TRACHEAL ANATOMY OF THE ANATIDAE AND ITS TAXONOMIC SIGNIFICANCE

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Summary

TRACHEAL and syringeal variations in waterfowl are summarized, based on a tracheal collection representing 84 out of the 143 species of Anatidae. Twenty seven species are illustrated with drawings, and photographs of 24 species are also included, comprising 29 of the 43 genera of Anatidae. The following major points are made:

1. The Magpie Goose (*Anseranas semipalmata*) is unique in its externally convoluted trachea, but the syrinx is small and simple in both sexes.
2. Species of the subfamily Anserinae have symmetrical tracheae in both sexes, which either lack bullae (Anserini) or have symmetrical bullae which are larger in males than in females (Dendrocygnini).
3. The Coscoroba Swan (*Coscoroba coscoroba*) and the Cereopsis Goose (*Cereopsis novaehollandiae*) have tracheae of the Anserini type, and the Freckled Duck (*Stictonetta naevosa*) has an extremely simple and primitive type of trachea and syrinx in both sexes.
4. Species of the subfamily Anatinae exhibit sexual dimorphism in the syrinx, and males of most species except stiff-tails (Oxyurini) possess asymmetrically enlarged syrinxes (bullae).
5. Enlargements of the tracheal tubes of male Anatinae occur in a few dabbling ducks (Anatini), most of the pochards (Aythyini) and most sea ducks (Mergini). Tracheal air sacs occur in some stiff-tails, and extra-tracheal sound production is also typical of this group.
6. Although males of most Anatinae possess entirely osseous bullae, partially membranaceous (fenestrated) bullae are found in all pochards and most sea ducks. The Marbled Teal (*Marmaronetta angustirostris*) and Pink-headed Duck (*Rhodonessa caryophyllacea*) also possess fenestrated bullae which are intermediate between the dabbling duck and pochard types.
7. The sea ducks exhibit the greatest variation in shape and structure of male tracheae, and specializations of the bronchi, tracheal tube, and musculature are frequent. The tribal separation of the eiders on the basis of their tracheal anatomy is not justified.

Although practically every genetically determined aspect of anatomy that varies among different species of animals has been used by biologists in attempting to assess evolutionary relationships, students of waterfowl have a particularly rich source of information available in the form of the trachea (" windpipe ") and the associated syrinx, the vocal organ of birds. Through differences in the size, shape, and structure of these organs, the different species (and often the two sexes of the same species) achieve the characteristic qualities of voice that provide for recognition among individuals and between species. Waterfowl of the family Anatidae lack the complex internal syringeal muscular structure of songbirds to achieve this specificity of vocalizations, and probably as a result of this have utilized simpler structural variations in the length, size and shape of the trachea and syrinx to provide auditory distinctiveness. It was realized very long ago that these variations of structure in different species were useful in judging relationships, and many early students of birds (Latham, 1798; Yarrell, 1827; Eyton, 1838) described and illustrated the tracheal anatomy of wildfowl. Heinroth (1911) was among the first fully to realize the value of tracheal variations in assessing waterfowl relationships, and attempted to summarize the major variations found in the Anatidae and relate them to their probable evolutionary relationships.

Delacour and Mayr (1945) also utilized tracheal anatomy in their revision of the Anatidae, and urged that attempts be made to collect and describe these structures from species which were still of uncertain relationships or for which the anatomy was unknown. Since collections of tracheae are very rare in museums, an attempt has been made to accumulate a representative collection at the Wildfowl Trust which may eventually serve as a reference collection for future research. These specimens have been obtained primarily from birds which have died at the Trust, and in somewhat over one year the number of species represented in this collection has reached 84.

Because the tracheae of numerous species have never been described, and also because no recent attempt has been made to summarize the major structural variations in the tracheae of waterfowl, the following summary of tracheal anatomy in the Anatidae is presented here. Since tracheal structure is fairly uniform within each tribe, the family will be discussed in such units, the sequence and composition of the tribes being basically that proposed by Delacour (1954-1959), but with some modifications as suggested by Johnsgard (1960, 1961).

SUBFAMILY ANSERANATINAE

Tribe Anseranatini

The Magpie Goose, *Anseranas semipalmata,* possesses a trachea which is one of the most distinctive of all birds'. Although the syrinx in both sexes is small and simple (Fig. 1), the trachea is extremely elongated, particularly in the male. Young Magpie Geese up to four months old have essentially straight tracheae like those of most other waterfowl, but the trachea soon lengthens by increasing the width of the tracheal rings, and begins to convolute outside the body cavity between the left breast muscle and the skin. This is more pronounced in males; in eight-month-old birds there are already obvious differences in the voices of the sexes, and the male's trachea is approximately half the length found in adult males (see photo section). The adult condition appears to be reached in two years, when a male's trachea is approximately 150 centimeters in length. The lower-pitched voice of adult male Magpie Geese is presumably the result of this greater trachea length.

SUBFAMILY ANSERINAE

Tribe Dendrocygnini

The whistling ducks (*Dendrocygna*) lack convoluted tracheae, but possess fairly complex syringeal structures, at least in males. In all eight species the male tracheae are symmetrically inflated at the syrinx to form rather oval-shaped structures (Fig. 1). The size of these chambers is relatively uniform in all species, but the shape differs somewhat in the various species and provides some clues to relationships. Thus the tracheae of male Indian (*D. javanica*), Wandering (*D. arcuata*) and Plumed (*D. eytoni*) Whistling Ducks are all very similar to one another and, to a lesser degree, to that of the Fulvous (*D. bicolor*). The tracheae of the White-faced (*D. viduata*) and Spotted (*D. guttata*) Whistling Ducks are, on the other hand, distinct from these and from one another. Those of the Cuban (*D. arborea*) and Red-billed (*D. autumnalis*) are not yet available for close comparison.

In the female sex the tracheal structure of all species is simpler and more uniform (see photo section). In two species (*D. arborea* and *D. autumnalis*) the syrinx is entirely osseous, while in the others the syrinx, although it is of similar shape, possesses a narrow membranaceous tympanum on the dorsal surface near the junction of the bronchi. In spite of these differences in the tracheal structure of the sexes in whistling ducks there is no obvious sexual dimorphism in the voices of *Dendrocygna*. Heinroth (1918) has also discussed the tracheal anatomy of whistling ducks.

Tribe Anserini

The true geese and swans are characterized by a remarkably uniform and relatively simple vocal apparatus. In no species are there any complex syringeal structures in either sex, and it is also true that practically no sexual dimorphism is present in the trachea or syrinx. In these species, as in the Magpie Goose, the source of sound production appears to be the vibration of the tympaniform membranes, which are situated where the bronchi join the trachea, and variations in pitch probably result from differences in the tension of these membranes as regulated by the syringeal muscles. In the true geese and the Coscoroba Swan (*Coscoroba coscoroba*) males possess normally higher pitched voices than do females, although the reasons for this are not yet clear. In most of the swans the sexes have voices of roughly the same pitch or the male's may be lower pitched. As is well known, the Trumpeter and Whooper Swans (*C. cygnus*) and also the Whistling and Bewick's Swans (*C. columbianus*) have tracheae which convolute inside the sternum, or breastbone, and it is presumably the increased length of these species' tracheae that is in part responsible for the marvellous trumpeting calls characteristic of these birds (see photo section). In the other swans the tracheae are unconvoluted and are uniform in diameter throughout. The trachea of the Coscoroba Swan is very similar to that of the Mute Swan (*C. olor*), suggesting that the Coscoroba is a true swan rather than a close relative of the whistling ducks (see photo section).

In the true geese (*Anser* and *Branta*) there is relatively little tracheal variation. The tracheae are straight, but vary in diameter in some species. It appears that the tracheal tubes of males tend to vary more than do those of the females. The syrinx is the same in both sexes and basically like those of swans and the Magpie Goose (see Fig. 1 and photo section).

The Cape Barren Goose (*Cereopsis novae-hollandiae*) has a tracheal structure (Fig. 1) like that of the true geese rather than of the very different form exhibited by the sheldgeese, and there are other reasons (Johnsgard, 1960a) for believing that this species provides a true link between the Anserini and the sheldgeese (Tadornini). The Freckled Duck (*Stictonetta naevosa*) has a trachea (illustrated in Fig. 1 after Campbell, 1899) with a simple syrinx and a tracheal tube which varies only slightly in diameter. As indicated earlier (Johnsgard, 1960a), it is possible that the Freckled Duck is more closely related to the true geese than to the ducks. The Freckled Duck and the Cape Barren Goose exhibit certain other primitive features that suggest that both species have been derived from early offshoots of the waterfowl stock and have no close living relatives.

SUBFAMILY ANATINAE

Tribe Tadornini

In the shelducks and sheldgeese, as well as in almost all the true ducks (Anatinae), there is considerable sexual dimorphism in tracheal structure and a corresponding difference in the adult voices of the two sexes. Females tend to have loud and low-pitched honking or quacking voices which are produced in the same manner as described for the preceding tribe. Males tend to have high-pitched, often whistling, voices, although they vary greatly. The whistling calls of males appear normally to originate in the tracheal "bulla," an enlarged area of the trachea in the region of the syrinx that acts as a sound chamber. In most species this is asymmetrical in shape, being enlarged towards the left side. The whistling sound appears to be produced by the rapid expulsion of air from the lungs, which rushes past the sound chamber and produces a whistle in the same manner as a mechanical whistle functions. Males of many species can also produce sound by the alternative means of vibrating the syringeal membranes.

In all the species of this tribe the tracheal tube is of uniform diameter in both sexes, and females of all species have simple, goose-like syringeal structures. Males of the sheldgeese (*Cyanochen, Chloëphaga, Neochen* and *Alopochen*) all possess tracheal bullae which consists of a simple inflated and relatively spherical bony chamber on the left side of the syrinx (Fig. 1 and photo section). The size of the bulla varies considerably in different species, but in all it is thin and rather uniformly ossified. In some shelduck (*Tadorna*) species (the "casarcas") the male's tracheal bulla is very small and almost rudimentary (Fig. 1), but the Radjah Shelduck's (*T. radjah*) bulla is fairly large. In the Common Shelduck (*T. tadorna*) it is also large and is equally inflated on both sides (see illustration in Heinroth and Heinroth, 1928).

Male steamer ducks (*Tachyeres*) have tracheae with typically inflated bullae that do not differ markedly from those of the sheldgeese, but behavioural evidence (Moynihan, 1958) suggests that they should be removed from the shelduck tribe. The bronchi of both sexes of steamer ducks are greatly enlarged (see Fig. 1 and photo section). The Crested Duck ("*Lophonetta*" *specularioides*) is here considered a member of the typical genus (*Anas*) of surface-feeding ducks.

Tribe Cairinini

Males of all species in this tribe have voices distinctly different from those of the females, and the degree of tracheal dimorphism varies considerably. It is least in the pygmy geese (*Nettapus*), in which the bulla of the male is only slightly indicated (Fig. 1). In the Spur-winged Goose (*Plectropterus gambensis*) the bulla is rounded and very unevenly ossified. The same uneven ossification is present in the White-winged Wood Duck (*Cairina scutalata*), but the bulla is large and is strongly flattened dorso-ventrally (see Fig. 1 and photo section). In both sexes of this species the bronchi are also markedly ossified (as is true also of the Trumpeter Swan and its near relatives), and perhaps the loud, honking voices of both sexes are somehow related to this. The trachea of the nearly-mute Muscovy Duck (*C. moschata*) lacks these unusual features, and males have a simple, wholly ossified, rounded bulla. The equally silent male Comb Duck (*Sarkidiornis*

melanotos) exhibits a relatively rudimentary bulla. In the Hartlaub's Duck *Pteronetta* (" *Cairina* ") *hartlaubi,* the male's tracheal bulla takes a form more like that found in *Anas,* being thick-walled and possessing a triangular bony protuberance at the ventral surface.

The North American Wood Duck (*Aix sponsa*) (Fig. 1) and Mandarin Duck (*A. galericulata*) have relatively simpler male tracheae, with thinner and more spherical bullae than is found in the Hartlaub's Duck. The trachea of the Maned Goose (*Chenonetta jubata*) is similar (see photo section), and the Brazilian Teal (*Amazonetta brasiliensis*) also has a bulla which is relatively large and spherical (Phillips, 1924).

It is now fairly clear that the Ringed Teal, *Callonetta* (" *Anas* ") *leucophrys,* is a member of the perching duck tribe (Johnsgard, 1960b). This is also supported by its male tracheal structure, which is roughly intermediate between those of *Nettapus* and *Aix* (Fig. 1).

Tribe Anatini

Besides the large genus *Anas,* several aberrant genera are included in this tribe of surface-feeding ducks. Of these, the tracheal anatomy of the Pink-eared Duck (*Malacorhynchus membranaceous*) and Blue Duck (*Hymenolaimus malacorhynchus*) is still undescribed and a knowledge of these species' tracheae might assist in interpreting their evolutionary relationships. The male Pink-headed Duck (*Rhodonessa caryophyllacea*) has a trachea with a fenestrated bulla that is distinct from the typical *Anas* shape but approaches that of the pochards (illustration in Fig. 1 after Garrod, 1875) and certain aspects of the adult plumage pattern also indicate that this species might be placed in the pochard tribe.* Torrent Ducks (*Merganetta armata*) have male tracheal bullae that are distinctly *Anas*-like (Niethammer, 1952) and which especially resemble that of the Salvadori's Duck (*Anas waigiuensis*).

Males of the approximately 36 species of *Anas* have tracheal structures that are relatively uniform, but which vary enough sometimes to indicate evolutionary relationships. These variations can be used to divide the genus into several fairly distinct groups. The wigeons (*Anas sibilatrix, A. penelope* and *A. americana*) comprise one such group. In these species the male bulla tends towards a spherical shape as found in *Aix* and some other perching ducks (see photo section). From this condition the Falcated Duck (*A. falcata*) and Gadwall (*A. strepera*) grade to the more typical situation found in the groups of species known as the " green-winged " teal (*A. crecca* and *A. flavirostris*) and " austral " teal (*A. gibberifrons, A. bernieri, A. castanea* and *A. aucklandica*). In these species the tracheal bulla is relatively small, but is strongly and evenly ossified, and forms a triangular point at the right ventral extremity (see photo section). The Cape Teal (*A. capensis*) also has a trachea of this shape (Fig. 1) and certainly belongs with this group of species rather than with the " spotted " teal (see below). The Baikal Teal (*A. formosa*) also has a bulla of this shape, but it is of rudimentary size and the absence of a lateral sound chamber probably accounts for the fact that, unlike the species already mentioned, the male Baikal Teal lacks a whistling note.

*A complete specimen of this species' trachea has been located by the writer in the British Museum (Natural History). It differs from the specimen on which the illustration by Garrod is based, and is even more pochard-like (see Fig. 3, p. 69).

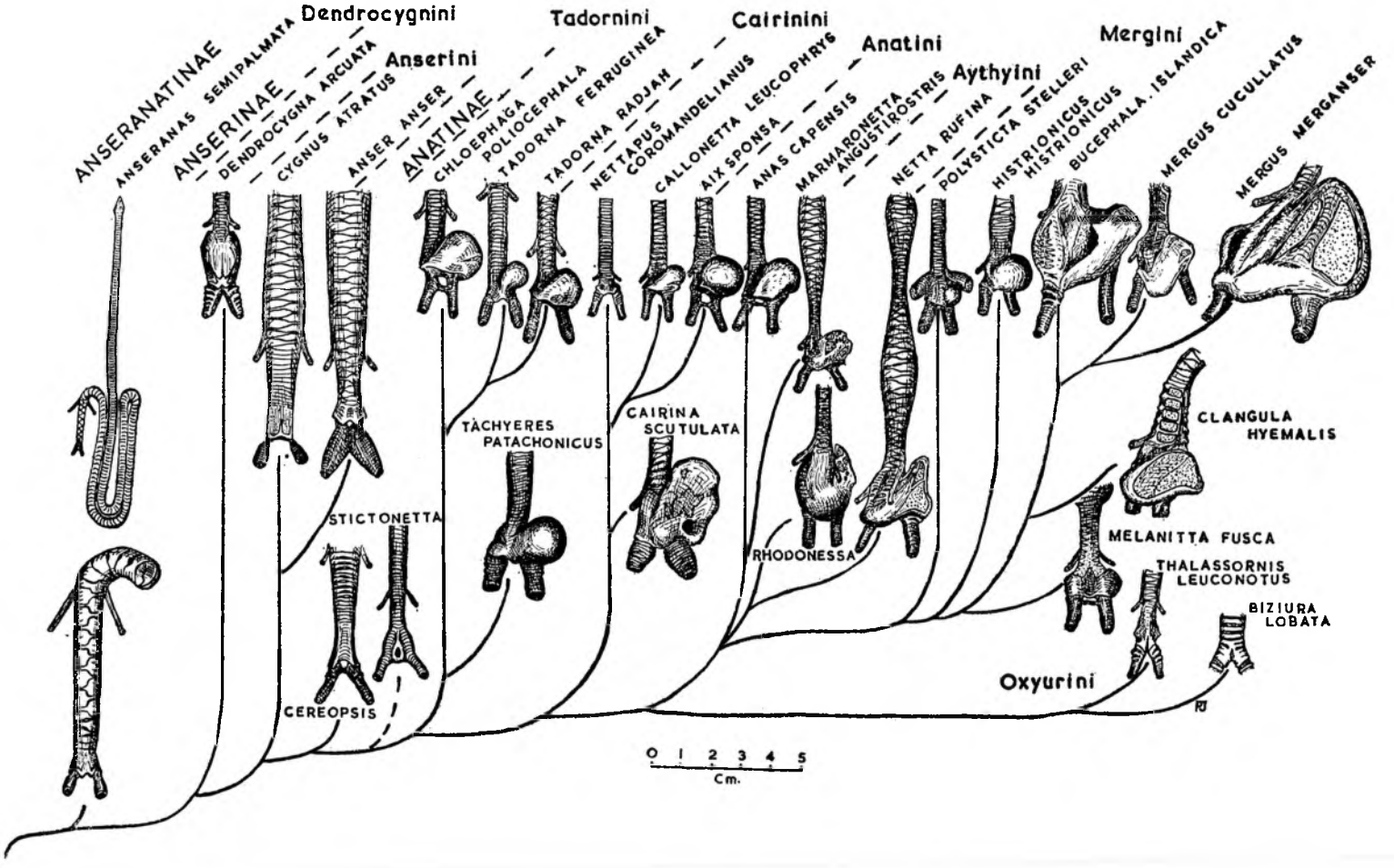
The " austral " teal in turn lead to the mallard-like and pintail-like ducks. On the basis of the shape of the tracheal bulla, the Salvadori's Duck (*Anas waigiuensis*) has been considered a near relative of the mallard group, but there is little in the species' behaviour which indicates it is a typical mallard and the bulla is also remarkably small. The African Black Duck (*A. sparsa*), which gives a stronger general appearance of being one of the mallard group, has a tracheal bulla which is relatively smaller than the typical mallard's. The Crested Duck (*Anas specularioides*) and Bronze-winged Duck (*Anas specularis*) have bullae of the same conformation as the mallard-like ducks (Phillips, 1924), but of decreased size and approaching the small bulla condition of the typical pintail-like ducks (*A. acuta* and *A. georgica*). Although the bullae are larger in the Bahama Pintail (*A. bahamensis*) and Red-billed " Teal " (*A. erythrorhyncha*), they are of the same shape as in the two preceding species and these four species comprise a homogenous evolutionary group.

The Silver Teal (*A. versicolor*) and Hottentot Teal (*A. punctata*) are unique among the species of *Anas* in that males possess a very marked enlargement of the trachea in the neck region. These two species are among the group termed " spotted " teal by Delacour (1954), but the other three species included by him in this group (Cape Teal, Red-billed Teal, and Marbled Teal) all appear to have closer relationships with other groups. The bulla shape of the Silver Teal (that of the Hottentot is unknown to me) is intermediate between the trangular shape of the pintail group and the rather globular shape of the blue-winged ducks (see photo section). This globular shape is found in the Garganey (*A. querquedula*), in which there is practically no asymmetry towards the left and the whistling voice typical of nearly all the preceding species is replaced by a low, wooden rattle. Most of the other blue-winged ducks also lack whistling voices (*A. discors* is the exception) and have small tracheal bullae situated more ventrally than towards the left (see photo section).

Behavioural evidence (Johnsgard, 1961) indicates that the Marbled Teal (" *Anas* " *angustirostris*) should be removed from the genus *Anas* and placed in a monotypic genus (*Marmaronetta*), adjacent to the pochard tribe. It possesses a male tracheal tube of gradually varying diameter such as occurs in male pochards (see photo section), and the bulla has several membranaceous fenestrae such as are typical of pochards and the Pink-headed Duck (Fig. 1).

Tribe Aythyini

The pochards exhibit an astonishing difference from the preceding tribe in the tracheal structure of males. Instead of a uniformly ossified and rounded bulla, there is a large, rather angular bulla on the left side which contains several membranaceous fenestrae, or " windows." As mentioned above, the Pink-headed Duck exhibits a transitional stage between the tracheal conditions of the Anatini and Aythyini, and has a crested and fenestrated bulla similar to those of male pochards (Fig. 1). In addition to this unusual bulla structure, the tracheal tubes in the males of most and perhaps all species of Aythyini are variable in diameter, with one or two enlargements (see photo section). The diameter of the tube in most species varies gradually, but in the Rosy-bill (*Netta peposaca*) the changes in diameter are abrupt. These diametric changes do not appear to have great taxonomic


ANSERANATINAE
ANSERANAS SEMIPALMATA
ANSERINAE
DENDROCYGNA ARCUATA
CYGNUS ATRATUS
Dendrocygnini
Anserini
ANSER ANSER
ANATINAE
Tadornini
CHLOEPHAGA POLIOCEPHALA
TADORNA FERRUGINEA
TADORNA RADJAH
NETTAPUS COROMANDELIANUS
Cairinini
CALLONETTA LEUCOPHRYS
AIX SPONSA
ANAS CAPENSIS
Anatini
MARMARONETTA ANGUSTIROSTRIS
NETTA RUFINA
POLYSTICTA STELLERI
Aythyini
HISTRIONICUS HISTRIONICUS
BUCEPHALA ISLANDICA
MERGUS CUCULLATUS
MERGUS MERGANSER
Mergini
TACHYERES PATACHONICUS
CAIRINA SCUTULATA
CLANGULA HYEMALIS
STICTONETTA
MELANITTA FUSCA
RHODONESSA
THALASSORNIS LEUCONOTUS
BIZIURA LOBATA
Oxyurini
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0 1 2 3 4 5
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significance, but there are some variations in the shape of the bulla itself which seem to suggest certain groupings. The genus *Netta* is relatively variable. The Red-crested Pochard (*N. rufina*) has two enlargements in the tracheal tube (Fig. 1) whereas the other two species of *Netta* have single enlargements. In the Rosy-bill, and also in the Tufted Duck (*Aythya fuligula*) and the scaup-like ducks the right side of the bulla is more inflated than in the other species.

Tribe Mergini

The sea ducks (here including the eiders, which have been placed by Delacour in a separate tribe) are the most variable in their tracheal anatomy of any single group of waterfowl. Partly because of this, Humphrey (1958) advocated the separation of the eiders from the other sea ducks and their placement near the Anatini. Indeed, the tracheae of eiders are remarkably like those of *Anas,* since the tracheal tubes are of uniform diameter and the bullae are completely and uniformly ossified and are of the same general configuration as those of some species of *Anas*. However, the Labrador Duck (*Camptorhynchus labradorius*) has an apparently similar tracheal bulla (Wilson, 1832), as does also the Harlequin Duck (*Histrionicus histrionicus*) (Fig. 1), although these two species otherwise appear to be relatives of the scoters (*Melanitta*) and the other sea ducks. The scoters are among the most aberrant of the ducks with regard to their tracheal anatomy, for in the Black Scoter (*M. nigra*) there is essentially no bulla, and in the Velvet (*M. fusca*) and Surf (*M. perspicillata*) Scoters the bulla is small and almost symmetrical (see Fig. 1 and photo section). In some species of scoters (especially *M. nigra*) and eiders (*Somateria*) the bronchi are greatly enlarged. The Steller's Eider (*Polysticta stelleri*) has a small bulla, but the associated muscles are highly developed, an unusual situation in view of the very silent nature of male Steller's Eiders (Fig. 1).

The Long-tailed Duck (*Clangula hyemalis*) possesses a trachea of relatively uniform diameter with a rather scoter-like bulla that is asymmetrically enlarged and fenestrated by one major and one minor " window " on the left side (Fig. 1). The Bufflehead (*Bucephala albeola*) has an undistinguished trachea which lacks swellings and has a small, simple bulla which is much like those of Velvet and Surf Scoters except that, as in the Long-tailed Duck, two membranaceous " windows " are present on the left side. In the goldeneyes (*Bucephala*) this basic form is more complex, but is certainly a modification of the type of bulla present in scoters and the Long-tailed Duck. In both species of goldeneyes the bulla is large and the two " windows " are placed more dorsally and anteriorly on the left side (Fig. 1). Unlike the Bufflehead and Long-tail, both species of goldeneyes have tracheae with distinct mid-tracheal swellings. In the Barrow's Goldeneye (*B. islandica*) this swelling is gradual and includes much of the tracheal tube, but in the Common Goldeneye (*B. clangula*) it is more abruptly restricted and is arranged in a cone-like

FIGURE 1. Ventral views of syrinxes of adult male Anatidae, arranged on a simplified evolutionary tree. The drawings of *Stictonetta, Tachyeres, Rhodonessa, Histrionicus* and *Biziura* are based on published illustrations and may not be to scale.

fashion that is " telescoped " normally but can be greatly extended (see photo section). This interesting adaptation no doubt is associated with the remarkable head-throw displays typical of the Common Goldeneye, which result in much greater neck-stretching than is the case during Barrow's Goldeneye display.

The mergansers (*Mergus*) exhibit a remarkable degree of variation in tracheal structure among the eight species. The Hooded Merganser (*M. cucullatus*) has a tracheal tube with one swelling near the bulla and a series of small " windows " just anterior to the bulla (Fig. 1). The bulla is shaped very much like those of the goldeneyes, with only a very small fenestra present on the side of the left chamber and a weakly ossified right chamber. The male Smew (*M. albellus*) has a tracheal tube rather uniformly enlarged over the female's, and the *sternotrachealis* muscles are also somewhat enlarged (see photo section), though not so markedly as in the Steller's Eider. The Smew's bulla is strongly enlarged towards the left, and the " windows " are much more noticeable than in the Hooded Merganser. The extremes of this tendency towards bulla inflation and development of large " windows " occur in the Red-breasted Merganser (*M. serrator*) and Goosander (*M. merganser*). In the male Red-breasted Merganser (see photo section) both the left and right chambers are greatly enlarged and contain fenestrae that are large and oval. The male Goosander has a tracheal tube with two enlargements and an asymmetrically inflated bulla with an extraordinarily large and fenestrated left chamber (Fig. 1). According to Humphrey (1955), the Brazilian Merganser (*M. octosetaceus*) has a trachea similar to that of the Red-breasted Merganser, whereas the Chinese (*M. squamatus*) and Auckland Island (*M. australis*) Mergansers agree more closely with the Goosander.

Tribe Oxyurini

The stiff-tail group is perhaps the most distinctive of all the tribes of waterfowl with respect to specializations for sound production. Although no species is known to have large or asymmetrical tracheal bullas, the auditory mechanisms are none the less of much interest. The Black-headed Duck (*Heteronetta atricapilla*), which appears to provide the most likely evolutionary " link " between the Oxyurini and the other waterfowl, has a simple male syrinx, a trachea which is enlarged near the middle of the tube, and lacks any tracheal air sacs. However, the oesophagus is enlarged and is probably inflatable and there is a large inflatable throat sac that connects with the mouth in males (Wetmore, 1926). Which of these structures is responsible for producing the various sounds which have been attributed to male Black-headed Ducks is uncertain.

Among the typical stiff-tails (*Oxyura*), the tracheal and oesophageal anatomy has been described for only a few species. The male North American Ruddy Duck (*O. j. jamaicensis*) has a simple trachea with a large air sac connecting with the dorsal side and which can be inflated at will. This sac serves as a " sounding board " for the bill-drumming, or " Bubble," display of the male, and is deflated to produce sound at the end of each display. The White-headed Stiff-tail (*O. leucocephala*) has a very similar display and so presumably has a similar tracheal air sac. In the Argentine Ruddy Duck (*O. vittata*) this sac is rudimentary, but the oesophagus of the male is enlarged and is apparently inflatable (Wetmore, 1926). In both this species and the

Australian Blue-billed Duck (*O. australis*) one of the common male displays is to inflate the neck, rear up in the water, and perform rapid preening-like movements of the bill against the breast which probably serve to deflate the oesophagus and produce sound. The Maccoa Duck (*O. maccoa*) male is reported to utter a loud " croaking " note without special head movements, and although it can inflate its neck it is not yet known whether this is the result of tracheal or oesophageal specializations. Likewise, the Masked Duck (*O. dominica*) male has a fairly loud voice, but the existence of inflatable neck structures has not been recorded.

The Musk Duck (*Biziura lobata*) has a trachea with a simple, bony syrinx that probably is the source of the male's whistling note (illustration in Fig. 1 after Beddard, 1898). Males also have an inflatable pouch (behind but not connected with the wattle) located below the tongue, which is possibly the origin of the male's well-known " plonk " call. The very aberrant White-backed Duck (*Thalassornis leuconotis*) seems to lack any form of inflatable air sacs or specialized oesophageal structure, but both sexes have loud, clear whistling voices that are reminiscent of whistling ducks or guinea pigs. The trachea of the male (Fig. 1 and photo section) is a simple tube with a rather long but not inflated bony bulla at the syrinx which is much like those of female whistling ducks. It seems most likely that this superficial similarity in the voice and trachea of the White-backed Duck to those of whistling ducks is the result of convergence, although this species also shows with the whistling ducks the previously undescribed feature of reticulated tarsi.

Discussion

As is true of many anatomical features, the value of the trachea for taxonomic purposes varies greatly in different groups. In the swans and true geese there is little inter-species variation in the basic structure of the trachea and syrinx, and accordingly the possibilities for taxonomic utilization appear to be reduced. In the shelducks (Tadornini), perching ducks (Cairinini) and dabbling ducks (Anatini) males of all species exhibit asymmetrical osseous tracheal bullas that often differ greatly within genera and sometimes provide strong clues as to relationships not otherwise evident (e.g., Cape Teal and Red-billed Teal). Tracheal evidence also points to distinctly different relationships in the case of the Pink-headed Duck and Freckled Duck from those which have heretofore been suggested.

The greatest degree of sexual dimorphism in tracheal structures occurs in the pochards (Aythyini) and especially the sea ducks (Mergini), in which the tracheal tubes and bronchi of males are often enlarged and the bullae are usually large and partially membranaceous. Here again the tracheal structure provides some interesting and valuable evidence for judging relationships (e.g.. Harlequin, Bufflehead, and Hooded Merganser), which are not always obvious from other evidence. Finally, in the stiff-tail group (Oxyurini) it seems likely that a combined study of the displays and the sound-producing structures of the various species of *Oxyura* would provide fascinating information on evolutionary relationships as well as on the inter-relationships between anatomy and behaviour.

As a final point, the evaluation of tracheal structures should be done with a full awareness of the actual vocalizations produced by the species being studied. For example, some species with outwardly similar male tracheal

structures (such as eiders and mallards) have extremely divergent vocalizations and thus the appearance of the trachea does not always indicate the type of vocalization produced. It is the latter which is of primary importance to the species, as well as to related species which live in the same region. Thus, simply because the trachea is an internal structure there is no reason to believe that it is less subject to convergent evolution than are certain external characteristics.

Opportunities for Future Studies

In spite of the fact that ornithologists have been interested in the tracheal anatomy of waterfowl for over a century, the tracheae of several species still remain to be described. The most important of these include the Pink-eared Duck and the Blue Duck, and the descriptions of male tracheae from such species as the Crested Duck, Bronze-winged Duck, Brazilian Teal, and numerous other species are inadequate and could be greatly improved with drawings or photographs. Likewise the male tracheal and oesophageal structures of the White-headed Stiff-tail, Maccoa Duck and Australian Blue-billed Duck should be examined and described. It is indeed fortunate that the tracheae of such now-extinct species as the Pink-headed Duck, Labrador Duck, and Auckland Island Merganser were described, for in each case important evidence for judging relationships has resulted which otherwise would have been entirely lost.

The means of preserving tracheae is exceedingly simple. The trachea is cut off at the base of the tongue and at the points where the bronchi enter the lungs. It can then be placed in an oxidizing solution such as hydrogen peroxide for bleaching and to loosen the excess connective tissues, and is finally dried and mounted. Submergence in a preservative such as formalin is a less satisfactory alternative procedure. The Wildfowl Trust would be pleased to receive tracheae from such species as are not usually represented in live collections.

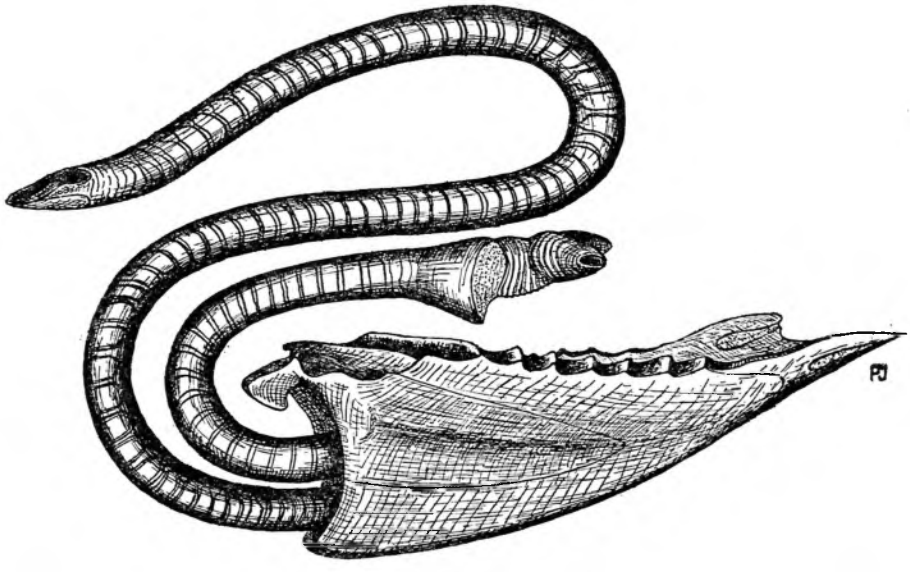

FIGURE 2. Lateral view of sternum and trachea of adult male Eastern Bewick's Swan (*Cygnus columbianus jankowskii*).

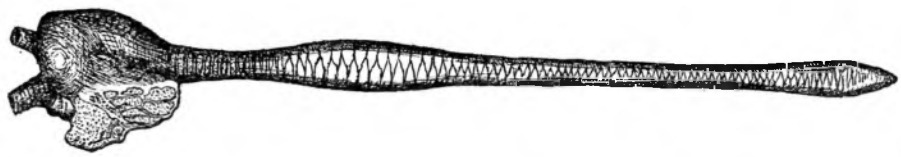

FIGURE 3. Trachea of male Pink-headed Duck, based on specimen of uncertain origin in the British Museum (N.H.). The view is a more directly ventral one than is the illustration on which the drawing in Fig. 1 was based and clearly shows the pochard-like bulla as well as the enlarged tracheal tube.

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References

BEDDARD, F. E. 1898. *The Structure and Classification of Birds*. Longmans, Green & Co., London. 548 pp.

CAMPBELL, A. J. 1899. On trachea of the Freckled Duck of Australia (Stictonetta naevosa). *Ibis* ser. 7, vol. 5 : 362-364.

DELACOUR, J. & MAYR, E. 1945. The family Anatidae. *Wilson Bull.* 57 : 3-55.

DELACOUR, J. 1954-1959. *The Waterfowl of the World*. 3 vol. Country Life, London.

EYTON, T. C. 1838. *A Monograph on the Anatidae or Duck-tribe, including the Geese and Swans*. Longmans, London. 178 pp.

GARROD, A. H. 1875. On the form of the lower larynx in certain species of ducks. *Proc. Zool.* Soc. Lond., : 151-156.

HEINROTH, O. 1911. Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Verh. V. Int. orn. Kongr., Berlin.* 1910. pp. 598-702.

HEINROTH. O. 1918. (Ueber das genus *Dendrocygna*). Jour. für Ornith. 66 : 241-244.

HEINROTH, O. & HEINROTH, M. 1928. *Die Vögel Mitteleuropas*. Vol. 3. H. Bermühler, Berlin.

HUMPHREY, P. S. 1955. The relationships of the sea ducks (Tribe Mergini). Ph.D. Dissertation, Univ. of Mich.

HUMPHREY, P. S. 1958. Classification and systematic position of the eiders. *Condor*, 60 : 129-135.

JOHNSGARD, P. A. 1960a. Comparative behaviour of the Anatidae and its evolutionary implications. *Wildfowl Trust Eleventh Annual Report* : 31-45.

JOHNSGARD, P. A. 1960b. The systematic position of the Ringed Teal. *Bull. Brit. Orn. Club* 80 : 165-7.

JOHNSGARD, P. A. 1961. The taxonomy of the Anatidae—A behavioural analysis. *Ibis* 103a : 71-85.

LATHAM, J. 1798. An essay on the tracheae or windpipes of various birds. *Trans. Linn. Soc. Lond.*, 4 : 90-125.

MOYNIHAN, M. 1958. Notes on the behaviour of the Flying Steamer Duck. *Auk*, 75 : 183-202.

NIETSHAMMER, G. 1952. Zur Anatomie und systematischen Stellung der Sturzbach-Ente (*Merganetta armata*). *Jour. für Ornith.* 93 : 357-360.

PHILLIPS, J. C. 1924. *A Natural History of the Ducks*. Vol. 2. Houghton Mifflin Co., Boston and New York.

WETMORE, A. 1926. Observations on the birds of Argentina, Paraguay, Uruguay and Chile. *Bull. U.S. Nat. Mus.* No. 133 : 448 pp.

WILSON, A. 1829. *American Ornithology*. Vol. 3. Philadelphia.

YARRELL, W. 1827. Observations on the trachea of birds; with descriptions and representations of several not hitherto figured. *Trans. Linn. Soc. Lond.*, 15 : 378-391.