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THE TAXONOMY OF THE ANATIDAE—A BEHAVIOURAL ANALYSIS

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Received on 14 May 1960

Delacour & Mayr's (1945) classic revision of the Anatidae took waterfowl behaviour into account to a much larger degree than had any previous classifications of the group. However, their utilization of behaviour was primarily at the tribal and generic levels, and no real attempt was made to use behaviour for determining intrageneric relationships. Thus far only Lorenz (1941, 1951-1953) has seriously attempted this with waterfowl, and his analysis of the relationships within the genus *Anas* (*sensu* Delacour & Mayr) has provided a remarkable insight into the evolution of this group. I have attempted to expand Lorenz's behavioural delineation of relationships within this genus to include all the living species, and have also attempted to do comparative behavioural analyses for the other genera and tribes in the family Anatidae. The publication of these studies in full detail will be done at a later date (Johnsgard, unpublished) but their taxonomic implications can be summarized here. The purpose of this paper is therefore to provide a more detailed set of behavioural definitions for the anatid groups proposed by Delacour & Mayr, and to suggest changes in intrageneric sequences of species, in generic relationships, and in a few cases the species composition of certain tribes of the Anatidae. Except where otherwise indicated, the species and generic nomenclature used is that of Delacour & Mayr (1945) or Delacour (1954-1959).

Acknowledgments. This work was done while the author was studying at the Wildfowl Trust, Slimbridge, on a National Science Foundation postdoctoral fellowship. I would like to express my sincere appreciation to the National Science Foundation for making this study possible and to the Wildfowl Trust personnel for their assistance in every possible way. For stimulating suggestions and unpublished observations I owe D. F. McKinney, P. Scott, and W. Von de Wall my sincere thanks, and the great source of inspiration that has been provided by the writings of K. Z. Lorenz and O. Heinroth cannot go unmentioned.

Observations. Each of the major taxonomic groups will be listed below, and defined so far as possible in behavioural terms. Whenever feasible, intrageneric and intergeneric relationships that are indicated behaviourally will be mentioned.

SUBFAMILY ANSERANATINAE

Tribe ANSERANATINI

There is no doubt that the Magpie Goose *Anseranas semipalmata*, deserves at least subfamilial distinction from the rest of the waterfowl. Besides its numerous anatomical peculiarities (Miller 1919; Delacour 1954), it has several behavioural peculiarities which set it apart and which may indicate affinities with the South American screamers (Anhimidae). The female, at least in captivity, usually builds several "dummy" nests which are rather swan-like heaps of vegetation, either of grass or herbs. The male is known to assist in nest building and assists with incubation as well, especially at night. The male also defends the nest vigorously. Both parents feed the young, the only known instance of parental feeding in the Anatidae; and it is possible that the bright orange bill and cinnamon head of downies act as a feeding "target" in the same manner as do head and bill specializations in various other groups of birds. Mutual preening, which is frequent in screamers (Stonor 1939), is rare in Magpie Geese. Males assist

in rearing the young and family bonds are strong, as in geese and swans. Threat behaviour is not strongly ritualized, and consists of cocking the neck and rapidly striking with the bill. At higher intensities the male strikes with the wings or may fly at the opponent, striking simultaneously with the bill and feet. Wing-shaking appears to be a low intensity threat, and also seems to function as a rudimentary "triumph ceremony" after aggressive encounters. Copulation takes place on land, but neither precopulatory nor postcopulatory behaviour has been adequately observed. There is apparently no wing-flapping or bathing after copulation. Flight intention signals are simply lateral head-shaking movements and associated calling.

Although it is apparent that the Magpie Goose is more closely related to the subfamily Anserinae than the Anatinae, it is not certain whether it most closely approaches the swans, geese, or whistling ducks. It seems most likely that the differentiation of these groups occurred after the isolation of ancestral Anseranatinae stock.

SUBFAMILY ANSERINAE

The subfamily of geese, swans and whistling ducks agrees with the preceding one in that there is little or no sexual dimorphism in plumages, voices, and behaviour, and the pair bond is relatively strong and permanent. Although sexual behaviour is remarkably uniform throughout the entire subfamily, threat behaviour is complex, varies greatly, and is of greater value in assessing intratribal relationships. In both tribes the male assists with nest building and rearing the young, but in only some species does the male take part in incubation. Of the two tribes, the Anserini might be considered to be the more generalized, but the Dendrocygnini is the more isolated as indicated by the absence of intertribal hybrids (Johnsgard 1960 a) involving whistling ducks. Therefore this tribe will be discussed first.

Tribe DENDROCYGNINI

The whistling ducks comprise a group of eight species which undoubtedly should be placed in a single genus *Dendrocygna*. Attesting to this is the fact that in their sexual behaviour (precopulatory and postcopulatory displays) all the species are nearly identical. Behaviourally the species differ primarily in their vocalizations and, to a lesser degree, their threat behaviour. Aggressive behaviour is highly developed and small groups often mutually threaten other birds. There does not, however, appear to be any real "triumph ceremony" present in the whistling ducks. There are two major threat displays, one being a "Head-back" posture with the neck cocked and ready to strike, and the other a "Head-low-and-forward" posture with the scapular feathers raised (Johnsgard, unpublished). Some species (*D. guttata*, *D. eytoni*) utilize the former posture almost entirely, whereas some (*D. aborea*, *D. autumnalis*, *D. viduata*) mainly use the latter. Flight intention movements consist of lateral head-shaking. Males help with incubation in most if not all species, which may account for the fact that there is normally practically no down present in the nest, as the eggs are almost continuously incubated. Mutual preening occurs in most, if not all, species, and is not restricted to mated birds. Family bonds appear to be strong, and individual recognition appears to be at least in part based upon variations in calls. In some species (*D. guttata*, *D. eytoni*, *D. bicolor*) these calls tend to be simple and are usually of only two syllables, while in the other species they are much more complex and are highly distinctive. In all the species studied precopulatory behaviour is almost identical, consisting of mutual behaviour that appears to be derived from bathing, drinking, or feeding movements. The birds usually copulate while in shallow water or when standing near shore. The male suddenly mounts the female before she assumes a prone posture, and treading lasts only a few seconds. As soon as it is completed, both birds call loudly and the pair rises in the water, side by side, usually raising the wing farthest from the other bird to a position directly vertical but folded at

the wrist. This is often accompanied by a vigorous paddling of the feet for a few seconds, after which the two birds return to their normal positions and usually go to shore where they both preen extensively. Two species (*D. autumnalis* and *D. arborea*) lack such an elaborate postcopulatory display, and copulation normally occurs on shore.

FIGURE 1. Evolutionary relationships in the Dendrocygnini (*Dendrocygna*). In this and the following figures the length of the branches indicates the probable degree of isolation from related species, and broken lines indicate uncertainty.

On the basis of behavioural differences and differences in the patterns of the downy young (Delacour 1954), the accompanying diagram (Fig. 1) illustrates the probable evolutionary relationships within the whistling duck group. Adult plumage patterns are of little value in showing relationships in this genus, and it is of interest that two species (*D. guttata* and *D. arborea*) which have outwardly similar adult plumages are probably not at all closely related. Both are island species (*arborea* West Indies, *guttata* East Indies) which are allopatric with nearly all other whistling ducks, and I believe that this dull, spotted adult plumage is a secondary, convergent, derivation.

Tribe ANSERINI

The swans and true geese are certainly closely related (Johnsgard 1960 a) and I agree with Delacour & Mayr (1945) that they should be placed in a single tribe. Unlike whistling ducks they do not become sexually mature before they are two or three years old, and in some swans possibly four years.

All swans and geese have a conspicuous "triumph ceremony" that is performed by members of a pair (or family) after the extrusion of an "enemy". This ceremony takes several forms. In some swans (*Cygnus olor*, *C. atratus*, and *C. melanocoryphus*) it consists of calling mutually while making vertical neck-stretching movements. In the other swans (*C. cygnus*, *C. columbianus*) it consists of calling mutually while rapidly waving the partially extended wings. In the geese it consists of mutually calling with necks outstretched horizontally and with bills almost touching. In some species (*Branta leucopsis*, *B. canadensis*) there are thrusting or waving movements of the neck in addition. Lower intensities of this "triumph ceremony" are utilized as greeting ceremonies.

In the swans, flight intention signals consist of mutual calling with strong upwards head-pumping movements (*C. cygnus*, *C. columbianus*), or simply slimming the plumage and holding the neck erect and motionless without calling (*C. olor*, *C. atratus*, probably *C. melanocoryphus*). In the geese pre-flight signals are mainly lateral head-shakes

combined with special vocalizations. In two species of geese (*B. canadensis*, *B. leucopsis*) chin-lifting movements are incorporated into the lateral head-shakes, producing a curious rotary movement that exhibits the white throats.

Threat in swans consists of ruffling the neck feathers, whereas in geese it consists of vibrating the neck feathers and the vertical striations of the neck feathers in most geese appear to function in making this threat display more conspicuous. Some swans (*C. olor*, *C. atratus*, *Coscoroba coscoroba*) raise their folded wings while threatening, whereas the others hold the wings close to the body or spread them widely. In several species of swans (*C. olor*, *C. atratus*, *C. columbianus*, *C. cygnus*) the general body shake is used as a threat display, and in a few (*C. melanocoryphus*, *C. olor*, *C. atratus*) wing-flapping is clearly used as a threat display as well.

In the true geese (*Anser* and *Branta*) as well as the Cape Barren Goose *Cereopsis novaehollandiae* the folded wings are often lifted repeatedly during threat display, and various neck postures indicate different levels of aggression. These postures appear to have some taxonomic value. Thus all *Anser* species have a "Forward" posture, and a "Diagonal neck" posture is typical of most species (Johnsgard, unpublished). All the *Branta* species have a "Forward" posture similar to that of *Anser* except that the head is not held so low and the bill is not tilted upwards, and an "Erect" posture (Blurton Jones 1960) replaces the "Diagonal neck" display in most species.

Although the male helps rear the young in all species, in only a few (*C. atratus*, probably *C. olor*) does the male take much part in incubation. Males of other species (*C. cygnus*, *C. columbianus*) have been observed incubating at times. Males of both geese and swans do a considerable amount of nest-building, and in three species of swans (*C. olor*, *C. atratus*, *C. melanocoryphus*) the young often ride on the female's (rarely the male's) back.

In all the true geese and swans precopulatory behaviour consists of a mutual head-dipping that may be derived from bathing, feeding, or possibly, nest-building movements. In the swans the bathing component is most conspicuous, but in some geese the head is not noticeably flicked sideways as in true bathing and the dipping movements are alternated with strong paddling actions similar to those used by feeding birds to stir up the water. In most geese the tail is strongly tilted upwards and the white under-tail coverts are clearly exhibited. Postcopulatory displays vary considerably. In the Mute Swan *C. olor* the pair rises high in the water breast to breast while paddling vigorously but without opening the wings, remaining in this posture for several seconds before subsiding. In the Black Swan *C. atratus* the two birds swim in a circle with necks extended diagonally upwards and heads pointed downwards. In the northern white swans (*C. cygnus* and *C. columbianus*) both sexes trumpet loudly as they rise up in the water with wings and necks extended and with bills pointing upwards. This type of postcopulatory behaviour is also typical of the true geese, except that the wings are not completely extended and often are only slightly raised while in a folded position. In all, however, the necks are extended and the bills are tilted upwards as both birds call. All swans and true geese except the Ne-ne *B. sandvicensis* normally copulate in water. The Ne-ne normally copulates on dry land although young birds may copulate while standing in shallow water or even while swimming. Precopulatory behaviour in the Ne-ne is clearly derived, however, from bathing movements, as is also true of the Canada Goose *B. canadensis* and Barnacle Goose *B. leucopsis*. The Coscoroba Swan, which is swan-like in its aggressive behaviour, has precopulatory and postcopulatory displays like those of the true geese, suggesting that it is a link between *Cygnus* and the *Anser-Branta* group.

The Cape Barren Goose is extremely goose-like in its voice and aggressive behaviour, possessing a well-marked "triumph ceremony" and threat displays which consist of wing-lifting and mutual pumping movements of the outstretched necks. Its anatomy is more anserine than tadornine (Verheyen 1953), but its downy young show distinct

relationships with the sheldgeese (Delacour 1954) and it probably constitutes a link between the true geese and the sheldgeese. Since in its behaviour it has more in common with the true geese, I prefer to include it in the Anserini rather than in the Tadornini as done by Delacour & Mayr (1945). Copulation in this terrestrial goose occurs on land, and the precopulatory behaviour lacks any bathing component, which indicates that the terrestrial existence is an ancient characteristic. Following copulation the birds perform a mutual "triumph ceremony" exactly like that performed after an aggressive encounter with other birds.

FIGURE 2. Evolutionary relationships in the Anserini.

A diagram of probable evolutionary relationships in the Anserini is shown in Fig. 2, which is based both on behavioural and morphological characteristics. Although not included in this figure, it is possible that the Freckled Duck *Stictonetta naevosa* should be included in the subfamily Anserinae (Johnsgard 1960 b), either in the Anserini or a separate monotypic tribe. However, this is based entirely on anatomical evidence (Verheyen 1953). No behavioural information is available for the species, nor is the downy plumage yet described. If the Freckled Duck proves, rather, to be anatine instead of anserine it seems likely that it should be considered a primitive shelduck rather than an aberrant surface-feeding duck (Boetticher 1952).

SUBFAMILY ANATINAE

Behaviourally most species of Anatinae differ from those of the preceding subfamilies in that pair bonds are less strong and tend to be renewed every year, often with different mates. The genetic and evolutionary implications of this are numerous (Johnsgard 1960 b), but the major result is that there tend to be two body moults, and thus two plumages, per year. One of these plumages, the nuptial, is associated with pair formation and is generally more elaborate in males than in females. Male courtship patterns tend to be more elaborate and more diversified, since pairs must be formed repeatedly during an individual's lifetime, usually in a matter of a few months. Female courtship patterns are more uniform than are males', and thus have greater utility in the establishment of relationships among the higher taxonomic categories. Precopulatory behaviour tends to be relatively uniform within tribes, and postcopulatory behaviour is usually fairly uniform within each genus. Unlike the preceding tribes, triumph ceremonies do not occur in most species, and pair bonds appear to be developed instead by the combination of female "inciting" (see Lorenz 1951-1953) and the preferred male threatening the indi-

cated "enemy" or, more often, "Turning-the-back-of-the-head" to his potential mate (Johnsgard 1960 c). In all but a few species the voices of the two sexes are distinctly different.

Tribe TADORNINI

The shelducks and sheldgeese link, behaviourally and morphologically, the true geese to the true ducks. In some genera (*Cyanochen*, *Chloephaga*, *Neochen* and *Alopochen*) there are no seasonal plumage differences and there may possibly be only one body moult per year. In one genus (*Cyanochen*) the voices of the sexes are essentially alike, but in all species there are major sexual differences in the tracheal structure. In the Abyssinian Blue-winged Goose *Cyanochen cyanopterus* there is a distinct "triumph ceremony", in which the two birds call mutually with necks extended almost vertically and bills nearly touching; but in the other genera the female has a distinct inciting behaviour and the male responds with threats or overt attack towards the enemy, alternating with sexual displays towards the female. The sexual displays tend to be relatively simple, but in the Orinoco Goose *Neochen jubatus* and some species of *Chloephaga* the sexual note, a double syllable note rather than the single syllable threat call, is accompanied by wing-lifting displays. This same distinction of sexual and threat calls holds for most species of *Tadorna* as well. Ritualized preening behind the wing is encountered for the first time in the Common Shelduck *Tadorna tadorna*, in which it is used as a courtship display as well as a precopulatory display in both sexes.

Precopulatory behaviour is practically identical in all the species of this tribe, and consists of mutual bathing movements. In some sheldgeese (*Chloephaga*) copulation occurs while the birds are standing in shallow water; in the other species studied it occurs in deeper water. In the genera observed to date (*Chloephaga*, *Alopochen*, *Tadorna*) postcopulatory displays are practically identical. The male holds on to the female's nape for several seconds as both birds call loudly, then the male releases her and assumes a "High-and-erect" posture (Johnsgard, unpublished), usually lifting the far wing in a manner similar to the postcopulatory display of whistling ducks (*Dendrocygna*). The female may raise her far wing slightly or may begin to bathe immediately.

Delacour & Mayr (1945) included the steamer ducks (*Tachyeres*) and the Crested Duck *Lophonetta cristata* in the present tribe, but Moynihan (1958) has advocated the removal of the steamer ducks to a separate tribe adjacent to the true shelducks; and the behaviour of the Crested Duck indicates clearly that it is a member of the genus *Anas* (Anatini). A diagram of evolutionary relationships based upon behavioural evidence is presented for the Tadornini in Fig. 3.

FIGURE 3. Evolutionary relationships in the Tadornini.

Tribe TACHYERINI

Moynihan's (1958) evidence indicates that the steamer ducks (*Tachyeres*) differ in numerous behavioural respects from the typical shelducks and probably warrant tribal separation from them. The most elaborate male posture of the Flying Steamer Duck *T. patachonicus*, the "Short-high-and-broad" (Moynihan 1958) is much like the "High-and-erect" sexual display of male shelducks, and it appears that female steamer ducks possess an inciting behaviour as well. Precopulatory behaviour appears to consist of mutual bathing in *T. patachonicus*, and postcopulatory display consists of both birds swimming apart in an alert posture while "Grunting" and "Head-flagging" (Moynihan 1958).

Tribe CAIRININI

Hybridization evidence (Johnsgard 1960 a), as well as tracheal anatomy and downy young patterns (Johnsgard, unpublished), indicate that the perching ducks belong between the shelducks and the surface-feeding ducks, rather than between the Aythyini and the Mergini as they were placed by Delacour & Mayr (1945). In addition to the species included in the tribe by these authors, the Ringed Teal is here included as a monotypic genus *Callonetta* (= *Anas leucophrys*) of perching ducks (Johnsgard, in press a). Behaviourally the perching ducks resemble the shelducks in that the included species are primarily hole-nesters. A few genera also require two years to reach maturity as in shelducks (*Cairina*, *Plectropterus*, *Sarkidiornis*), but pair bonds are much weaker than in that tribe, and in at least two genera (*Cairina*, *Sarkidiornis*) pair bonds are practically absent. It is probable that the remarkable size dimorphism in the sexes of these genera is related to the fact that copulation is achieved by a simple raping of females by the largest and strongest males. In these larger forms there is relatively little dimorphism of plumage, and in addition displays tend to be simple, with the same postures used for aggression as for courtship.

Hartlaub's Duck *Cairina hartlaubi* shows some affinities with these larger forms, but differs considerably in plumage, its downy young, its one-year period to maturity, and in its behaviour, all of which are more specialized and show affinities with the Anatini. Therefore this species is retained in a monotypic genus *Pteronetta* (Salvadori 1895, Cat. Birds Brit. Mus. 27 : 63).

The rest of the perching ducks are characterized by being smaller, more specialized forms (*Nettapus*, *Callonetta*, *Aix*, and *Amazonetta*) that mature in their first year, have little size dimorphism in the sexes but have considerable plumage dimorphism in which the male plumages are of more complex patterns, with metallic coloration more restricted in occurrence. An "eclipse" plumage is found in three species. Pair bonds are stronger in all these more specialized species, displays and vocalizations are more complex, and overt aggressive behaviour is much less frequent. Females of all these species also have conspicuous inciting displays which tend to be more ritualized than those of female shelducks. The voices of the females are, with a single exception (*Amazonetta*), remarkably unusual and lack the familiar "quacking" note of most female surface-feeding ducks. Courtship displays in the males consist mainly of ritualized shaking and drinking movements as well as ritualized preening behind the wing. In a few species (*Aix*, *Amazonetta*) the male has a "Turning-of-the-back-of-the-head" display (Lorenz 1951-1953) and in several genera (*Callonetta*, *Aix*, *Amazonetta*) the male has a marked "Chin-lifting" display (Lorenz 1951-1953).

Precopulatory displays are unusually variable. In a few genera (*Cairina*, *Sarkidiornis*) they are practically absent. In other genera (*Chenonetta*, *Amazonetta*, *Aix galericulata*) mutual bathing or head-bobbing movements are utilized. In still others (*Callonetta*, *Aix sponsa*) there is little or no mutual head movement and the female assumes a receptive posture usually after mutual drinking displays. Postcopulatory behaviour differs in the

two sexes, with the female simply beginning to bathe immediately and the male usually calling as he swims away from the female or turns and faces her. The postcopulatory display of the Brazilian Teal *Amazonetta brasiliensis* is remarkably like that of the Aythyini, but since the precopulatory displays are altogether different this appears to be the result of convergence. Flight intention movements in the perching ducks consist of rather slow pointing movements of the head and bill.

All the genera of the Cairinini are well marked, and the tribe, although undoubtedly valid, is an unusually heterogeneous assortment of species. Probable relationships within the tribe are indicated in Fig. 4. The tribe is certainly closely related to the

FIGURE 4. Evolutionary relationships in the Cairinini.

Anatini and several genera show clear affinities with that group. Thus *Pteronetta* approaches the Anatini in downy young patterns (Delacour 1954) and in some aspects of display, *Aix* shows its affinities by the remarkable number of *Aix-Anas* hybrids (Johnsgard 1960 a) and *Amazonetta* is similar to *Anas* in the female's vocalizations.

Tribe ANATINI

The marked success of this tribe, in terms of numbers of species and individuals, is probably related to three facts:—that the included species have generalized feeding and nesting requirements; that they mature in one year; and that they have a high reproductive potential.

Little is known about the behaviour and relationships of the three very highly specialized species that are tentatively included in this tribe. These are the Torrent Duck *Merganetta armata*, the Pink-eared Duck *Malacorhynchus membranaceus* and the New Zealand Blue Duck *Hymenolaimus malacorhynchus*. The Pink-headed Duck *Rhodonessa caryophyllacea*, included by Delacour & Mayr (1945) in this tribe, is here considered a member of the Aythyini on the basis of its plumage pattern, and tracheal structure (Garrod 1875). Likewise the Ringed Teal *Anas leucophrys* is considered (Johnsgard 1960 d) a perching duck, and the Crested Duck *Lophonetta cristata*, placed by Delacour & Mayr (1945) in the Tadornini, is here placed in the genus *Anas* on behavioural evidence. Finally, the Marbled Teal *Anas angustirostris* shows so many behavioural characteristics of the Aythyini that it is considered by me to comprise a direct link with that tribe and is placed here in the monotypic genus *Marmaronetta* (Reichenbach 1852, Av. Systeme Nat. : 9).

Behaviourally the genus *Anas* can be readily defined. The females of all species have marked inciting displays which are relatively uniform in both appearance and auditory characteristics. Females of all species also have distinctive "Decrescendo calls" (Lorenz 1951-1953), ranging in syllables from one to over twenty. Males of most, if not all, species have a marked "Turning-of-the-back-of-the-head" display (Johnsgard 1960 c) as well as a courtship call ("Burp" of Lorenz 1951-1953). Males of most species have ritualized "Preening-behind-the-wing" displays as well (Johnsgard 1960 c). Flight intention movements consist of rapid neck-jerking and lateral head-shakes. Precopulatory displays in all species consist of mutual head-pumping; and postcopulatory displays consist of bathing by the female and, in the male, calling once ("Burping" or "Bridling" of Lorenz 1951-1953) with or without any additional displays.

Fairly complex courtship displays are typical of males of most species. The "Grunt-whistle", "Bridling", "Head-up-tail-up" and "Down-up" (Lorenz 1951-1953) are the major *Anas* displays, and are typical of most species other than the wigeons, blue-winged ducks, and a few others. It is evident that one or more of these displays has been secondarily lost in various species; and in other species some of these displays are linked in differing combinations resulting in a display specificity for each species. Courtship displays in the wigeon group consist primarily of ritualized aggressive behaviour, and in the blue-winged ducks ritualized feeding and up-ending are the primary courtship postures.

Behavioural evidence such as the presence of the "Head-up-tail-up" and postcopulatory "Bridling" postures indicates that the Cape Teal *Anas capensis* belongs with the green-winged teal group rather than with the other "spotted" teal. The Crested Duck *Anas specularioides*, by its "Decrescendo call" and "Nod-swimming" (Lorenz 1951-1953) in the female, the "Grunt-whistle" in the male, and the typical *Anas* copulatory behaviour, appears to be a close relative of the Bronze-winged Duck *A. specularis*; and the two species probably belong between the mallard-like ducks and the pintail group. The mallard-like ducks are extremely homogeneous in their behaviour. The Australasian Grey Ducks and Black Ducks *A. superciliosa* are considered conspecific with the Spotbilled Ducks *A. poecilorhyncha*. The American Black Duck *A. rubripes* is doubtfully distinct from the Common Mallard *A. platyrhynchos* (see Johnsgard 1959), and the Mexican Duck (*diazi*), Florida Duck (*fulvigula*) and Mottled Duck (*maculosa*) are clearly subspecies of the Common Mallard (Johnsgard 1959).

FIGURE 5. Evolutionary relationships in the Anatini (genus *Anas* only).

A diagram of probable relationships within the genus *Anas* is shown in Fig. 5. The African Black Duck *A. sparsa*, while undoubtedly a member of this genus, has so many unusual characteristics in its display that it is not easily placed in any linear sequence of species. Not enough is known about the Salvadori's Duck *A. waigiensis* to ascertain its relationships; it may be a highly specialized mallard-like duck or it may be more closely related to the African Black Duck.

The Marbled Teal *Marmaronetta angustirostris* deviates from *Anas* in several behavioural respects. The female lacks a "Decrescendo call", and her inciting behaviour is peculiar. The male has a "Turning-of-the-back-of-the-head" display, but its primary courtship posture is not at all *Anas*-like. Another male display is very similar to the "Sneaking" (Hochbom 1944) posture of the Aythyini, and the precopulatory displays (mutual drinking and preening dorsally) are totally unlike any species of *Anas* and are very much like those of the Aythyini. Likewise the postcopulatory displays are almost identical to those of the Aythyini. In its adult plumage and downy pattern (Delacour 1956) the Marbled Teal is closer to *Anas* however, and it is therefore tentatively retained in the Anatini.

Tribe AYTHYINI

The pochard tribe is a remarkably homogeneous group of species, behaviourally as well as anatomically. Besides the two genera (*Netta* and *Aythya*) that were placed in this group by Delacour & Mayr (1945), the extinct Pink-headed Duck *Rhodonessa caryophyllacea* is here included in the tribe on plumage and anatomical grounds (Garrod 1875). The very close relationships of the Aythyini to the Anatini are, however, indicated by the connecting genera *Marmaronetta* and *Rhodonessa*.

Behaviourally the pochards differ from the Anatini in that female pochards lack "Decrescendo calls" (with the possible exceptions of *Netta rufina* and *N. peposaca*). Courtship displays of males include the "Kinked-neck call", "Coughing" (another type of courtship call in which the tail and folded wings are twitched slightly), the "Head-throw", "Sneaking", and "Neck-stretching" (Johnsgard, unpublished; Hochbaum 1944). These displays are very similar in form in all species, but differ primarily in their associated vocalizations. Female pochards have an inciting behaviour somewhat similar to that of *Anas* females, and males of most, if not all, species "Turn-

FIGURE 6. Evolutionary relationships in the Aythyini.

the-back-of-the-head" to inciting females (Johnsgard 1960 c). Mutual "Preening-behind-the-wing" also occurs in many species (Johnsgard 1960 c).

Precopulatory behaviour in most species consists of mutual drinking and preening dorsally, with an *Anas*-like head-pumping being found in a rudimentary way in four

species. As soon as the female begins to flatten out on the water, the male mounts. Postcopulatory display in males is identical in all the species studied thus far (13 out of 16). The male calls once, then swims away from the female in a characteristic "Bill-down" posture (Johnsgard, unpublished). The female may adopt this same posture for a short time but usually begins to bathe immediately. Pre-flight signals consist of rapidly repeated chin-lifting movements combined with lateral head-shaking.

A diagram of probable relationships appears in Fig. 6. This sequence is much like that proposed by Delacour & Mayr (1945), except that the Ring-necked Duck *Aythya collaris* is here considered to be a close relative of the typical pochards rather than the scaups and Tufted Duck *A. fuligula*. In addition to behavioural evidence, this relationship is also indicated by the plumage patterns of the downy young and adult females.

Tribe MERGINI

The Tribe Mergini is here used in the original sense of Delacour & Mayr (1945), including the eiders which were later (Humphrey 1958; Delacour 1959) separated from the other sea ducks and placed adjacent to the Anatini in the tribe "Somateriini". As shown elsewhere (Johnsgard, in press c), the eiders are not closely related to the surface-feeding ducks, and probably are best retained in the present tribe. The generic nomenclature used here is that of Delacour & Mayr (1945), except that Steller's Eider *Polysticta stelleri* is separated into a monotypic genus in accordance with anatomical (Humphrey 1958) and behavioural evidence. There is no behavioural evidence, however, that Steller's Eider provides an evolutionary link with the Anatini, but instead it exhibits several distinct affinities with the typical sea ducks such as the scoters (*Melanitta*). The Mergini's closest relatives are probably the Aythyini (Johnsgard, in press c), but they differ from them mainly in that most species are salt-water forms that consume primarily animal material and do not become sexually mature before their second or third year.

Behaviourally, females of most if not all species have inciting displays which, although differing somewhat in form (Johnsgard 1960, in press b, c), are all identical in function and are probably homologous. Aside from the inciting call and the warning note, females of most species are relatively silent, but males vary greatly in their degree of vocalization development. Male courtship displays also vary to an astonishing degree, even among closely related species, and are often extremely complex. The only male displays which appear to be fairly constant throughout the tribe are the "Upwards-stretch" and "Wing-flapping" (Myres 1959).

Copulatory behaviour is much more conservative and therefore is more useful in assessing relationships. In all species studied the female assumes the receptive, or prone, position some time before the male actually mounts, during which the male performs various precopulatory displays. These usually include drinking, stretching, shaking and preening movements which may be different from the corresponding normal comfort movements or identical with them. In a few species some of the courtship displays are also performed. The male finally mounts, but in some species (*Bucephala clangula*, *B. islandica*, *Mergus cucullatus*) does so only after performing a complicated, stereotyped sequence of displays (Myres 1959; Johnsgard, in press b). During treading, males of some genera (*Melanitta*, *Bucephala*, *Mergus*) loudly "Flick-the-wings" (Myres 1959) and in some (*Bucephala*, *Mergus*, *Somateria*) the male retains hold of the female's nape for several seconds after treading is completed, so that the two birds "Rotate" (Myres 1959) in a circle. Females of all species begin to bathe immediately after being released by the male, but male postcopulatory displays are varied. In some genera (*Melanitta perspicillata*, *Somateria*) the male performs a single courtship display immediately after treading, "Steams" (Myres 1959) away from the female (*Somateria*, *Bucephala*, *Mergus cucullatus*), or does not display at all (*Clangula*, *Histrionicus*, *Melanitta fusca*) (Myres 1959). Flight intention movements consist only of lateral head-shaking in all species studied.

A diagram of probable relationships in the Mergini is presented in Fig. 7, which is based primarily on behaviour and to a lesser degree on morphology.

FIGURE 7. Evolutionary relationships in the Mergini.

Tribe OXYURINI

The stiff-tailed ducks are the most poorly studied group of the entire family, and in only one species, the North American Ruddy Duck *Oxyura jamaicensis*, has the behaviour been adequately described. Of the four genera, two (*Oxyura* and *Biziura*) might be considered as typical stiff-tails. The Black-headed Duck *Heteronetta atricapilla* appears to be the least specialized anatomically and shows some similarities in structure (Delacour 1959) and behaviour to the Anatini. The White-backed Duck *Thalassornis leucotis*, on the other hand, is certainly a highly specialized form and is perhaps the most isolated of all the species of Anatinae. It is perhaps most convenient to retain it in the Oxyurini rather than erecting a special tribe for this single species, but it is doubtful if it is actually very closely related to the other stiff-tails.

Behaviourally the group is difficult to characterize because so little is known of most species, but it appears that auditory signals play a more important role in the sexual behaviour of the stiff-tails than in the other tribes (Johnsgard 1960 b). Associated with this is the fact that in males of three genera (*Oxyura*, *Biziura*, *Heteronetta*) there are inflatable structures which are derived from the air sacs, oesophagus or pharynx and which presumably are the sources of most of the male courtship calls. Females are unusually silent birds. A whistled call is found in males of a few species (*Thalassornis*, *Heteronetta*, *Oxyura dominica*) and is presumably syringeal in origin. In *Thalassornis* both sexes have a curious whistling voice that is similar to the voices of whistling ducks (*Dendrocygna*), and the tracheal structure of this species is also somewhat like that of whistling ducks (Johnsgard, unpublished).

In at least two species (*Oxyura jamaicensis* and *O. leucocephala*) the major courtship display consists of the male repeatedly striking his bill on an inflated tracheal air sac. In two other species (*O. australis*, *O. vittata*) and perhaps a third (*O. maccoa*) the display call is produced by the inflation and subsequent deflation of the oesophagus by jerky head and neck movements. Jerky head movements are also a part of the display of male Black-headed Ducks and may function in a similar way, but there is no head movement during calling in the White-backed Duck. A cocked-tail display is found in all species of *Oxyura* as well as in *Biziura*, but it is not present in *Thalassornis*, and in *Heteronetta* the tail is only slightly cocked. Precopulatory and postcopulatory

behaviour is only known for three species (*O. jamaicensis*, *O. australis* and *Biziura lobata*), and in all cases these displays are greatly different from copulatory displays in other tribes.

Behavioural evidence favours the species limits used by Delacour (1959), rather than those of earlier classifications. Figure 8 shows the probable intratribal relationships based on the relatively scanty behavioural and anatomical evidence that is available at present.

FIGURE 8. Evolutionary relationships in the Oxyurini (genus *Oxyura* only).

Summary of intra-family relationships. To place these tribal groups in an overall perspective, and to include various aberrant genera that are not shown in the previous diagrams, an inclusive diagram showing all the genera of the Anatidae has been prepared (Fig. 9). In this diagram 43 genera are accepted and are placed in ten tribes. It is possible that one additional monotypic tribe, the "Stictonettini", should be erected for *Stictonetta naevosa*, but too little evidence is at hand at present for any definite decision. This suggested arrangement compares with 40 genera, placed in nine tribes, by Delacour & Mayr (1945), and ten tribes with 41 genera by Delacour (1954–1959).

SUMMARY AND CONCLUSIONS

It is concluded on behavioural analysis that the classification of the Anatidae proposed by Delacour & Mayr (1945) is fundamentally a sound one, and almost complete agreement is reached with these authors on the larger taxonomic categories. Some of Delacour's (1954–1959) more recent modifications are accepted (the merging of *Merganetta* into the Anatini and the erection of the Anseranatinae) whereas others (the erection of the Somateriini) are rejected. A summary of suggested modifications in tribal composition, generic limits, and other major points follows:

1. The subfamilial separation of *Anseranas* (Delacour 1954) is upheld.
2. *Cereopsis* is included in the Anserini rather than the Tadornini, but is considered to represent a definite link with the Tadornini.
3. *Stictonetta* probably belongs in the Anserinae on anatomical grounds and perhaps constitutes a monotypic tribe, but it is tentatively included in the Anserini.
4. Moynihan's (1958) tribal separation of *Tachyeres* is followed.
5. *Lophonetta* is considered congeneric with *Anas*.
6. The Cairinini are placed between the Tadornini and Anatini rather than between the Aythyini and Mergini.
7. *Anas leucophrys* is considered to be a perching duck and is placed in the monotypic genus *Callonetta* between *Nettapus* and *Aix*.
8. *Cairina hartlaubi* is placed in the monotypic genus *Pteronetta* and is considered to be a possible link between the Cairinini and the Anatini.
9. *Anas angustirostris* is considered to be a link between the Anatini and the Aythyini and is placed in the monotypic genus *Marmaronetta*.
10. *Rhodonessa* is considered, on anatomical grounds, to be a member of the Aythyini rather than the Anatini.
11. The eiders are retained in the Mergini rather than being separated into a tribe "Somateriini" as proposed by Humphrey (1958).
12. The generic separation of *Polysticta stelleri* (Humphrey 1958) is upheld and this species is believed to provide a link between the typical eiders and the other sea ducks.

FIGURE 9. Evolutionary relationships among the genera of Anatidae. The position of *Stictonetta* is somewhat speculative.

13. Delacour's (1959) division of *Oxyura* into six species (*dominica*, *jamaicensis*, *leucocephala maccoa*, *vittata* and *australis*) is upheld.
14. *Thalassornis* is tentatively retained in the Oxyurini, but it is extremely aberrant and probably is not very closely related to the other species of this group.

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