny margins are raised up dorsally and frayed out. The distal fourth of the tongue is slightly split into a right and left half but far less than in *Coereba*. This broader, shorter, and decidedly less tubular tongue is in conformity with the slightly broader bill.

Loxops coccinea he describes as "short, in conformity with the bill, but ending in a frayed-out single brush, which, like the whole

ART, 19

¹⁵ Fauna of British India. E. W. Oates. Birds, vol. 2, p. 372.

¹⁶ Gadow, H. Structures of Certain Hawaiian Birds. The Birds of the Sandwich Islands, Wilson and Evans, London, 1890-99, pp. 219-241.

organ, is formed exactly like that of the other Drepanididae." The tongue of *Hcmignathus olivaceus* is "short and less tubular, being intermediate in structure and appearance between those of *Himatione* and *Vestiaria*.

Psittirostra psittacea (fig. 140) has a flat, fleshy tongue in which the long, horny curled portion is absent. The tip is blunt and not frayed. The appearance is almost exactly as if the tubular portion of the tongue of *Hemignathus procerus* had been cut away leaving the basal uncurled portion.

An entirely different arrangement is seen in the finchlike *Telespyza cantans*, however (fig. 136). Here the entire tongue is thick and fleshy, much as in some of the finches (compare *Passerculus rostratus*, fig. 137), with an uprolling of the thick margins to form a fleshy rolled tubular tongue not at all the same in appearance or arrangement as the tubular tongues of the foregoing forms, made up, as they are, by a prolongation and curling of the natural thin horny tip of the standard tongue.

It is apparent, therefore, that in this family there is a wide range in tongue forms, from which no reliable evidence as to relationship is to be drawn, as is evidenced by the error made by Doctor Gadow in the case of *Loxioides*.

The Coerebidae have tongues that are curled, split, and frayed, but not all to the same degree, and a fine series of modifications can be traced through this family. Thus in *Glossoptila (Euneornis)* campestris the tongue is practically flat in the posterior two-thirds. The anterior third shows a moderate upcurling of the lateral margins, with delicate fraying into a fringe that rolls inward but does not meet the opposite side. The tip is bifid, thus converting this portion into two very imperfect semitubular fringed projections. *Cyanerpes cyanea* (fig. 138) has the anterior one-half curled in much the same manner, while the tip may or may not be bifurcated.

Cyanerpes lucidus shows very little fraying of the margins of the tube, while *C. caeruleus* is deeply cleft and frayed. In *Chlorophanes spizu* (fig. 4) the tube is becoming more perfect by a close approximation of the upcurled edges. Finally in *Coereba bananivora* (fig. 5) the edges completely overlap, forming a true tube which by splitting becomes double tubes, the curling margins of which are much frayed. This same appearance is seen in *Coereba portoricensis* and *Diglossa plumbea*, the latter of which shows a surprisingly long tongue in comparison to the short bill.

The Meliphagidae have elongate quadruple tongues. The curled tongue first splits into a right and left half with marked fraying of the edges, forming two fringed tubes, and these are again deeply split and frayed, so that four elaborately frayed brushy tips are formed. The whole organ is as long or longer than the bill.

VOL. 67

The appearance is illustrated by Myzomela rubratra (fig. 6), and the same appearance is seen in M. nigriventris and M. sanguinolenta. Whether the bird and tongue be a large one, as Tropidorhynchus and Microphilemon, or of moderate size, as Meliphaga (Ptilotis) carunculata, there is a surprising conformity to the pattern described. This same long quadruple tongue is present also in Meliornis australasiana, Acanthorhynchus tenuirostris, Myzantha garrula, and Acrulocercus braccatus.

So far as is known this extraordinary quadruple brushy tongue is limited to and characteristic of this family. It is an interesting fact that the formation of the multiple tubular and brushed tongues of these several families of flower-frequenting birds follows different lines of development using one or more of the fundamental tendencies of the type tongue to curl, split, and fray. Thus, as has been demonstrated, the Nectariniidae have almost purely *tubular* tongues, the Drepanididae *tubular* tongues with *frayed margins*, the Coerebidae combine *curling*, *splitting*, and *fraying*, to form double tubes, while the Meliphagidae carry this to the degree that *four curled brushy tips* are formed.

Among the Mniotiltidae there is a rather wide range of variation. As is the case with the type pattern these are tipped with horny thin translucent tissue which may form nearly one-half of the organ (see fig. 142, Dendroica dominica) or may be absent, which was the case in a second specimen of the same species and is also illustrated by Vermivora celata lutescens (fig. 143) and Dendroica petechia gundlachi (fig. 144). The tongue may be a thin, flat structure as in Catharopeza bishopi (fig. 145), Dendroica occidentalis (fig. 146), and Dendroica palmarum (fig. 147), or curled at the tip as in Granatellus francescae (fig. 148), by upcurling of the fraying margins a process which is carried to its greatest extreme in this family by Dendroica tigrina (fig. 2). There may be rather marked differences in shape as is evidenced by a tongue of Wilsonia canadensis (fig. 149), which is very broad at the middle, while others from the same species showed this to a lesser degree or not at all. Certhidea salvini (fig. 150) has a rather thick fleshy tongue, grooved shallowly and rather suggestive of the fringilline type.

There is thus in this group considerable variation even in such a small series as in the one genus Dendroica, as may be observed by the following figures: *D. nigrescens* (fig. 151), *D. auduboni* (fig. 152), *D. vigorsii* (fig. 153), *D. discolor* (fig. 154), *D. petechia* (fig. 155), *D. striata* (fig. 156), *D. castanea* (fig. 157), *D. fusca* (fig. 158), and *D. virens* (fig. 159). Other members of this family are *Teretistris fernandinae* (fig. 160), *T. fornsi* (fig. 161), *Wilsonia citrina* (fig. 162), *Wilsonia pileolata pileolata* (fig. 163), *Vermivora luciae* (fig. 164), *Compsothlypis americana* (fig. 165), *Oporornis tolmiei* (fig.

166), Helmitherus vermivorus (fig. 169), Icteria virens (fig. 168), and Oreothlypis gutturalis (fig. 167).

Family Tanagridae.—In some of this group the tongue is flat and thin, as in *Tachyphonus* (fig. 170) and in *Tanagra (Euphonia)* violacea (fig. 171). In others it is fleshy, as in *Thraupis darwini* (fig. 172), Stephanophorus leucocephalus (fig. 173), and Ramphocelus brasilius (fig. 174), while in the very large billed Pitylus grossus (fig. 175) the tongue is cylindrical and fleshy while the anterior half is hollowed out and scoop-shaped, very suggestive of some of the finches. *Phaenicophilus poliocephalus* has a longer tongue (fig. 177), which is considerably frayed at the tip.

The Ploceidae have a structure very similar to the finches, with a cylindrical fleshy tongue having a depression anteriorly to form a scoop. This is illustrated by *Munia punctulata* (fig. 178). The horny under surface is often folded over the dorsum to form a grooved tongue as in some of the finches and as is illustrated by *Steganura paradisea* (fig. 179). This is seen also in *Ploceus megarhynchus*, *P. benyalensis*. and a species of *Foudia* from St. Helena Island.

The Icteridae, as typified by *Icterus cucullatus nelsoni* (fig. 180), and *Icterus icterus* (fig. 3), have upcurled frayed margins to the tongue which may be deeply split to form double frayed semitubular tips. This is found also in *I. parisorum*, *I. wagleri*, *I. bullocki*, *I. mesomelas*, and *I. northropi*, all of which have tongues very suggestive of the Coerebidae with less advanced degrees of curling.

The blackbirds, as exemplified by *Molothrus atronitens* (fig. 181), have upcurled margins without fraying, forming a guttered organ with the tip somewhat whipped out. This is seen in *Agelaius phoeniceus*, *A. tricolor*, *Molothrus ater*, and *Dolichonyx oryzivorus*. *Gymnostinops montezumae* has little curling; the tip is bifurcated and frayed, while *Megaquiscalus major macrourus* has a bifid curled and much frayed organ, much like *Icterus*. *Pseudoleistes* (fig. 182) has a thin tongue somewhat curled and whipped out at the tip.

The Fringillidae have cylindrical fleshy tongues, which show much variation. Ordinarily the horny under surface projects beyond the tip, and this is often frayed and somewhat curled so that a small scoop-shaped end is formed. This same horny under surface invests the lateral margins of the tongue and often curls over the dorsal surface as indicated in *Loxia leucoptera* (fig. 185). The tongue may have long posterior branches as in the odd form assumed by *Passer domesticus* (fig. 183), or, as is usually the case, they are closely compressed to the basihyal portion. It may have simply a flat surface, as indicated in *Oberholseria chlorura* (fig. 186), or there may be a deep groove formed as in *Zamelodia melanocephala* (fig. 191). In the genus *Passerculus* the grooving is very marked so that in some of the species a rolled or tubular tongue is formed (see fig. 137 *Passerculus rostratus*).

In conclusion it is obvious that the tongues of birds subserve many different uses, a wide range of function that is paralleled by changes in form, ranging from simple rudimentary nodules of flesh to the highly complex multiple tongues of the flower-frequenting birds. Furthermore, when classified as to adaptations, eight natural groups are formed, to which many of these differing patterns may be assigned.

The type pattern of tongue is composed of a fleshy basal part which is tipped with a more or less extensive thin horny translucent anterior portion, which has an inherent tendency to curl, bifurcate, and fray laterally. One or all of these tendencies are utilized to produce many adaptive modifications, a fine series of which may be traced through the flower-frequenting birds, where they undergo the greatest development, producing elaborate and complex tubular, brushy, and multiple tongues.

Fundamentally the tongue is a paired structure arising, as it does, from the second and third visceral arches, and upon this foundation must be constructed all the variations seen. Practically, however, in the fully developed organ the alterations have become so great, through fusion of some parts and suppression or exaggeration of others, that it is not possible to select a fundamental pattern from which all others may be derived, but, instead, many of these must be recognized.

With regard to the taxonomic value of this organ in birds the evidence is conflicting. Much of it tends to support the conclusion that it is of little or no value, since, either from similarity of diet or due to convergent evolution, appearances of affinity are formed where no true relationship exists. Furthermore, differences in structure are seen in closely allied birds where presumably the diet is the same.

On the other hand, in many families, in spite of changes in response to diet a uniform and characteristic pattern is traceable which gives definite indications of affinity and provides valuable taxonomic features. Among the groups in which this is true are the Ardeidae, Phoenicopteridae, Anatidae, Picidae, Trichoglossidae, Buteonidae, Falconidae, Trochilidae, and possibly the Meliphagidae, Bucconidae, Ramphastidae, Corvidae, and Nectariniidae. To these with more study, others may be added.

BIBLIOGRAPHY

BAIRD, S. F.

1864, November. Review of American Birds, pp. 161-2.

BATH, W.

1906. Die Geschmacksorgane der Vögel and Krokodile. Arch. Brontologie, vol. 1, pp. 1-47.

BEDDARD, F. E.

- 1891. On the Tongue of Zosterops, Ibis, ser. 6, no. 3, p. 510.
- 1898. Note on the tongue of *Podargus*. Structure and Classification of Birds, p. 234.
- 1903. On the Modifications of Structure in the Syrinx of the Accipitres, with Remarks Upon Other Points in the Anatomy of That Group. Proc. Zool. Soc. London, 1903, vol. 2, pp. 157–163.
- 1903. A Note Upon the Tongue and Windpipe of the American Vultures, with Remarks on the Interrelation of the Genera Sarcorhamphus, Gypagus and Cathartes. Proc. Zool. Soc. London, 1903, vol. 2, pp. 386-392.

BOTEZAT E.

1910. Morphologie, Physiologie und Phylogenetische Bedeutung der Geschmacksorgane der Vögel. Anatomischer Anzeiger, vol. 36, pp. 428– 461.

CHAINE, M. J.

- 1904. Remarques Sur La Musculature de la Langue des Oiseaux, Comptes Rendus de la Société de Biologie, Paris, vol. 56, pp. 991–2.
- 1905. La Langue des Oiseaux, Bull. Scient. de la France et de la Belgique, vol. 39, pp. 487-504.

EVANS, A. H.

1899. Birds. Cambridge Natural History. Macmillan & Co.

GADOW, H.

- 1883. On the Suctorial Apparatus of the Tenuirostres. Proc. Zool. Soc. London, 1883, pp. 62–69.
- 1890-99. Structure of Certain Hawaiian Birds. The Birds of the Sandwich Islands. Wilson and Evans, London, pp. 219-241.

GARROD, A. H.

1873. Tongue of Steatornis caripensis. Proc. Zool. Soc., London, p. 531. GIEBEL, C.

- 1858. Die Zunge der Vögel und ihr Gerüst, Zeitschrift für die Gesammten Naturwissenschaften, vol. 11, pp. 19–53.
- 1862. Zur Anatomie der Papageien. Zeitschr. für die Ges. Naturw., vol. 19, pp. 133-152.

KALLIUS, E.

1905. Beitrage zur Entwickelung der Zunge Anas boschas L. Passer domesticus L., Anat. Hefte, vol. 28, pt. 2. Vögel, pp. 311–586.

LIEBER, ADOLPH.

1907. Vergleichende Anatomie der Spechtzunge. Zoologica, vol. 20, pt. 51, Stuttgart '07. LINDAHL, JOSHUA.

1879. Some New Points in the Construction of the Tongues of Woodpeckers. Amer. Naturalist, vol. 13, p. 43-44.

LUCAS, F. A.

- 1896. The Taxonomic Value of the Tongue in Birds. The Auk, vol. 13, No. 2, April, 1896, pp. 109-115.
 - The Tongues of Woodpeckers, Bulletin No. 7, U. S. Dept. of Agric., Division of Ornithology and Mammalogy.
 - 1897. The Tongues of Birds. Report of U. S. National Museum, 1895, pp. 1003-1020.

MACGILLIVRAY, WILLIAM.

- 1839. Note on tongue of Setochalcis vocifera. In Audubon, J. J., Ornithological Biography, Edinburgh, 1839, vol. 5, p. 306.
- 1839. Description of tongue of Antrostomus carolinensis. Audubon, J. J., Ornithological Biography, Edinburgh, 1839, vol. 5, pp. 402–403.
- 1839. Tongue of Chordciles virginianus. Same reference, p. 407.
- 1840. Tongue of Caprimulgus europaeus. History of British Birds, London, vol. 3, pp. 630 and 634.

MARSHALL, M. E.

1905. Note on the Tongue of *Phalaenoptilus*. Proc. Amer. Philos. Soc., vol. 44, p. 215.

MUDGE, G. P.

1901. Lingual Myology of Parrots. Proc. Zool. Soc. London, vol. 1, p. 277-8.

OATES, E. W.

Tongue of Chalcoparia. Fauna of British India. Birds, vol. 2, p. 372. WALLACE, A. R.

1870. Note on the tongue of Chalcoparia, Ibis, p. 49.

WETMORE, ALEXANDER.

1918. On the Anatomy of Nyctibius with Notes on Allied Birds. Proc. U. S. National Museum, vol. 54, pp. 577–586.

EXPLANATION OF FIGURES ILLUSTRATING BIRD TONGUES

PLATE 1

- No. 1. Planesticus migratorius.
 - 2. Dendroica tigrina.
 - 3. Icterus icterus.
 - 4. Chlorophanes spiza.
 - 5. Coereba bananivora.
 - 6. Myzomela rubratra.

34

ę.,



Series Illustrating Multiple Tubular Tongues, Modifications of a Generalized Type Pattern. (×3)

FOR EXPLANATION OF PLATE SEE PAGE 5







9 11 TONGUES ADAPTIVELY MODIFIED FOR AN OMNIVOROUS DIET, FISH FARE, RAPTORIAL FEEDING, OR FOOD STRAINED FROM WATER. (No 11 ONE-HALF NATURAL SIZE, OTHERS 23) FOR EXPLANATION OF PLATE SEE PAGE 8



- No. 7. Callipepla squamata.
 - S. Puffinus griseus.
 - 9. Querquedula eyanoptera.
 - 10. Mergus servator.
 - 11. Phoenicopterus ruber.
 - 12. Buteo lincatus elegans.

- No. 13. Xenopicus albolarvatus.
 - 14. Colaptes cafer collaris.
 - 15. Melanerpes formicivorus bairdii.
 - 16. Sphyrapicus thyroideus.
 - 17. Conurus auricapillus.
 - 18. Carpodacus cassini.
 - 19. Hemignathus procerus.
 - 20. Anhinga anhinga.
 - 21. Pyrotrogon neglectus.
 - 36



Spearing Tongues. Tongues of Seed and Fruit Feeders, Flower Frequenters, and rudimentary Types. $(\times 3)$



- No. 22. Gavia pacifica.
 - 23. Gavia immer.
 - 24. Colymbus nigricollis californicus.
 - 25. Fulmarus glacialis glupischa.
 - 26. Ciconia ciconia.
 - 27. Larus heermanni.
 - 28. Larus occidentalis.
 - 29. Erismatura jamaicensis.
 - 30. Gallinula galeata.

No. 31. Nycticorax naevius.

32. Ardea herodias.

33. Botaurus lentiginosus.

34. Butorides virescens anthonyi.

35. Cereopsis novaehollandiae.



FOR EXPLANATION OF PLATE SEE PAGE 13

U. S. NATIONAL MUSEUM

PROCEEDINGS, VOL. 67, ART. 19 PL. 6



FOR EXPLANATION OF PLATE SEE PAGE 15

- No. 36. Gypaëtus barbatus.
 - 37. Buteo borealis calurus.
 - 38. Cathartes aura septentrionalis.
 - 39. Falco sparverius phalaena.
 - 40. Circus hudsonius.
 - 41. Polyborus plancus.
 - 42. Buteo albicaudatus.
 - 43. Accipiter cooperi.
 - 44. Surnia ulula.
 - 45. Opisthocomus cristatus.
 - 201. Chrysolophus pictus.

No. 46. Heteroscelus incanus.

- 47. Rallus levipes.
- 48. Limnodromus griscus scolopaceus.
- 49. Aramus vociferus.
- 50. Recurvirostra americana.
- 51. Rynehops nigra.
- 52. Eurypyga helias.
- 53. Fulica americana.
 - 40



Tongues of Gruiformes and Charadriiformes (Nos. 49 and 52 \times 2, Others \times 3)

U. S. NATIONAL MUSEUM



TONGUES OF VARIOUS BIRDS. (NCS. 59 AND 61 \times 2, Others \times 3 $^{\circ}$ For explanation of plate see page 17

- No. 54. Actitis macularia.
 - 55. Sterna antillarum.
 - 56. Sterna forsteri.
 - 57. Ereunctes pusillus.
 - 58. Oxyechus vociferus.
 - 59. Ionornis martinica.
 - 60. Charadrius semipalmatus.
 - 61. Haematopus palliatus.
 - 62. Colinus virginianus cubensis.
 - 63. Histriophaps histrionica.
 - 64. Geopelia cuneata.
 - 65. Zenaida vinaceorufa.
 - 66. Columba gymnophthalma.

- No. 67. Geococcyx californianus.
 - 68. Geococcyx californianus. (to show differences in length).
 - 69. Saurothera dominicensis.
 - 70. Psitteuteles chlorolepidota.
 - 71. Aprosmictus cyanopygius.
 - 72. Melopsittacus undulatus.
 - 73. Calopsitta novaehollandiae.
 - 74. Todus multicolor.
 - 75. Ceryle alcyon.
 - 76. Spcotyto cunicularia hypugaea.
 - 77. Asio wilsonianus.





FOR EXPLANATION OF PLATE SEE PAGE 19

No. 78. Tyto pratincola.

- 79. Otus asio bendirei.
- 80. Spiloglaux novaezealandiae.
- 81. Chordeiles acutipennis texensis.
- 82. Macropteryx coronata.
- 83. Bucco bicinctus.
- 84. Lophoceros melanoleucus.
- 85. Collocalia, sp (from Lucas).
- 86. Calypte anna.
- 87. Pteroglossus frantzii.
- 88. Dryobates villosus hyloscopus.
- 89. Dryobates nuttalli.

- No. 90. Pitta erythrogaster.
 - 91. Myiochancs richardsoni.
 - 92. Pyrocephalus rubinus mexicanus.
 - 93. Sayornis sayus.
 - 94. Sayornis nigricans.
 - 95. Nuttallornis borealis.
 - 96. Empidonax griseus.
 - 97. Tyrannus verticalis.
 - 98. Tolmarchus gabbi.
 - 99. Myiarchus dominicensis.
 - 100. Furnarius agnatus.
 - 101. Sittasomus, sp.
 - 102. Gymnocichla nudiceps.
 - 103. Thamnophilus bridgesi.
 - 104. Oligura superciliaris.
 - 105. Myadestes townsendii.
 - 106. Hylocichla guttata.
 - 107. Mimus polyglottos leucopterus.





No. 108. Sialia mexicana.

- 109. Toxostoma redivivum pasadenense.
- 110. Cinclus mexicanus.
- 111. Thryomanes bewicki charienturus.
- 112. Catherpes mexicanus punctulatus.
- 113. Certhia familiaris zelotes.
- 114. Lanius ludovicianus gambeli.
- 115. Petrochelidon lunifrons.
- 116. Polioptila caerulea obscura.
- 117. Dulus dominicus.
- 119. Vireo, sp.
- 118. Lawrencia nana.
- 120. Vireo belli pusillus.
- 121. Sitta carolinensis aculeata.
- 122. Sitta pygmaea.
- 123. Penthestes gambeli baileyae.
- 124. Baeolophus inornatus.
- 125. Psaltriparus minimus californicus.
- 126. Auriparus flaviccps.
- 127. Xanthoura luxuosa (apparently injured).
- 128. Aphelocoma californica.

- No. 129. Pica nuttalli.
 - 130. Cyanocitta stelleri frontalis.
 - 131. Scissirostrum dubium.
 - 132. Nucifraga columbiana.
 - 133. Strepera graculina.
 - 134. Sturnella neglecta.
 - 135. Zosterops atrifrons.
 - 136. Telespyza cantans.
 - 137. Passerculus rostratus.
 - 138. Cyanerpes cyanea.
 - 139. Chalcoparia phoenicotis.
 - 140. Psittarostra psittacea.
 - 141. Hermotimia, sp.





169

168

167

166

No. 142. Dendroica dominicia.

143. Vermivora celata lutescens.

144. Dendroica petechia gundlachi.

145. Catharopeza bishopi.

146. Dendroica occidentalis.

147. Dendroica palmarum.

148. Granatellus franciscae.

149. Wilsonia canadensis.

150. Certhidea salvini.

151. Dendroica nigrescens.

152. Dendroica auduboni.

153. Dendroica vigorsii.

154. Dendroica discolor.

155. Dendroica petechia.

156. Dendroica striata.

157. Dendroica castanea.

158. Dendroica fusca.

159. Dendroica virens.

160. Teretistris fernandinae.

161. Teretistris fornsi.

162. Wilsonia citrina.

163. Wilsonia p. pileolata.

164. Vermivora luciae.

165. Compsothlypis americana.

166. Oporornis tolmiei.

167. Oreothlypis gutturalis.

168. Icteria virens.

169. Helmitherus vermivorus.

170. Tachyphonus, sp.

- No. 171. Tanagra (Euphonia) violacea.
 - 172. Thraupis darwini.
 - 173. Stephanophorus leucocephalus.
 - 174. Ramphocelus brasilius.
 - 175. Pitylus grossus.
 - 176. Tanagra, sp.
 - 177. Phaenicophilus poliocephalus.
 - 178. Munia punctulata.
 - 179. Steganura paradisea.
 - 180. Icterus cucullatus nelsoni.
 - 181. Molothrus atronitens.
 - 182. Pseudoleistes, sp.
 - 183. Passer domesticus.
 - 184. Tiaris olivacea.
 - 185. Loxia leucoptera.
 - 186. Oberholseria chlorura.
 - 187. Ammodramus savannarum bimaculatus.
 - 188. Spinus pinus.
 - 189. Passerculus savannarum alaudinus.
 - 190. Oryzborus, sp.
 - 191. Zamelodia melanocephala.
 - 48





 \bigcirc

No. 192. Pipilo aberti.

193. Chondestes grammacus strigatus.

194. Passerculus beldingi.

195. Amphispiza belli.

196. Spizella passerina arizonae.

197. Passerella iliaca stephensi.

198. Junco hyemalis thurberi.

199. Passerella iliaca.

200. Pipilo crissalis senicula.

43316 - 25 - 4