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Functional Morphology of the Tongue in the Nutcracker (*Nucifraga caryocatactes*)

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The nutcracker *Nucifraga caryocatactes* belongs to a group of bird species that use their beak and tongue as tools for obtaining food, such as seeds from hard-to-reach cones or nuts from shells. The aim of the present study, carried out with a scanning electron microscope, was to define the morphological features of the tongue of the nutcracker, which seems to be adapted to its environment through specific methods of obtaining food. One of the characteristic features of the nutcracker's tongue is the unique structure of the anterior part of the tongue, which has two long and highly keratinized processes – a product of the renewable keratinized layer of the epithelium covering the ventral surface of the tongue. These dagger-like processes, which are a modified "lingual nail," take a major role in levering up and shelling seeds, which are transported over the short sulcus-shaped body of the tongue. A unique feature of the nutcracker's tongue is the groove separating the body from the root. Two rows of highly keratinized, mechanical, conical papillae are located at the junction of the body and the root. These papillae are mechanically protective elements for passing food particles in the form of seeds. Among lingual glands, only the posterior lingual glands on the root of the tongue have been observed. Their secretion agglutinates dry food before it is swallowed. Results of the present study indicate that the nutcracker's tongue is an efficient tool resembling a lever that is helpful in shelling seeds.

Key words: tongue, lingual papillae, lingual nail, nutcracker, scanning electron microscopy (SEM)

INTRODUCTION

The wide variation in the morphology of the beak and structures of the oral cavity in birds is related to the adaptation of strategies for obtaining food, feeding methods, and different kinds of food and climate conditions (Iwasaki, 2002). The microstructure of the tongue has been examined in many species of birds, e.g., in parrot, penguin, little tern, owl, white-tailed eagle, hen, quail, and bean goose (Homberger and Brush, 1986; Iwasaki and Kobayashi, 1986; Homberger and Meyers, 1989; Iwasaki, 1992; Iwasaki, 1997; Kobayashi et al., 1998; Jackowiak and Godynicki, 2005; Rossi et al., 2005; Jackowiak et al., 2006; Emura and Chen, 2008).

In terms of their anatomy, avian tongues show a fundamental similarity to the divisions of the mammalian tongue (apex, body, and root). Large species-specific differences in shape and size are thought to be modifications allowing the tongue to function as a specialized tool for obtaining and processing food (McLelland, 1975, 1979; Komarek et al., 1986; Vollmerhaus and Sinowatz, 1992). This specialization may lead to a remarkable variety of surface structures of the mucosa, as in Anatidae, which are specialized in grazing, pecking, and filtration of food particles (van deer Leeuw et al., 2003; Bels, 2006). Contrastingly, in species that swallow food whole, such as cormorant or stork, there is a great structural reduction of the tongue (Campbell and Lack, 1985; Jackowiak et al., 2006). In ostriches, a short tongue is the main organ secreting mucus, which prevents oral mucosa from drying (Jackowiak and Ludwig, 2008).

Bird tongues are characterized by a wide variety of mechanical papillae useful for the manipulation of food, filtration of liquid, and transport of food particles on the lingual surface. Another specific feature displaying variations are the types of mucosa epithelium, such as keratinized and/or non-keratinized types.

The aim of this work is to characterize the morphology of the tongue of the nutcracker tongue (*Nucifraga caryocatactes)*, a bird belonging to the Corvidae family. This species is omnivorous. The composition of their diet depends on the food source available, which in the spring, summer, and autumn consists of invertebrates, small vertebrates, fruit and

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seeds, but in winter only seeds (Cramp 1988, Cichocki 2005, Rolando, 2008). In the literature dealing with the behavior of the nutcracker, Cramp (1988) states that it has an unusually forked tongue, which enables the bird to obtain seeds in a specific way, especially the seeds of the conifers thus resembling the feeding behaviour of woodpeckers and crossbills (Cramp 1988; Osiejuk 1991). The present macro- and microscopic study is focused on characterizing the microscopic features of the nutcracker's tongue, as well as explaining how its adaptation to obtaining food.

MATERIAL AND METHODS

The microscopic study was conducted on the tongue of adult nutcracker, donated by the Poznań Zoological Garden. Immediately after dissection, the tongues were fixed in 10% formalin and then documented with a digital camera (Sony DSC – S75, Japan) with lens attachment (Carl Zeiss, Vario-Sonnar, Germany).

For observations under a scanning electron microscope (SEM), fixed samples of particular parts of the tongue were dehydrated in a series of ethanol (70%–99.8%) and acetone, and subsequently dried to a critical point with CO_2 (Critical Point Dryer K850, Emitech, England). All specimens were mounted on aluminium stubs covered with carbon tabs, sputtered with a 15 nm layer of gold (Sputter Coater S 150B, Edwards, England) and observed under the SEM ZEISS 435 VP (Oberkochen, Germany) at an accelerating voltage of 15–20 kV.

RESULTS

The tongue of the nutcracker is approximately 2.4 cm long. Three main parts can be distinguished: the apex, body, and root (Fig. 1). The apex of the tongue terminates in two flexible processes, which are 0.7 mm long. The apex and sharp ends of the processes are directed downwards (Fig. 2). The overall length of the apex and the body of the tongue is 1.2 cm. The root of the tongue is located at a lower level than its body, and has a length of approximately 0.5 mm (Fig. 2). A difference in the color of some parts of the tongue was noted on macroscopic observation. The processes and the strand of conical papillae at the end of the root of the tongue have a darker brown color (Fig. 1, 2).

Our observations of the nutcracker showed that the epithelium covering the ventral surface of the tongue produces a highly keratinized layer, which is projects towards the front of the apex and splits into two slightly concave processes on its edge (Fig. 3). The width of these two flat plates at the point of junction with the surface of the apex is between 1.8 mm and 2.5 mm. In some places they undergo stratification into two parts (Fig. 4). The surface cells of the processes peel off in the form of lengthwise squamae (Fig. 5). The epithelium of the dorsal surface of the apex of the tongue overlaps the processes and the polygonal surface cells undergo

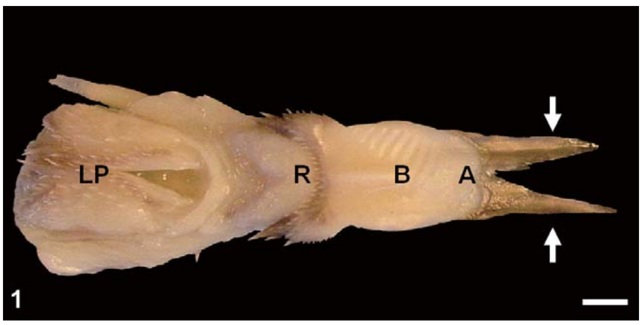

Fig. 1. Dorsal view of the tongue of the nutcracker. Arrows show two elongated processes of the apex. A, apex, B, body, R, root, LP, laryngeal prominence. Scale bar, 3 mm.

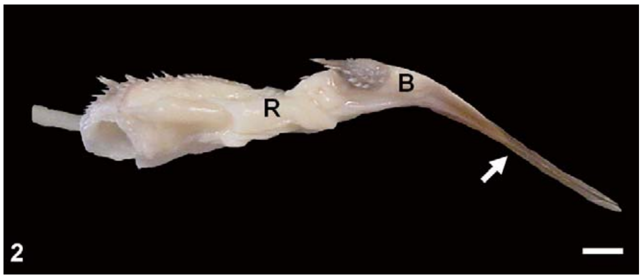

Fig. 2. Lateral view of the tongue of the nutcracker. Arrow shows elongated processes, pointed diagonally, B, body, R, root. Scale bar, 3 mm.

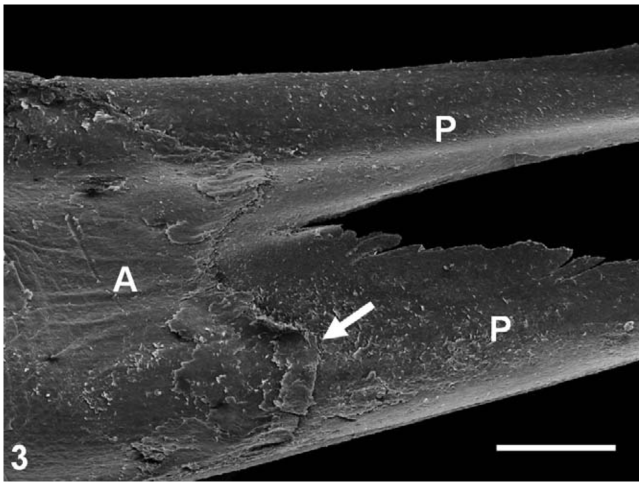

Fig. 3. Dorsal view of the lingual apex of the nutcracker. White arrow shows layer of dorsal epithelium of the apex, which overlaps the base of processes. A, apex of the tongue, P, keratinized processes. Scale bar, 1 mm.

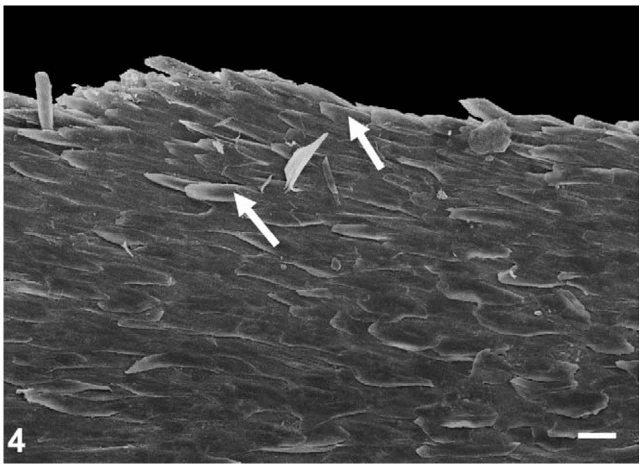

Fig. 4. Lateral view of the top of both processes undergoing splitting into two parts (white arrow). Scale bar, 100 μm.

exfoliation (Fig. 3).

Fig. 6 shows the body of the tongue with two flat entoglossal cartilages, which are located parallel to each other. They form the internal frame of the tongue. Entoglossal cartilages become narrower in the apex region, and disappear at the junction of the apex and horny processes. Spaces between cartilages fill out the fibrillar connective tissue. The height of epithelium on the dorsal surface of the body is 167 μm, and on the ventral surface between 127 μm and 178 μm. The horny layer is 65.3 μm thick. The surface cells of the epithelium of the body of the tongue are polygonal and the outlines of nuclei can be viewed at higher magnification (Fig. 7). Lateral surfaces of the apex and body, along their entire length, are raised before the lamina propria of the mucosa (Fig. 6). In addition, a crest has been observed on the smooth surface of the body in the medial region. The edges of the posterior part of the body of the tongue widen towards the sides, forming two lateral conical papillae (Fig. 8). The base of these papillae is approximately 1.4 mm wide, and is covered with numerous small secondary papillae (Fig. 9). The body of the tongue just before the lateral papillae is 4.8 mm wide. Two crests of conical papillae are formed on the posterior edge of the body of the tongue (Fig. 8). The anterior crest is composed of smaller conical papillae, which are 287–319 μm high. The sharp ends of these papillae are ragged and directed slightly upwards (Fig. 10). The posterior crest is composed of larger conical papillae, which are between 565 μm and 720 μm high. Pointed ends of the papillae are directed downwards and towards the tail, and predominate over the flat surface of the root of the tongue (Fig. 9, 10). Conical papillae forming both crests are covered with a horny layer undergoing exfoliation (Fig. 10).

Between the body and the root, there is a cleft 230 μm wide, into the middle of which the ducts of the mucous

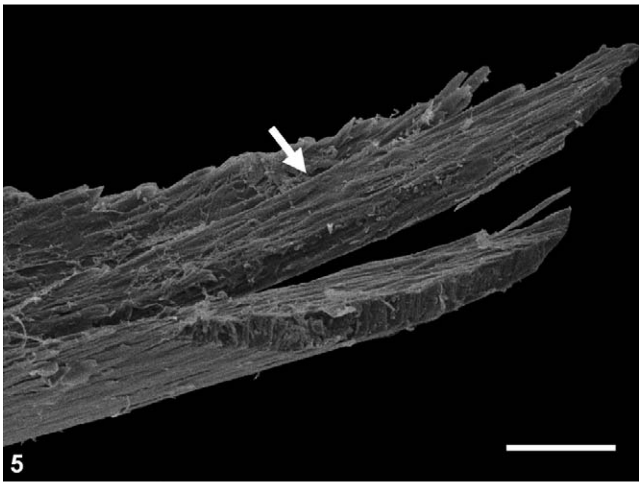

Fig. 5. A higher magnification view of the surface of the keratinized processes. White arrows show single cells exfoliate in form of lengthwise squamae. Scale bar, 30 μm.

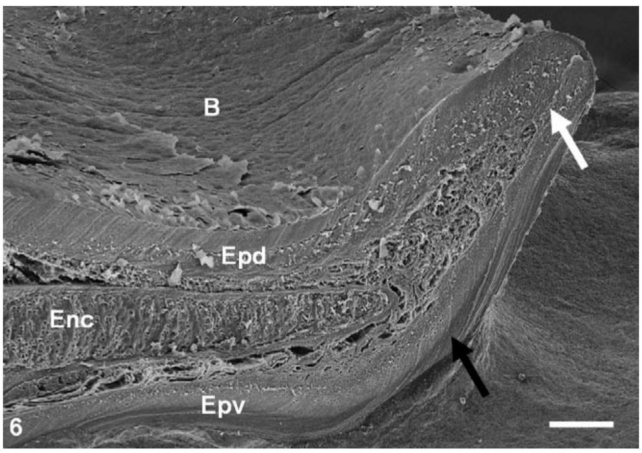

Fig. 6. Cross-section through the body of the nutcracker's tongue. White arrow shows raised edge of the body of the tongue. Black arrow points to the keratinized layer of the ventral epithelium. B, body of the tongue, Epd, dorsal epithelium, Epv, ventral epithelium, Enc, entoglossal cartilage. Scale bar, 200 μm.

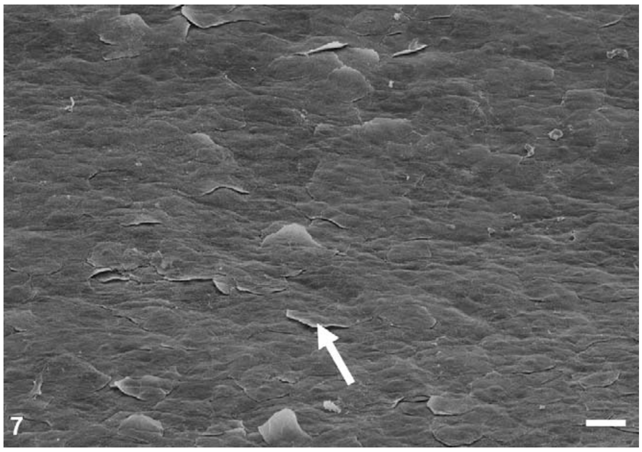

Fig. 7. A higher magnification view of the dorsal epithelium of the body of the tongue. White arrow shows single exfoliated cells with cell nuclei. Scale bar, 30 μm.

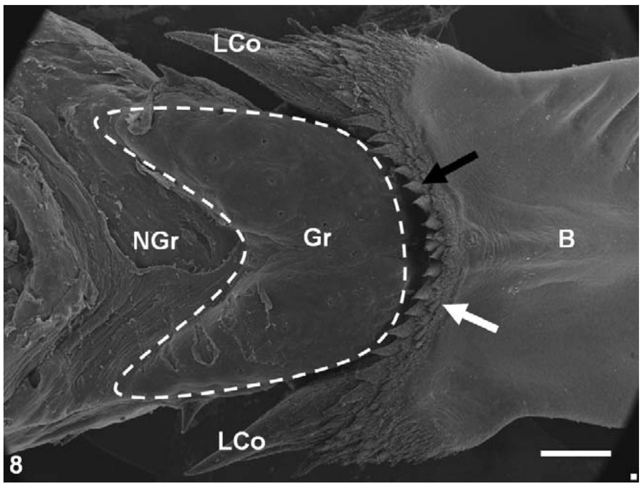

Fig. 8. Dorsal view of the posterior part of the body and root of the tongue. White arrow shows anterior crest of conical papillae. Black arrow shows posterior crest of conical papillae. B, body of the tongue, Lco, large conical papillae, dotted line marks area of glandular part of the root (Gl), Ng, non-glandular part of the root of the tongue. Scale bar, 1 mm.

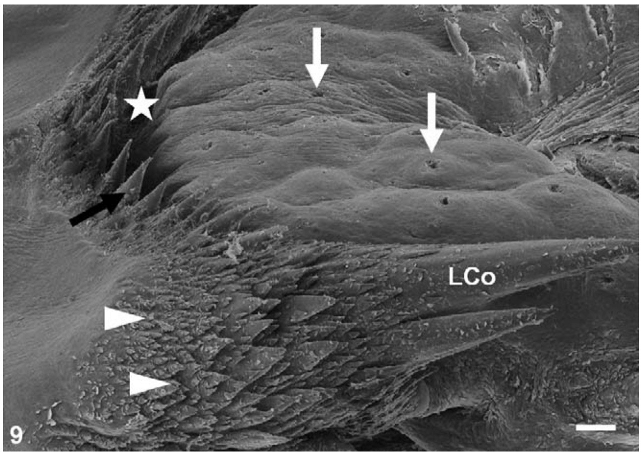

Fig. 9. Lateral view of the posterior part of the body and root of the tongue. Black arrow shows posterior crest of conical papillae. White arrows point to the openings of the mucous glands. Star shows the cleft between body and root of the tongue. Arrowheads show small secondary papillae on the large conical papillae (Lco). Scale bar, 300 μm.

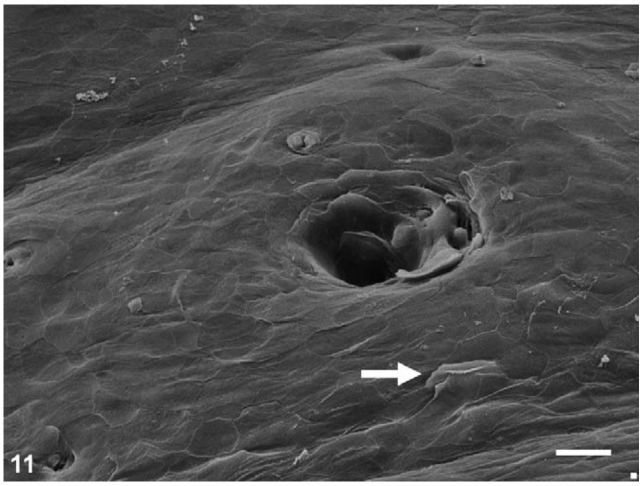

Fig. 11. Higher magnification view of the opening of the mucous gland on the surface of the lingual root . White arrow shows exfoliated cells with cell nucleus. Scale bar, 30 μm.

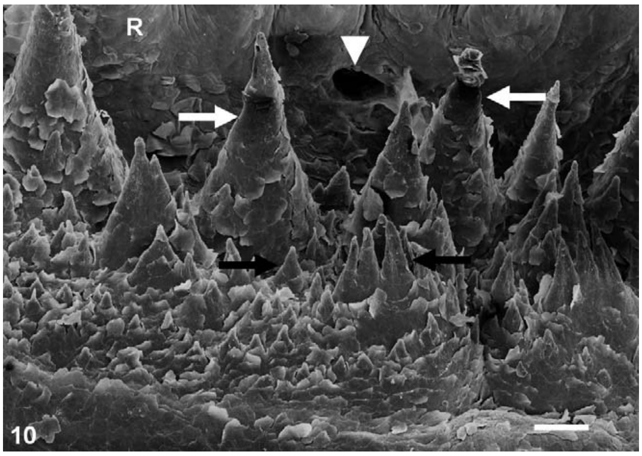

Fig. 10. Frontal view of the double crest of conical papillae on the posterior part of the tongue body. Black arrows show anterior crest. White arrows show posterior crest of conical papillae. Arrowheads show the openings of the mucous gland in the cleft. R, root of the tongue. Scale bar, 100 μm.

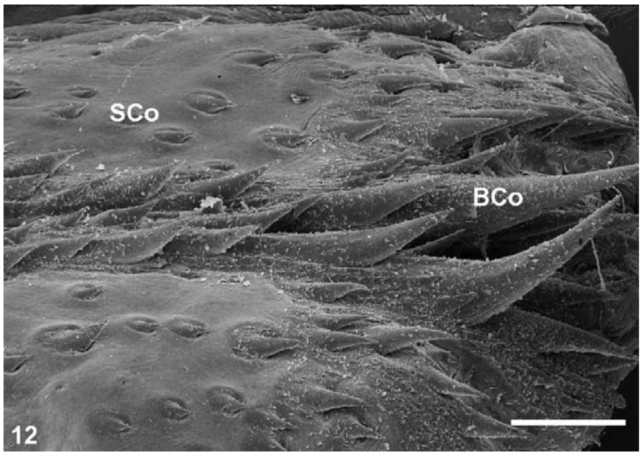

Fig. 12. Dorsal view of the surface of the laryngeal prominence. Bco, big conical papillae, Sco, small conical papillae. Scale bar, 1 mm.

glands of the root open (Fig. 9). Two parts can be distinguished in the structure of the root of the tongue: the glandular part, which is crescent-shaped, and the non-glandular part, which borders the laryngeal prominence (Fig. 8). There are about mucous gland 19 openings in the glandular part, which average 78 μm in diameter. Cells on the surface are polygonal and undergo exfoliation (Fig. 11). The laryngeal prominence is covered with large conical papillae, distributed medianwise along the laryngeal cleft and with numerous small conical papillae, which are distributed irregularly (Fig. 12).

DISCUSSION

The tongue of the nutcracker maintains the typical anatomical structure for vertebrates, i.e. the division of the tongue into three parts, i.e., apex, body and root, whereas the morphology and proportions of the individual parts are species-specific. The features that are specific in this respect include a short apex with a pair of long keratinized processes whose length exceeds the size of the tongue, and a short body of the tongue that is separated from the root by a distinct groove. To date, Iwasaki has described a similar structure in the little tern (Iwasaki, 1992), belonging to the Corvidae family, whose diet consists of fish, and which possesses a strong beak as a prehensile organ. Iwasaki (1992) reported an extension of the anterior part of the tongue up to 6/7 of the tongue length and a slight bifurcation of the apex.

The side view of the nutcracker's tongue reveals an interesting geometry of the tongue, directed towards the bottom of the beak cavity, forming sharp-ended and slightly concave dagger-like keratinized plates. This anterior structure suggests that the nutcracker's tongue is a specialized organ that, together with its beak, enables the bird to shell the seeds of conifers. The method of extraction of seeds from cones is similar to methods of feeding used by the great spotted woodpecker (Osiejuk 1991, 1994, 1998), which places cones picked in an "anvil," such as a crevice in a stone or in the trunk of a tree. A similar method is used by nutcrackers for hazelnuts and acorns (Cramp 1988, Cichocki 2005). In the first phase, the nutcracker breaks or partially breaks off the outer scales of the husk of the cone with its hard beak and then strips the remaining parts of the husk with the lower part of the beak, thus exposing the seeds that adhere to the base of the husk. Using the keratinized processes of the lingual apex, the bird levers the seeds out of the claw-like base of the seed wing (Cramp, 1988). Apart from seeds, the nutcracker also feeds on insects, e.g. wasps and bees, which it rubs against branches of trees in order to remove the sting, before swallowing them whole. While searching for insects under the bark and in the crevices of trees, the nutcracker hits the bark with its beak, like a woodpecker, and the processes makes it possible to acquire food discovered in this way.

To date, there have been no reports of the microstructure of the tongue apical processes in other birds. Macroscopic observations of the long processes allow us to define them as grooves in the mucosa, which have been described in vertebrates as a bifurcated or bifid tongue (Emura and Chen, 2008; Iwasaki, 1992). However, the SEM images showed that the processes are the modified structures of the epithelium of the ventral surface of the tongue that correspond to the description of the keratinized layer defined in birds as the "lingual nail". The "lingual nail" is defined as a single keratinized plate that most often takes the shape of the apex (Homberger and Brush 1986; Homberger and Meyers, 1989; Jackowiak and Godynicki, 2005). Only in geese and ducks has this "lingual nail" been observed to protrude slightly beyond the edge of the apex of the tongue (Jackowiak et al., 2009). Due to the significant hardness of this keratinized layer, we presume its function is protective, possibly even similar to an external skeleton, in tongues that are lacking entoglossal cartilage in the apical region. The division of the flat, common keratinized layer into two processes results in the structure of the anterior part of the tongue being filled with two parallel cartilages of the hyoid apparatus. Splitting the ventral keratinized layer takes place following the pattern of oval cartilages, and is likely to affect the inner structure of the keratinous layer. Formation of the concave surface of the processes and the rolling-up of the edges of the processes are also caused by the resilience of keratin. The presence of a pair of cartilages of the hyoid apparatus is rare in birds, as usually only a single cartilage extends to the apex of the tongue. Double cartilages have been observed in the penguin, but no processes of the "lingual nail" type have been found in that species (Kobayashi et al., 1998).

The nutcracker feeds mainly on seeds of 2–5 mm in diameter of Norway spruce, mountain pine, Scots pine, and larch, which grow as large as 1 cm, especially in the Swiss pine. The size of pine seeds corresponds to the width of the keratinized processes and the seeds fit into the space formed by the groove-like body of the tongue. Birds usually accumulate seeds in the widening of the oesophagus behind the larynx, transport, and bury them in different places, creating a larder for the winter. This behavior may be environmentally adaptive for the nutcracker, as seeds are a high-energy source of food.

The conical papillae on the posterior region of the body and the laryngeal prominence are structures of mechanical importance during transport of food over the lingual surface. The papillae are usually tilted towards the oesophagus and are holding elements, which prevent the food from moving back towards the beak cavity. The arrangement of conical papillae on the arch plan has been described in many species of birds, although the number of the so-called giant conical papillae is generally smaller than in the nutcracker (Iwasaki and Kobayashi, 1986; Iwasaki, 2002; Jackowiak and Godynicki, 2005). The presence of giant papillae with smaller secondary papillae has not to our knowledge been described previously in birds. A unique structural feature of the nutcracker's tongue is the perpendicular groove between the body and root of the tongue. The groove is situated above the junction of the hyoid bones and the more flexible hyoid cartilages. Because of this division, two segments of the mucosa are formed which can be moved further from, or closer to, each other, which probably removes the possible tensions in the mucosa related to the fact that the tongue extends significantly from the beak cavity, and that the anterior part with the processes is bent while seeds are being shelled from cones.

In other birds, e.g. in the chicken, partridge, pheasant, white-tailed eagle, bean and domestic goose, the body of the tongue with conical papillae is situated higher than the root of the tongue (Iwasaki and Kobayashi, 1986; Homberger and Meyers, 1989; Jackowiak et al., 2004; Rosii, 2005). An exceptional case has been reported in the ostrich, in which the mucosa of the body forms a smooth fold which pulls over 1/3 of the root of the tongue (Jackowiak and Ludwig, 2008).

The passage of dry food over the surface of the tongue is supported by lingual glands on the root. The secreted mucus moisturizes and agglutinates seeds, making them easier to transport to the oesophagus. In birds, the anterior and posterior lingual glands in the mucosa are usually distinguished (Iwasaki and Kobayashi, 1986; Kobayashi et al. 1998; Liman et al. 2001; Jackowiak and Godynicki 2005; Rossi et al. 2005). In the majority of species, the anterior glands are situated in the body of the tongue, and the posterior glands are distributed in the root of the tongue. In the nutcracker, we have found a reduction of the anterior lingual glands. The reduction of lingual glands in the nutcracker is connected with the thin lamina propria around the entoglossal cartilages.

The results of the observations of the structure of the nutcracker's tongue and their consistency with behavioural observations allows us to conclude that the nutcracker tongue is characterized by a unique morphology of the apex and the posterior part of the body, and functions as a highly specialized organ used for shelling seeds and the acquisition of insects and their larvae.

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