SALIVARY GLANDS IN THE GRAY JAYS *(PERISOREUS)*

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UNIQUE morphologic specialization in a single species or genus provides one of the best approaches into the entire subject of adaptation and the evolution of new groups. Further, if the animal possessing the unique specialization lives in an unusual or strenuous habitat, then the action of the evolutionary processes is frequently easier to understand. The gray jays of the genus *Perisoreus* form an excellent basis for the discussion of some of these problems as they are permanent residents in the far northern coniferous forests—one of the most strenuous habitats available to passerine birds. Gray jays must possess adaptations to the cold of winter and the ability to utilize the limited food supply available during the winter. The question of protection against the cold shall not be considered as I wish to concentrate on the problem of food gathering. This latter problem has been overlooked by ornithologists because the gray jays, like most other permanent residents in the northern forests, were not known to have any marked feeding adaptations. But the discovery of a pair of "woodpecker-sized" mandibular mucous glands in the gray jays reopens the question of their feeding habits. Mucous glands as large as those found in the woodpeckers are, to the best of my knowledge, not known in any other passerine bird. This leads to the question of whether this structure is a special adaptation in the gray jays for life in the northern coniferous forests. These questions cannot be answered directly because of a lack of information on the function and biological role of the glands, but I shall speculate on them because of their bearing on the general topic of adaptation of birds to the northern forests as well as their importance to the evolution of the gray jays.

DESCRIPTION OF THE GLAND

The pair of mandibular glands was present and equally well developed in the three adult specimens of *P. canadensis* examined, indicating that they are a normal feature of this species. The glands were also present in the two specimens of *P. infaustus* dissected, but they were considerably shrunken because of preservation and long storage in alcohol. Whether the glands are present in the third species of this genus, *internigrans,* is not known. Topographically, the glands lie in the same position and have the same general appearance as do the mucous glands of the woodpeckers. When the head is examined from beneath, the paired mandibular glands can be seen lying between the mandible and the hyoid bones (Figure 1B). At their anterior end, a small, flattened medial projection may be seen. This flattened appendix extends somewhat forward of the main portion of the gland and disappears into the floor of the mouth lateral to the tongue at a point just level with the center of the eye. The main collecting ducts, which lie within this

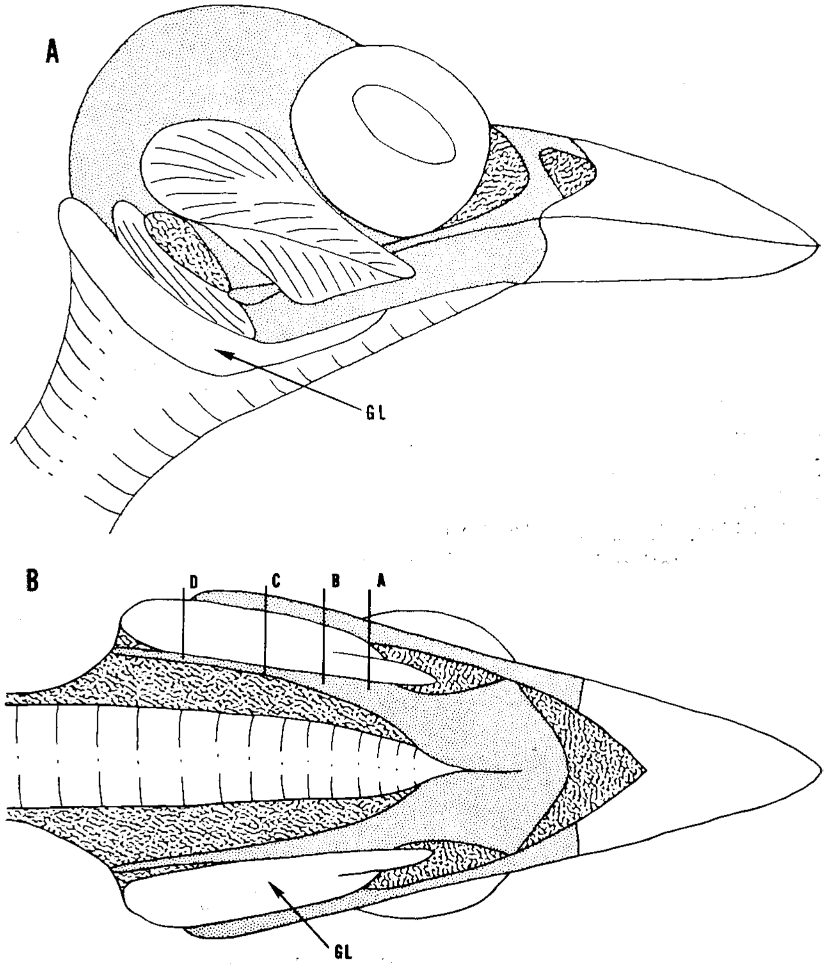


Figure 1. The mandibular gland of the Gray Jay *(Perisoreus canadensis)* seen from the side (A) and from beneath (B). The gland (GL) lies between the mandible and the hyoid bones and extends around the back of the skull to reach a point just dorsal to the origin of the *M. depressor mandibulae*. The lines crossing the gland in the ventral view indicate the levels at which histological sections were cut.

medial projection, as will be shown below, pass through the floor of the mouth to open into the buccal cavity near the lateral edge of the tongue. When viewed from the side (Figure 1A), the gland can be seen curving dorsally around the posterior end of the mandible to reach a point just above the dorsal end of the *M. depressor mandibulae.* When removed from the head, this "moon-shaped" gland is seen to be twisted on its longitudinal axis so that its posterior end no longer faces dorsally, but somewhat medially. As would be expected, the general shape of the gland conforms to the shape of the head—that is, it fits in between the other structures without interfering structurally or functionally with them (see Dullemeijer, 1958, pp. 77-78). In size, the gland is approximately 24 mm. long, 6 mm. wide at its greatest width and 4 mm. thick (maximum).

According to the most recent classification for the avian salivary glands (Antony, 1920; see also Farner, 1960, pp. 413-414), the enlarged gland in the Gray Jay is part of the *Gl. mandibularis.* Most probably it is the *Gl. mandibularis medialis,* although it is difficult to distinguish and identify the various components of the *Gl. mandbularis* complex with certainty. It should be pointed out that the *Gl. mandibularis medialis* of the Gray Jay is almost certainly not homologous with the large mucus-secreting gland in the woodpeckers. Unfortunately, Antony was not clear in her discussions of the "woodpecker gland." In her listing of the salivary glands in birds (p. 550), she considers the "woodpecker gland" to be a completely separate gland, the *Gl. picorum;* but in a table showing the distribution of the salivary glands in the woodpeckers, she includes the *Gl. picorum* as a subdivision of the *Gl. manibularis.* Thus, it is not certain whether the *Gl. picorum* is part of the *Gl. mandibularis* complex; but, even if it is, it would be an anterior part of that gland, not a medial and more posterior part as is the mandibular gland of the gray jays.

The gross histologic structure of the mandibular gland can be understood by an examination of the figures (see Figures 2A–2D). The collecting ducts gather together on the medial side of the gland, forming the flattened appendix seen in the ventral view of the head. In the anterior sections, the collecting ducts comprise more than half of the cross-sectional area, while in the posterior slides, the ducts become smaller, pass to the internal surface of the gland, and gradually drop out with a corresponding disappearance of the medial appendix. The epithelial cells lining the collecting ducts appear to be a pseudostratified columnar type with a striated border. The secretory cells are arranged in long tubules, which run parallel to the longitudinal axis of the gland. A heavy theca of connective tissue surrounds each tubule as well as the entire gland. In the posterior half of the gland only secretory tubules are present; the collecting ducts have dropped out completely. Lumina and small ducts can be seen inside the tubules. The secretory cells appear to be arranged in rows radiating out from the central duct of each tubule. The cells are relatively tall for secretory cells, with rounded nuclei that lie at the basal end of the cell, but are not pressed against the floor as is usual for mucus-secreting cells. These observations on the cellular structure are not conclusive because of the fixation, nor could any additional details be ascertained. It was not possible to determine the type of secretion from a histological examination of the gland cells.

The suspected mucus-secreting nature of the gland was confirmed by the application of several histochemical procedures (see Gomori, 1952, and Lillie, 1954, for description of these tests). Staining with Paraldehyde Schiff reagent (PAS), with PAS combined with a diastase digestion, and with toluidine blue were all positive, which proves quite conclusively that the granules within the secretory cells are mucoid and hence that this gland secretes mucus.

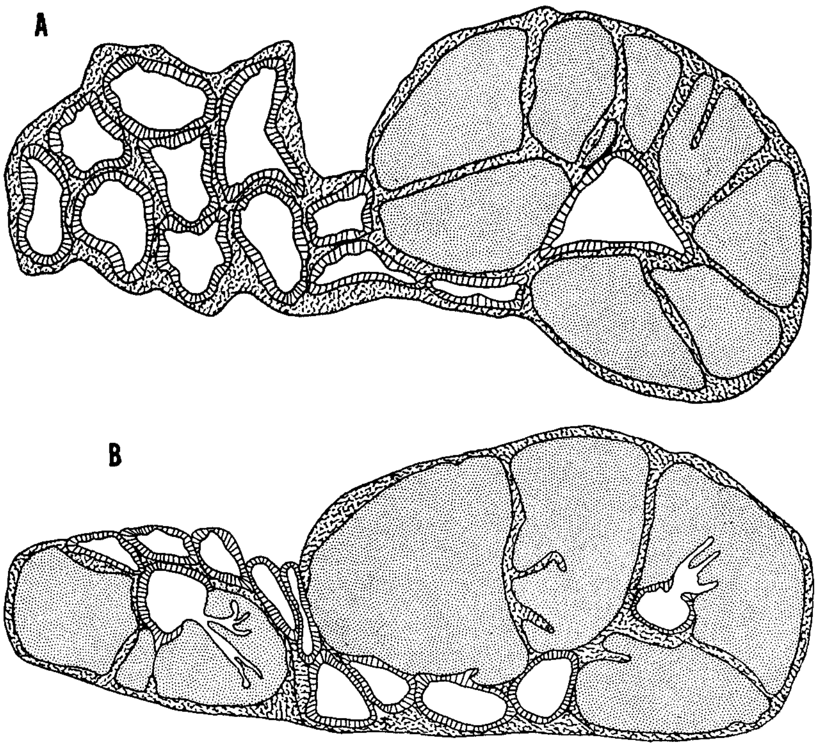
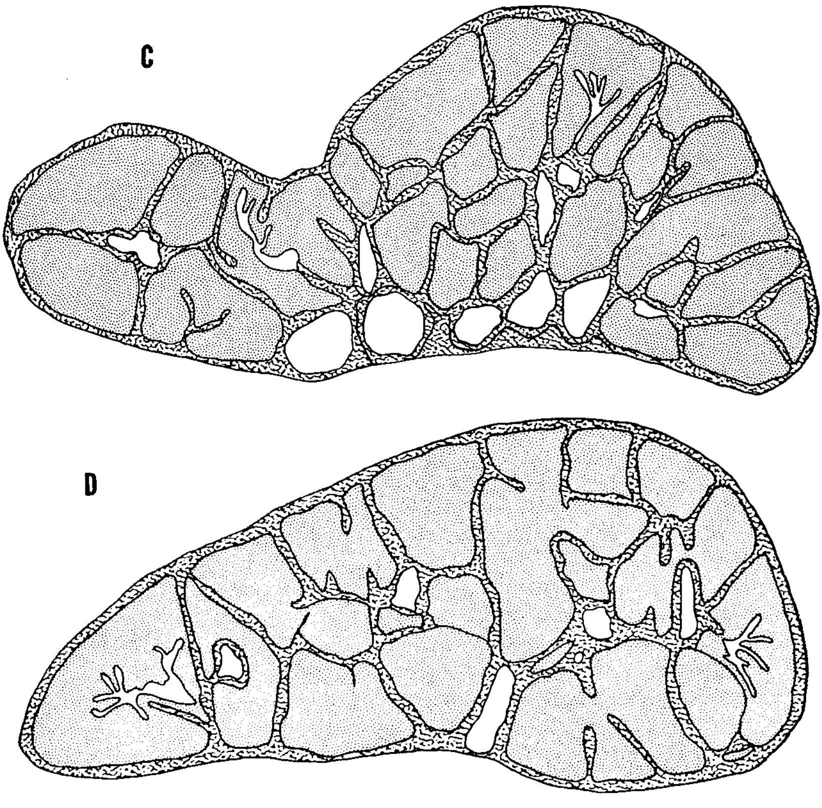


Figure 2. Semischematic drawings of the histological structure of the mandibular gland of the Gray Jay *(Perisoreus canadensis)*. The Figures A to D were traced from sections cut from the levels A to D shown in Figure 1B. The sections are oriented with their ventral side upwards and their medial side to the left. Magnification of the sections is, for technical reasons, not the same; Figures A and B are enlarged about two to three times more than Figures C and D. The secretory tubules are shaded by stippling, the

Mandibular Glands in other Corvids

Before it is possible to inquire into the adaptive value of the large mandibular glands in the gray jays, it is necessary to ascertain whether this structure is unique in this genus. Specimens of the following forms were dissected: *Garrulus glandarius, Cyanocitta cristata, C. stelleri, C. coerulescens, Pica pica, Nucifraga columbiana, Corvus brachyrhynchos, C. corona,* and *C. frugilegus.* All had an area of small mandibular glands lying in the floor of the mouth as described for various members of this family (see, Cholodkowsky, 1892; Hölting, 1912; Greschik,



connective tissue by a broken-line pattern, and the collecting ducts are left blank with their walls shown by vertical lines in Figures A and B. In Figure A, the collecting ducts are bunched together on the medial side of the section; this is the medial projection seen in Figure 1B. Note how the collecting ducts then pass to the middle of the dorsal side of the gland (Figures B and C) before becoming completely scattered in the posterior part of the gland (Figure D).

1913; and Antony, 1920). Although this area is extensive in some species, no species have a gland equal in size to that found in the gray jays. Special care was taken in dissecting the rook because Antony (1920, p. 600) reported the *Gl. mandibularis externa* in this species to be 30 mm. long and 6 mm. wide. I dissected several adult rooks and found the *Gl. mandibularis externa* as well as the usual field of small mandibular glands. The *Gl. mandibularis externa* is buried within the floor of the mouth and is hidden for most of its length by the mandible. This gland appeared to be smaller than the figures given by Antony (precise measurements were not possible), but in any case it is considerably smaller in absolute and relative size than the mandibular gland of the Gray Jay. Although I was not able to examine all genera of the Corvidae, it may be tentatively concluded that the large mandibular glands in the gray jays are a unique feature in the corvids and are probably unique in the passerine birds. Additional evidence is needed before this conclusion can be fully accepted; this can be obtained while skinning birds as the glands lie directly under the skin. I would like to suggest that collectors examine all specimens of corvids, and other passerine birds if possible, for the presence of large mandibular glands.

DISCUSSION

Why should a pair of woodpecker-sized mucous glands have evolved in the gray jays, birds living in the far northern coniferous forests? Normally, mucus from salivary glands has the function of lubricating the mouth (see Farner, 1960, p. 414). Among birds with greatly enlarged salivary glands, the mucus is sticky and serves as a cementing substance for nest construction (*e.g.*, swifts) or to coat the tongue, thereby transforming it into a "lime-stick" suitable for capturing insects or other food (*e.g.*, woodpeckers). In the case of the gray jays, the most reasonable working hypothesis is that the mucus coats the tongue and changes it into a lime-stick. The tongue of these birds is a normal corvid tongue—flat with some fringing at the tip—which is completely suitable for tongue probing. The use of the tongue would allow the gray jays to obtain food such as seeds still in coniferous cones and insects in bark crevices, which they could not reach with their short, blunt bill. But do the gray jays obtain food by tongue-probing and if so, why?

A search was made through the literature to ascertain whether gray jays have been observed feeding by means of tongue probing. However, aside from numerous statements on the camp-robbing habits of these birds, I have found little about the food habits and feeding methods of the gray jays and nothing of help for the present problem. Here I wish to enter a plea for observations on their feeding methods, especially during the winter when food would be scarce. These observations would be difficult to make because of the rarity of these birds and the fact that they can be shy and elusive during parts of the year, but this information is absolutely essential for solving the function of the mandibular glands. Perhaps the observations could be made on captive birds by presenting them with food (*e.g.*, coniferous cones containing seeds) that they can only reach with their tongues. Nevertheless, there is some indirect evidence supporting the hypothesis of tongue probing. First is the availability of food to the gray jays during the winter; the food supply, not the cold, is the more restricting factor to birds in the north. While the ground is covered with snow, the food supply is almost entirely restricted to what can be found on trees. And this food is most probably largely limited to what is concealed in crevices in the bark and so forth; any insects, their eggs, and so forth lying on exposed surfaces would probably be rapidly washed away by storms or may be too small to be utilized by gray jays. Besides insects in bark crevices, this food would include seeds still in coniferous cones. Second, the bill of these birds is blunt and would not permit them to obtain this food directly. Third, there are indications that the gray jays do eat pine seeds. Peterson, *et al.* (1954, p. 204) make the brief statement that the Siberian Jay is: "Agile in clinging to tips of pine branches to reach cones," which I was able to confirm in some observations on this species in northern Sweden during the summer of 1960. I saw several individuals of Siberian Jays clinging to the tips of branches and seemingly feeding on the cones hanging there, but I was not close enough to determine whether they were using their tongue in any way. Mrs. Lawrence informed me in a letter that during the winters when evergreen seeds are scarce, Gray Jays appeared at feeding stations in Ontario in greater numbers, which lead her to suspect that cone seeds may contribute an important part of the diet of these jays. She added that, unfortunately, she has never observed them eating seeds from cones. Mr. Helminen informed me, also by letter, that there are scattered reports of Siberian Jays in Finland eating coniferous seeds or cones during the winter, but he was not able to supply any further details. These few facts constitute all of the support for the tongue-probing theory, which must remain as a hypothesis until more evidence has been gathered.

It is, nevertheless, of interest to speculate further on the part played by the mandibular glands in the adaptation and evolution of the gray jays for which I shall assume the correctness of the tongue-probing hypothesis. Next it is important to know what percentage of their total food is obtained in this manner. It may be assumed that, during the summer months, only a small part of the food is attained by probing, while, during the winter, a major share of the total food is obtained by tongue probing. Again, these assumptions must be verified or rejected by direct observations, but until definite evidence is available, I shall accept them as tentatively correct. Hence, it may be concluded that, in addition to other necessary adaptations such as resistance to cold, the gray jays are able to live permanently in the northern forests because of their ability to gather food by tongue probing. Further, it may be concluded that these anatomical features that enable the gray jays to tongue probe constitute the most important feeding adapations of this genus. The mandibular glands are one of these important feeding adaptations, and probably they are the most basic one. All of the other anatomical features—the tongue, hyoid muscles, and so forth—involved in tongue probing are little, if any, changed from the typical corvid condition and may be considered to have been preadapted for the new feeding method. Only the mandibular glands are vastly different between the gray jays and other corvids, and they are the sole anatomical feature (*i.e.*, a mucus-secreting salivary gland) whose development determines whether a corvid bird can probe with a sticky tongue. Thus, the development of the mandibular glands was the critical morphologic innovation in the strictest sense of the concept (see Miller, 1949) that enabled the gray jays to enter their present ecological niche. One of the most interesting aspects of the mandibular glands as a critical innovation is that they are not a new structure, but only the enlargement and modification of a structure already present in the Corvidae. The enlargement of a gland is a rather simple evolutionary change, which shows how a simple modification can become the critical innovation permitting the development of a new feeding method and the utilization of a new ecological habitat, and might even have been the factor responsible for the evolution of a new genus of corvid birds.

The evolution of the large mandibular glands and the establishment of the gray jays as permanent residents in the northern forests can be easily visualized. The ancestral form may have had a distribution such as found in some present-day jays (*e.g., Cyanocitta* or *Garrulus*)—covering the temperate and northern forests with the birds breeding in the northern parts of the range migrating to the southern parts—or they may have been temperate forest birds expanding to the north. These birds would have had the normal corvid arrangement and development of salivary glands, and most likely made no special use of their tongue in feeding. Yet, the tongue was probably slightly sticky because of the normal supply of mucus to the mouth. Two associated changes, one behavioral and the other morphologic, had to occur before the evolution of the large mandibular glands could begin; both of these changes are well within the normal range of reaction or variation of corvid birds. The behavioral change was that the birds began to probe into crevices with their tongue to reach the food lodged there, this action being well within the ability of these normally curious birds. The success of this new feeding action would depend upon the stickiness of the tongue. The morphologic change was an increase in the size of the mucous glands and hence the supply of mucus; however, it did not matter which of the salivary glands increased in size. The new, but inefficient, tongue-probing method allowed the birds to utilize a previously unattainable food supply and may have permitted them to remain longer in the northern parts of their range before moving south with the onslaught of winter. If it was advantageous for the birds to remain north longer in the fall, then the new feeding method would have a definite selective value and those birds able to probe with their tongue would have a selective advantage. Why the new feeding method was advantageous—whether there was competition from other species in the temperate regions or whether the birds breeding early in the spring left more offspring—is of no importance; it is only necessary to assume that remaining in the northern part of the range was advantageous. At first only a part of the population would possess the beginnings of the new feeding method, and these would have been able to remain in the northern area slightly longer in the fall. As the genetic factors controlling the increase in the size of the mucous glands and the ability of probing with the tongue increased in the population, the efficiency of the tongue probing increased and the birds were able to remain in the north longer and longer in the fall until finally some individuals, by virtue of their now better-developed ability to tongue probe, were able to remain during mild winters. Specialization of tongue probing, including the size of the mucous glands, has reached the point that today the gray jays must move south only during the severest winters. From this suggested evolutionary history, it can be seen that the behavioral and morphologic changes occurred simultaneously and slowly during the entire phylogeny of the gray jays, and that even the very first changes were under the control of natural selection.

It may be asked: if the large mucus-secreting mandibular glands are essential adaptations in the gray jays, why have similar glands not developed in other permanent residents of the northern forests? The answer may lie in the fact that the feeding methods of the ancestors of most of these birds were suitable, *i.e.*, preadapted, to life in these forests and did not have to be altered as the birds entered the new habitat. Woodpeckers, nuthatchers, chickadees, finches, shrikes, and so forth all feed on food that is available in the northern forests during the winter, so that these birds can become permanent residents if they are able to resist the cold. Moreover, it is possible that some of these birds have special feeding adaptations that are yet unknown.[1] But the most interesting fact is that *Perisoreus* is, with the exception of *Pinicola,* which has doubtless evolved from a northern-adapted finch, the only genus of passerine birds endemic to the northern coniferous forests; all other permanent residents of these forests are members of widespread genera. This may be coupled with the fact that the gray jays are the only known passerine birds with a special feeding adaptation to this habitat. This may be only a coincidence. But in any case this correlation deserves additional study.

[1] Tichomirov (1925) has reported "larger" mandibular glands (= *Gl. mandibularis externa?*) in some species of chickadees. From his figures this gland appeared to be as large, relatively, as the *Gl. mandibularis externa* of the rook, and hence it is considerably smaller, relatively, than the mandibular gland of the gray jays. It has been noted by some observers that the gray jays feed in a manner similar to chickadees. These observations allow two assumptions. The first is that chickadees can also tongue probe. The second is that the mucus from the large mandibular glands in one or both forms has a totally different function.

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SUMMARY

A pair of woodpecker-sized, mucus-secreting mandibular glands has been found in the gray jays; these are a unique feature in the Corvidae and are probably unique in the passerines. The mucus from these glands presumably coats the tongue, thereby making it sticky and suitable for probing into crevices for insects and under the scales of cones for seeds during the winter when other food is scarce. The mandibular glands are thus probably the basic feeding adaptation in these species and appear to be the critical innovation that has allowed the development of a new method of feeding and the invasion of a new ecological niche.

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