

THE AUK

A QUARTERLY JOURNAL OF
ORNITHOLOGY

VOL. 90

JULY 1973

No. 3

MORPHOLOGY OF THE SUBLINGUAL POUCH AND TONGUE MUSCULATURE IN CLARK'S NUTCRACKER

WALTER J. BOCK, RUSSELL P. BALDA, AND STEPHEN B. VANDER WALL

THE food harvesting and storing behavior of many species of crows and jays is well-known to ornithologists, although little is known about subsequent utilization of these stores. The habits are best developed in the two species of nutcracker (*Nucifraga*: Corvidae) that gain their common and scientific names from their habit of opening nuts and pine cones to obtain the enclosed seeds. Harvesting, transporting, storing and use of pine seeds and hazelnuts by the Eurasian Nutcracker (*Nucifraga caryocatactes*) has long been known (Swanberg 1951, 1956; Turcek and Kelso 1968; Löhrl 1970). This species carries seeds in an expandable sublingual pouch that was discovered over 100 years ago, but apparently was described in detail first by Portenko (1948). Far less is known about Clark's Nutcracker (*Nucifraga columbiana*). This species is known to harvest pine seeds and to feed seeds to its young (Mewaldt 1956). Davis and Williams (1964:10) infer, without citing any authority, that Clark's Nutcracker stores seeds for winter use. Aside from a brief statement by Richmond and Knowlton (1894:305), no one had reported Clark's Nutcrackers carrying seeds, and we could find no mention in the literature of a sublingual pouch in this species.

During the course of an ecological-behavioral study of Clark's Nutcracker, Vander Wall and Balda (MS) discovered that these birds harvest, transport, and then store pine seeds in a communal caching area. The birds used the seeds during the next breeding season as adult food (e.g. for courtship feeding and reproductive energy) and to feed their young. Vander Wall and Balda also discovered that these birds carry seeds in an expandable sublingual pouch. Preliminary dissections showed that the sublingual pouch in Clark's Nutcracker is similar to that Portenko described for the Eurasian Nutcracker. Moreover, it was immediately clear that the sublingual pouch is a critical morphological

feature in these birds' seed harvesting-storage behavior. The entire yearly cycle of Clark's Nutcracker is attuned to their manner of using pine seeds which, with a number of attendant morphological and behavioral traits, comprises an adaptive syndrome of seed storage and utilization. We decided to analyze all morphological, behavioral, and ecological aspects of seed use by Clark's Nutcracker to obtain as complete an understanding as possible of this intriguing syndrome. This paper treats the sublingual pouch and tongue musculature. Ecological and behavioral information are taken from Vander Wall and Balda (MS) unless otherwise cited.

The large sublingual pouch in *Nucifraga columbiana* poses several interesting morphological questions in addition to the necessary description of its morphological form and its function. It is a novel feature in the Corvidae, being an adaptation associated with the seed storage and utilization complex in nutcrackers. Yet food transportation and storage is widespread among the Corvidae (Turcek and Kelso 1968) and the question arises of the possible evolutionary antecedents of the nutcracker sublingual pouch in other corvids. Equally interesting is that the sublingual pouch varies from a flat diverticulum when empty to a large, bulging sack when filled with seeds. The full sublingual pouch is a large structure that dominates the entire sublingual region of the head in terms of space requirements. Hence the pouch has primary influence over neighboring morphological features in terms of space demands and partly in terms of shape requirements (Dullemeijer 1958); surrounding structures exert less influence in this respect. Hence other structures in the sublingual region must conform to the morphological demands the pouch imposes. Determination of the exact manner and degree to which the sublingual pouch impinges on surrounding features would help answer the question of the morphological interactions between different features during evolutionary change. The effect of the sublingual pouch on the tongue musculature is especially interesting because of their close morphological proximity, because the selection forces acting on the pouch and on the tongue muscles can be separated clearly, and because modifications in the tongue muscles in *Nucifraga* from the typical corvid condition (e.g. *Corvus*) and from that seen in another pine seed transporting and storing species, the Piñon Jay (*Gymnorhinus cyanocephalus*), can be ascertained empirically.

MATERIALS AND METHODS

Specimens of *Nucifraga columbiana* and of *Gymnorhinus cyanocephalus* were preserved in 10% formalin. Nutcrackers with empty pouches and with pouches filled with seeds were obtained for comparative study of the tongue muscles under different conditions of the pouch. Both males and females were collected, as were

several birds of the year. Attempts to expand the pouch in a few specimens were not successful. The cotton wadding used to stuff the pouch stuck in the mouth and expanded the oral cavity, not the pouch. Anyone repeating our experiment must take care to lift the tongue out of the way and to place wadding material directly into the pouch below the tongue.

Detailed dissections were performed on a series of 10+ specimens of *Nucifraga columbiana*, one of which had its sublingual pouch stuffed with seeds. Comparative studies were made on the sublingual pouch and tongue muscles of one specimen of *Nucifraga caryocatactes*, two specimens of *Gymnorhinus cyanocephalus* and previous dissections of *Corvus*. *Gymnorhinus* was chosen because this bird also gathers, carries, and stores pine seeds (Balda and Bateman 1971, Ligon 1971), but does not possess a pouch. Description and figures of the tongue musculature of *Corvus* and *Gymnorhinus* are to be published elsewhere (Bock and Shear, MS).

All dissections were made under a dissecting microscope and using an iodine solution to stain the muscles (Bock and Shear 1972). Illustrations were drawn directly from the dissections with a camera lucida. The muscles were cleared of connective tissue and fat, properly arranged for the illustration, and then pinned in a wax-bottomed dish. Special care was taken to show the exact arrangement of the muscle fibers and the attachments of the muscles to bones and other features. Three dimensional arrangement of the muscles could be shown only in some figures; in others, some muscles were cut or displaced to expose others. Outlines of muscles are indicated with a heavy line and the fibers with a thinner line. Collagenous fibers are indicated by dashed lines.

Measurements of muscle fiber length and of gross physiological cross section (cross-sectional area of all muscle fibers) were made during dissection of the tongue muscles of specimens with empty pouches. These measurements, especially those of cross-sectional area are rough and serve only as an indication of the gross morphological parameters of the tongue muscles.

Description and terminology of the tongue muscles are based upon the general review of passerine tongue muscles by Bock and Shear (MS).

DESCRIPTION

SUBLINGUAL POUCH

The sublingual pouch occupies much of the space between the mandibular rami ventral to the tongue apparatus (Figures 1, 2, and 3). Its opening into the oral cavity is very broad and extends from the area anterior to the base of the corneous tongue, along the lateral sides of the tongue base, to terminate at a point opposite the posterior end of the glottis. The lateral openings appear in dorsal view as narrow slits between the tongue and the mandibular rami. In essence these slits separate the base of the tongue from the sides of the mouth and permit the entire corneous tongue to be raised. Thus a broad oval opening into the pouch is formed; the aperture extends posterior beneath the tongue as far as the glottis (e.g. anterior edge of the trachea). No constrictor muscle or other special mechanism to close the pouch exists, although the tongue could serve as a trap door over the broad aperture into the sublingual pouch. The pouch is a simple diverticulum of the floor of the mouth cavity, its walls being a continuation of the epithelium and mucosa lining the oral cavity. The pouch wall is not noticeably thicker than the mouth lining, but it may contain more collagenous and/or elastic fibers. The wall of the empty pouch is deeply wrinkled (Figure 2), which permits its expansion as the pouch is filled with seeds.

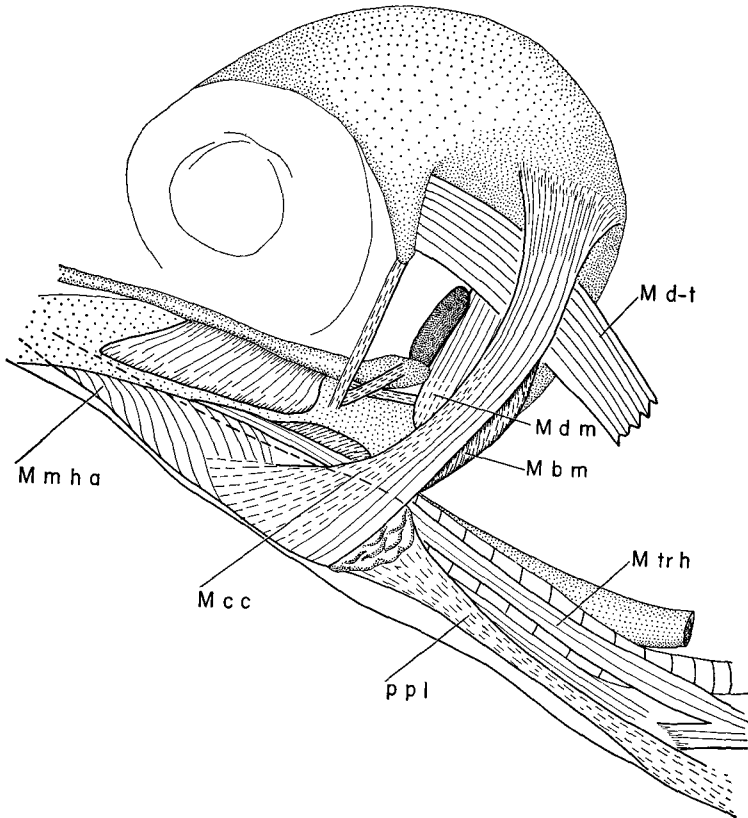


Figure 1. Lateral view of the head of *Nucifraga columbiana* to show the sublingual pouch (outline indicated partly with dashed lines) and the muscles (M m h a and M c c) supporting its ventral surface. Abbreviations for all figures: M b m, M. branchiomandibularis; M b m a, M. branchiomandibularis anterior; M b m p, M. branchiomandibularis posterior; M c c, M. cucullaris caput portion; M c g, M. ceratoglossus; M c h, M. ceratohyoideus; M d m, M. depressor mandibularis; M d-t, M. dermatemporalis; M hg a, M. hypoglossus anterior; M hg o, M. hypoglossus obliquus; M g g, M. genioglossus; M m h a, M. mylohyoideus anterior; M m h p, M. mylohyoideus posterior; M s h, M. serpihyoideus; M st h, M. stylohyoideus; M th h, M. thyrohyoideus; M tr h, M. tracheohyoideus; M tr l, M. tracheolateralis; p p l, posterior pouch ligament.

The pouch wall was examined under a dissecting microscope with high magnification for an intrinsic layer of muscular tissue. None could be seen; hence if the pouch has intrinsic musculature, it would probably be smooth muscle forming a sheet of microscopic thickness. No histological sections of the pouch wall were prepared.

The free posterior end of the pouch projects ventroposteriorly through M. mylohyoideus, separating this muscle into two parts (Figures 2 and 3). Ventrally

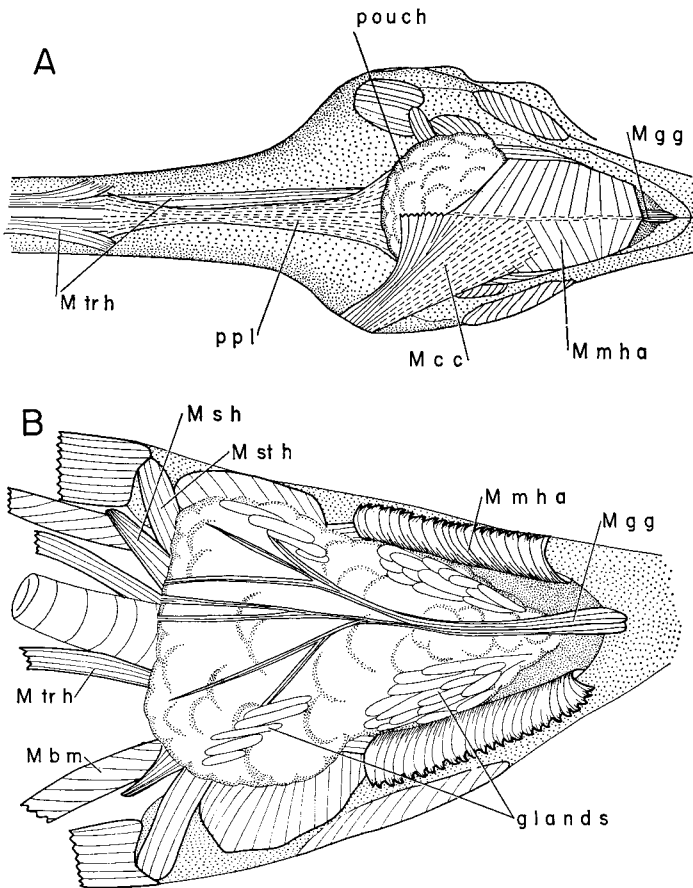


Figure 2. Ventral view of the head of *Nucifraga columbiana* to show the sublingual pouch. (A) Superficial muscles (M m h a and M c c) left in place except for the right half of the M c c, which was removed to expose the pouch. (B) The superficial muscles removed to expose the entire pouch. Note the branching M g g and the mandibular glands on the ventral surface of the pouch.

the pouch is covered by the *M. mylohyoideus* anterior and the caput portion of the *M. cucullaris* (Figures 1, 2A, and 9); these muscles and the skin support the pouch from below. No special ligaments or aponeuroses support the pouch; but because of its extensive opening into the oral cavity, the pouch wall gains considerable support from its long connection with the mouth floor. A long posterior ligament extends from the posterior end of the pouch, along the ventral surface of the trachea, to attach at the common insertion of the *M. dermatemporalis* and the *M. tracheolateralis* onto the skin of the neck (Figures 2A and 9). A thin band of muscle lies on the ventral surface of this ligament, connecting the posterior border of the caput portion of the *M. cucullaris* with the junction of the *M.*

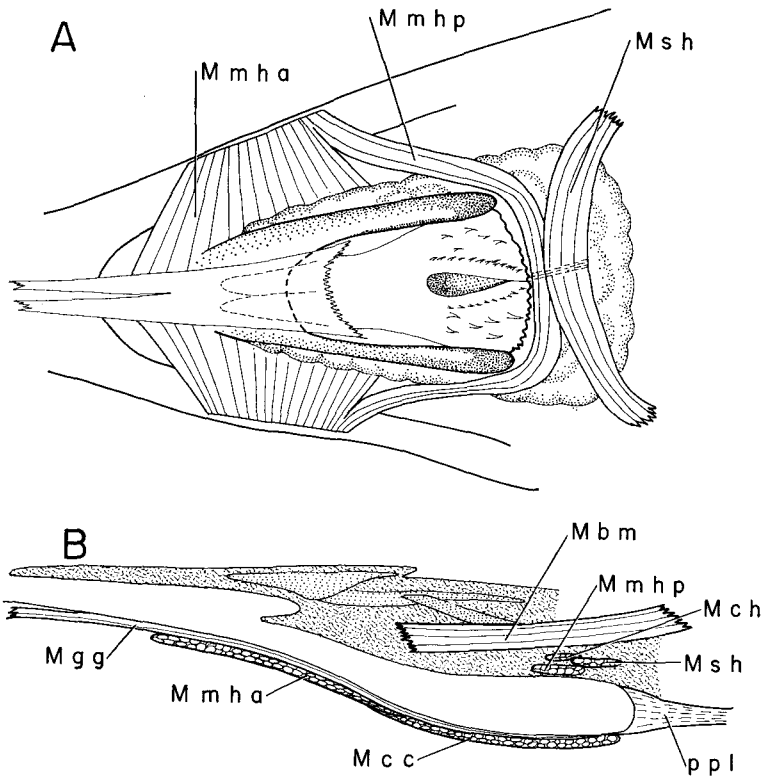


Figure 3. (A) Dorsal view of the mouth cavity of *Nucifraga columbiana* showing the opening of the pouch anterior and lateral to the tongue. Note the *M m h a* passing ventral to the pouch and the *M m h p* and *M s h* passing dorsal to the posterior end of the pouch. (B) Approximate midsagittal section of the tongue and pouch to show the position of the *M g g*, *M m h a*, and *M c c* ventral to the pouch and the position of the other tongue muscles (e.g. *M m h p*, *M c h*, *M s h*, and *M b m*) dorsal to the pouch. Note how the pouch passes between the two parts (*M m h a* and *M m h p*) of the *M. mylohyoideus*.

dermotemporalis and the *M. tracheochoyoideus*. This muscular layer is very thin and is easily destroyed when removing the skin.

The paired genioglossal muscles are closely affixed to the ventral surface of the pouch. Each muscle divides several times with the branches spreading over the ventroposterior surface of the pouch (Figure 2B). These muscle slips were traced until they faded into the tissue of the pouch wall.

All tongue muscles, except the *M. genioglossus*, the *M. mylohyoideus* anterior, and the *M. cucullaris* caput portion, lie lateral or dorsal to the sublingual pouch, as does the entire tongue skeleton. The posterior slip of the *M. mylohyoideus* curves about the lateroposterior corner of the pouch opening (Figure 3A) to insert on the medial raphe dorsal to the pouch. Comparison of Figures 2, 3, and 4, noting

especially the relationships shown in Figure 3B, clearly demonstrates the position of the sublingual pouch relative to the tongue musculature.

Two pairs of salivary glands lie on the ventral surface of the pouch (Figure 2B). Most likely these are mandibular glands. Although their ducts were not traced, they probably open into the pouch or into its anterior opening.

We found the sublingual pouch in all immature and adult nutcrackers we examined. It is already present in a juvenile only 8 weeks old. The pouch is equally well-developed in males and females and remains fully formed throughout the year. No signs of regression could be seen as has been reported for the sublingual pouch of auklets (Portenko 1948; Speich pers. comm.).

We examined the sublingual pouch (empty state) in one specimen of *Nucifraga caryocatactes* was similar in all essential details to that in *columbiana*. Because only one specimen of the Eurasian Nutcracker was available, no comparison of the relative sizes of the pouches in the two species of nutcrackers was possible. Our observations agree in most details with Portenko's (1948) description of the sublingual pouch in *caryocatactes*. He showed the opening of the pouch to be narrow; we suspect that the pouch opening in all forms of *caryocatactes* is similar to that in *columbiana*. We could find no evidence of a "sublingual frenum" that divides the lower part of the pouch into two halves; the pouch in the specimen of *caryocatactes* examined was undivided as were the pouches in all specimens of *columbiana* we examined.

TONGUE MUSCLES

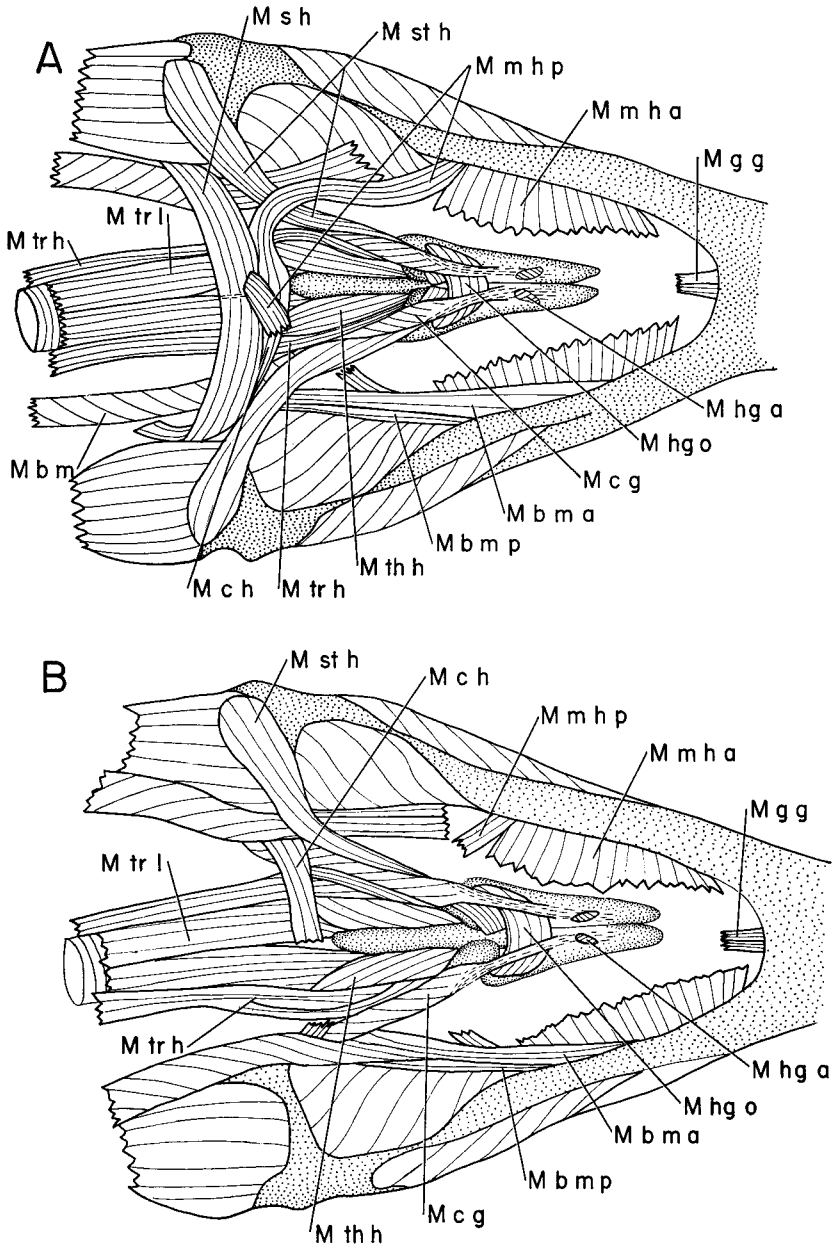
Each tongue muscle is described for *Nucifraga columbiana* with careful attention to possible modifications resulting from the evolution of the sublingual pouch. Because each muscle is illustrated in several figures, no individual reference to figures is made in the description of each muscle; the reader should examine Figures 4-8 before reading the muscle descriptions. Functions of the tongue muscles in *Nucifraga* are similar, in most respects, to those in *Corvus* as can be judged from their morphology. Hence no comments on function are included except for those muscles having special functions in *Nucifraga*; the reader is referred to the functional descriptions in Bock and Shear (MS). Comparisons of the morphology of each muscle are made between *Nucifraga columbiana*, *N. caryocatactes*, *Corvus*, and *Gymnorhynchus cyanocephalus*; the last lacks a specialized pouch but transports piñon seeds to storage areas in its esophagus.

A) M. cucullaris, caput portion (M c c)

Origin: Dorsolateral surface of the skull, dorsal to the origin of the M. depressor mandibulae (Figure 1).

Insertion: Midventral raphe with its contralateral reciprocal and by a broad thin aponeurosis onto the ventral surface of the posterior part of the M. mylohyoideus anterior (Figure 2A). The raphe of the M. cucullaris is a continuation of that of the M. mylohyoideus anterior; it is not bound to the ventral surface of the pouch.

Structure: A thin, straplike, parallel-fibered muscle lying superficial to other features in the posterior part of the head. Its fibers pass lateral (superficial) to the M. dermatotemporalis, and then cover much of the M. depressor mandibulae and the distal end of the hyoid horn. A thin broad aponeurosis extends from the anterior border of the muscle and spreads fanlike over the posterior half of the M. mylohyoideus anterior. The M. cucullaris covers (i.e. passes beneath) the posterior



portion of the sublingual pouch as a sling. Its fibers are very long, about 40 mm, so that the length of the entire sling is 80 mm.

The posteriormost fibers of the *M. cucullaris* appear to curve posteriorly near the ventral midline and continue as a narrow, thin strap of muscle along the mid-ventral line just under the skin to the junction of the *M. dermotemporalis* and *M. tracheohyoideus*. These fibers are hard to dissect because of their position just under the skin and their extreme thinness; they are also closely associated with the posterior pouch ligament and can be mistaken easily for collagenous fibers.

Function: Support of the posterior portion of the sublingual pouch. The long fibers of this muscle can stretch as the pouch fills with seeds and expands ventrally.

Comparison: Details of this muscle could not be observed in *caryocatactes*; it is present but may be less developed than that in *columbiana*. The caput portion of the *M. cucullaris* is very well developed in *Nucifraga*, far better than in any other passerine bird to our knowledge. It is so weakly developed in *Corvus* and *Gymnorhinus* that it cannot be readily dissected and demonstrated in these genera.

B) *M. mylohyoideus*

The expansion of the sublingual pouch has divided the normally continuous mylohyoideus muscle sheet into two distinct parts, which are united only at their origin (Figure 3A). Because they are morphologically and functionally distinct, each part is described separately.

1) *M. mylohyoideus anterior* (M m h a)

Origin: Fleshy in a thin line along the medial face of the mandibular ramus just ventral to its dorsal rim and just dorsal to the insertion of the *M. branchio-mandibularis*.

Insertion: On a midventral raphe with its counterpart ventral to the sublingual pouch.

Structure: A thin, parallel-fibered muscular sheet. The anterior fibers are transverse or slant slightly forward, while the posterior fibers angle sharply posteriorly, dorsal to the broad aponeurosis of the *M. cucullaris*.

The length of the midventral insertion of the *M m h a* is 25 mm while its origin measures 10 mm. The anterior fibers are 10 mm long (mandible to mid-ventral raphe) and the longest posterior fibers are 25 mm, thereby the sling of the combined muscles varies from 20 mm to 50 mm. The physiological cross section of the muscle is about 2 sq mm.

Function: Support of the anterior portion of the sublingual pouch. As the ventral wall of the pouch is continuous with the floor of the mouth, the function of the *M m h a* in *Nucifraga* is basically similar to that in other passerine birds.

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Figure 4. Ventral view of the entire tongue musculature of *Nucifraga columbiana* after removal of the sublingual pouch. (A) All muscles left in place, but with the insertions of the *M m h a* and *M g g* severed. (B) The *M s h*, the *M m h p*, and the left side of the *M c h* removed. Note that most tongue muscles are dorsal to the common insertion of the *M m h p*, *M s h*, and *M c h*, which lies dorsal to the pouch as shown in Figure 3B.

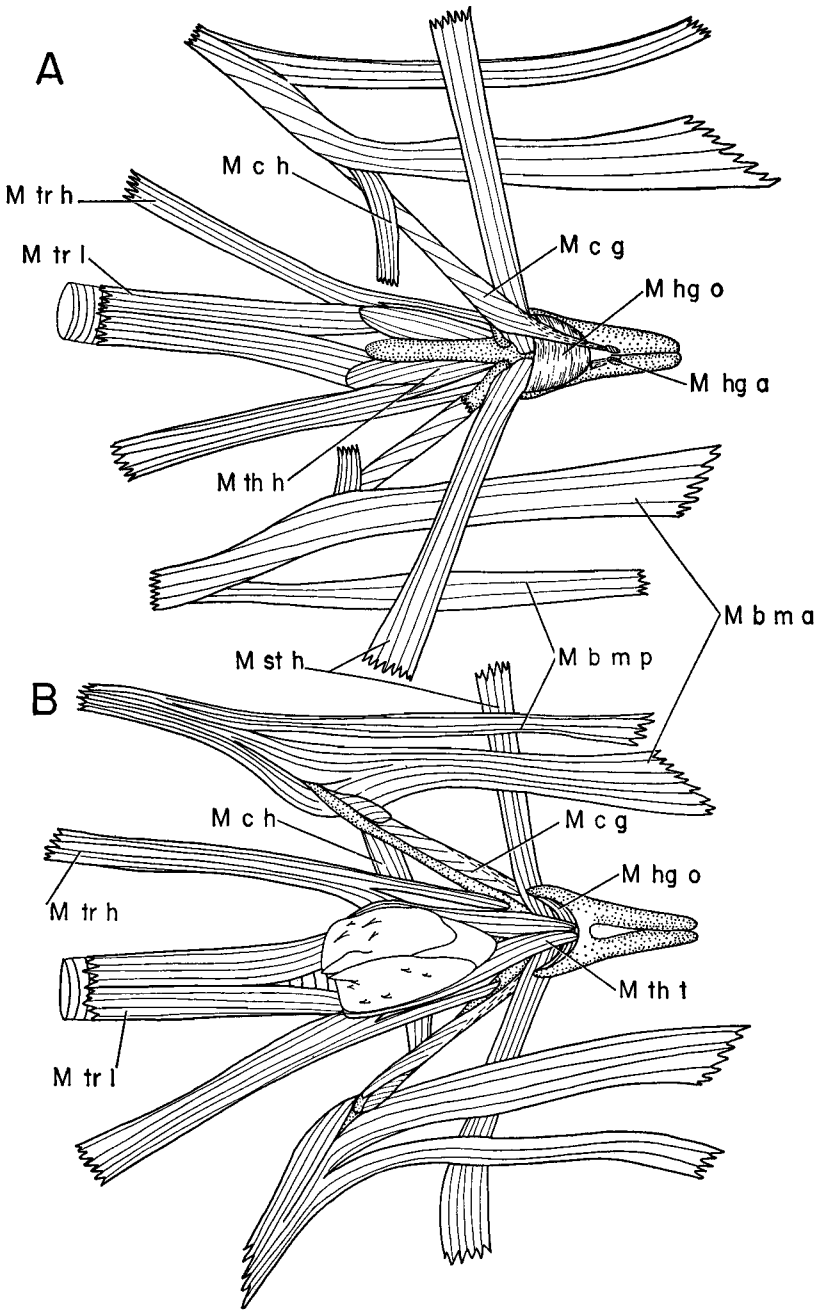


Figure 5. Tongue muscles of *Nucifraga columbiana* after removal of the tongue apparatus from the head. (A) Ventral view. (B) Dorsal view.

The long fibers, especially those of the posterior half, stretch as the pouch expands ventrally.

Comparison: See below under *M m h p*.

2) *M. mylohyoideus posterior* (*M m h p*)

Origin: From the medial face of the mandibular ramus, continuous with the origin of the *M m h a*.

Insertion: On a midventral raphe with its contralateral opposite, dorsal to the sublingual pouch (Figure 3B); this raphe is bound to those of the *M. serpihyoideus* and *M. ceratohyoideus*, but has no attachment onto the surface of the pouch (or the urohyale).

Structure: A thin, straplike, parallel-fibered muscle containing about 10% of the total fibers of the *M. mylohyoideus*. After leaving its origin and separating from the *M m h a*, the *M m h p* turns sharply and runs posteriorly, dorsal to the *M. branchiomandibularis* (Figure 4A), until it reaches the dorsolateral corner of the sublingual pouch (Figure 3A). At this point, the muscle curves medially to reach its insertion. In the specimen figured (Figure 4A), the inserting ends of the paired *M m h p* overlap each other and part of the *M. serpihyoideus*. In other specimens (Figure 3A), the two ends simply abut against each other at the midventral raphe and lie completely anterior to the *M. serpihyoideus*.

The *M m h p* is 2 mm wide at its insertion and has a fiber length of about 15 mm. Its physiological cross section is approximately 0.2 sq mm.

Function: An antagonist for the insertions of the *M. serpihyoideus* and the *M. ceratohyoideus* to preclude permanent posterior shift of these muscles. This function of the *M. mylohyoideus* also exists in all other passerine birds. Because of its curved path about the dorsolateral corner of the sublingual pouch, the *M m h p* may also function to maintain the position of the pouch or of the posterior end of its opening but this appears unlikely.

Comparison: The anterior and posterior parts of the *M. mylohyoideus* in *caryocatactes* are similar to those in *columbiana*. In *Corvus*, *Gymnorhinus*, and all other passerine birds, the *M. mylohyoideus* is a single continuous sheet of muscle fibers comparable to the combined anterior and posterior portions of this muscle in *Nucifraga*. The sublingual pouch simply divides the *M. mylohyoideus* into two parts in the nutcrackers and forces the fibers of the posterior part to deviate away from a straight course between their origin and insertion. Modification of the posterior portion appears to be great morphologically, but the basic function of this part of the *M. mylohyoideus* is little modified. The anterior part of the *M. mylohyoideus* in *Nucifraga* is scarcely modified from the corresponding portions in other passerine birds.

C) *M. genioglossus* (*M g g*)

Origin: Fleшы from the posterior edge of the mandibular symphysis with the medial borders of the paired muscles abutting.

Insertion: Fleшы on the other surface of the ventroposterior end of the sublingual pouch.

Structure: A straplike, parallel-fibered muscle with very long fibers in relation to fiber number. The muscle is about half as thick as broad and has the smallest number of fibers of all the tongue muscles except for the tiny *M. hypoglossis* anterior. Each genioglossus muscle divides several times with the branches diverging

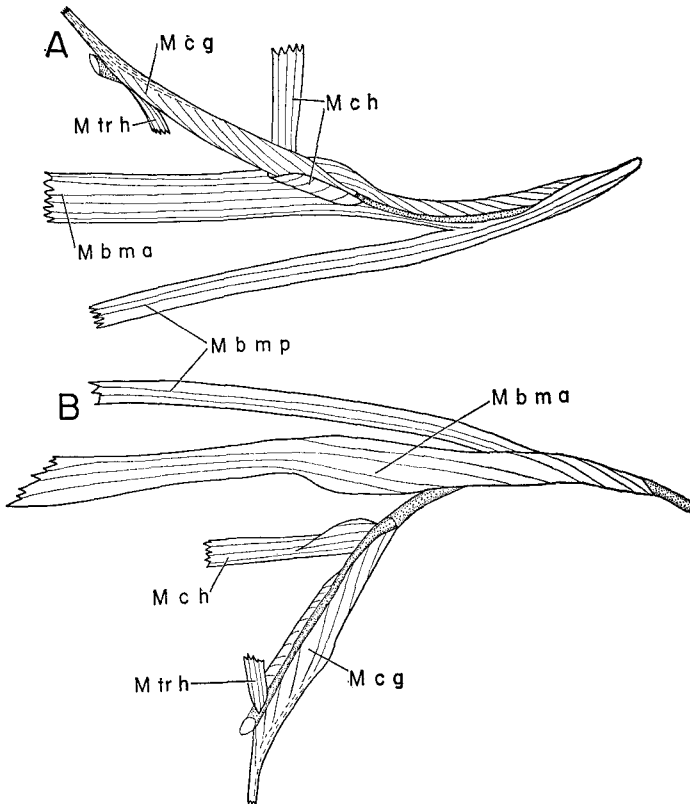


Figure 6. Hyoid horn and attached muscles of *Nucifraga columbiana*. (A) Approximate dorsal view with the anterior end to the left and medial surface toward the top of the figure. Insertion of part of the M st h onto the anterior end of the ceratobranchiale is not shown. (B) Ventromedial view with the muscles partly unwrapped from the hyoid horn.

over the surface of the pouch. None of the fibers of the M g g reach the tongue proper.

The length of the fibers in this muscle is 30–35 mm and the physiological cross section is approximately 0.3–0.35 sq mm.

Function: Apparently to return the empty pouch to its collapsed shape and position, although it does not provide the force to empty the pouch. The spread of the branches of the paired muscle is well-suited for collapsing the pouch.

Comparison: The M g g of *caryocatactes* is similar to that in *columbiana*. In all other passerine birds this muscle inserts on the tongue proper, either on the ventrolateral edge of the paraglossale, the anterior edge of the cricoid cartilage, the mucosa between the cricoid cartilage and the paraglossalia, or a combination of these insertions. The muscle is usually divided once just before its insertion except in those few forms having a single insertion. The size of the M g g varies

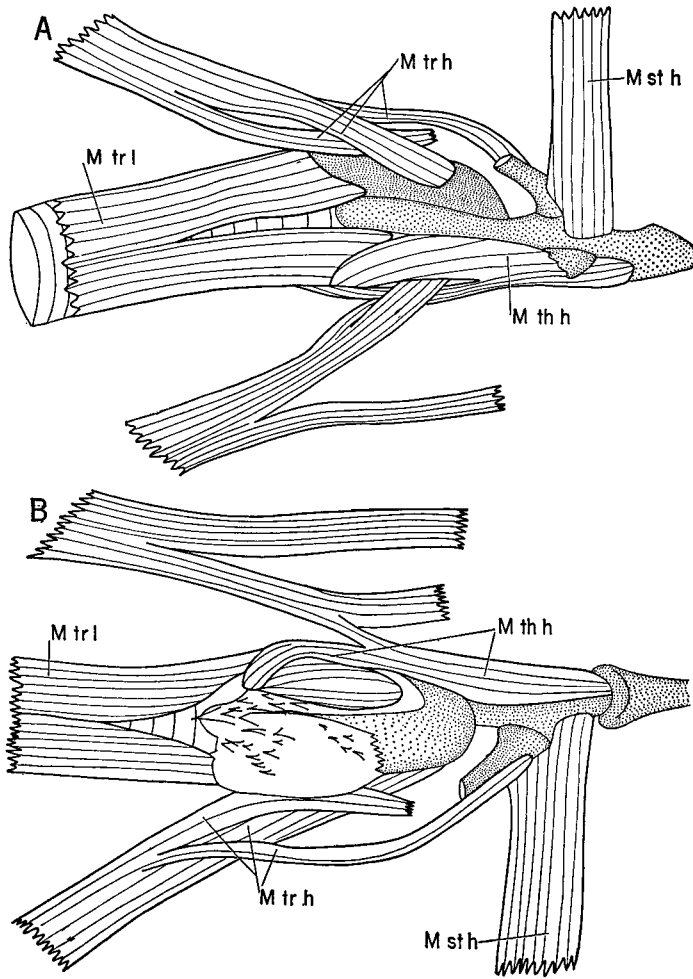


Figure 7. Medial tongue muscles of *Nucifraga columbiana* after removal of the paraglossalia and the hyoid horns. (A) Ventral view. (B) Dorsal view. The muscles have been removed or arranged to provide maximum clarity of all muscles.

considerably in passerines; it is relatively very small in corvids. Its insertion could not be ascertained with certainty in *Corvus* although it can be dissected easily in many small insectivorous and nectarivorous birds. In all other corvids examined, the *M g g* reaches the tongue and inserts somewhere in the mucosa between the paraglossalia and the cricoid cartilage. This muscle is relatively larger in *Nucifraga* than in other corvids, but it is not so well-developed relatively as in some heavy billed finches (e.g. *Hesperiphona vespertina*) or in some nectar feeders (e.g. *Arachnothera*, Bock, pers. observ.).

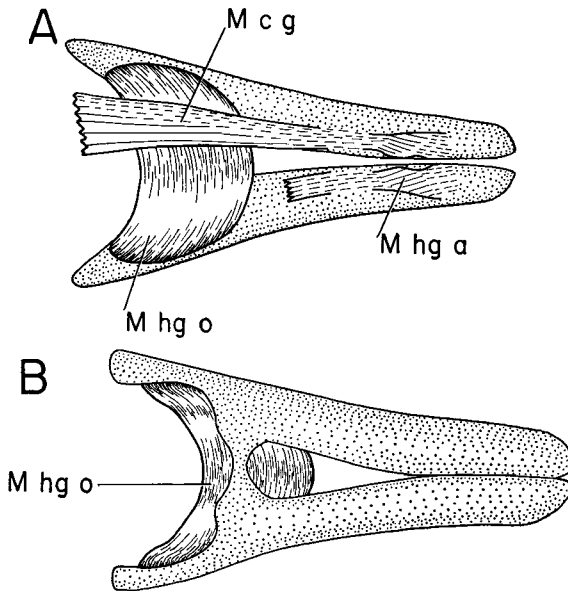


Figure 8. Paraglossalia and attached muscles of *Nucifraga columbiana*. (A) Ventral view. (B) Dorsal view.

The *M g g* of *Gymnorhinus cyanocephalus* is peculiar in that the normally paired muscles are completely united from their origin to a point about $\frac{3}{4}$ of the distance to their insertion. After splitting, each genioglossal muscle passes posterolaterally around the lateral surface of the tongue. Each muscle splits again into half, and the two thin slips curve lateral and dorsal to the *M. stylohyoideus* and *M. ceratoglossus*, and finally insert into the mucosa just anterior to the cricoid cartilage.

D) *M. serpihyoideus* (*M s h*)

Origin: Ventrolateral corner of the occipital plate medial to the origin of the *M. depressor mandibulae*.

Insertion: On a midventral raphe with its contralateral mate; the anterior end of this raphe is bound to that of the *M. mylohyoideus* posterior.

Structure: A thin, straplike, parallel-fibered muscle that broadens slightly at its insertion and is almost circular in cross section at its origin. The two muscles form a sling about the posterior part of the tongue apparatus.

The muscle is 4 mm wide at its insertion and has a fiber length of 18 mm; hence the total length of the sling is 36 mm. Its physiological cross section is about 0.8 sq mm to 1.0 sq mm.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus cyanocephalus*.

E) *M. stylohyoideus* (*M st h*)

Origin: Fleshy from the lateroventral surface of the mandibular ramus at the anterior border of the insertion of the *M. depressor mandibulae*.

Insertion: Fleshy onto the lateroventral surface of the basihyale just anterior to its ceratobranchial articulation and onto the ventral surface of the articulating head of the ceratobranchiale. The insertions of the paired stylohyoideus muscles approach each other on the ventral surface of the basihyale at the ceratobranchial articulation, but diverge anteriorly.

Structure: A thin, straplike, parallel-fibered muscle with long fibers. The *M st h* lies dorsal to the sublingual pouch with only its origin visible in ventral view. After its origin, the muscle passes ventral (superficial) to the *M. branchio-mandibularis*, and then dorsal to the *M. mylohyoideus posterior*. It lies along, but is not tightly bound to, the anterior border of the *M. serpihyoideus*. The muscle runs along the ventrolateral surface of the *M. ceratoglossus* until the anterior end of the hyoid horn; here it curves dorsolaterally and passes dorsal to the tendon of the *M. ceratoglossus*; and finally it inserts on the ventral surface of the basihyale and ceratobranchiale.

The *M st h* has a fiber length of 23 mm and is about 2 mm wide throughout its length. Its physiological cross section is approximately 1.0 sq mm.

Comparison: The *M st h* in *caryocatactes* is similar to that in *columbiana* except that the insertion on the ceratobranchiale head is reduced in the former. This muscle is basically similar to that in *Corvus* and in *Gymnorhinus*. The insertion of this muscle on the ceratobranchiale in the nutcracker is unusual but does not represent a major modification.

F) *M. branchiomandibularis* (*M b m*)

This muscle is divided as usual into a large anterior part (*M b m a*) and a small posterior part (*M b m p*).

Origin: Fleshy from the medial surface of the mandibular ramus anterior to the mandibular fossa and ventral to the origin of the *M. mylohyoideus*. The origin of the *M b m* extends quite far anteriorly along most of the origin of the *M. mylohyoideus*. The two parts arise contiguously with the posterior head being ventroposterior to that of the anterior head.

Insertion: Fleshy onto the very distal end of the epibranchiale.

Structure: Both parts are straplike, parallel-fibered muscles whose basic structure is obscured by their twisting path about the hyoid horn. The two parts diverge gradually from the mandibular ramus and pass ventral to both parts of the *M. mylohyoideus* and dorsal to the *M. serpihyoideus* and *M. stylohyoideus* before reaching the hyoid horn. The *M b m a* passes ventral to the ceratobranchiale and folds about the hyoid horn from below; the fibers on the medial side twist about the hyoid horn from ventral to dorsal as they extend toward their insertion. The *M b m p* passes dorsal to the ceratobranchiale and covers the seam formed by the upfolded edges of the anterior portion.

The *M b m* lies lateral and dorsal to the sublingual pouch.

Fiber length of the *M b m a* is 50 mm and that of the *M b m p* is 45 mm. Their physiological cross sections are 4.0 sq mm and 0.75 sq mm respectively.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus*.

G) *M. ceratohyoideus* (*M c h*)

Origin: Fleshy from the lateral surface of the ceratobranchiale just anterior to its articulation with the epibranchiale.

Insertion: On a midventral raphe with its opposite member. The raphe of in-

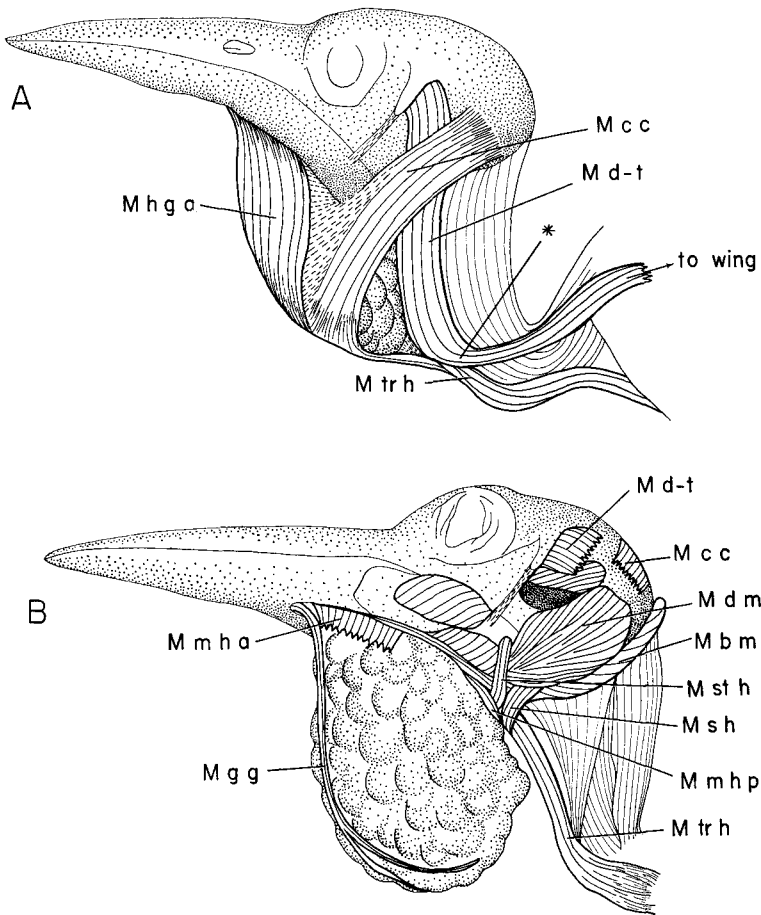


Figure 9. Lateral view of the head of *Nucifraga columbiana* with a full pouch. (A) All superficial muscles are left in place. Note that the dermal muscles all attach to the skin of the neck at one point (marked with an asterisk) to which the posterior pouch ligament and superficial band muscles also attach. (B) The superficial muscles are removed to reveal the pouch, the head is tilted slightly. Note the M g g on the ventral surface of the pouch and the other tongue muscles tucked over the posterodorsal corner of the pouch.

sersion of the M c h is dorsal to that of the M. mylohyoideus posterior; these raphes are bound together and their posterior end is continuous with that of the M. serpihyoideus. The raphe of insertion of the M. ceratohyoideus is not bound to the urohyale.

Structure: A thin, straplike, parallel-fibered muscle. From their origin the fibers run forward to curve around the lateral and ventral surface of the ceratobranchiale and then pass medially to their insertion; hence the M c h makes a half turn about the hyoid horn.

The M c h has a fiber length of 14 mm and its width at the insertion is 2 mm. Its physiological cross section is about 0.5 sq mm.

Comparison: Similar to that in *Corvus* and *Gymnorhinus cyanocephalus*, and hence different from most other passerine birds in which the muscle originates from the medial edge of the ceratobranchiale, and hence does not make a half turn about the lateral edge of the hyoid horn.

In the one specimen of *caryocatactes* available, about 10% of the fibers of the M c h originate directly from the medial surface of the ceratobranchiale while the remaining fibers arise from the lateral surface. Fibers do not arise from the intervening ventral surface of the ceratobranchiale although it is clear that shift of the origin of this muscle between the medial and lateral surfaces of the hyoid horn was via the ventral surface either by slow spreading of the origin or by a single "jump" between the medial and lateral surface by the origin of individual fibers. The difference in the origin of the M c h in the two species of nutcrackers is interesting as it shows the likely course of evolution, but it has no taxonomic significance.

H) *M. ceratoglossus* (M c g)

Origin: Fleshy from the ventrolateral surface of the entire length of the ceratobranchiale.

Insertion: All or almost all fibers attach onto a stout tendon along the lateral surface of the muscle that inserts on a ventral tubercle of the paraglossale just anterior to the paraglossal-basihyal articulation. Muscle fibers attach to the tendon right up to its insertion on the paraglossale. In some specimens, a small number of fibers on the dorsal side of the muscle insert directly onto the ventral edge of the paraglossale between the *M. hypoglossus obliquus* and the ventral tubercle.

Structure: A long, unipinnate muscle with a large number of moderately long fibers; it is presumably the strongest tongue muscle, but develops little torque because of its extremely short moment arm. Insertion of fibers along the entire tendon and directly on the paraglossale in the nutcrackers is a result of the short basihyale and relatively long fibers of this muscle.

The fiber length of the M c g is 9 mm with the angle of pinnation being about 15°. The length of the ceratobranchial origin is 13 mm with the physiological cross section about 5-6 sq mm.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus*; the fleshy insertion of a few fibers on the paraglossale in the nutcrackers is a minor difference from other corvids.

I) *M. hypoglossus anterior* (M hg a)

Origin: Fleshy from the ventral surface of the paraglossale and from the ligaments binding the two paraglossalia together.

Insertion: On the anterior surface of the ventral tubercle of the paraglossale.

Structure: A minute, unipinnate muscle with short fibers intermeshed with collagenous fibers. The fibers run lateroposteriorly from their origin to insertion. In some specimens the M hg a had additional fibers lying lateral to the main mass shown in Figure 8A, and some in the interparaglossal space. These fibers form a thin, somewhat diffuse layer and are difficult to maintain undamaged while removing the epithelial covering of the paraglossalia, i.e. the corneous tongue.

The fiber length of the M hg a is 1.0 mm. The width of the muscle is about 0.5 mm and the physiological cross section is 0.1 to 0.2 sq mm.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus cyanocephalus*.

J) *M. hypoglossus obliquus* (M hg o)

Origin: Fleshy from the medioventral surface of the posterior surface of the paraglossale.

Insertion: Fleshy on the contralateral muscle at the midventral surface below the basihyale.

Structure: A parallel-fibered, straplike muscle forming a sling between the paired paraglossalia, which passes below the anterior end of the basihyale. Actually the two muscles have merged to form a single transverse muscle; no medial raphe exists. The M hg o forms a very flat sling as the ventral surface of the basihyale lies almost on the same horizontal plane as the areas of origin on the paraglossalia. The fibers are relatively short in this species compared to the fiber length of the *M. ceratoglossus*.

Fiber length of the M hg o varies between 3.0 and 4.0 mm with the posterior fibers being the longest; hence the total length of the muscular sling varies from 6 to 8 mm. The width of the muscle along the the midventral line is 4 mm, and the physiological cross section is approximately 3 sq mm.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus*.

K) *M. tracheochoideus* (M tr h)

Origin: Fleshy from the anterior surface of the midventral region of the furcula, and from the skin of the neck at a point approximately midway between the trunk and the head (Figure 2A).

Insertion: Fleshy by three separate slips that divide just before their insertions (Figure 7). The largest slip (75% of total fiber number) inserts on the ventral surface of the cricoid cartilage just below its lateral edge and at a point level with the anterior end of the glottis; this slip passes between the two heads of the *M. thyreochoideus*. A small slip (10% of the fibers) merges with the dorsal head of the *M. thyreochoideus*. The third slip (about 15% of the fibers) from the dorsolateral part of the muscle extends forward to insert on the dorsal surface of the ceratobranchial head just distal to the insertion of the *M. stylochoideus* on this bone.

Structure: A straplike, parallel-fibered muscle with extremely long fibers. The attachment of this muscle on the skin of the neck is at the point where the posterior pouch ligament attaches.

Fiber lengths of the M tr h is about 90 mm. The width of the muscle just before it divides is 3.0 mm and its physiological cross section is approximately 0.6–0.75 sq mm.

Function: Because of its attachment to the posterior pouch ligament, the M tr h may serve to regulate the position of the pouch and may prevent excessive movement (swaying) of the distended, filled pouch. Attachment of the posterior end of the *M. cucullaris* to the M tr h by a thin band of muscle fibers may serve as an anchor to prevent a forward shift of the *M. cucullaris* and *M. mylochoideus* anterior.

The other functions of the M tr h are similar to those in other passerine birds.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus*. Variations in the size of the several slips of insertion are minor.

L) *M. tracheolateralis* (M tr l)

Origin: Presumably from the syrinx; the origin was not dissected in *Nucifraga*.

Insertion: Fleshy on the ventral surface of the cricoid cartilage. Most of the fibers insert along the posterior and medial edge of the origin of the *M. thyreochoideus*, but some fibers extend forward beneath the medial border of the *M. thyreochoideus* to insert deep to this muscle just posteromedial to the insertion of the main slip of the *M. tracheochoideus*.

Structure: A straplike, parallel-fibered muscle with very long fibers. It is very broad and spreads over most of the trachea including its dorsal surface. This muscle is not a member of the tongue musculature proper, but must be mentioned because of its close morphological association with the tongue apparatus.

Fiber length of the M tr l is about 90–100 mm. Its width is 5.0 mm, but its physiological cross section is 0.5 sq mm or less.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus cyanocephalus*.

M) *M. thyreochoideus* (M th h)

Origin: Fleshy from the cricoid cartilage. The main head arises from the ventral surface of the cartilage between the major insertions of the *M. tracheochoideus* and the *M. tracheolateralis*. The small dorsal part (5% of the fibers) originates from the dorsolateral edge of the cartilage where it receives some fibers from the *M. tracheochoideus*. Both heads of origin merge before they reach the anterior border of the cricoid cartilage.

Insertion: Fleshy on the basihyale, covering almost the entire lateral and dorsal surfaces of the bone between its ceratobranchial and paraglossal articulations. The area of insertion extends from a point just dorsal to that of the *M. stylochoideus* to the middorsal line and forward to the posterior edge of the broad anterior expansion of the basihyale forming the paraglossal articulations.

Structure: A stout, parallel-fibered muscle with relatively short fibers corresponding to the short basihyale.

Fiber length of the M th h is 12 mm. The muscle is about 2 mm wide, across its dorsal surface just anterior to the cricoid cartilage. Its physiological cross section is approximately 1.0 sq mm.

Comparison: Similar to that in *N. caryocatactes*, *Corvus*, and *Gymnorhinus*.

THE FILLED POUCH

Two specimens with naturally filled pouches were available for dissection (Figure 9). The volume of the nuts in the pouch of the specimen figured displaced 5.0 cc of water and occupied a volume of approximately 10–12 cc in the intact pouch.

Upon removal of the skin, the distended pouch and slinglike muscles are visible (Figure 9A). Fibers of the *M. mylochoideus* anterior and the *M. cucullaris* caput portion are stretched to almost double their length when the pouch is empty, the *M. cucullaris* stretching to 60 mm and the posterior fibers of the *M. mylochoideus* anterior to 35–40 mm. The sheet of collagenous fibers between these muscles is stretched thin. A small part of the posterior end of the pouch can be seen behind the *M. cucullaris*. The *M. dermatotemporalis* (a part of the *M. cucullaris*) is very broad and extends down the neck just behind the pouch to the common attachment of these dermal muscles on the skin (marked by an asterisk in Figure 9A). The position of the *M. dermatotemporalis* varies with bending of the neck. From this point

the *M. dermatemporalis* continues to its attachment on the proptagium of the wing, now termed the *M. cucullaris pars proptagialis* (George and Berger 1966: 316–317). The *M. tracheohyoideus* (= *M. ypsilotrachealis* of some authors, George and Berger 1966: 263–264) extends from its origin on the clavicle to attach (some fibers only) on the skin of the neck with the *M. dermatemporalis*, and then continues forward (hidden in Figure 9A, but visible in Figures 9B and 2A) to insert on the cricoid cartilage and the ceratobranchiale. A very narrow, thin band of muscle fibers connects the posterior, midventral edge of the *M. cucullaris caput* part with the attachment of the *M. tracheohyoideus* and *M. dermatemporalis* on the skin; this ventral band is usually smaller than that shown in Figure 9A and is easily damaged while removing the skin. The posterior pouch ligament lies immediately dorsal to this muscular band (Figures 1 and 2A). Thus the pouch is supported by muscular slings and is bound to the neck and steadied against excessive lateral swinging by the combination of the *M. dermatemporalis*, *M. tracheolateralis*, and connecting muscular and collagenous fibers.

Upon removal of the superficial muscles, the pouch pulls forward and away from the ventral surface of the neck (Figure 9B). The stretched *M. genioglossus* spreads over the ventral surface of the pouch. Some of the main tongue musculature is just visible at the dorsoposterior corner of the pouch. These muscles lie lateral and dorsal to the distended pouch and are slightly, if at all, displaced from their normal position. In any case the filled pouch does not interfere with the normal functioning of the tongue apparatus, as can be inferred from the morphology.

The muscles about the pouch, *M. mylohyoideus* anterior and *M. cucullaris*, are too thin and presumably too weak to assist significantly in emptying the filled pouch. The function of the *M. genioglossus* to collapse the empty, but still extended pouch can be readily appreciated from Figure 9B.

DISCUSSION

The sublingual pouch of the nutcrackers is a diverticulum of the floor of the oral cavity opening in front of the corneous tongue. It has received several names, but the most accurate descriptive term for this feature is "sublingual pouch." It definitely should not be called a "crop" or a "neck pouch" as frequently done in the literature. The term "throat pouch" (Swanberg 1951, 1956) and the German "Kehlsack" (Löhrl 1970) are ambiguous, although not wrong, but are best dropped from usage. In any case "Kehlsack" should be translated as "throat sac" and not as "crop" (= *der Kopf*) as done in the English summary of Löhrl's paper (1970).

The sublingual pouch of nutcrackers is a neomorph and is not homologous as a sublingual pouch with similar oral diverticula found in several species of auklets (Alcidae) and in the rosy finches (*Leucosticte*, Fringillidae) as suggested by Portenko (1948). These pouches share no morphological similarities that suggest they are homologous as diverticula of the floor of the oral cavity. It is most reasonable to conclude that they evolved independently in each of these groups (i.e. are independent neomorphs), and hence may be regarded as convergent features

with the similar function of carrying food. Food objects may be carried in the pouch without interfering with other functions of the mouth and esophagus; hence the bird can select some food items to be transported in the pouch and can eat other food items. The pouch permits the bird to gather a large number of objects, be they minute marine invertebrates, pine seeds or insects, and thereby allows the birds to transport a greater amount of food each time it makes the long trip between the feeding ground and the nesting or caching site. The pouch in *Leucosticte* and other cardueline finches may have evolved under the control of a selection force associated with a stored food supply for long winter nights or perhaps a few days of unfavorable weather.

COMPARISONS WITHIN *Nucifraga*

We noted no essential differences in the morphology of the sublingual pouch or the tongue muscles in the two species of *Nucifraga*. The tongue muscles of *caryocatactes* appear to be larger than those of *columbiana*, which would be expected as the Eurasian species is a considerably larger bird. It is not possible to ascertain from our dissections whether *caryocatactes* has a larger pouch, either relatively or absolutely, than that of *columbiana* because of a lack of material of the Old World species. The relationship of the pouch to the tongue muscles is the same in both species. Thus it is not possible to determine from our dissections whether this adaptation is better developed in either species. We would judge that the sublingual pouch and associated morphological features are approximately equally developed in the two congeners.

Our studies substantiate the basic morphological findings of Portenko (1948) for *caryocatactes*.

MORPHOLOGICAL RELATIONSHIP WITH OTHER FEATURES

The sublingual pouch lies ventral to all features of the jaw apparatus and the tongue apparatus except the most superficial tongue muscles—the M. genioglossus, the M. mylohyoideus anterior, and the M. cucullaris caput portion (a dermal muscle). Its distal end projects through the M. mylohyoideus and thereby divides this muscle into two unequal parts. The small M. mylohyoideus posterior lies dorsal to the pouch and retains its morphological connection with M. serpihyoideus and M. ceratohyoideus. When the pouch is empty, it is a flat sack that lies between the superficial muscular slings of the M. mylohyoideus and M. cucullaris and the tongue apparatus. It would not interfere in any way with the normal functions of the tongue apparatus, including the superficial muscular slings, or of the jaw apparatus.

No evidence exists to suggest a regression of the pouch in adults during the nonbreeding and nonseed gathering seasons. The pouch apparently develops early in the life of the individual nutcracker; we found one in a young bird approximately 8 weeks old. Seasonal regression of the pouch is not feasible because the birds utilize it during the entire courtship and nesting period and during the late summer and autumn harvest. Moreover the empty pouch is flat and does not interfere with other features so that regression is of no real advantage.

Maximum expansion of the pouch as it fills with seeds has little effect on the normal functions of the tongue apparatus or the jaws. Most of the tongue musculature lies dorsal to the filled pouch (Figure 9) and operates normally in spite of the distended throat. Because of its large opening anterior to the base of the corneous tongue, the pouch can be filled and emptied easily. Presumably the tongue helps in directing seeds into the entrance of the pouch and in preventing them from escaping. One possible disadvantage is that the weight of the filled sac is supported almost completely by the lower jaw; only that part supported by the slinglike *M. cucullaris* is not. When the sublingual pouch is full, it places a larger load on the mandible, which must be overcome by the jaw muscles during any normal action of the jaw apparatus. The extra energy required by the jaw muscles during contraction would not be needed if the seed carrying pouch had been a croplike expansion of the esophagus. A major advantage is that the sublingual pouch allows the bird to separate food types, eat one kind, and carry off the other, which is not possible with a crop.

The evolution of the sublingual pouch influenced mainly those tongue and dermal muscles lying ventral to it in the intermandibular space; this effect is examined carefully for each muscle, considering both the empty and filled pouch.

a) *The M. cucullaris caput portion* underwent no modification in its basic morphology; it remained a parallel-fibered, slinglike muscle superficial to all other structures in the ventroposterior part of the head. The enlarging sublingual pouch in the nutcrackers with its need for additional support when filled resulted in a considerable enlargement of this dermal muscle to form a definite sling about the posterior part of the pouch. Increased physiological cross-sectional area (fiber number) is associated with greater demands of support. Fiber length also increased to permit maximum stretching as the pouch is filled. The aponeurosis extending from the anterior edge of the *M. cucullaris* to the *M. mylohyoideus* is a new specialization. Thus the *M. cucullaris caput portion* changed from a thin muscle that cannot be dissected and observed by gross methods in

most passerine birds to an easily observable muscular sling in the nutcrackers.

b) *The posteroventral extension* of the sublingual pouch split the *M. mylohyoideus* into two unequal parts that appear as quite distinct muscles and quite different from the configuration of the *mylohyoideus* in other corvids. Upon closer examination, this division of the *M. mylohyoideus* is a rather minor morphological change with both portions of the muscle maintaining their usual morphology and functions. The *M. mylohyoideus* anterior remains a sheetlike muscle spanning the space between the mandibular rami and functioning to support the anterior part of the pouch. It acquired a strong connection with the *M. cucullaris* via their continuous midventral raphe and the broad aponeurosis of the latter muscle. Length of the posterior fibers of the *M. mylohyoideus* anterior has probably increased to permit sufficient stretch when the pouch expands. Little if any increase in physiological cross section of this muscle accompanied the evolution of the sublingual pouch. The function of the *M. mylohyoideus* anterior in nutcrackers is basically the same as in other passerine birds in which this muscle supports the floor of the mouth and the tongue. When empty, the flat collapsed pouch does not interfere with the action of this muscle. When the pouch is filled with seeds, the *M. mylohyoideus* anterior acts as a sling to support it (Figure 9), but can no longer support the tongue apparatus or other parts of the oral cavity. Yet, function of the muscle is basically unchanged because the sublingual pouch is simply an extension of the mouth floor.

Because of the new connection between the *M. mylohyoideus* anterior and the *M. cucullaris* caput portion, these muscles serve as antagonists and prevent each other from shifting anteriorly and posteriorly respectively when they contract or when the pouch expands. Although these muscles form a supporting sling, we doubt that they provide a significant force for emptying the filled pouch. Their total cross-sectional area appears too small to provide the needed force to empty a filled pouch. Field observations suggest that nutcrackers empty the pouch by inertia mechanisms. They open their bill and swing the head up and down, which would bring the seeds forward and out of the pouch.

The *M. mylohyoideus* posterior appears quite different morphologically from the posterior fibers of the *mylohyoideus* muscle in other corvids, but this difference results mainly from the curved path of these fibers about the sublingual pouch. These fibers may have increased in length with the evolution of the pouch, but their attachments did not change. And the basic function of the *M. mylohyoideus* posterior as an antagonist for the *M. serpihyoideus* and *M. ceratohyoideus* is identical to that in other passerines.

Although the change in structure and function of the *M. mylohyoideus* appears to be considerable with the evolution of the sublingual pouch, the greatest modification in this muscle is its being split into two segments, each of which remain similar in form and function to the corresponding portions of the *mylohyoideus* in other passerine birds. A greater morphological change would have resulted if the expansion of the sublingual pouch severed the *M. mylohyoideus* from its common attachment with the *M. serpihyoideus* and *M. ceratohyoideus*. The antagonistic relationship of these muscles is so important that we suspect an enlarging sublingual pouch could escape the confines of the *mylohyoideus-serpihyoideus* muscular sling only by penetrating the *M. mylohyoideus*.

c) *The sublingual pouch* evolved as a broad diverticulum extending almost completely across the intermandibular space and elongating posteriorly as a blind sack. As the pouch grew it intercepted the course of the *M. genioglossus*, which usually runs from the mandibular symphysis along the floor of the mouth dorsal to the *M. mylohyoideus* to reach the lateral and dorsal surface of the corneous tongue anterior to the glottis. As the sublingual pouch grew posteriorly, the fibers of the *M. genioglossus* had to elongate to reach about the pouch, and had to be sufficiently long to stretch when the pouch filled. Disruption of the normal function of this muscle would be maximal when the pouch was empty because the contracting muscle would have to develop tension about the folded end of a flat, soft sack. The *M. genioglossus* appears to be vestigial or almost so in the *Corvidae* (Bock and Shear MS). Selection forces favoring continued attachment of the *M. genioglossus* on the tongue muscle are weak or no longer present. Presumably it lost its insertion onto the tongue when the enlarging pouch in *Nucifraga* penetrated the *M. mylohyoideus*, if not before. Even before the *M. genioglossus* lost its attachment to the tongue, it would have acquired the function of collapsing the empty sublingual pouch because it ran along and was bound to the outer (ventral) surface of the pouch. Once the muscle lost its tongue insertion, it could subdivide several times, with the small subdivisions spreading out and inserting over a wide area of the ventro-posterior surface of the sublingual pouch, and would possess the sole function of collapsing the empty pouch. Thus the enlarging pouch has modified the morphology and the function of the *M. genioglossus* from its usual role of a tongue muscle to one associated only with the pouch; this is the greatest change the evolution of the sublingual pouch has produced in any neighboring structure.

Evolution of the *M. genioglossus* from a tongue muscle to a pouch muscle in nutcrackers represents a classical example of preadaptation, with the muscle acquiring a new function and subsequently losing its

original function. The sequence of morphological and associated functional changes, origin of new selection forces, loss of old ones, and modification in biological roles is especially clear.

In a purist sense, the *M. genioglossus* in *Nucifraga* should be renamed because it no longer inserts on the tongue; however, such action would obscure homologies more than it would clarify morphological and functional changes.

The evolution of the large sublingual pouch, which is a dominant morphological feature in terms of space requirements in the floor of the mouth, has occurred with remarkably little change in surrounding structures. The tongue and most of the tongue muscles have not been modified. It is of particular interest that a new and large morphological feature has evolved with so little modification of neighboring elements. It shows that the development of a major component in space requirements and a central feature in an important adaptive complex need not necessarily impinge on surrounding structures. Each case must be analyzed individually as stressed by Dullemeijer (1958).

ADAPTIVE SIGNIFICANCE

The function of the sublingual pouch is that of a receptacle in which the bird can place seeds while they are being collected and carried to the caching grounds. It is used in like fashion during the breeding season to bring seeds from the caches to the breeding grounds, but we include both aspects under a single heading of harvesting and transportation. Nutcrackers obtain seeds by hammering cones and pulling the scales off with violent tugs of the bill (Turcek and Kelso 1968, Löhr 1970, Vender Wall and Balda MS). Moreover seeds are carefully examined and bad ones rejected. Thus the jaw apparatus must be fully usable, and preferably free of previously gathered seeds. A pouch permits the bird to hold seeds and frees the jaws for additional gathering. The sublingual pouch, being a sack off the main track of the alimentary canal, allows the bird to separate food items and to eat those (e.g. insects) that cannot be stored. Increase in the size of the pouch permits the bird to gather more seeds per collecting trip and hence reduces the number of times the bird must traverse the long distance between the harvesting and the caching sites.

The biological role of the pouch is associated with the use of the stored seeds. In Clark's Nutcracker this supply of stored energy is used during the following reproductive season as a source of food for adults and more importantly for the young birds. The plentiful food supplies of autumn are thus made available for reproduction the following spring during a period of greatly reduced food availability. The stored seeds

permit Clark's Nutcrackers to nest very early in the spring (see Mewaldt 1956, Vander Wall and Balda MS) with an assured food supply. The young birds fledge by late spring, and hence have more time to gain experience before the onset of difficult conditions the following winter. And it frees the adults of the young birds early in the summer before the onset of molt (Mewaldt 1958), which precedes the pine seed harvesting in the fall. Thus, the biological role and adaptive significance of the sublingual pouch is associated with early nesting. Indeed the complete yearly cycle of Clark's Nutcrackers is based upon its harvesting, caching, and utilizing the abundant fall supply of seeds for reproduction, all of which are dependent upon the sublingual pouch. This drastic modification in the yearly cycle of these nutcrackers occurred with a relatively minor morphological change.

It should be noted that the Clark's Nutcracker (Vander Wall and Balda MS) and the Eurasian Nutcrackers (Swanberg 1951, 1956) are two of the few species of birds known to store overwinter a major portion of the energy supply required for reproduction. The only other species in which food is definitely known to be stored overwinter for reproduction is the Piñon Jay (Balda and Bateman 1971, Ligon 1971).

Food harvesting and storage in the Eurasian Nutcracker is by pairs of birds that mate for life and hold their territory for life. Food is frequently harvested outside the territory, but is cached in definite locations within the territory; the holders of the territory defend stored food against other individual nutcrackers that will steal it. Food harvesting and storage starts after the family group is broken up when the young disperse. Only the mated pair harvest and store food (Swanberg 1951, 1956).

In Clark's Nutcracker, seed harvesting and caching is undertaken by all members of the flock, and the food is stored in a communal cache. The members of the flock breed in a restricted area close to the cache, and all use the seeds in the communal cache for adult food and especially for nestling food (Vander Wall and Balda MS). The breeding structure in Clark's Nutcracker appears to be the more advanced state, which evolved from a system like that present in the Eurasian Nutcracker. Communal seed harvesting, caching, and utilization by all members of a flock, including immature birds which do not breed until they are over 1 year old, appear to constitute true altruistic behavior controlled by kin selection.

EVOLUTION OF THE SUBLINGUAL POUCH

The origin and specialization of the sublingual pouch in *Nucifraga* is correlated with the evolution of food caching habits in this genus. Because

food transportation and storage is widespread in the Corvidae (Turcek and Kelso 1968), antecedents of the sublingual pouch may be sought among other members of the Corvidae. Several genera of this family have specializations of the buccal cavity or of the esophagus to facilitate carrying of food objects over long distances.

Eigelis and Nekrasov (1967) showed that *Pica pica* and several species of *Corvus* carry seeds in the buccal cavity. The cavity volume is increased by lowering the floor of the mouth between the rami by relaxation of the M. mylohyoideus, the corneous tongue is drawn backwards, and the result is a shallow pouch located anterior to the tongue. The birds fill this pouch and entire oral cavity with seeds. The buccal pouch in *Corvus* and *Pica* described by Eigelis and Nekrasov represents a primitive type of pouch from which the sublingual pouch in *Nucifraga* could have evolved. Change from the *Corvus*-type pouch to the *Nucifraga* pouch involved posteroventral growth of the pouch to penetrate the M. mylohyoideus (which would allow greater expansion and hence greater seed carrying capacity), increase in size of the M. cucullaris caput portion, and modification of the M. genioglossus.

Hence we may conclude that the sublingual pouch did not originate in *Nucifraga*, but was already present as a less specialized buccal pouch in the corvid ancestor of the nutcrackers. Evolution from the ancestral pouch to the specialized sublingual pouch required a small number of relatively simple morphological changes. The resulting modification in the yearly cycle of the nutcrackers represent a major evolutionary change. These birds can harvest and store food for reproduction during the previous autumn when seed supplies are most abundant, compared to other corvids that store food for presumed use during short periods of scarcity.

Communal harvesting, caching, and utilization of seeds by the Clark's Nutcracker appears to have evolved from the territorial nesting and food storage behavior of the Eurasian Nutcracker. We could not ascertain any corresponding modification in the structure of the sublingual pouch and conclude that its morphology is suited for both systems of seed carrying and storage.

The second type of pouch present in the corvids is found in the European Jay (*Garrulus glandarius*) which has an expansible esophagus (Eigelis and Nekrasov 1967). Piñon Jays also carry seeds in an expandable portion of the esophagus (Balda pers. observ.). The two types of carrying sacks, (a) the antelinguar buccal cavity (*Corvus*, *Pica*) and the sublingual pouch (*Nucifraga*) and (b) the expansible esophagus (*Garrulus*, *Gymnorhinus*), are two paradaptations (Bock 1967) in the Corvidae for food transportation.

ACKNOWLEDGMENTS

We would like to thank several friends whose contributions added greatly to the success of this study. Dorothea Goldys used special skill and care in her illustrations, which permit a real comprehension of the spatial relationships of the sublingual pouch and tongue apparatus. T. Goslow did the initial dissections that demonstrated the pouch, suggested the importance of the morphological study, and read the final manuscript. The officials of the British Museum (Natural History) permitted us to dissect the sublingual pouch and tongue muscles of a specimen to *Nucifraga caryocatactes*. Our special appreciation goes to Leon Kelso who provided us with valuable advice and assistance throughout the study. We are especially indebted to him for supplying us not only with references to important Russian literature on nut-crackers, but also the English translations. Support for the field work was supplied by a grant to Balda from The Institutional Research and Studies Committee, Northern Arizona University. The morphological portion of this study was supported by a grant to Bock from the National Science Foundation (NSF-GB-6909X). We wish to thank both institutions.

SUMMARY

The sublingual pouch in *Nucifraga columbiana* is a diverticulum of the mouth floor, opening anteriorly and laterally to the corneous tongue. Its broad opening lacks constrictor muscles. The posterior end of the pouch penetrates the *M. mylohyoideus* and is attached by a ligament to the skin of the neck. The pouch wall is thin and lacks an intrinsic muscular layer.

The *M. cucullaris* caput portion is well-developed, as is the *M. mylohyoideus* anterior. The two muscles insert along a continuous mid-ventral raphe and are bound together by a broad aponeurosis from the anterior edge of the *M. cucullaris*; they form a sling about the pouch. The small *M. mylohyoideus* posterior curves about the posterolateral corner of the pouch and inserts dorsad to the pouch on a common raphe with the *M. serpihyoideus* and *M. ceratohyoideus*. The *M. genioglossus* no longer reaches the tongue, but divides several times and inserts broadly on the posteroventral surface of the pouch. All other tongue muscles lie dorsad to the pouch and have a typical passerine morphology.

The empty pouch is a flattened sack lying between the *M. mylohyoideus* anterior and *M. cucullaris* and the oral cavity plus the tongue apparatus. The filled pouch is greatly expanded ventrally, stretching the muscular sling, but does not affect the normal functioning of the tongue. The *M. genioglossus* apparently serves to collapse the empty pouch.

The sublingual pouch and tongue musculature in *N. caryocatactes* are similar to those in *N. columbiana*. It was not possible to determine whether the pouch was larger in the larger sized *caryocatactes*.

The sublingual pouch functions as a sack for carrying pine seeds and

hazelnuts from the harvesting areas to the caching sites. It permits the birds to carry a larger load on each flight to the cache and hence to store more food. Adult birds eat the stored seeds during the following nesting season. Both nutcracker species use the stored seeds as the primary food for nestlings. Hence the sublingual pouch is an adaptation in the annual cycle of these birds that evolved from an unspecialized antelingual buccal cavity found in other corvids.

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Department of Biological Sciences, Columbia University, New York, New York 10027, and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86001. Accepted 21 July 1972.