DOI: 10.1478/C1A0901004

Atti della Accademia Peloritana dei Pericolanti
Classe di Scienze Fisiche, Matematiche e Naturali
ISSN 1825-1242

Vol. LXXXVII, C1A0901004 (2009)

GLYCOSAMINOGLYCANS IN THE TONGUE OF BIRDS

CONCETTA CALABRÒ,[a]* MARIA PIA ALBANESE,[a] CLARA BERTUCCIO,[a]
AND LILIANA RESTUCCIA[b]

ABSTRACT. We examined the literature to verify whether adaptations and modifications in the structure and glandular secretions of birds' tongues are related to habitat and can be ascribed to evolutionary processes. The data are discussed in relation to species taxonomy, following the Sibley and Ahlquist classification [C. G. Sibley and J. E. Alquist, *Philogeny and Classification of Birds. A study in molecular evolution* (Yale University Pres, New Haven, 1990)]. The following conclusions are drawn: gustatory papillae and taste buds are present in varying numbers in most species. The composition of gland secretions is also found to be variable. Proteic secretion is documented in *Larus modestus*, *Sula variegata*, *Fulica atra* only. Acid proteoglycans both with sulfomucins and carboxymucins, and also glycoproteins, are consistently found. Sialic and hyaluronic acids are found in many species. Our overview indicates that the presence or absence of gustatory papillae is related to adaptation processes that these structures undergo in response to environmental factors, and that the absence of front tongue glands can be ascribed to habitat and feeding habits. Referring to the Sibley and Ahlquist classification, proteins are present in the glandular secretion of less evolved species, whereas more evolved species exhibit a gradual decrease in proteins with the exception of hyaluronic acid, which is absent, and a progressive increase in glycoproteins and acid proteoglycans.

1. Introduction

Early studies on the tongue of birds were carried out only from the morphological and structural points of view [1, 2, 3]. In the second half of the twentieth century lingual secretion was also examined in order to solve problems concerning the physiology of taste, besides testing the structure of papillae, where present, and the lingual glands. The lingual secretion has also been studied [4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15]. The aim of the current study is to ascertain whether there is a relation between the type of diet and the chemical composition of the glandular secretion and whether the habitat can exert an influence on the structure of the tongue and on the chemical composition of the secretion. A study on the tongue of *Larus ridibundus* [8] and *Larus modestus* [14] showed substantial differences in the distribution of the lingual glands of two species which live in different habitats. More specifically, these differences were present in the anterior and posterior glands of *Larus ridibundus* and in the posterior glands only of *Larus modestus*, with a

ORDER	SPECIES
ANSERIFORMES	
CICONIFORMES	*Podiceps nigricollis* *Sula variegata* *Ardeola grayii* *Falco chiquera* *Halietus leucogaster* *Milvus migrans* *Larus ridibundus* *Larus modestus*
GALLIFORMES	*Coturnix coturnix*
CORACIIFORMES	*Alcedo atthis*
CUCULIFORMES	*Eudynamis scolopacea* *Centropus sinensis*
PSITTACIFORMES	*Psittacula cyanocephala*
APODIFORMES	*Apus affinis*
STRIGIFORMES	*Athene brama*
GRUIFORMES	*Amauronis phoenicurus* *Fulica atra*
PASSERIFORMES	*Turdus philomelus* *Turdus merula* *Nectarina asiatica* *Passer domesticus* *Garrulus glandarius*

TABLE 1. Birds belonging to AVES NEOGNATA under consideration in the present work.

presence of hyaluronic acid in the latter species. This led us to believe that the distribution and the secretion of the lingual glands are influenced by the habitat and by the way food is swallowed. The numerous studies carried out on the physiology of taste and on the histological and histochemical characteristics of the tongue with respect to habitat have not hitherto been considered in an evolutionary context. On this basis, we considered it of interest to examine modifications and adaptations of the tongue and the chemical composition of its secretions during evolution: from primitive birds to the more evolved species. In order to take into account the histological and histochemical features of the tongue's evolution, the data are here discussed in the Sibley and Ahlquist classification [16]. The tongues dealt with in the present overview belong to birds of the super order of Neognates.

2. Materials and Methods

In this paper we consider the results obtained by several authors on the birds' tongue. As mentioned above, we interpret them in an evolutional key, in the framework of the Sibley and Ahlquist classification. The classification is based on DNA-DNA hybridization studies and has been accepted by the British Ornithologists' Union (see Table 1).

3. Results

Several types of glands have been described in birds' toungues, that differ in the chemical composition of the secretion: glands producing a proteic secretion; type I glands secreting glycoproteins, sulfomucins, sialomucins, no hyaluronic acid; type II glands secreting glycoproteins, sialomucins and sulfomucins, and hyaluronic acid; type III glands secreting sulfomucins only; type IV glands secreting glycoproteins, acid proteoglycans with sulfomucins, and sialic acid; type V glands secreting glycoproteins, acid proteoglycans with sulfomucins and carboximucins; type VI glands secreting glycoproteins and acid proteoglycans with carboxylic, and sulphate groups, sialic and hyaluronic acids, no glycogen; type VII glycoproteins, proteoglycans with carboxylic and sulphate groups, and hyaluronic acid.

No species of the Anseriform Order was examined. Among the Ciconiformes, *Podiceps nigricollis Sula variegata*, *Ardeola grayii*, *Falco chiquera*, *Haliaetus leucogaster*, *Milvus migrans*, *Larus ridibundus*, and *Larus modestus* were considered.

- *Podiceps nigricollis* [12]. The tongue is triangular shaped, covered with keratinized stratified epithelium in the anterior half, with rare gustatory papillae and taste buds located in the posterior part of the tongue near to the glandular ducts. Anterior and posterior type I glands, with cells secreting glycoproteins, sulfomucins, sialomucins, no hyaluronic acid, are observed (see Table 2 where all the data that we have collected have been summarized).
- *Sula variegata* [15] lives on the southern coast of Peru. It has a triangular shaped tongue with concavity on the ventral face and two lateral bulges. It is covered with pluristratified cuboidal epithelium. It has no gustatory papillae and taste buds and has lingual posterior glands only. There are two types of glands, one secreting basic proteins with $-NH_2$ and $-S-S$ radicals, the other, type VI glands, secreting glycoproteins and acids proteoglycan with carboxilic and sulphate groups, sialic and hyaluronic acids, but no glycogen.
- *Ardeola grayii* [12] has a triangular tongue keratinized in the anterior half. Rare gustatory papillae anteriorly and taste buds posteriorly are present. In the tongue anterior and posterior glands are shown. The former are ramified, the latter alveolar. The anterior ones are type I glands, with cells secreting glycoproteins, sulfomucins without hyaluronic acid and sialomucins; the posterior ones are type III glands, with cells secreting sulfomucins only.
- In *Falco chiquera* [7] the anterior part of the tongue is keratinized and has only rare gustatory papillae and rare taste buds in the posterior half. It has anterior and posterior type IV glands with cells secreting glycoproteins, acid proteoglycans with sulfomucins, and sialic acid.
- In *Haliaetus leucogaster* and *Milvus migrans* [7] the triangular-shaped tongues are keratinized in the anterior half, with rare gustatory papillae and taste buds posteriorly located. In the tongues of both species anterior ramified glands and posterior simple tubular glands have been described. The anterior glands of *Haliaetus leucogaster* are type II glands with cells secreting glycoproteins, sialomucins, sulfomucins, and hyaluronic acid; the posterior ones are type I glands, with cells

secreting glycoproteins without hyaluronic acid, sulfomucins, sialomucins, and type III glands, with cells secreting sulfomucins only.

- In *Milvus migrans* the anterior glands are type I glands secreting glycoproteins, sulfomucins without hyaluronic acid, and sialomucins; the posterior ones are type III and IV glands.
- *Larus ridibundus* [8] and *Larus modestus* [14] have been examined. The former species lives in the Straits of Messina, the latter in the southern coast of Peru.
- The tongue of *Larus ridibundus* is keratinized in the apical portion, without papillae and taste buds, with anterior and posterior glands. The anterior glands are type V glands secreting glycoproteins, acid proteoglycans with sulfomucins, and carboximucins; the posterior ones are type I glands. The tongue of *Larus modestus* has no papillae and taste buds. Lingual ramified glands are found posteriorly. It is possible to distinguish glands secreting mostly basic proteins with groups $-NH_2$; type VII glands secreting glycoproteins, acid proteoglycans with sulphate and carboxylic groups and hyaluronic acid are also revealed.

In the Galliformes *Coturnix coturnix* has been examined [15]. In their tongue there are rare gustatory papillae, numerous taste buds, and anterior and posterior type VII glands.

Among the Coraciformes *Alcedo atthis* [7] has been examined. The tongue has rare papillae and taste buds, and anterior and posterior lingual glands. In both there are only type I glands secreting glycoproteins, sialomucins and sulfomucins without hyaluronic acid.

Among the Cuculiformes two species, i.e. *Eudynamis scolopacea* and *Centropus sinensis*, have been examined [12]. Both species have a keratinized tongue at the tip, rare papillae and rare taste buds, tubular anterior glands and simple tubular posterior glands. The anterior glands of *Eudynamis scolopacea* are type II glands with cells secreting glycoproteins, sialomucins and sulfomucins with hyaluronic acid, and type III glands secreting sulfomucins. The posterior glands are type II and type IV glands. In *Centropus sinensis* both anterior and posterior glands are type I glands with cells secreting glycoproteins, sulfomucins without hyaluronic acid and sialomucins.

Psittacula cyanocephala, out of Psittaciformes, and the Apodiformes *Apus affinis* [12] have been examined. The tongue in both species have rare papillae and taste buds, located in the posterior portion, and anterior and posterior glands. In *Psittacula cyanocephala* there are type I glands. In *Apus affinis* the anterior glands are ramified tubular type I glands with cells producing glycoproteins, sulfomucins, sialomucins and type III glands producing sulfomucins; the posterior glands are type III and type IV glands.

Among the Stringiformes *Athene brama* [7] has been considered. The tongue, keratinized proximally, has rare gustatory papillae and taste buds in the posterior part only and anterior and posterior type I glands.

Among the Gruiform *Amauronis phaenicurus* and *Fulica atra* have been examined.

- The tongue of *Amauronis* [12] is keratinized in the anterior half with rare papillae and taste buds. There are anterior and posterior glands: the former ones are type I and type III glands; the posterior ones are type IV glands.
- In *Fulica atra* we have shown that the tongue is strewn with papillae and taste buds, the lingual glands are tubular and are located only posteriorly. There are two

kinds of glands: the first type secreting basic proteins with amine groups $-NH_2$ and with $-S-S$ radicals, tyrosine; type VII glands are also found, secreting glycoproteins, acid proteoglycans with sulfomucins, carboxymucins, and hyaluronic acid.

Five species of the order of the Passeriformes have been examined: *Turdus phylomelus*, *Turdus merula*, *Nectarina asiatica*, *Passer domesticus*, and *Garrulus glandarius*.

- We have shown that the tounge of *Turdus phylomelus* [11] has rare papillae, numerous taste buds, and type IV glands only in the posterior portion.
- In *Turdus merula* [15] rare gustatory papillae and numerous taste buds are present; the secretion of the anterior and posterior type V glands is composed of glycoproteins, acid proteoglycans with sulfomucins and carboximucins.
- In *Nectarina asiatica* [12] the tongue has rare papillae and buds, and both anterior and posterior glands: the anterior ones are type I glands producing glycoproteins, sialomucins, and hyaluronidase resistant sulfomucins; the posterior ones are type I and IV glands.
- In *Passer domesticus* [7] the tongue has rare papillae and no taste buds, and anterior and posterior type I glands.
- In *Garrulus glandarius* [13] the tongue has no papillae and no taste buds; it has posterior type IV glands secreting glycoproteins, acid proteoglycans with sulfomucins and carboximucins, and sialic acid.

4. Discussion

The results obtained by studies on the tongue of birds reveal that gustatory papillae and taste buds are present in variable quantity in almost all the species examined. They are absent only in the following five species: *Sula variegata*, *Larus modestus*, *Larus ridibundus*, *Fulica atra*, and *Garrulus glandarius*. The absence of gustatory papillae both in less evolved species (*Sula variegata*) and in more evolved ones (*Garrulus glandarius*) is probably due to an adaptation process of these structures within the environment. The anterior lingual glands are absent only in *Sula variegata*, *Larus modestus*, *Fulica atra*, *Turdus philomelus*, and *Garrulus glandarius*. The absence in *Sula variegata* and *Garrulus glandarius* is not due to an evolutionary factor but to a regression in relation to their habitat. This can be deduced by the fact that every animal species lives in its own ecological niche, where it finds favourable environmental conditions for its development and where it adapts. In two species, *Sula variegata* and *Larus modestus*, both living in the same habitat (the southern coast of Peru), we observed the absence of anterior glands.

In *Larus ridibundus*, living in the Straits of Messina, both anterior and posterior glands are present; in *Larus modestus*, posterior glands only. The difference between these two species of seagull might be due to their respective habitat and to the way they capture their prey. As far as the chemical composition of the secretion produced by the lingual glands is concerned, we compare it on the posterior glands because only these are present in all the species that have been examined. We have not always been able to detect the presence of proteins in this secretion, and we observed instead that these substances are detectable histochemically in a few species like *Sula variegata*, *Fulica atra*, and *Larus modestus*; they are absent in other species such as *Turdus philomelus*, *Turdus merula*, *Coturnix coturnix*,

BIRDS	GUSTATORY PAPILLAE	TASTE BUDS	ANTERIOR GLANDS	POSTERIOR GLANDS
Podiceps nigricollis	rare	rare	Type I	Type I
Sula variegata	no	no	absent	Proteic secretion Type VI
Ardeola grayii	rare	rare	Type I	Type III
Falco chiquera	rare	rare	Type IV	Type IV
Haliaetus leucogaster	rare	rare	Type II	Type I−III
Milvus migrans	rare	rare	Type I	Type III−IV
Larus ridibundus	no	no	Type V	Type I
Larus modestus	no	no	absent	Proteic secretion Type VII
Coturnix coturnix	rare	numerous	Type VII	Type VII
Alcedo atthis	rare	rare	Type I	Type I
Eudinamis scolopacea	rare	rare	Type III	Type II−IV
Centropus sinensis	rare	rare	Type I	Type I
Psittacula cyanocephala	rare	rare	Type I	Type I
Apus affinis	rare	rare	Type I−III	Type III−IV
Athene brama	rare	rare	Type I	Type I
Amauronis phaenicurus	rare	rare	Type I−III	Type IV
Fulica atra	numerous	numerous	absent	Proteic secretion Type VII
Turdus phylomelus	rare	numerous	absent	Type IV
Turdus merula	rare	numerous	Type V	Type V
Nectarina asiatica	rare	rare	Type I	Type I−IV
Passer domesticus	rare	absent	Type I	Type I
Garrulus glandarius	no	no	absent	Type IV

TABLE 2. Gustatory papillae, taste buds, and glands of birds under consideration in the present work.

and *Garrulus glandarius*. In all the species examined the glycosaminoglycans are always present, especially in the more evolved species, as well as the acid proteoglicans containing both sulfomucins and carboximucins; sialic acid is detected in all except in *Fulica atra*, *Larus ridibundus*, *Turdus merula*, and *Coturnix coturni*x. Hyaluronic acid has been documented in *Sula variegata*, *Fulica atra*, *Larus modestus*, *Eudynamis scolopacea*, and *Coturnix coturnix*.

The substances involved in a possible evolutionary process of the glandular secretion are the proteins, the glycosaminoglycans, and the hyaluronic acid among the acid proteoglicans. In fact we can verify that the substances present in the glands of the less evolved specie are the proteins; in the passage towards a more evolved species we observe their gradual decrease and the corresponding increase of glycosaminoglycans, while hyaluronic acid – whose presence is detected only in a few species – is always absent in the more evolved species. However, these conclusions are only based on a general view because data on species belonging to different orders, both Paleognati and Neognati, are still unavailable.

References

[1] S.D. Roper, "The cell biology of Vertebrate taste receptors", *Annual review of Neuroscience* **12**, 329-353, (1989).

[2] W. Bath, "Die Geschmacksorgane der Vogel und Krokodile", *Arch. Fur Biontologie* **1**, 5-47 (1906).

[3] K. Heidrich. " Die Mund - Schlundkopfhohle der Vogel und ihre drussen", *Morph. Jahrr.* **37**, 10-69 (1908).

[4] C. J. Duncan., "The sense of taste in birds", *Ann. Appl. Biol.* **48**, 409-414 (1960).

[5] S. Fujii and T. Tamura, "Histochemical studies on the Mucin of the chicken: salivary glands", *J. Fac. Fish Anim. Husb. Hiroshima Univ.* **6**, 354-355 (1966).

[6] M. N. Nalavade, "Studies on mucopolysaccharides of the tongue", Ph.D. Thesis, Department of Zoology, Shivaji University, Vidyanagar, Kolhapur 416004, Maharashtra, India (1975).

[7] M. N. Nalavade and A. T. Varute, "Histochemical studies on the mucins of the Vertebrate tongues XI : Histochemical analysis of mucosubstances in the lingual glands and taste buds of some birds", *Acta Histochem.* **60**, 18-31 (1977).

[8] G. Zaccone, "Mucopolisaccharides histochemistry of the avian tongue histochemical features of the lingual glands in *Larus ridibundus* L", *Acta Histochem.* **60**, 67-77 (1977).

[9] M. P. Albanese Carmignani, and C. Calabrò, "Aspetti strutturali ed istochimici delle ghiandole linguali dell'uccello acquatico *Fulica atra* (Ralliformi, Rallidae)", *Atti 47º Convegno UZI Boll. Zool. Suppl.* **46**, 6-7 (1979).

[10] M. P. Albanese Carmignani, and C. Calabrò, "Aspetti strutturali ed istochimici delle ghiandole linguali dell'uccello acquatico *Fulica atra* (Ralliformi, Rallidae)", *Riv. Biol. Norm. Patol.* **5**, 3-16 (1979).

[11] M. P. Albanese Carmignani, and C. Calabrò "Studio strutturale ed istochimico della lingua e delle ghiandole linguali di *Turdus philomelus* Brehm (Aves, Turdidae)", *Riv. Biol. Norm. Patol.* **7**, 3-12 (1981).

[12] J. N. Gaikwad, "Studies on mocosubstances of vertebrate tongues", Ph.D. Thesis, Department of Zoology, Shjvaji University, Vidyanagar, Kolhapur 416004. Maharashtra, India (1981)

[13] F. Cannata, "Studio strutturale ed istochimico della lingua e delle ghiandole linguali di *Garrulus glandarius*", *Riv. Biol. Norm. Patol.* **8**, 45-57 (1982).

[14] M. P. Albanese Carmignani, and L. Acosta Pomar, "Aspetti istochimici delle ghiandole linguali di *Larus modestus* L", *Mem. Biol. Mar. Ocean* **13**, 175-193 (1983).

[15] M. P. Albanese Carmignani, F. Cannata, C. Calabrò, and L. Acosta Pomar, "Studio istochimico del secreto prodotto dalle ghiandole linguali di *Sula variegata* L, *Turdus merula* L, *Coturnix coturnix* L (Aves)", *Atti 51º Convegno UZI Boll. Zool. Suppl.* **53** 18 (1986).

[16] C. G. Sibley and J. E. Alquist, *Philogeny and Classification of Birds. A study in molecular evolution* (Yale University Pres, New Haven, 1990).

[a] Dipartimento di Biologia Animale ed Ecologia Marina
Università degli Studi di Messina
Contrada Papardo
98166 Messina, Italy

[b] Dipartimento di Matematica
Università degli Studi di Messina
Contrada Papardo
98166 Messina, Italy

* To whom correspondence should be addressed. E-mail:concetta.calabro@unime.it

Presented: 14 May 2008; published online: 29 June 2009.