The Avian Tongue

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Birds are considered unique in the animal kingdom for many reasons. Some of the classic reasons are: having feathers, not having teeth, and having the ability to fly. The one feature that is not mentioned is their tongue. It should be, because of the wide variety of shapes and features that bird tongues have. A bird's tongue can be very long, very short, feathered at the tip, have barbs of various sizes, and in some species show specific adaptations for feeding. This doesn't mean that birds that have similar adaptations are closely related. In many species the tongue has evolved through convergent evolution. Convergent evolution is the independent evolution of similar features in species not closely related.

While this paper concentrates on the tongue, you can't separate the tongue from the rest of the oral cavity. For example, the size, shape, and structure of the beak is extremely important since it works with the tongue to catch/collect, manipulate and swallow food (Lucas 1895). Depending on the species, the beak is equally or more important than the tongue for feeding.

It also should be noted that even though some birds' tongues show a remarkable adaptation to a particular feeding method, it doesn't mean that they don't eat other foods. An example is the hummingbird. Their tongue is adapted to acquiring nectar, but insects are also an important element of their diet.

This paper is divided into four sections, the first section, 'Avian Tongue Morphology', describes the tongue and its structure. The second section, 'Relationship of Diet to the Avian Tongue', discusses various types of tongues and diet with a few examples. The third section, 'Other roles of the Avian Tongue' details some of the other roles of the bird tongue besides eating, and the fourth section contains the 'Conclusions and Observations'.

The various bird tongue pictures and drawings are not drawn to scale. This is partly because the actual size was not included on the original drawings and there is little information on tongue sizes. Additionally, varying nomenclature is used for the same bone in the literature. This paper is using the Handbook of Avian Anatomy: Nomina Anatomica Avium (Baumel 1993)

1 Avian Tongue Morphology

Tongues are part of the 'lingual apparatus' and are located in the floor of the lower mandible (beak). The lingual apparatus includes the cartilaginous and bony skeletal structure of the tongue's hyoid apparatus (Figure 1), glands, muscles, nerves, blood vessels, and various connective tissues. (D. M. Homberger 1989) Extrinsic connective tissue, including extrinsic muscles, connects the lingual apparatus to the skull.

Two types of muscles are associated with the tongue. Intrinsic tongue muscles are muscles that connect the various hyoid skeleton bones (Section 1.1) and allow the hyoid bones to move relative to each other and thus change the shape of the tongue. Extrinsic muscles anchor the tongue to bones outside the hyoid apparatus and allow the tongue to change position. (wikipedia, Tongue 2014) (D. Homberger 1986). Human tongues have intrinsic and extrinsic muscles, but almost all birds have only extrinsic muscles. (Huang 1999) Parrots are one of the few birds that have intrinsic muscles controlling tongue movement. (D. Homberger 1986)

The tongue is covered in epithelium (Section 1.2) which can be partially keratinized (hardened) and covered with papillae (Section 1.4). In some birds, the horny tongue tip has a tendency to fray (Figure 9). (Proctor 1993) Bird tongues may also have tactile receptors that help in identifying and position food before swallowing. (Olsen 2011) Some birds have temperature receptors (sensitive to cold) on their tongue. (Beason 2003)

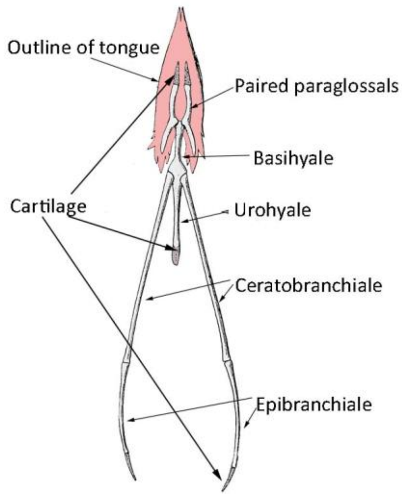


Figure 1. Hyoid of a Peewee shows the various bones that make up the hyoid and where the tongue is usually located. (Lucas 1895)

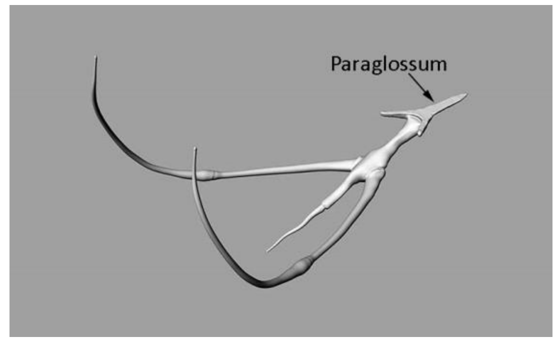


Figure 2. 3D rendering of a domestic chicken's hyoid from a set of drawings (D. M. Homberger 1989) by Darby Johnston.

1.1 Bones of the Tongue – the Hyoid Apparatus

The articulated group of bones and cartilage, that support and control tongue movement, is called the hyoid apparatus. All vertebrates have hyoids. In mammals the hyoid mainly supports the larynx. In birds, the hyoid helps define the shape of the tongue and its movement and ability to extend/retract. The paraglossum and the rest of the hyoid bones (Figure 1) control tongue movement, provide attachments for extrinsic muscles, and keep the apparatus in place. (Lucas 1895)

In birds, the hyoid apparatus varies in size, shape and the number of bones (maximum of 9). The paraglossum (syn: entoglossum) is embedded in the tongue. The paraglossum can be one unpaired bone (Figure 2) or two paired bones called the paired paraglossals (Figure 1) which can be fused together. (D. Homberger 1986) The urohyale (syn: caudal basibranchiale) can be present (Figure 1 & Figure 2) or not (Figure 25). The muscles that are attached to the hyoid apparatus control the movement of the tongue and help to keep the apparatus in place. (Landsborough 1964) (Portman 1961) In swans, parrots and most other birds, the hyoid horns extend backward from the tongue on either side of the larynx (Figure 3). In birds with long horns (e.g., woodpeckers and hummingbirds) the horns curve around the skull terminating at the front of the skull. (Podulka 2004)

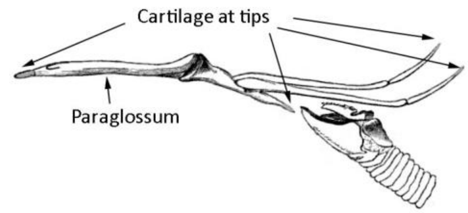


Figure 3. Placement of the hyoid to the upper larynx of a swan. (Owen 1866) The hyoid bones are ossified cartilage and the tips may still be cartilage.

The hyoid horns and their muscles are encased in sheaths. The sheath is two layers of connective tissue with lubricating fluid in between. Where the sheath and horns is anchored depends on the species. For example, in woodpeckers that extend their tongue the most, it can be anchored at the left nostril or encircle the right eye. (Figure 26) When the tongue is extended the branchiomandibularis muscle contracts and the horns are pulled out of the sheaths. When the tongue is retracted, the cricohyoideus muscle contracts and horns are pulled back into the sheaths. (D. Homberger 1999) (D. M. Homberger 1989) (Bock 1999) The muscles that control the extension of the tongue must be at least three times as long as the distance that the tongue is protruded. (Bock 1999)

In some birds, such as herons and egrets, the horns are located well below the mandible and do not move relative to the sheaths. This limits the movement of the hyoid and tongue but it increases the space between the palate and the hyoid skeleton so they can swallow large food whole. (D. Homberger 1999)]

The shape and size of the various hyoid bones are indicative of what the tongue looks like and how it functions. If the paraglossum is well developed, then the tongue is thick and fleshy (Figure 5). If the paraglossum is small and mostly cartilage, then the tongue is small and probably unimportant (Figure 37, Figure 39). Long hyoid horn bones mean that the tongue can be protruded well outside the lingual cavity. (Figure 25, **Error! Reference source not found.**). (Lucas 1895)

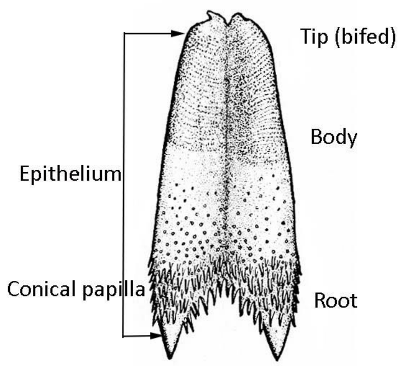


Figure 4. American Kestrel (Gardner 1925) showing the various parts of the tongue, the epithelium and the backward facing conical papillae.

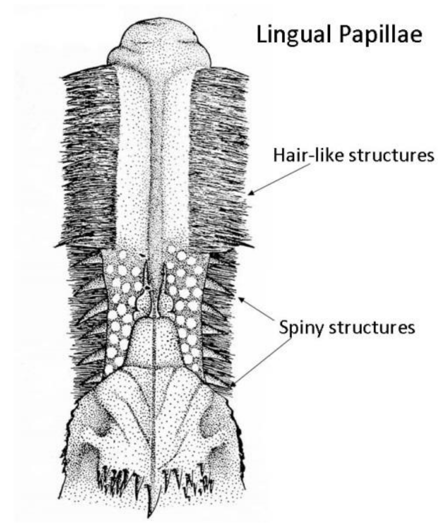


Figure 5. Ruddy Duck (Gardner 1925) showing the lingual papillae that is used for filter feeding.

1.2 Epithelium

The layer of cells covering a bird's tongue is called the epithelium (Figure 4). The epithelium can vary in thickness and it can also be hardened (keratinized). This keratinization is usually near the tip or the sides of the tongue. (Landsborough 1964) In some cases, when the tip of the tongue is keratinized, it creates the "lingual nail" that is found in some birds such as ducks and geese.

1.3 Lingual Nail

The tongues of ducks, geese and swans and other birds such as the parrot, chicken and white-tailed eagle have what is called a 'lingual nail'. The lingual nail is found at the tip of the tongue and is a strong and hard keratinization of the epithelium. In geese the nail extends to edges of the tongue's apex. It is believed that this structure is flexible enough that it can be stretched. In some birds, it may be used as a spoon for lifting grains. (H. S.-S. Jackowiak 2011)

1.4 Papillae

Papillae (Figure 4, Figure 5) are hair or barb like structures on the tongue and are keratinized processes of the epithelium. (H. S.-S. Jackowiak 2011) The papillae vary in shape and size (Figure 4 and Figure 5) and are useful in keeping food on the tongue, holding onto food, or moving towards the esophagus. (Iwasaki 2002) Most birds have rear-directed papillae, usually near the root, that helps them to swallow food. (Gill 1994) The woodpeckers are one exception and do not have rear-directed papillae. (Lucas 1895)

The Papillae Crest is the name given to the V-shaped row of conical papillae that point backwards towards the throat and is located between the body and root of the tongue. It is present in many birds such as geese, quail, birds of prey, terns, nutcrackers, etc. It facilitates the movement of food towards the esophagus. It also helps prevent regurgitation. (Erdogan 2013)

1.5 Salivary Glands

In birds, salivary glands are found in various places on the tongue including the root and body. These glands produce saliva and mucus which helps to protect against bacteria and moistens food before swallowing. (Gill 1994) Most birds only have mucus-secreting cells. (Husveth 2011) (D. Homberger 1986) Some woodpeckers secrete sticky mucus which coats the tip of their tongue and aids in extracting ants and insects. (Bock 1999) Salivary glands are absent in some species such as the Great Cormorant. (King 1984)

Amylase, an enzyme for breaking down starch into sugar, has been found in the saliva of some birds such as chickens, turkeys, and geese. It unclear how much of a role it plays in digestion of food because food is usually swallowed whole or in chunks and doesn't stay in the mouth cavity long. (Husveth 2011) One theory is that it is only used in the crop to help digest food. (Marshall 1960)

Some swifts use their mucus rich salvia to build their nests. These nests are used by humans to make bird's nest soup. (Marshall 1960)

1.6 Taste Buds

Initially, in the 1800's when taste buds were discovered, they were not thought to exist in birds. It wasn't until the early 1900's that birds' taste buds were found. Humans have over 10,000 taste buds and are primarily found on our tongue. Birds have significantly less. For example, chickens have around 24, pigeons 27-59 and parrots 300-400. (Portman 1961) (Proctor 1993) The placement of birds' taste buds is also different. In birds, they are primarily found at the base of the tongue and on the roof or floor of the mouth. It is believed that they are not found on the anterior (front) part of the tongue because it is frequently hard and horny.

Studies have shown that birds are able to differentiate a variety of tastes which varies between birds of the same species and different species. (Landsborough 1964) For example, birds can taste sweet, salt, brine, bitter, lipids (fats) and sugar concentrations. (Gill 1994) Sanderlings (*Calidris alba*) and Dunlins (*Calidris alpine*) have been shown to be able to use their taste receptors to recognize where worms have been crawling in sand and hummingbirds can distinguish different types of sugars and concentrations. (Beason 2003)

1.7 Color and markings

Some nestlings' tongues are marked with spots, a band, or both. Mannikens, such as the Magpie Mannikin and the Bronze Mannikin, have a black band; the Tricolored Parrotfinch has two lateral spots, and the Grey-headed Silverbills tongue has two black spots and a band near the tip. The Locust Finch's tongue is more dramatic because it has red spots and the Pheasant Coucal nestling tongue is red with a black tip. (del Hoyo 2011) Like the nestlings' gape, these are considered to be directive marks or targets for the parent to place food. (Landsborough 1964)

Figure 6. Laughing Gull showing its red tongue (Nancy Johnston, http://nejohnston.org/birds)

Little information has been published about the color of adult tongues. Gardner (Gardner 1925) mentions that adult bird tongues can be pink, black, light blue and that some swallows have brown spots and road runners have a flesh-colored tongue mottled with black. A picture on the web showed a Blue-and-Gold Macaw with a blue tongue, but it was not clear if this tongue color is found in the wild. Another bird with a color tongue is the Yellow-crested Manakin which has a bright yellow tongue and gape. (del Hoyo 2011)

Use of color in adults may serve as a threat and warning colorization and may be a factor in displays in some seabirds such as the auks. (Thomson 1964)

1.8 Growth of the Tongue

Frederick Lucas (Lucas 1895) showed that bird tongues grow after they are hatched. This is most dramatic in birds such as woodpeckers and hummingbirds (Figure 7). Birds with short adult tongues, such as the chimney swift and screech owl, also show growth (Figure 8) but not as dramatically.

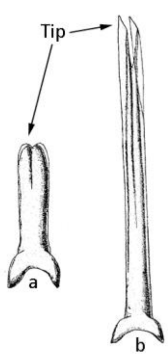


Figure 7. Green-throated Carib Hummingbird showing the tongue at hatching (a) and after leaving nest (b). (Lucas 1895)

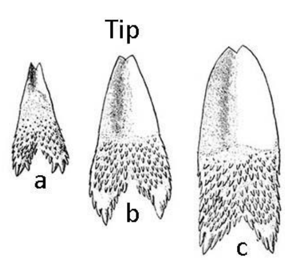


Figure 8. Screech Owl showing the tongues growth from embryo (a), nestling (b), and adult (c). (Lucas 1895)

2 Relationship of Diet to the Avian Tongue

In the previous section we discussed avian morphology. To try and organize and bring order to all the various varieties of tongues, researchers have proposed various ways to classify them. J.G. Harrison (Landsborough 1964) proposed five functions that a birds' tongue provides: collecting food, eating, swallowing, taste and touch, and nest building. In 1925/1926, Gardner proposed eight categories based on diet: omnivorous birds, fish eaters, food strained from water, flesh feeders, probed food, seed and nut eaters, flower frequenters and rudimentary. (Gardner 1925) Others have arranged by taxonomy. This paper will organize tongues by type, with a few examples of each type. Some birds can be in more than one type.

2.1 General Purpose Tongues

A general purpose tongue is basically a tongue that does not show significant diet adaptations. A variety of foods can be eaten, including insects, small seeds, grain, etc. and this varies by species. Birds that belong in this category have tongues that are thick or thin, narrow or wide, rounded or pointed at the tip, have feathering and/or bifurcated at the tip, etc. Birds in Lucas's system (Lucas 1895), under the category 'Omnivorous' belong here and this includes most passerines (songbirds), galliformes (chicken, quail, etc.). Shorebirds have also been included in this category.

2.1.1 Passerines -- Passerformes

Passerines (songbirds) make up more than half of all birds found. Because of the diversity of birds in this class, their diet variation is extensive and includes insects, seeds, nuts, grains, fruit, invertebrates, reptiles, small birds, small mammals, fish, crustaceans, carrion (American Crow), human food scraps. (del Hoyo 2011) Even though the diet varies among species, most passerines tongues look remarkably similar. The tongues width varies and they frequently have backward facing papillae near the root of the tongue for moving food towards the esophagus. (Lucas 1895) Their tongues tend to fray and split at the tip. (Erdogan 2013)

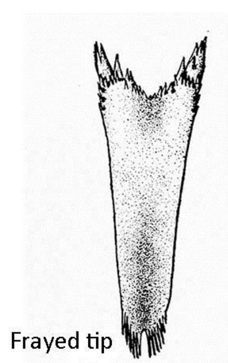


Figure 9. Pygmy Nuthatch (Gardner 1925) showing the feathering at the tip.

Figure 10. Picture by Bob Lewis (https://www.wingbeats.org/) showing the feathered tip of a Pygmy Nuthatch

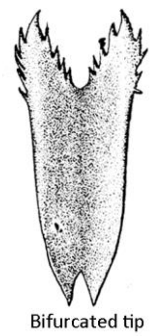


Figure 11. Say's Phoebe (Gardner 1925) showing the bifurcated tip.

The Cape May Warbler (Figure 12) has a different tongue from the other warblers and most other songbirds. The tongue is curled and semi-tubular towards the tip. During the summer they feed on insects and in the winter on nectar and the juice of berries. They will even visit hummingbird feeders. (del Hoyo 2011)

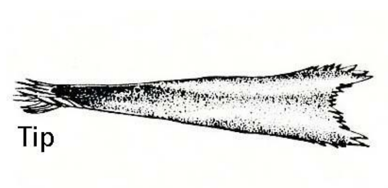


Figure 12. Cape May Warbler showing the semi-tubular tip. (Gardner 1925)

2.1.2 Galliformes

Galliformes include chickens, quail, turkeys, pheasant, etc. Much research and information on the tongues of these birds has been done on domestic chickens. Partly this has been done because of the commercial importance of these birds.

Two methods of feeding have been observed in domestic chickens: slide-and-glue and throw-and-catch. In the slide-and-glue method, the food particle is first picked up with the beak. Then the mucus covered tongue moves the food particle to the esophagus. In the throw-and-catch method, as the head moves upward, the beak opens wide and the tongue retracts and moves the food backwards. These two methods can be combined. (Bels 2006)

2.1.3 Shorebirds

Shorebirds have a variety of feeding methods and the role of the tongue varies and in some cases, the beak plays a more important role. There does not seem to be anything unique about their tongue except for the amount and size of the papillae found.

It is believed that shorebirds obtain food by:

1. Pecking at food at the surface (e.g., sand or rocks) and then using the slide-and-glue method or the throw-and-catch method described in Section 2.1.2 to swallow the food. (Bels 2006).
2. Probing for prey that lives under the surface (e.g., sand) with their beak that has touch receptors. The food is probably swallowed as in step 1.
3. Surface tension transport is using the surface tension of water surrounding prey to move prey from their gaping beak to the mouth. Initially observed in phalaropes,

Least Sandpiper and Western Sandpipers have also been observed using this method of feeding. (Rubega 1997)

4. More recently studied is the consumption of biofilm by some shorebirds. Biofilm is made up of a variety of microorganisms (e.g., bacteria, protozoa, fungi, algae, etc.). A study of Western Sandpipers and Dunlins has shown that they eat biofilm using their densely bristled tongues covered with mucous. (Elner 2005)   Biofilm consumption may be as high 45-59% of the total energy intake during migration. (Kuwae 2008)

2.2 Spiny Tongues – Fish Eaters

Birds in this category have significant papillae (spines) on their tongues. They primarily eat fish and the papillae aid in the catching, positioning and consumption of the fish. The papillae come in various sizes and shapes and can be found in other parts of the lingual cavity. Also, their beaks frequently have spiny ridges on the cutting edges (tomia) of the mandibles.

2.2.1 Penguins (Spheniscidae)

Penguins' tongues have many large and backward facing pointed papillae (barbs) that cover the surface of the tongue. (Kobayashi 1998) (Figure 13) As can be seen in (Figure 14), the roof of the mouth also has backward facing pointed papillae.

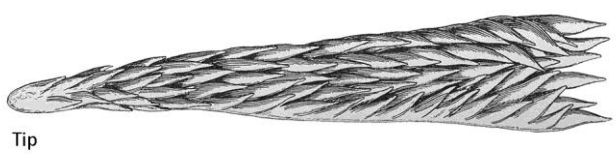


Figure 13. Drawing of a King Penguin tongue (Lucas 1895)

Figure 14. Note the spines on the roof of the mouth of the Fiordland Crested Penguin. (http:www.photovolcanica.com)

2.2.2 Merganser (Anatidae)

The fish-eating Red-breasted Merganser has serrations on its slender beak matched by a series of sharp, reverted, horny papillae on the thin tongue (Figure 15). The spines are in two rows, backward facing, from the apex to the root of the tongue. They are sharp and hard, and aid in the ability to hold and swallow fish. An interesting fact is the Hooded Merganser which also mainly eats fish, does not have the spiny papillae. (Lucas 1896)

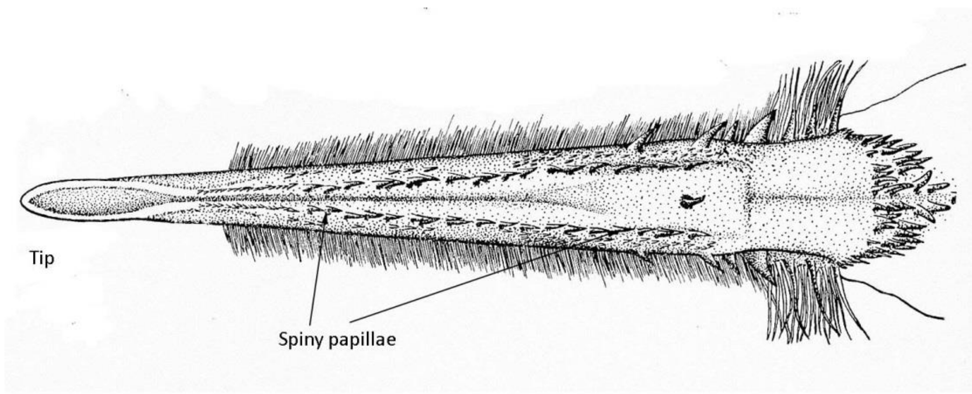


Figure 15. Red-breasted Merganser (Gardner 1925)

2.2.3 Seabirds

Many seabirds including shearwaters and petrels have spiny tongues, but not to the extent that penguins do. (Lucas 1895). The Razorbill, Common Murre and the murrelets are fish eaters but they have a narrow beak and the tongue is highly keratinized. To catch fish they use their tongue to press the fish against their palate.

2.3 Spiny Tongues - Filter Feeders

Filter feeders strain food particles and other suspended matter from water and mud. Some of the notable filter feeders include flamingos, many ducks and geese, prions and avocets.

There are at least a couple of different methods for how filter feeders filter out food particles. One method is to swing the beak from side to side and using the beak to strain food from water/mud as it goes through their beak. (wikipedia, Northern Shoveler 2014) (Holliday 2006)

The second method is depressing the tongue and using it like a pump to allow water/mud to fill the oral cavity and then the tongue is pressed against the palate and the water/mud is ejected sideways between the papillae capturing the solid food particles. (Erdogan 2013)

2.3.1 Ducks, geese, swans (Anatidae)

Ducks, geese, and swans have a variety of feeding methods and include grazing, pecking, breaking off shellfish, fishing, and filter-feeding. Some of the major duck filter-feeders are the Mallard, shovelers such as the Northern Shoveler and teals such as the Blue-winged Teal.

While geese may still do some filter feeding, their tongue and beak is better adapted to cutting the vegetable parts of plants and to eating seeds. The serrations on a goose's beak are thick and resemble blunt teeth. In conjunction with the spiny papillae on the muscular tongue the goose is able to clip vegetation close to the ground by gripping and tearing off the plant stems. (Figure 17) For grains, the lingual nail may act as a spoon to pick up seeds. (H. S.-S. Jackowiak 2011) (van Grouw 2013)

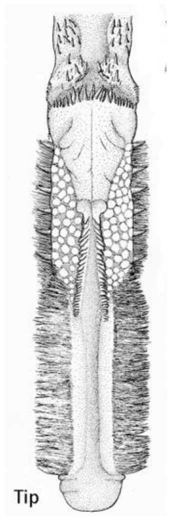


Figure 16. Tongue of Cinnamon Teal (Gardner 1925) showing the filtering papillae. This arrangement is more efficient for filter feeding than the goose. (H. S.-S. Jackowiak 2011)	Figure 17. Domesticated Goose shows the spiny papillae on the side of the tongue and the tomia on the upper and lower beak. Both aid in the grabbing and breaking off grass. (Nancy Johnston, http://nejohnston.org/birds)

2.3.2 Flamingos (Phoenicopteridae)

Flamingos are the best known filter feeders (Figure 18). They feed on brine shrimp and blue-green algae. They use both methods of filter feeding described in 2.3, but they do so with their beak upside down (the upper mandible on the bottom). For larger food items, they also feed by using the ‘catch and throw’ mechanism in which the role of the tongue is not known. (Holliday 2006) (Landsborough 1964) (wikipedia, Flamingo 2014)

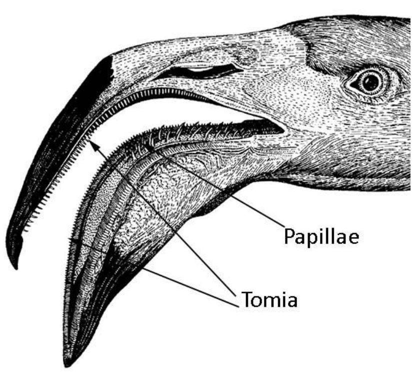


Figure 18. Flamingo showing the backward facing papillae on the tongue and the tomiaon the beak. Both are used for filter feeding. (Zweers 1995)

Figure 19. Flamingo showing how they feed with the beak upside down. (Nancy Johnston, http://nejohnston.org/birds)

2.3.3 Prions (Procellariidae)

The three largest prions (whalebirds) filter feed. They have tooth-like or comb-like ridges on the beak, but it is unclear if the tongue has matching papillae. One of the ways that they filter feed for zooplankton is to use their feet to skim swiftly over the surface of the water with wings outstretched, and the beak, or head, submerged. (del Hoyo 2011) (wikipedia, Prion (bird) 2014)

They will also use their tongue to create suction to draw water and prey into their mouth and then to squeeze out the water leaving the prey behind. (Klages 1992)

2.3.4 Avocets (Recurvirostridae)

One of the ways that avocets feed is by moving their head back and forth through water or mud to capture food. The tongue helps direct the food for swallowing. (del Hoyo 2011) The tongue itself is short and fills only a small part of the lower beak. The tongue is also smooth (Figure 20) and does not have papillae like other filter feeders but they have hard projections on their palate.

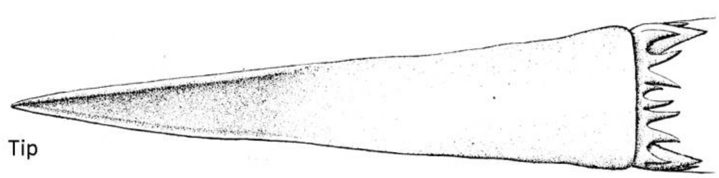


Figure 20. American Avocet tongue showing the smooth surface. (Gardner 1925)

2.4 Fleshy tongues

Birds of prey are in this category. They tend to have large, thick and fleshy tongues with backward facing spikes at the root of the tongue. (van Grouw 2013) The spines can be in either a single or multiple rows. The tongue tip is usually keratinized epithelium and can be bifurcated. (Gardner 1925)

2.4.1 Hawk, Eagles, and Falcons

Hawks, eagles and falcons are mostly carnivorous and eat a variety of different sized animals. Rodents, insects, other birds, lizards, snakes, etc. are all popular food. (del Hoyo 2011) Smaller food items can be swallowed whole and larger items are eaten by tearing off smaller chunks. Except, for the number of backward facing conical papillae near the root of the tongue (Figure 21), there doesn't seem to be any diet tongue specific modifications.

2.4.2 Owls (Strigidae, Tytonidae)

Owls' diet and tongue is similar to those of hawks, eagles and falcons (Figure 22). They will either swallow smaller prey whole or tear larger prey apart. (del Hoyo 2011) The tip of the Barn Owl tongue is almost totally keratinized epithelium (Gardner 1925) while the Ural Owl's tongue is not keratinized. (S. C. Emura 2008)

2.4.3 Vultures (Accipitridae, Cathartidae)

A vulture's tongue is somewhat different than other birds of prey such as a hawk or eagle. They are principally carrion eaters and their tongue has a rasp like edge (Figure 23), which probably helps pull the flesh from the bones. (Gardner 1925) (wikipedia, King Vulture 2014)

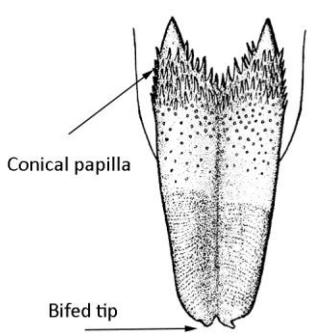


Figure 21. American Kestrel (Gardner 1925) Tongue is 1.5 cm long (S. O. Emura 2008)

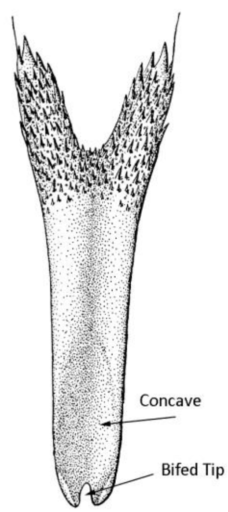


Figure 22. Barn Owl (Gardner 1925)

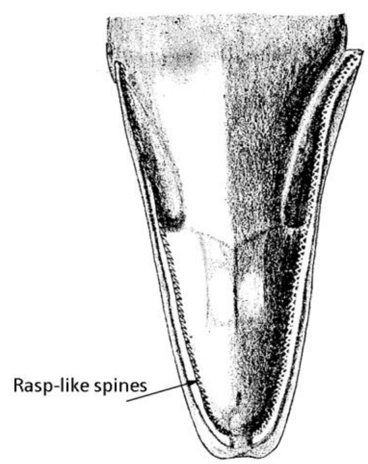


Figure 23. Turkey Vulture (Gardner 1925)

2.5 Protruding tongues

In this category are the birds that extend their tongue to acquire food. This includes woodpeckers, hummingbirds, flowerpeckers, honeyeaters, and sunbirds. Woodpecker and hummingbirds are discussed here.

2.5.1 Woodpeckers (Picidae)

Woodpeckers are the classic example of birds that extend their tongue to obtain food. The amount of extension of a woodpeckers' tongue depends on the species. For example, sapsuckers eat sap and can't extend their tongues as far as flickers and green woodpeckers that forage for insects and larvae in trees. (Bock 1999)

The ability to extend the tongue is directly related to the length of the hyoid horns. For the greatest extension, the horns and the attached muscles and sheaths extend around the brain case to the right nostril or encircle the right eye (Figure 26) depending on the species. (van Grouw 2013)

In Section 1.1, it was described how the horns move in woodpeckers and other birds that extend their tongues. A special feature of the woodpecker hyoid is that the paraglossum is smaller and stiffer than in other birds (Figure 25). They also have two intrinsic muscles that enable the woodpecker to move the tip of the tongue in all directions to better get insects out of tunnels.

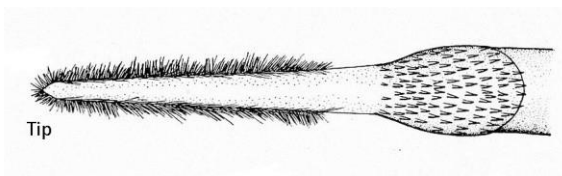


Figure 24. Williamson's Sapsucker showing the hair-like structures on tongue for gathering sap. (Gardner 1925)

The tip of the tongue for insect eating woodpeckers can be barbed for spearing insects (**Error! Reference source not found.**) or have hair-like structures coated with sticky mucus secreted by their salivary glands to help capture them. (Bock 1999). Sapsuckers have the shorter tongues and their tongues have hair-like structures (Figure 24) for gathering sap from trees. (Podulka 2004)

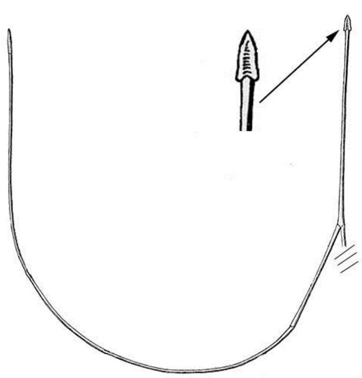


Figure 25. Hyoid apparatus of a flicker Yellow-backed Chattering Lory (*Colaptes auratus)* with the tip expanded. Just hatched woodpeckers tongue and hyoid horns are not fully grown when hatch. They tongue grows as they age. (Gardner 1925)

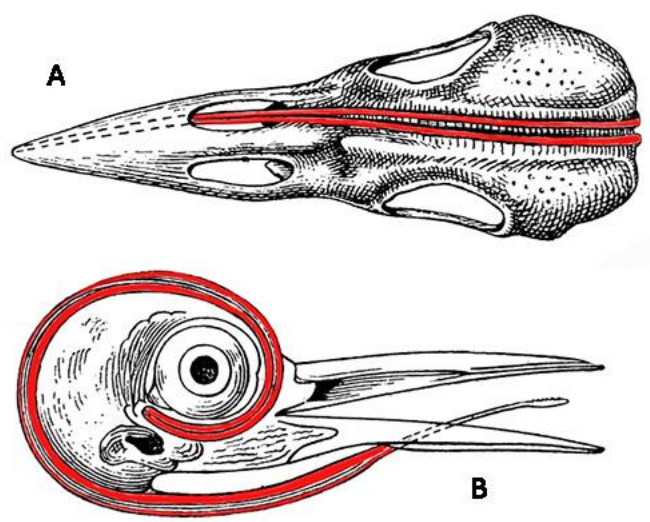


Figure 26. Pictures of the hyoid apparatus (red). A: shows how the horns go around the skull and terminate in the right nostril, e.g., Northern Flicker. B: shows how the horns can go around the eye, e.g., *picus*. Modification of a picture from http://etc.usf.edu/clipart/

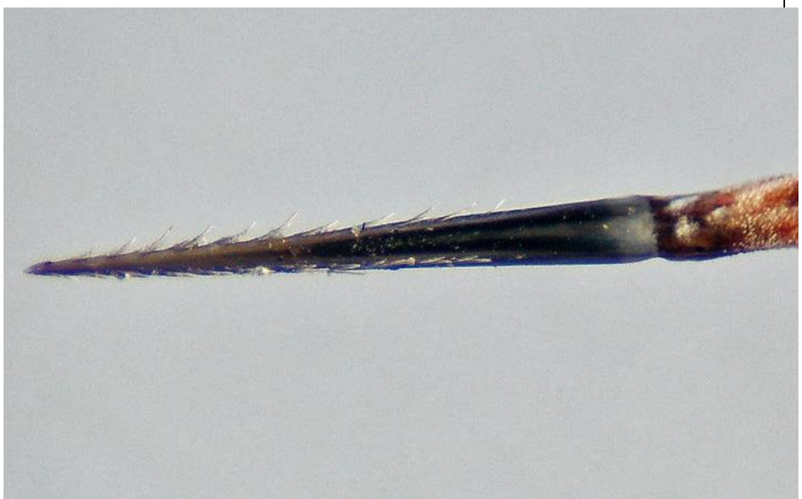


Figure 27. Red-bellied Woodpecker tongue tip showing the rear-facing barbs used for extracting larvae from trees. Chris Kargel (http://www.livingstonbirds.com/photos/red-bellied_woodpecker/) used with permission.

2.5.2 Hummingbirds (Trochilidae)

Hummingbirds' main diet is pollen and nectar, but insects are also important. Hummingbird tongues are partially bifurcated, starting at the tip, into two branches (Figure 28). (Paton 1989)

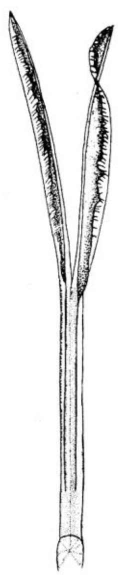


Figure 28. Anna's Hummingbird showing the feathered bifurcated tip. (Gardner 1925)

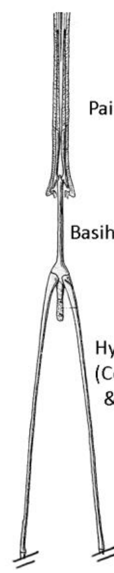


Figure 29. The paired paraglossum are cartilaginous and are joined for approximately the distal half. As the tongue extends, the horns are pressed forward through a fibrous sheath. (D. Homberger 1999) Picture: (Lucas 1895)

Hummingbirds were long thought to use capillary action to acquire nectar. Recently, through the use of high-speed photography, it has been shown that this is not the case. Their long tongue is bifurcated at the tip with lamellae (fringe) at each tip and two grooves running from the tip toward the tongue's base (Figure 28). (Rico-Guevara 2011) The bifurcation is approximately half the length of the tongue. (Lucas 1891) When not feeding, the tongue tips are together and the lamellae are tightly furled creating a flatten tube. When entering the nectar, the tongue tips spread apart and the lamellae unfurl. When the tongue leaves the nectar, the tongue tips twist around their long axis and the lamellae furl, trapping the nectar inside. This happens very fast (50ms) and seems to require no muscular effort on the hummingbird. It is still not clear how the nectar is swallowed, but it is believed that when hummingbirds extend and retract their tongue after feeding they may be squeezing nectar from their tongue. (Rico-Guevara 2011) Whether this same mechanism carries to other nectar eating birds is unknown, but the researchers Rico-Guevara and Rubega believe so.

The tongue seems to be unimportant for the capture of insects, an important food source for hummingbirds.

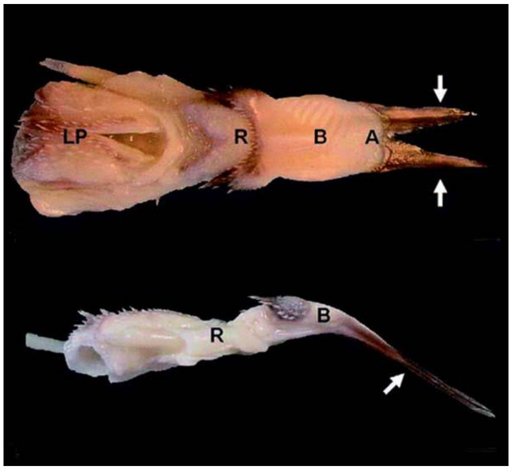
Figure 30. Picture showing the hummingbird tongue furled together. The extending of the tongue outside of a flower may be forcing remaining nectar out of the tongue to be swallowed (Rico-Guevara 2011). Picture by Bob Lewis (https://www.wingbeats.org/)

2.6 Tongues that help in extracting nuts/seeds

A variety of bird species eat seeds and nuts including most parrots and some passerines. Seed and nut eaters usually have thick fleshy and strong tongues.

2.6.1 Nutcrackers (Corvidae)

Nutcrackers are a medium sized bird and the North American nutcracker is the Clark's Nutcracker. Nutcrackers can eat a variety of foods, but the unique aspect of their diet is when they use their beak and tongue to extract seeds from cones and nuts from shells. The tongue apex is made of two pointed processes that are at the end of the paired paraglossals and point downward. They are a highly keratinized dagger like structure. It is believed that the Nutcracker tongue and beak work together to grasp and shell the seeds of conifers. The beak breaks off the husk and the tongue uses the apex to lever seeds out. (H. S.-S.-L. Jackowiak 2010) The pointed processes are likened to a modified 'lingual nail'. (Erdogan 2013)



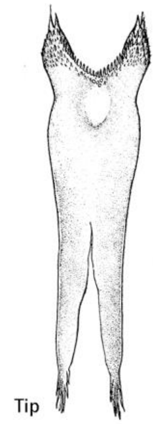


Figure 31. Dorsal (top) and lateral (bottom) view of the Spotted Nutcracker tongue. The tongue is approximately 2.4 cm long and the pointed processes are .7 mm long. (H. S.-S.-L. Jackowiak 2010).	Figure 32. Drawing of Clark's Nutcracker by Gardner (Gardner 1925)

2.6.2 Finches (Fringillidae)

In finches (fringillids andestrildids), various studies have been performed relating the size of the seed eaten to the size of the beak. The tongue is used to position the seed between the rims of the beak and to help keep it there while cracking, and also to rotate the seed to husk it. (Van der Meij 1973) (del Hoyo 2011)

2.6.3 Parrots (Psittacines)

Parrots have a fleshy tongue with intrinsic muscles to control tongue movement. The hyoid still supports the tongue as in other birds, but because of the intrinsic muscles they can move the tongue around more like mammals. Another unique feature is the wrinkled and folded tongue epithelium which allows the tongue more freedom to be stretched. (D. Homberger 1986)

Many parrots, macaws, cockatoos eat nuts and seeds and have an upper mandible (beak) that is stepped (or shaped) to provide cracking spaces for seeds of different sizes. The nut is turned by the tongue until the groove or seam is positioned on the cutting edge of the lower mandible. The tongue holds the seed in place while the bird's jaw splits the seed in half. The tongue also separates out and discards the husk. Small seeds are swallowed whole. (van Grouw 2013) (del Hoyo 2011)

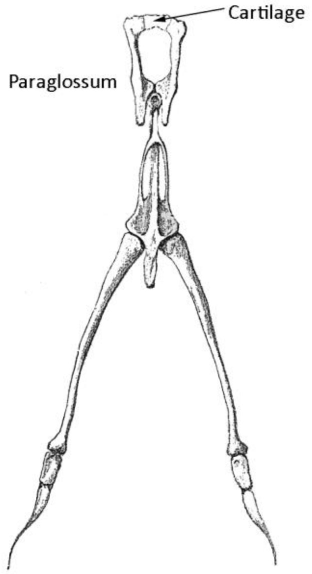


Figure 33. Hyoid of Lorius flavopalliatus (Mivart 1895)

Figure 34. Military Macaw showing muscular tongue. Michael Durham (www.Durmphoto.com), used with permission

2.7 Brush-like Tongues

Brush tip tongues are used by a few bird species to feed on nectar and pollen. Lories and Honeyeaters are the prime examples.

2.7.1 Lories

Lories, the Swift Parrot and the Philippine Hanging-parrot primarily feed on pollen and nectar and have an unusual tongue. The tongue is long and the tip looks like an old time shaving brush. The tip is made up of papillae designed to brush up pollen and nectar from flowers. When the tongue is not extended, the papillae lie flat. (del Hoyo 2011)

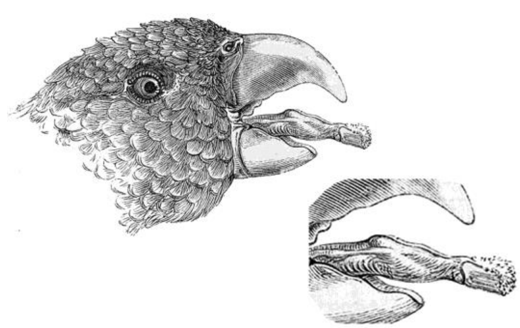


Figure 35. The close up view shows the bristles at the tip of the tongue of a Lorius. (Beddard 1898) (after Garrod)

2.7.2 Honeyeaters

All honeyeaters have long tongues and therefore might also be included in Section 2.5, “Protruding Tongues”. But, some of these honeyeaters also have brush tipped tongues which they use to eat nectar. The number of bristles on their tongue tips varies between 50 and 100.

Their long extensible tongue is flicked rapidly and repeatedly into a flower and the upper beak compresses out any nectar when the beak is closed. (wikipedia:Honeyeater) (Olsen 2011)

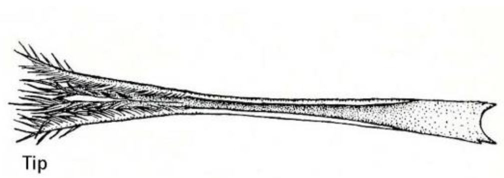


Figure 36. Micronesian myzomela is a honeyeater that primarily feeds on nectar but will eat insects and small invertebrates. (Gardner 1925)

2.8 Rudimentary Tongues

There are some species of birds where it is believed that the tongue plays a minimal role in eating. Rudimentary tongues are usually much smaller than the beak and tend to be simple in form. These tongues are not used to catch, collect, manipulate or used to direct the food to the esophagus. Some of the bird species that have been mentioned having such tongues are the cormorant (H. A. Jackowiak 2006), pelican, (del Hoyo 2011), ostrich (Tivane 2011) and the kingfisher (Gardner 1925). In cormorants and pelicans, fish is the main dietary source. While some kingfishers eat fish, other species in this family eat frog, snakes, spiders, insects, etc. (wikipedia, Kingfisher 2014), and ostriches eat plants and some invertebrates. (wikipedia, Ostrich 2014)

2.8.1 Cormorant (Phalacrocoracidae)

The cormorant's tongue is located in the center of the lower beak with a reduction in the posterior part of the tongue. The tongue is immobile and mushroom shaped. (Figure 37) It is also keratinized with no lingual glands. (H. A. Jackowiak 2006) (Figure 37) Cormorants use a 'catch and throw' mechanism to swallow fish. (Zweers 1995)

Darters, who are in the same order as cormorants, also have a small tongue that is probably unimportant. (Figure 40)

2.8.2 Ostrich (Struthionidae)

The ostrich tongue is also considered rudimentary, though it does contain numerous mucous glands for moistening the beak cavity. (H. S.-S. Jackowiak 2011) The tongue is short, sits in the center of the lower beak, and is 'U' shaped. The hyoid apparatus is unique in that both the paired paraglossals and the basihyale are cartilaginous and not calcified as in many other birds. (Tivane 2011)

2.8.3 Other Ratites

Other ratites, besides the ostrich, have small tongues in relationship to the length of their beak, and the tongues are considered rudimentary or vestigial organs. Ratites, such as the emu and cassowaries, use a single 'catch and throw' movement to position the food. During this, the tongue is depressed to the floor of the mouth which creates an enlargement of the mouth. This seems to be the only role that the tongue plays. (Erdogan 2013)

2.8.4 Pelicans (Pelecanidae)

Pelicans' tongues are small, especially compared to their beak size (Figure 38). But, in the case of Pelicans, the tongue muscles control the pouch and permits the pelican to expel the water after a catch. (del Hoyo 2011) It is harder to consider their tongues as not being important.

2.8.5 Kingfisher (Alcedinidae, Hacyonidae, Cerylidae)

While the kingfishers' tongues are small (approximately 1.8 cm long), occupying ½ of the beak, their tongue contains well developed salivary glands, and the posterior part of the tongue body and the root is covered with numerous fine processes. (El-Fattah 2013) Thus, their tongues seem to play a role in moistening food and the fine processes may aid in swallowing it.

Figure 37. Double-crested Cormorant tongue (Nancy Johnston, http://nejohnston.org/birds)

Figure 38. Brown Pelican showing the small tongue in front of the pouch. (wikipedia, Pelican 2014)

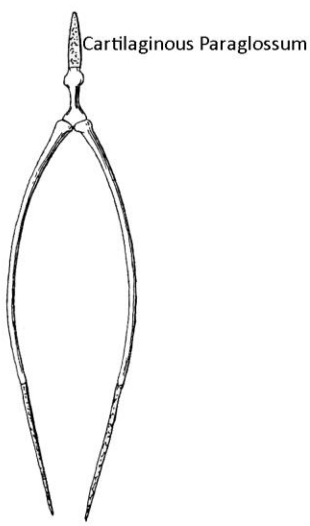


Figure 39. Cormorant hyoid. Notice the small paraglossum bone that has not ossified. (Lucas 1895)

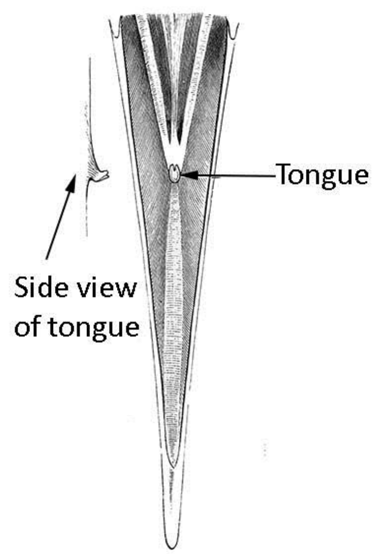


Figure 40. Notice how small the tongue is in this Darter in relationship to the beak size. (Lucas 1895)

3 Other roles of the Avian Tongue

Besides eating, avian tongues play other roles in the life of a bird. Some of those roles are described here: courtship behavior, gular fluttering and singing.

3.1 Courtship Behavior

There are a few birds where the tongue plays a minor role in courtship behavior. For example, along with other courtship displays, both the male Grey-headed Silverbill and Magpie Mannikin will quiver their protruded tongue towards the female. (del Hoyo 2011)

When displaying, Darters use their hyoid horns to stretch the gular sac. (wikipedia, Darter 2014)

3.2 Gular Fluttering

Birds will flutter the gular area (area that joins the lower mandible to the neck) when overheated to reduce internal heat. When the muscle along each hyoid horn contracts it flexes the horn and causes the gular skin to flutter. The bird's beaks are slightly gaped, but do not move during the fluttering. In the case of the Horned Owl, the tongue moves forward and backward in synchrony with the flutter. (Bartholomew 1968) It has been reported that gular fluttering may account for 35% of the heat loss of a chicken.
(http://www.ornithology.com/Lectures/Metabolism.html)

3.3 Singing

Most birds have a syrinx (or two) which plays a similar role as a human's larynx. Sounds are created by airflow over the syrinx and it is believed that these sounds are modified by structures such as the mouth cavity, beak and tongue. How much effect the tongue and these other structures have is still being investigated but it is not believed that the tongue has a large role in singing. (Podulka 2004) However, one experimental study showed that in Parrots tongue placement caused significant frequency changes. (Beckers 2004) Olsen (Olsen 2011) reports that a spoon-shaped tongue is important in parrot speech for the talking species.

4 Conclusions and observations

There is great diversity in the shape of avian tongues. They are thick/thin, long/short, triangular, tubular, bushy, smooth, or covered with spines. For some birds the tongue plays an important role in eating, while in others the tongue is unimportant. Even with this diversity, most bird tongues are relatively simple and are not specialized to eating only one type of food.

While there is quite a bit of research available on the tongues of birds, there are still many species where little is known about their diet and the role that the tongue, or even the beak, plays in the acquisition and consummation of food. Part of the problem is the difficulty is studying the tongue in live birds. New methods, such as high speed photography, are helping to solve some of these questions, but many challenges remain. For example, Rico-Guevera and Rubega used high speed photography to understand how hummingbirds acquire nectar (Rico-Guevara 2011), but they acknowledge that they don't yet understand how hummingbirds swallow the nectar.

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