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THE FAMILY ANATIDAE

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A MORE natural grouping of species with a better understanding of their affinities expressed in a simpler taxonomy has been one of our principal objects for many years. Among the most popular groups of birds, the waterfowl, as the Anatidae are known, have perhaps been more arbitrarily classified than any other. Because of the general interest attached to these birds, we have thought that it might be useful to revise the group and to state our views on the relationships within it. Delacour (1933, 1936, 1938) has already published several papers on the subject. But since their appearance our knowledge has advanced considerably, and the present paper is a corrected, expanded, and up-to-date version, in English, of these earlier articles.

For over 20 years Delacour maintained in the park of the Chateau de Clères, in Normandy, the greatest collection of live waterfowl ever gathered. All existing species of swans, geese, tree ducks, and sheldrakes were represented in it; and of all the other ducks, only 26 species were missing. They lived under conditions approaching those of the wild state, and consequently they bred freely and displayed their natural behavior, including their courtship. In addition, we have observed many of the rarer exotic species in their natural habitat, and we have extensively studied museum series at the American Museum and elsewhere.

We also have benefited by the work of many authors, ornithologists, sportsmen, and breeders, particularly by the excellent pioneer studies of Dr. O. Heinroth (1910; 1911; and with M. Heinroth, 1928). For many years, Delacour has exchanged views, notes, and specimens with Dr. K. Lorenz, of Vienna, on the subject of the display and affinities of the Anatidae, with a view to later joint publication. The files kept at Clères were destroyed by a fire in 1939. We know that Dr. Lorenz has since published a paper on the subject, but this is unfortunately not yet available to us (Lorenz, 1941). It will be interesting to compare his conclusions with ours.

The classification of ducks which has been accepted up to the present is more than 50 years old. In spite of criticism by a number



BAIKAL TEAL, *Anas formosa*

of recent authors, it has been more or less followed in all recent works, such as Phillips' "A Natural History of the Ducks" (1922-26); Peters' "Check-List of Birds of the World" (1931); and the fourth edition of "The A.O.U. Check-List of North American Birds" (1931). In fact, Salvadori's classification in the "Catalogue of Birds in the British Museum" (Vol. 27, 1895) is in some ways more acceptable than several later ones. All these systems have the weakness of being based exclusively on a small selection of morphological characters, primarily on the shape of the bill and feet. Nothing could be more misleading, for the form of bill or feet is entirely functional and undoubtedly often recently acquired, representing merely a secondary adaptation that is repeated in widely separate groups. It is useful in distinguishing species but has certainly no deeper phylogenetic significance. Non-adaptive morphological characters are far more useful taxonomically. The most important of these in the duck family are: pattern of tarsus (whether scutellate or reticulate in front), a very fundamental character in the family; plumage pattern in both adults and young, the downy young of most of the nine main groups in the family having a very characteristic pattern; presence or absence of a double annual molt; posture, general body proportions, length of neck, and shape of head, all of which show characteristic differences among the nine main groups; characteristics of the internal anatomy, especially the structure and shape of the syrinx and trachea (as Heinroth has repeatedly pointed out¹). Similarly, biological characters—almost entirely ignored by the currently adopted systems of classification—are of paramount importance to the classifier, for habits and behavior are deeply rooted and are usually the product of very ancient evolution. In the duck family the main points are pair formation, displays, nesting, and feeding habits. To be satisfactory and reliable, any system must be based on the greatest possible number of known characters, and an over-valuation of a few primarily functional characters has led to great confusion in the taxonomy of the Anatidae.

Several branches, for example, the pochard group, the goldeneye-merganser-scoter group, and the stiff-tailed duck group, have developed into divers par excellence, and are structurally rather similar to one another. However, their non-adaptive characters, such as the general proportions of the body, the color pattern of the downy young, the structure of the syrinx, and the courtship performances, are sufficiently different among the three groups to suggest that the three are not at all closely related.

A further instance is that of the so-called geese. In addition to the typical geese of the *Anser-Branta* group, there are a number of

¹ We refer to his detailed account (O. and M. Heinroth, 1928:226-229). The taxonomic advantage of this structure lies in the fact that its shape is not easily modified by any peculiar adaptations of a given species. It tends to be phylogenetically conservative.

“goose-like” genera such as the Cape Barren Goose (*Cereopsis*), the Pied Goose (*Anseranas*), the Maned Goose (*Chenonetta*), the South American “geese” (*Chloëphaga*), the Egyptian Goose (*Alopochen*), and the group commonly known as sheldrakes (“*Casarca*” and *Tadorna*), all of which are characterized by rather large size and long legs, many by grazing habits. They are the “ungulates” of the duck family. Again the evidence is rather strong that the goose-like features were acquired independently by the several groups. This adaptability poses a problem to the classifier of the duck family which by no means has been solved entirely. However, even though the position of certain species and genera is still uncertain, the study of live specimens and the consideration of previously neglected morphological characters have shed much light on the relationship of the birds included in this family.

This might be an appropriate place to state again our views on the subject of zoological nomenclature. We have always stood for the strict application of the law of priority, but according to the rules and opinions of the International Commission. These provide for corrections in evident cases of misprints, of lapsus calami, and of errors in transcription. There is sometimes a certain difficulty in determining the validity of the evidence for such mistakes, but moderate degrees of common sense and classical scholarship are usually sufficient to enable a zoologist to make up his mind. To retain the original spelling of a name, however wrong it evidently is, constitutes a retrograde solution too easy and too uncritical. It is a great pity that both the A.O.U. and the B.O.U. committees on nomenclature have recently chosen to follow such a course. We are absolutely opposed to it, now as in the past,² and consequently we correct all misprints, lapsus calami, and errors in transcription. Also, according to the same rules, the endings of the adjectival species names should agree with the gender of the genus, and Greek endings should not be latinized. Furthermore, we conserve long-used names, unless the necessity for a change is unequivocally established.

We believe in large genera, since it is the function of the generic name to express relationship (as an aid to the memory), not distinctness, which is expressed by the species name. Even Peters, who is certainly not a splitter, recognizes in the family of Anatidae 62 genera for 167 species (an average of 2.7 species per genus), and 42 (70 per cent) of his genera are monotypic. The A.O.U. Check-List goes even further. Such nomenclature comes dangerously close to being monomial. The modern broadening of the species concept (Mayr, 1942:102–122) necessitates a corresponding adjustment of the genus limits. In the classification here presented we recognize 40 genera for 144 species (3.6 species per genus). It is interesting to find that a number of the vernacular names for the waterfowl—swans, scoters,

² See Delacour, 1931, *L'Oiseau*, n. s. 1:438–440.

eiders, mergansers—delimit natural groups more accurately than the generic names currently used by taxonomists. It has been our endeavor to bring the generic nomenclature of the duck family back to an expression of these natural groups. The proponents of generic splitting forget that if morphological difference is acknowledged as an inevitable generic criterion, sooner or later nearly every species will deserve a genus of its own. Generic subdivision carried to extremes not only places an unbearable burden on the memory of the taxonomist, but also completely obliterates the difference between the weak and the really distinct genera. The differences separating *Anser*, *Philacte*, and *Chen*; *Anas*, *Nettion*, and *Dafila*; *Aix* and *Dendronessa*; or *Somateria*, *Arctonetta* and *Polysticta*, are certainly very slight compared with the differences separating *Anser*, *Cygnus*, and *Coscoroba*; or *Chloëphaga*, *Alopochen*, and *Tadorna*; or *Anas*, *Malacorhynchus*, *Tachyeres*, and *Stictonetta*. Since no category above the genus can be expressed in the scientific name, the splitter has no way of making a distinction between “weak” and “good” genera. We consider this another strong argument in favor of recognizing only pronounced genera. (Mayr, 1942:280–291.)

A NEW CLASSIFICATION OF THE ANATIDAE

The new classification of the duck family that we propose attempts to do two things: to arrange the species in related groups and in a natural sequence, and to adjust the nomenclature of species and genera to progressive concepts of these categories.

Following the popular classification of this family, the first taxonomists divided the waterfowl into: swans, geese, ducks, and mergansers. As more and more was learned about the anatomy as well as about the habits of members of the family, it was realized that this simple division was unsatisfactory. For example, Linnaeus included in the duck genus *Anas* such widely divergent species as the river ducks of the mallard and teal type, the diving ducks of the scaup-pochard group (“*Nyroca*” = *Aythya*), the diving ducks of the goldeneye-scooter-eider group (Mergini), the tree ducks (*Dendrocygna*), and the sheldrakes (*Tadorna*). Although subsequent classifiers recognized some of these subdivisions, they were guided in their reclassification mainly by the shape of the bill or by the presence or absence of the diving habit.

All the ducks, geese, and swans, including even the most aberrant species, are so much alike in their basic structure and habits that there can be no doubt that those modern authors are right who include all waterfowl in a single family, the Anatidae. Within this family a number of groups of genera can be recognized, but they are clearly arranged in two main groups, which we admit as two sub-families:

(1) Anserinae. This subfamily includes the swans, geese, and the whistling ducks ("tree" ducks). The attributes of the group are a "goose-like" posture and body shape (with a long neck); a tarsus reticulated in front; a single annual molt; absence of sexual dimorphism in plumage, voice, and structure of the syrinx. Displays are simple and are similar in the two sexes.

(2) Anatinae. This subfamily includes the rest of the Anatidae. The attributes of the group are a tarsus that is scutellated in front (with a few exceptions); a double annual molt; sexual dimorphism in plumage (frequent), in voice and structure of syrinx (usual). Displays are usually elaborate and different in the two sexes.

Within each subfamily further subdivisions are recognizable. We use the term tribes (with the ending *-ini*) for such groups of genera, following a custom that is widespread in entomology. The reasons for the recognition as well as for the delimitation of these tribes will be found in the following discussion. The phylogenetic relationships within the duck family are diagrammed in Figure 1.

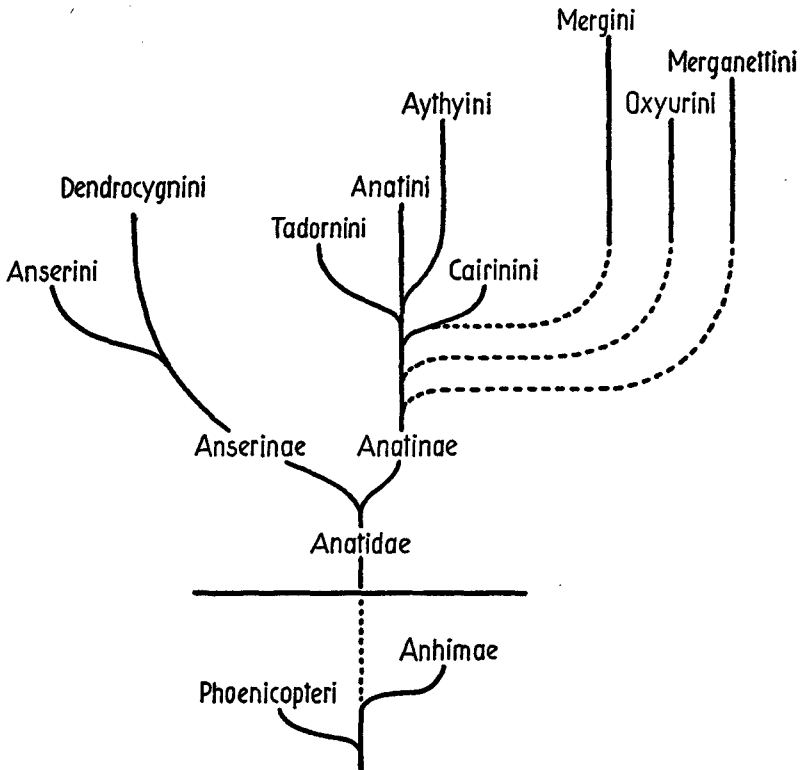


Figure 1. Diagram of the theoretical relationships of the subfamilies and tribes of the Anatidae.