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Mini review

Function-related morphological characteristics and specialized structures of the avian tongue

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SUMMARY

As a reflection of different life styles and environment, the tongue of vertebrates, which plays a major role in the intake and swallowing of food, displays significant morphological differences. The gross form and microscopic structure of the avian tongue differ greatly according to lifestyle. The avian tongue plays a fundamental role in many functions such as capturing, filtering, sucking and manipulating food in order to compensate absence of subsidiary organs like teeth in the oropharyngeal cavity. Variations in lingual papillae play an important role in feeding of birds, as they represent a structure similar to teeth in the upper and lower beaks and can be used to hold and direct food in the oropharyngeal cavity. Tongues of birds exhibit common as well as varying anatomical characteristics in terms of surface morphology, structure and topographical distribution of lingual papillae as well as distinct specialized structures, epithelial layers, taste buds and lingual glands. This review evaluates the important morphological peculiarities of the tongue in birds, focusing on the relationship between anatomical features and feeding functions.

1. Introduction

Since birds have no teeth, the functions of organs in the oropharyngeal cavity are confined to prehension and the incomplete breaking up of their food. The development of the upper and lower jaws of birds into beaks and the absence of teeth, lips and cheeks with functional muscles limit the manipulation of foods (Nickel et al., 1977; King and McLelland, 1984; Reece, 1996). The lingual apparatus, which is one of the organs in the oropharyngeal cavity and responsible for the regulation of these functions, consists of various elements that influence one another mechanically, such as cartilaginous and bony skeletal elements, muscles and salivary glands (Homberger and Meyers, 1989).

The floor of the oral cavity, which is a trench-like depression between the mandibular rami of the lower beak, accommodates the tongue in many avian species. Its shape is adapted to that of the lower beak and, thus, the tongue assumes a variety of forms (Hodges, 1974; Nickel et al., 1977; Erdoğan et al., 2012b) (Fig. 1). The outline of the tongue is basically triangular, and the tongue fits perfectly on the lower beak, in galliform and passerine birds (Iwasaki and Kobayashi, 1986; Homberger and Meyers, 1989; Dehkordi et al., 2010; Jackowiak et al., 2010; Parchami et al., 2010a; Erdogan and Alan, 2012; Erdoğan et al., 2012a,b). The tongue is elongated and oval, with many projections, in lamellirostrate birds (King and McLelland, 1984; Iwasaki et al., 1997; Hassan et al., 2010; Jackowiak et al., 2011); lance-shaped in near-passerine birds, such as woodpeckers and sapsuckers (Goodge, 1972; Bock, 1999; Emura et al., 2009a); tassled, fringe-shaped or brush-like in nectarivorous birds (Rand, 1961, 1967; Paton and Collins, 1989; Wiens, 1992; Downs, 2004; Rico-Guevara and Rubega, 2011); elongated and bulky in birds of prey (Jackowiak and Godynicki, 2005; Emura et al., 2008a,b; Erdoğan et al., 2012a); mushroom-like in cormorants (Jackowiak et al., 2006); rasp-like, with enormous projections or a barbed appearance, in penguins (Samar et al., 1995; Kobayashi et al., 1998); and relatively small with no functional projections, in ratite birds (Jackowiak and Ludwig, 2008; Crole and Soley, 2009a,b, 2010; Guimarães et al., 2009; Santos et al., 2011; Tivane et al., 2011) (Fig. 1).

There have been many investigations of tongue anatomy in birds, with a focus on species-specific morphological details. The various shapes of the tongues and lingual structures themselves have been analyzed by gross anatomical observation with conventional dissection techniques, by light microscopy, by scanning and transmission electron microscopy and by histochemical methods. Such research has focused mainly on the surface morphology of the avian tongue; on the structure and topographical distribution of lingual papillae and other functional projections or specialized structures; on the chemical and functional features of epithelial layers, taste buds, lingual glands and movable lingual elements,

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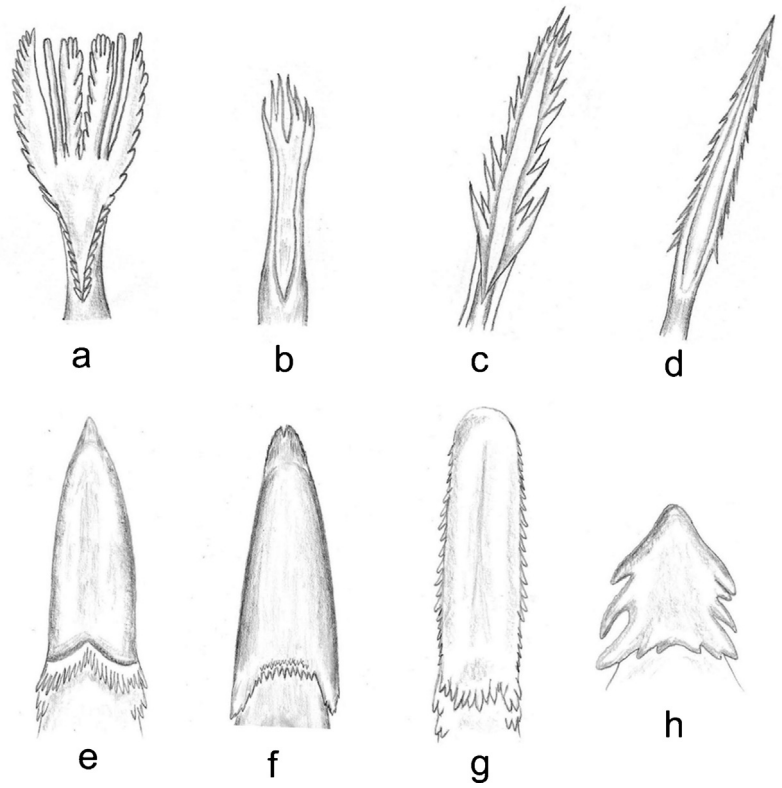

Fig. 1. Diagrams of some tongue shapes. (a) Brush-like or fringe-shaped tongue (nectarivorous birds, flowerpeckers-Passeriformes), (b) tube-like tongue (nectarivorous birds, Zosteropidae), (c) tube and brush-like tongue (sunbirds-Passeriformes), (d) lancet-shaped tongue (woodpeckers-Piciformes), (e) dagger-like or triangular tongue (chicken-Galliformes), (f) bifid apex in tongue (magpie-Passeriformes), (g) oval shaped tongue (goose-Anseriformes), (h) star shaped tongue (emu-Struthioniformes).

such as the hyoid apparatus and muscles; and on physiological relationships between morphological and functional variations in these structures and feeding habits.

2. Functional and adaptational specialization is reflected by morphology

The avian tongues exhibit adaptations specific for the collection, manipulation and swallowing of foods (Sturkie, 2000; Harrison, 1964) (Tables 1 and 2). The diversity of feeding adaptations among birds is reflected in the form and function of their feeding apparatus, and morphological adaptations of avian tongues are also closely associated with discrete eating habits and lifestyle in different environments, in addition to the shape of the lower beak (Nickel et al., 1977; Emura et al., 2008a,b; Parchami et al., 2010a,b). If their environment changes organisms must adapt or specialize to survive. Thus, feeding adaptation in conjunction with specialization of the feeding apparatus, in particular the tongue, is essential for birds, which have very high metabolic activity and energy requirements as compared to other vertebrates.

2.1. Adaptation to collecting of foods

Specialization of the tongue for the collection of foods has resulted in many morphological variations, such as long, narrow and protrusible probes, spears, brushes and capillary tubes (King and McLelland, 1984) (Fig. 1). In birds whose tongues are used for collecting foods (Table 1), the tongue can be extended from the oropharyngeal cavity for this purpose. Such tongues typically have lateral barbs, needle-like processes at the lingual apex and a dorsal surface that is roughened by numerous spinous papillae (Fig. 1). The tongue may also be coated with sticky mucous secretions from the large salivary glands (King and McLelland, 1984; Bock, 1999; Sturkie, 2000; Emura et al., 2009a). A good example of such adaptation is the tongue of the woodpecker, which extends a considerable distance from the oropharyngeal cavity to catch insects and larvae inside trees (King and McLelland, 1984; Ryan, 2003) (Figs. 1 and 2, Tables 1 and 2). In the wrynecks (*Jynx*) and the woodpeckers, hyobranchial horns (or horns of the hyoid apparatus) are remarkably elongated and wind around the back of the skull (Fig. 2). Whereas in some species, such as the green woodpeckers (*Picus viridis*), two horns enter the right nasal cavity (Fig. 2), and the horns of wrynecks terminate in the left nasal cavity, horns of the orange-backed woodpeckers (*Reinwardtipicus validus*) are attached near the base of the bill (King and McLelland, 1984). In a few forms, such as the North American hairy woodpeckers (*Picoides villosus*), the hyoid horns do not enter the right nostril but, instead, encircle the right orbit (Goodge, 1972; Bock, 1999). The various species of woodpeckers differ in terms of the distances probed with their tongues to find food, from very short distances in sapsuckers (*Sphyrapicus*) to very long distances, as much as 10–12 cm, in green woodpeckers (*Picus*) and flickers (*Colaptes*) (Bock, 1999). It is likely that, in ancestral woodpecker species that began to seek grubs deeper in trees, those woodpeckers with mutations that increased growth of hyoid horns had a fitness advantage, being able to extend their tongues farther to reach prey. By contrast, the sapsuckers, for example, drill tiny holes in trees and then use their short tongues to eat the oozing sap on the tree's exterior and the insects that stick to it (Goodge, 1972; Ryan, 2003).

The tongues of most nectarivorous birds, such as flowerpeckers, honeyeaters, sunbirds and hummingbirds, are also usually highly protrusible and capable of being thrust in and out of flowers to harvest nectar, pollen and small insects (King and McLelland, 1984) (Table 1). Tongues of many nectarivores have specified morphological features, being split, fringed, curled or tubular, and are closely adapted to the geometry of the flowers on which they feed (Wiens,

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