SKULL PNEUMATICITY

Skull Pneumaticity in Wildfowl in relation to their Mode of Life

by Dr Jeffery G. Harrison

THE bones of birds contain air—an adaptation which results in a relative lightness for flight. This is a generally accepted fact, but one which may well require modifying as our knowledge of the air systems of birds grows. The large, highly pneumatic skull of an owl is one of the best examples of this adaptation, but by no means all birds have such skulls, and this is particularly true of wildfowl.

I have so far studied the skulls of 68 different species of wildfowl, and although I still have some gaps to fill, the findings do indicate a high degree of functional adaptation, although much remains to be discovered. I have yet to find a single skull which is fully pneumatised. There is a basic pattern of pneumatisation which appears to be common to most geese, the swans and dabbling duck. This is illustrated in Figs. A–C. After hatching, air cells invade the skull from the nasal apparatus and auditory capsules and soon give rise to stage A, in which air is present in the nasal bone and has spread medially from both mastoid areas to meet in the mid-line. The main airless area of bone in the vault of the skull has three thickened ridges of bone, in which air subsequently develops to give rise to stage B. This is shown in the X-ray photograph of a Shoveler's skull, transilluminated by a small electric bulb placed within the skull. In stage C, a fourth pneumatised bar has developed from the postero-lateral border of the orbit as an extension of the air in the base of the skull. This is the most advanced stage seen so far in those species in this group.

Turning now to the diving duck, a different state of affairs is found, as in only one species does the air invade the skull to a similar extent. This is in the Red-crested Pochard, which is the least diving of the diving species. In the others, air develops in the auditory capsules and occasionally meets in the mid-line (Goldeneye, Barrow's Goldeneye, Scaup and Tufted Duck), while only one species examined has had minimal air in the nasal bone, this being a Pochard. Other species (Velvet and Common Scoter, Eider, Maccoa and Ruddy Duck, Smew and Red-breasted Merganser) have the air limited to the mastoid areas and base of the skull. The nasal bones are airless and the supporting ridges in the vault of the skull are well developed. This is illustrated in Fig. D.

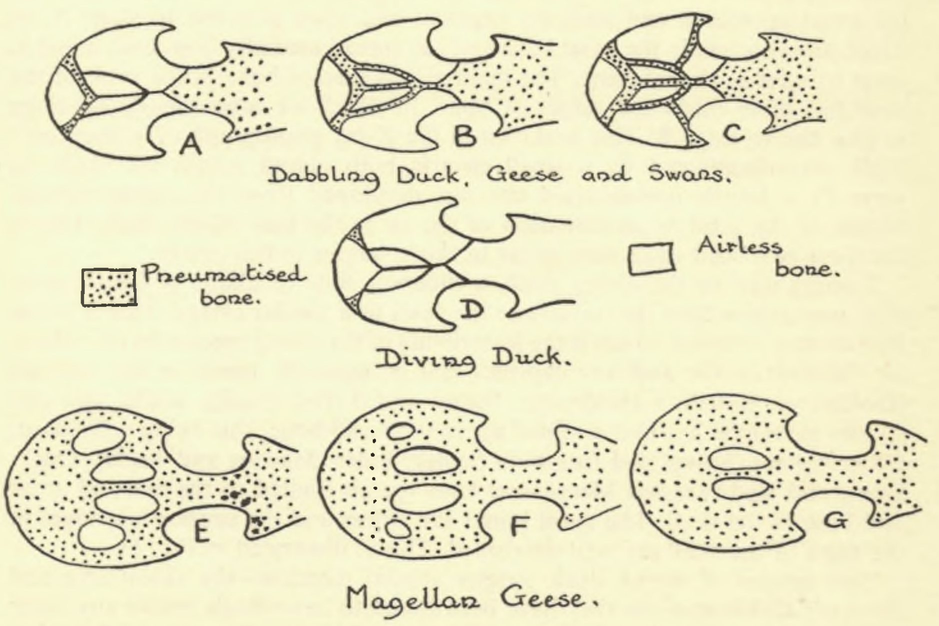
Two species of diving duck require special mention—the Goldeneye and Barrow's Goldeneye—as they have been found to have skulls unlike any other duck. In these, there is a huge air sinus extending over the vault of the skull, as an extension of the nasal apparatus. The sinus is larger in drakes than in ducks, and may reach back to the anterior border of the occipital bone in some drakes. The X-ray photographs show this in an adult drake Goldeneye (straight X-ray), and in an adult duck after the injection of radio-opaque lipiodol into the nose in order to fill this sinus.

Before discussing the possible significance of these findings, it is necessary to mention one or two other species. The Falkland Island Flightless Steamer Duck has a skull of much interest, as it conforms to that which I have described as typical of a diving duck. Placed by Delacour tentatively near the *Tadornini* (Shelduck), this species is an expert diver. The Shelduck skull, on the other hand, conforms to that of the geese–dabbling duck group. A single adult Mountain Blue Duck had a skull as shown in Fig. A. Considered by Delacour to be possibly a highly aberrant *Anas*, the species dives for food.

The Magpie Goose is thought to represent an ancestor of the present geese and duck (Delacour). It is not surprising therefore that its skull is quite distinct, although I have only been able to examine one so far, an immature which died at the Trust. There is a heavy medial ridge of bone only, and two areas of airless bone in the frontals of a distinctive pattern.

The South American Sheldgeese appear interesting. Of fourteen adult Greater Magellan Geese examined, all except one show more pneumatisation than I have previously described (Figs. E–G). Four immatures and the other adult show that the pneumatisation proceeds along the lines of the thickened ridges, as in other wildfowl. The Kelp Goose similarly develops pneumatisation almost to stage E, while retaining the airless occipital bone, but only two examples have been seen.

How are these findings to be correlated to the mode of life? At the present stage of this research, it seems possible that it might be related to diving. Birds



Skull vaults seen from above to show the relationship of pneumatised and airless bone which possess fully pneumatised skulls, such as the great order of perching birds, owls, etc., do not dive. On the other hand, other diving species such as the Cormorants, Grebes, Auks and certain diving Petrels possess skulls comparable with those of deep diving duck, such as the Scoters. All wildfowl are capable of diving, even such species as the Mute Swan (often in the face of danger), and I have an Eastern Greylag Goose which frequently dives and swims strongly under water, obviously enjoying it. I have records of Mallard diving for small fish and Mandarins feeding by diving.

The species with the most air in their skull-bones are the Greater Magellan Goose and the Kelp Goose. These are described by Delacour as 'distinctly land birds' and 'largely pedestrian' respectively. Pneumatisation then decreases to that seen in the swans, the other geese and the dabbling duck. Finally we reach the stage of minimal pneumatisation, as found in the true diving duck. It seems likely, therefore, that the reason for this lack of air within the skull-bones of wildfowl is functional in origin. In further support of this, there is the fact that other species of underwater divers, quite unrelated to wildfowl, have comparable skulls. Also, if Delacour is right in his classification of the Falkland Island Flightless Steamer Duck, we then have two related species, this and the Shelduck, with differing skulls, the one a diving and the other a dabbling duck by habit.

It seems to be a common factor among those species which dive that skull pneumatisation is diminished, the diminution varying directly with the efficiency of the species as an underwater diver. Air within the skull would presumably be subjected to underwater pressure changes when diving, and lack of pneumatisation may be an adaptation to avoid unpleasant effects from this. The following table shows the volume to which 120 cubic feet of free air would be reduced at different depths:

Depth	*Positive Pressure*	*Absolute Pressure*	*Volume*
Surface	0 lb. per sq. inch	1 atmosphere	120 cu. ft.
33 feet	14·7 lb. per sq. inch	2 atmospheres	60 cu. ft.
66 feet	29·4 lb. per sq. inch	3 atmospheres	40 cu. ft.

Scott and Boyd give feeding depths for diving duck as follows:

Tufted Duck	—	food obtained by diving in shallow water.
Pochard	—	rarely more than 20 feet.
Goldeneye	—	not more than 20 feet.
Scaup	—	food obtained principally in shallow water.
Eider	—	up to 50 feet.
Common Scoter	—	30–60 feet.

With this in mind, my findings so far suggest that the Tufted Duck, Pochard, Scaup and Goldeneye do tend to have a little more air in their skulls than the Scoters, Eider, Stiff-tails and Saw-bills.

Another factor which may be significant is skull buoyancy, for a fully pneumatised skull would tend to rise when submerged, which would be an obvious disadvantage when feeding. In contradiction to this, there is the skull of the two species of Goldeneye, which are so completely different from all other diving duck examined. The relatively large size of their heads is due to the air sinuses over the dome of the skull, and these must play a part in skull buoyancy. It seems possible that the sinus air could form a reserve supply when the Goldeneyes are feeding shallowly submerged. Further data on diving times is needed to see if Goldeneyes can, in fact, dive for longer periods than diving duck without air sinuses, bearing in mind that the deeper the dive the greater will be skull buoyancy and the less available the air.

While studying these wildfowl skulls I have been struck by the very complicated naso-lacrymal apparatus in duck, particularly certain diving species, and it is likely that a new field of research awaits to be explored here, and the findings may well link up with this work on skull pneumaticity. The whole should make an intriguing study. I am conscious of many gaps still to be covered —the Long-tailed Duck, Bufflehead and the Torrent Ducks, to mention but a few. That I have been able to examine so many is due to the kindness of Mr Peter Scott and the scientific staff of the Trust, who have taken so much trouble to get me specimens that have died in the collection, and also to Mr Philip Wayre and Mr Walter Salmon, who have sent me specimens from their collections which had died. Captain J. V. Wilkinson, D.S.C., G.M., R.N., collected me some most valuable wildfowl, while in command of H.M.S. *Protector* in Antarctic waters, and for many examples of British wildfowl I am indebted to members of the Kent Wildfowlers' Association. I am also most grateful to Dr Hugh Hay, Consulting Radiologist, who has been so helpful with the X-rays on my behalf; as has Mr Gordon Anckorn with the photography.

South Georgia Teal (*Anas g. georgica*)

THE SOUTH GEORGIA TEAL

by G. B. Spenceley

SOUTH GEORGIA, a small speck on the map of the South Atlantic, is an island, mountainous and snowbound, surrounded by the world's most stormy seas.

It was discovered by Captain James Cook in 1775 when he was sailing south in search of the mythical southern continent. Although in the same latitude as Cape Horn, geographically and climatically it belongs to the Antarctic. From the Weddell Sea flow cold ocean currents which maintain a low temperature, and the winds which blow from the west, uninterrupted by land, make South Georgia one of the stormiest places in the world.

The Teal were among the birds noted by Captain Cook on the first landing on the island. At the beginning of the present century they were probably abundant in all the coastal areas. The German expedition in 1890 observed several flocks of about a hundred individuals at Royal Bay. Unfortunately the