FEEDING ADAPTATIONS IN WHISTLING DUCKS (*DENDROCYGNA*)

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Waterfowl have radiated into a variety of niches by evolving such diverse feeding structures as serrated bills for capturing fish (*Mergus*) and lamellated bills for sifting food items (*Anas* and especially *Spatula*). Goodman and Fisher (1962) thus described and analyzed the feeding apparatus in a number of representative anatids, placing particular emphasis on the bones and musculature of the head. More recently Kear and Burton (1971) described in detail the feeding adaptations of the New Zealand Blue Duck (*Hymenolaimus malacorhynchos*) in an effort to understand the function of this species' bill flap.

We recently reported structural adaptations in the locomotor behavior (Rylander and Bolen MS) and the foot structure (Bolen and Rylander 1974) in four species of whistling ducks: the Black-bellied Whistling Duck (*Dendrocygna autumnalis*), the Fulvous Whistling Duck (*D. bicolor*), the Plumed Whistling Duck (*D. eytoni*), and the Wandering Whistling Duck (*D. arcuata*). The distinctive adaptations for terrestrial and aquatic locomotion in these species and their phylogenetic implications prompted us to examine their feeding apparatuses for evidence of parallel evolution between the two species representing sympatric populations in North America (*D. autumnalis* and *D. bicolor*) and the two species that are sympatric in Australia (*D. eytoni* and *D. arcuata*).

Materials and Methods

Our data were obtained from at least two adult specimens of each of the four species. Measurements were made with dial calipers, or in some cases with an ocular micrometer incorporated in a binocular dissecting microscope. To measure the length of the semicircular canal, we carefully removed the medial part of the periotic bone with a steel cutting burr on a rotary electric tool. Once the semicircular canal was opened at each end, a human hair was inserted, cut with iridectomy scissors to a length equal to the canal, then removed from the canal with forceps and measured.

To measure the height of a lamella (i.e. the greatest distance that it projects into the maxillary cavity), one of the lateral edges of the maxilla was shaved with a scalpel, parallel with the axis of the maxilla, until a cross section of the lamellae at their maximum heights was exposed. The height of each lamella was then easily measured with an ocular micrometer.

Brain sections could not be prepared adequately because of deterioration, so we estimated the size of the optic and vestibulocochlear lobes by measuring the length and width of the depressions in the skull accommodating these lobes. We prepared an outline of the profile of the upper mandibular cavity by tracing a photograph of a clay cast of this cavity.

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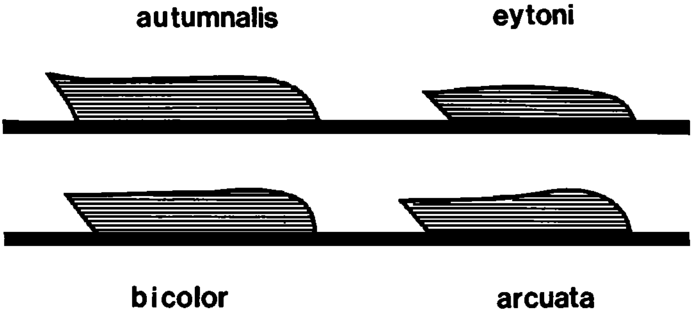

Figure 1. Outlines of whistling duck bill shapes traced from photographs. Note the generally parallel-sided outline of *D. eytoni* and *D. autumnalis* and the flared tips of *D. bicolor* and *D. arcuata*.

RESULTS

Our results are summarized in Figures 1–6, which show significant differences among the four species with regard to morphological features normally associated with feeding. On the basis of the features, the four species clearly segregate into two sets: (1) *D. autumnalis* and *D. eytoni*, and (2) *D. bicolor* and *D. arcuata*, each set having a representative in Australia and a representative in North America. Moreover, the morpho-

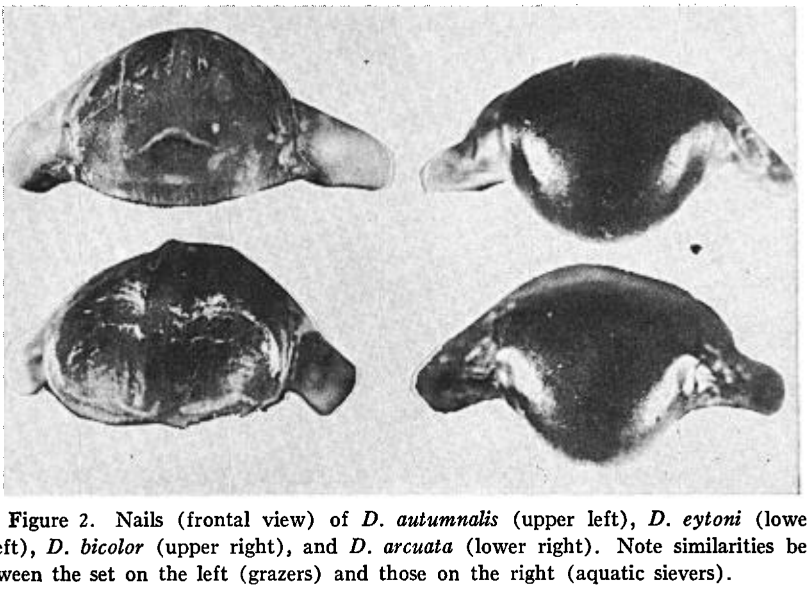

Figure 2. Nails (frontal view) of *D. autumnalis* (upper left), *D. eytoni* (lower left), *D. bicolor* (upper right), and *D. arcuata* (lower right). Note similarities between the set on the left (grazers) and those on the right (aquatic sievers).

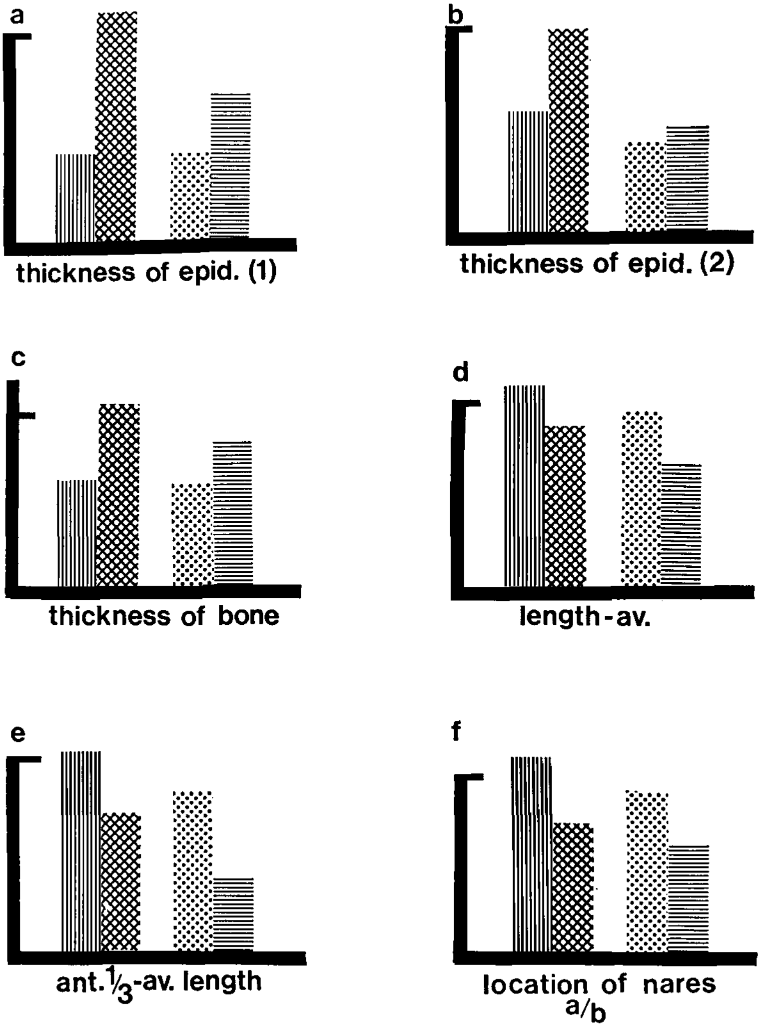

Figure 3. Morphological characters in *D. bicolor* (vertical hatching), *D. autumnalis* (cross-hatching), *D. arcuata* (dots), and *D. eytoni* (horizontal hatching). The horizontal marker on the ordinate represents the following values: a = 0.5 mm; b = 1.0 mm; c = 2.0 mm; d = 0.5 mm; e = 1 mm; f = 0.4 mm. These graphs thus indicate (a) the thickness of the epithelium covering the surface of the maxilla; (b) the thickness of epithelium lining the maxillary cavity; (c) the thickness of the maxillary bone at the midline, beneath the nail; (d) the height (i.e. length) of the lamellae, when viewed in cross section; (e) the height of the lamellae in the anterior ⅓ of the maxilla only; and (f) the location of the nares, with reference to Figure 6.

logical data can be related to certain ecological similarities within each set of species.

The first set, *D. autumnalis* and *D. eytoni*, primarily graze on land whereas the second set, *D. bicolor* and *D. arcuata*, feed almost entirely in the water by means of a sievelike feeding mechanism. The food and feeding habits of the species are contrasted in detail elsewhere (Frith 1967, Bolen and Forsyth 1967, Lavery 1967).

Terrestrial grazers.—*D. autumnalis* and *D. eytoni* strip vegetation when grazing and the following structural characters may serve as adaptations for this action: (1) attenuated or at least parallel-sided maxilla (Figure 1); (2) a less pronounced nail (Figure 2); (3) thicker bone and integument at the distal end of the maxilla (Figure 3a, 3b, 3c); (4) relatively large optic and vestibulocochlear lobes (Figure 4c, 4d); (5) more proximal nares (Figures 3f, 6); and (6) a greater angle formed by the axes of the brain and skull (Figures 4f, 6).

Aquatic sievers.—Studies of aquatic feeding in several ducks, not including *Dendrocygna*, indicate that water is typically drawn into the mouth by a pumping-suction action of the tongue and is then expelled out the side of the bill through the lamellae (see Goodman and Fisher 1962). This forms a sieving action that filters out food particles from the water. The following structural characters, when compared in degree of development with the grazing species of each sympatric pair, seemingly represent adaptations in *D. bicolor* and *D. arcuata* for the sieve type of feeding: (1) maxilla somewhat flared at the tip (Figure 1); (2) a highly developed nail (Figure 2); (3) a greater average height (i.e. length in cross section) of the lamellae especially in the anterior part of the maxilla where seining presumably occurs to a greater extent (Figure 3d, 3e); (4) relatively larger hyoid apparatus (Figure 4a, 4b); (5) a more expansive maxillary cavity distally (Figure 5); and (6) more lamellae along the inner edge of the upper mandible (*D. autumalis* and *D. eytoni* possess about 82–85% of the lamellae per mm of tomium length found in aquatic sievers, Table 1).

DISCUSSION

All of the characters reported in our study seem related to the expected demands made by the two feeding niches represented by each set of species, even though the biomechanics of grazing and aquatic feeding in waterfowl are not yet clearly understood.

Conceivably the more attenuated maxilla, less pronounced nail, and more highly developed bone and integument at the distal end of the maxilla in the grazing species are important adaptations for meeting the mechanical demands of grazing.

TABLE 1

LAMELLAE NUMBER FOR FOUR SPECIES OF WHISTLING DUCKS[1]

Pair	Species	N	Average no. lamellae	Tomium length mm	Lamellae/ tomium length	Ratio A/B
1	A) *D. autumnalis*	5	52.2	54.4	0.96	
	B) *D. bicolor*	2	62.5	53.5	1.17	82
2	A) *D. eytoni*	3	48.3	46.7	1.03	
	B) *D. arcuata*	2	58.5	48.5	1.21	85

[1] Note similarities between the respective species within each set of dendrocygnids (e.g. *D. autumnalis* with *D. eytoni*) and the similarity between pairs of species.

In the aquatic sievers, the relatively larger ceratohyal and basihyal that support musculature for moving the distal tongue bone (hyoglossal) suggest a greater capacity for flexing the tongue, due perhaps not only to the increased musculature, but also to a mechanical advantage from the relatively smaller hyoglossal. The more expansive maxillary cavity may increase the volume of the "pump" (although, alternatively, the smaller cavity in the two grazing species may be the result of a trend toward a more massive maxilla distally).

In their revision of anatid taxonomy Delacour and Mayr (1945) recognized the adaptive nature of bill shapes in waterfowl; previously bill shape was often regarded as a morphological basis for distinguishing waterfowl taxa. Our examination of bill shape compared the area of the bill, taken from photographs, as a percentage of the total area encompassed by an imaginary rectangle determined by the bill's widest point and its length. This comparison, shown in Table 2, revealed remarkably similar results for each member of the same ecological set (i.e. 78% for *D. autumnalis* and 79% for *D. eytoni*). Moreover, there was likeness in the relative amount of divergence between each pair of species (91 vs. 94), although one pair is considerably larger than the other.

Delacour (1954: 47) noted that all dendrocygnids are apparently rather nocturnal but that, among the eight species, *D. autumnalis* is the most nocturnal of the group. Hersloff et al. (1974) recently examined the visual sensitivity in *D. autumnalis* and found a preponderance of rods in its retinal structure. The relatively large optic and vestibulocochlear lobes in *D. autumnalis* and *D. eytoni* suggest that, as grazers, these species may exhibit somewhat greater optical and auditory abilities than do the tactile straining species, *D. bicolor* and *D. arcuata*, skills that may be useful for feeding at night. The significance of the greater angle formed by the axes of the brain and skull in the two grazing species is also not clear. Neither is there an apparent explanation for the more proximally situated nares in the grazing species. A relatively

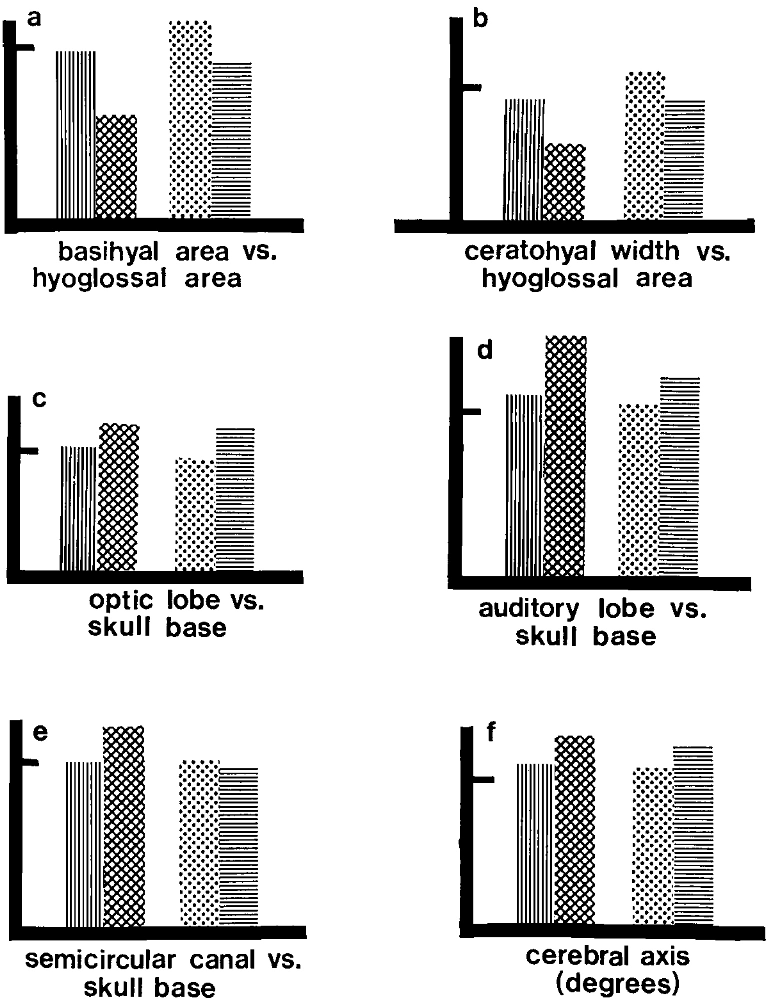

Figure 4. Morphological characters in *D. bicolor* (vertical hatching), *D. autumnalis* (cross-hatching), *D. arcuata* (dots), and *D. eytoni* (horizontal hatching). The horizontal marker on the ordinate represents the following values: a = 0.30; b = 0.1; c = 0.3; d = 0.02; e = 0.1; f = 100 degrees. These graphs thus indicate (a) the ratio between the area on the dorsal surface of the basihyal and the corresponding area of the hyoglossal; (b) the ratio between width of the ceratohyal at its widest part and the area of the dorsal surface of the hyoglossal; (c) the volume of the cavity in the skull containing the optic lobe in relation to the area of the skull base (= basitemporal plate, p on Figure 6); (d) the same type of ratio as in c, but using the auditory lobe cavity instead of the optic lobe cavity; (e) the length of the vertical semicircular canal related to the area of the basitemporal plate; and (f) the angle xyz in Figure 6, xy being perpendicular to the spinal cord as it passes through the foramen magnum.

TABLE 2

BILL AREA EXPRESSED AS THE PERCENTAGE OF AN IMAGINARY RECTANGLE ENCLOSING THE BILL[1]

Pair	Species	Bill area X	Rectangle area Y	Percent X/Y	Ratio A/B
1	A) *D. autumnalis*	43.25	55.20	78	
	B) *D. bicolor*	42.00	48.59	86	91
2	A) *D. eytoni*	27.12	34.20	79	
	B) *D. arcuata*	33.75	40.18	84	94

[1] Note relative similarities between the respective species within each set of dendrocygnids (e.g. *D. autumnalis* with *D. eytoni*) and the similarity between pairs of species.

longer olfactory passage in the aquatic forms could of course reduce the chances of inhalation of water, whereas more proximally situated nares in grazing species could conceivably protect the delicate nasal epithelium from accidental penetration and injury by coarse vegetation. While no direct evidence suggests that these differences in naris location serve such purposes, the data are remarkably consistent between the two sets of species we studied. The relatively large semicircular canals in *D. autumnalis,* most strikingly seen in the vertical canals (Figure 4e), are probably related to this species' unique perching habits; it is the only one of the four species we studied that regularly perches in trees, on wire fences, or other structures (see Rylander and Bolen 1970).

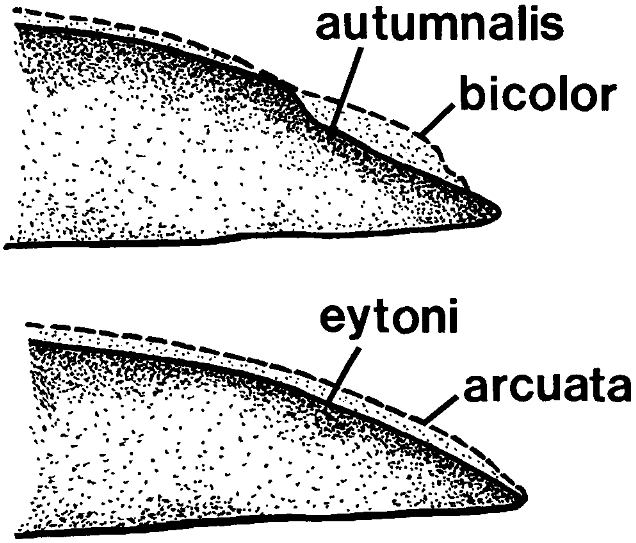

Figure 5. Profiles of the maxillary cavities of *D. eytoni*, *D. autumnalis*, *D. bicolor*, and *D. arcuata* prepared from photographs of clay impressions of the cavities.

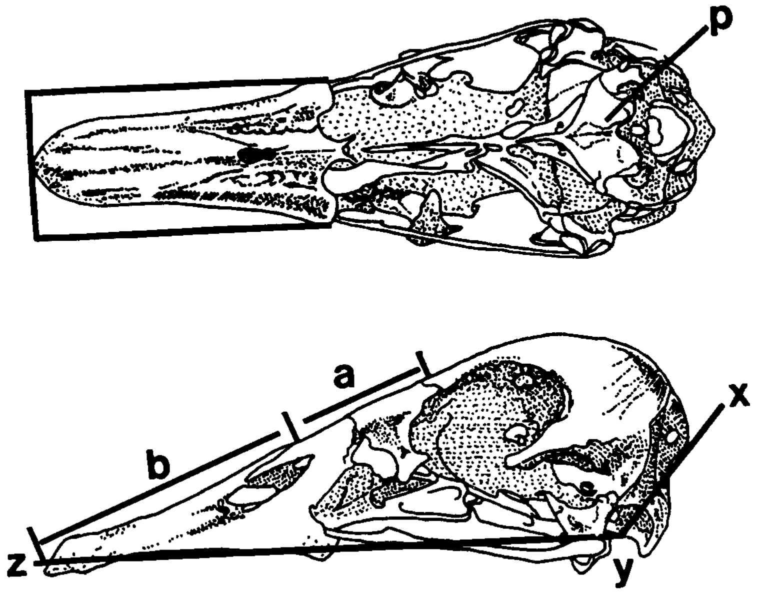

Figure 6. Top: ventral view of skull, indicating the rectangle constructed to calculate data in Table 2, and basitemporal plate, p, the area of which was used to calculate ratios in Figure 4c, 4d, and 4e. Bottom: lateral view of skull, showing the distances a and b used to calculate ratios referred to in Figure 3f, and angle (xyz) formed by plane perpendicular to the axis of spinal cord at the foramen, and the axis of the skull as indicated.

Caution must obviously be exercised when interpreting these morphological distinctions in terms of ecological differences. On the other hand, the two pairs of whistling ducks form distinctive sets on the basis of their locomotion and locomotor apparatus (Rylander and Bolen MS), and the case for parallel evolution in *D. eytoni* and *D. autumnalis* becomes even stronger as additional similarities are found that can be related to their niches. Rylander and Bolen (MS) have also discussed the phenetic relationships and the courses of evolution that *D. autumnalis* and *D. eytoni* may have followed to their present status.

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SUMMARY

The feeding apparatuses of four species of whistling ducks were compared and related to the niches they occupy. The Black-bellied Whistling Duck (*D. autumnalis*) and Plumed Whistling Duck (*D. eytoni*) are predominately grazing species whereas the Fulvous Whistling Duck (*D. bicolor*) and Wandering Whistling Duck (*D. arcuata*) feed on aquatic vegetation while swimming and diving, and presumably employ a seining mechanism while feeding.

When North American representatives of *D. autumnalis* and *D. bicolor* were compared with each other, and the Australian pair *D. eytoni* and *D. arcuata* were similarly compared, the structural differences between the land feeders and water-feeding species were found to be strikingly alike within each group. These correlations included (1) bill shape; (2) shape of the mandibular cavity; (3) relative number of maxillary lamellae; (4) structure of the maxillary lamellae; (5) structure of the hyoid apparatus; (6) relative development of structures associated with sight, hearing and equilibrium; and (7) location of the nares.

LITERATURE CITED

BOLEN, E. G., AND B. J. FORSYTH. 1967. Foods of the Black-bellied Tree Duck in south Texas. Wilson Bull. 79: 43–49.

BOLEN, E. G., AND M. K. RYLANDER. 1974. Foot adaptations in four species of whistling duck. Wildfowl, in press.

DELACOUR, J. 1954. Waterfowl of the world, vol. 1. London, Country Life Ltd.

DELACOUR, J., AND E. MAYR. 1945. The family Anatidae. Wilson Bull. 57: 3–55.

FRITH, H. J. 1967. Waterfowl in Australia. Honolulu, East-West Center Press.

GOODMAN, D. C., AND H. I. FISHER. 1962. Functional anatomy of the feeding apparatus in waterfowl. Carbondale, Southern Illinois Univ. Press.

HERSLOFF, L., P. N. LEHNER, E. G. BOLEN, AND M. K. RYLANDER. 1974. Visual sensitivity in the Black-bellied Tree Duck, a crepuscular species. J. Comp. Physiol. Psychol., in press.

KEAR, J., AND P. J. K. BURTON. 1971. The food and feeding apparatus of the Blue Duck *Hymenolaimus*. Ibis 113: 483–493.

LAVERY, H. J. 1967. Whistling ducks in Queensland. Adv. Leaflet 917, Div. Plant Industry, Dept. Primary Industries, Queensland, Australia.

RYLANDER, M. K., AND E. G. BOLEN. 1970. Ecological and anatomical adaptations of North American tree ducks. Auk 87: 72–90.

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