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Order ANSERIFORMES

Medium-sized to large aquatic, marine and terrestrial birds. Three families: (1) Anhimidae (screamers), (2) Anseranatidae (Magpie Goose) and (3) Anatidae (true wildfowl); Screamers confined to South America, Magpie Goose confined to Aust. and New Guinea, and rest cosmopolitan. Suggestion that the order is distantly related to Phoenicopteriformes and Ciconiiformes (see Sibley & Ahlquist 1972) now seems unlikely. Claims for some anatomical similarities with gamebirds such as Cracidae, suggesting distant affinity with Galliformes via Anhimidae and Anseranatidae (Simonetta 1963; Johnsgard 1968; Bock 1969), strongly rejected by Olson & Feduccia (1980).

All members of the Anseriformes are web-footed (in some semi-palmate) swimming (some now almost terrestrial) and diving birds that are filter-feeders or are derived from aquatic filter-feeders. They differ from Galliformes in almost every anatomical feature (see Olson & Feduccia 1980). The unique filter-feeding mechanism is diagnostic of the order. Two groups of filter-feeding birds probably evolved from some charadriiform origin; in one, the specialized mechanisms for filtering evolved in the lower mandible (flamingoes); in the other, the upper mandible housed the specialized tongue used to provide the pump-action for filtering. The complex structure of the bill and its operation during filter-feeding in a typical duck has been investigated recently (Zweers 1974; Zweers et al. 1977; Kooloos 1986; Kooloos & Zweers 1989; Kooloos et al. 1989). Sensory apparatus of the bill associated with this filtering function is likewise complex (Berkhoudt 1980). The typical bill, representing the fundamental apparatus unique to the order, acts as a double-action suction-pump in which fluid is drawn in at the tip and expelled past filter plates at the sides and rear. The tongue and internal shape of the bill provide the elaborate piston effects and the lamellae or fine plates, common to all members of the order, act as the sieves. Lamellae trap the food, which is then brushed free and swallowed by the combined actions of tongue and lamellae. Vestigial lamellae occur in screamers (Olson & Feduccia 1980). Filtering is the original feeding method and departures from it towards adaptations for grazing in geese, serrated edges for catching fish in 'saw-billed' ducks (mergansers and allies) or superficially fowl-like bill of screamers, are all derived features (Olson & Feduccia 1980). Anhimidae, however, being extralimital, are not considered further.

The innovative modern classification of the ducks, geese and swans, and the systematic order proposed by Delacour & Mayr (1945, 1946) and Delacour (1954–64), was modified by Johnsgard (e.g. 1965a, 1968) in the light of further studies, particularly on behaviour and social signals, and new information on little known species. Woolfenden (1961) and Livezey (1986) have prepared phylogenetic analyses of the order based on morphological characters, and the classification by Livezey has been followed by some recent works (e.g. Madge & Burn 1988). Madsen *et al.* (1988) provide important additional information from DNA studies and give a partial classification of the order. We have adopted the classification of Johnsgard in Peters with some modification concerning only those species within our area. Our reasons for these changes are as follows but the arrangement of species fits closely the proposed classification of the order given by Sibley *et al.* (1988) and Madsen *et al.* (1988). The arrangement is consistent with the persuasive argument presented by Olson & Feduccia (1980) concerning the origin and evolution of the order. The fossil *Presbyornis* (Eocene; North America) and the endemic *Stictonetta* (Freckled Duck) and *Malacorhynchus* (Pink-eared Duck) of Aust. have special significance in this respect (see Olson & Feduccia 1980).

Special features of Stictonetta are: reticulated anterior face of tarsus; lack of a syringeal bulla; no speculum; unpatterned downy young (see Frith 1964a,b). Structure of the trachea and syrinx described by Ramsey (1878) and in more detail by Campbell (1889) and in Campbell demonstrate the lack of any development of a swollen bulla in drake. Claim by Frith (1964a, 1965, 1967, 1982) that tracheal loop occurs in mature drake is unconfirmed in many hundreds of birds examined (G.F. van Tets). Long neck. Uropygeal wax esters like those of some swans (Edkins & Hansen 1972) but chemotaxonomy difficult to interpret because similarities also shown with Cereopsis, Branta, Cairina, Tadorna, Mergus and Melanitta (Jacob & Glaser 1975). Brush (1976) has shown that the featherproteins are unique. Verheyen (1953) on skeletal characters (cranial & post-cranial) concluded that it was sufficiently distinct to be separated from other waterfowl. Clearly it shows a large number of 'primitive' characters. Olson & Feduccia (1980) emphasize several feature of the cranium that are unique in living ducks: the markedly recurved rostrum and mandible and the expanded lachrymal. Livezey (1986), largely from osteological characters, supports traditional conclusions that it is the last branch of the waterfowl with reticulate tarsi and places it after the geese and swans. Faith (1989) has shown that many of these skeletal characters might be explained on divergence between diving, dabbling and grazing adaptations. Recent DNA studies (Madsen et al. 1988) lend some support to an earlier suggestion, based on behaviour and some morphological features, of possible similarity with Oxyurinae (Johnsgard 1965b). Fullagar et al. (in press) add support to idea that Stictonetta has several behavioural similarities with stiff-tails. The uniqueness of this species has been widely supported, but in the past the absence of information about its behaviour and ecology ensured that it remained doubtful to which other group of wildfowl it was most closely related. Many of these deficiencies have now been resolved (see text elsewhere) and the argument for a link with stiff-tails has become more compelling. Plumages, social signals and vocalizations are all in some way most readily comparable to *Oxyura* and *Biziura* but specially to *Heteronetta*. A seasonally colourful bill in the male most closely matches the condition found in *Heteronetta* but also in most stiff-tails; sequence of moults follow unusual pattern found in at least some, if not all, stiff-tails but not known in other wildfowl, notably the presence of a post-juvenile moult including wings. Many characteristics of breeding biology (nest-construction and choice of site; small clutch-size; predisposition to dump laying; appearance and quantity of down used in lining nest; unpatterned ducklings) are features shared with most stiff-tails. In particular the unusual copulation involving greatly elongated pseudopenis is most closely comparable with features shown only by stiff-tails.

Major recommended works of reference are: **Comprehensive accounts**: Delacour (1954–64); Todd (1979); Phillips (1922–26) [ducks]; Scott (1972) [swans]; Owen (1980) [geese]. **Regional accounts**: Palmer (1976) [Nearctic]; BWP [w. Palaearctic]; Bauer & Glutz von Blotzheim (1968–69) [Europe]; Frith (1982) [Aust.]. **Field guides**: Scott (1988); Madge & Burn (1988). **Special studies**: Hochbaum (1955, 1973) and Sowls (1955) [migration and habits]; Johnsgard (1965a) [complete review of behaviour]; Hochbaum (1944); Driver (1974) and Kear & Berger (1980) [species monographs].

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Family ANATIDAE wildfowl

Waterbirds (some more or less terrestrial) with rather short legs and front toes connected by webs; hallux elevated and reduced. Though considerable adaptive diversity in outward appearance, size, colours of plumage, behaviour, and ecology, homogeneous in many characters, as attested by numerous, often fertile, interspecific hybrids reported, chiefly in captivity (see Gray 1958). About 160 species in six sub-families: (1) Dendrocygninae (whis-tling-ducks); (2) Oxyurinae (stiff-tails and Freckled Duck); (3) Anserinae (swans and geese); (4) Tadorninae (shelducks, sheldgeese and steamer-ducks); (5) Anatinae (dabbling ducks and allies); (6) Merginae (eiders, scoters, mergansers and allies).

Body, broad and rather elongated in many, though more rotund in some, especially diving species. Plumage, thick and waterproof; contour-feathers distributed over distinct feather-tracts with underlying coat of down. Neck, medium to long. Wings generally rather small; mostly pointed, fairly broad in many, but narrower in some highly migratory species. Small claws on first and second digits occur in most. Spurs-horny sheathed bonesoccur in several species as projections near carpal joint; attached either to radial carpal or the metacarpal. Wingspurs are found in the Tadorninae and Sarkidiornis, Plectopterus and Merganetta in the Anatinae. Eleven primaries; p9 nearly always longest, p11 minute. Wide range in number of secondaries, from 12 to 24, innermost (tertials) often long and brightly coloured; diastataxic. Many species, particularly in Tadorninae, Anatinae and Merginae have a specialized, contrastingly coloured patch (speculum) on upper surface of inner wing, important for sexual and social signalling. Most fly fast and have large, high-keeled sternum. Tail, short and square or slightly rounded in most; long in some diving species (serving as rudder), pointed or with elongated central feathers in some others. Tail-feathers, 14-24 but varying even in single species. Bills show much adaptive variation but typically of medium length, broad, often flattened centrally and distally but high at base, and rounded at tip with horny nail at tip, producing slight terminal hook; covered with soft skin. Edges of mandibles with rows of lamellae, showing different development in various ecological types and taxonomic groups; most highly specialized in surface plankton-feeders, least so in species (such as scoters Melanitta) that swallow molluscs whole. Tongue, thick and fleshy; epithelium covered with papillae and horny spines. Lower part of tibia and tarsus bare; front toes connected by webs (reduced in a few species), hind toe elevated. Gait, striding or waddling. Oil gland, feathered. Aftershaft, reduced or absent. Special intromittent copulatory organ present in males; vascularized sac everted from wall of cloaca, protruded by muscular action; facilitates sexing by examination (Hochbaum 1942). even of small young. Salt-secreting nasal glands subject to adaptive variation in size, even in same species; enlarged in forms inhabiting saltwater or brackish habitats, modifying profile of head considerably. In many species, males have remarkably lengthened, bent, or locally widened trachea forming resonating tubes; also syringo-bronchial sound-boxes (bullae), either fully ossified or with membranous fenestrae. These vocal structures highly characteristic of species or larger taxonomic units (see Eyton 1838 and, especially, Johnsgard 1961, 1971). Considerable diversity in types of plumage: male and female similar, nearly similar, or show extreme sexual dimorphism. In all species, except some sheldgeese, flight-feathers moulted simultaneously, producing period of flightlessness lasting 3-4 weeks. Two body-moults per cycle. Young precocial and nidifugous, covered with thick down; pattern often cryptic and characteristic of taxonomic groups within sub-families. Able to swim soon after hatching.

Cosmopolitan, but absent from continental Antarctica and some islands. Usually on or close to water. Highly vulnerable to human pressures on habitats. Labrador duck Camptorhynchus labradorius extinct during last century, and three more (Crested Shelduck Tadorna cristata, Pink-headed Duck Rhodonessa caryophyllacea, Auckland Merganser Mergus australis) probably so this century. A few species domesticated: Swan Goose Anser cygnoides, Greylag Goose A. anser, Muscovy Duck Cairina moschata, and Mallard Anas platyrhynchos (Goodwin 1965); some populations of a few more (Mute Swan Cygnus olor, Canada Goose Branta canadensis, Egyptian Goose Alopochen aegyptiacus) kept in semi-domesticated or feral conditions.

N. forms often highly migratory and tied to Arctic or high latitudes for breeding, exploiting brief but productive period each year to raise young; for many of these species autumn movements preceded by marked moult-migrations by males to special areas for period of flightlessness. More sedentary in warmer latitudes, specially in equatorial regions. The term 'boreal' for these n. wildfowl is useful to draw attention to the marked differences between the breeding ecology of n. high-latitude wildfowl compared with many s. hemisphere species for which the term 'austral' has been used (Fullagar *et al.* 1988). In general, most austral species are more sedentary and certainly lack spectacular migrations. Regular movements in most s. hemisphere species are at best only local. Occasional much wider dispersal is often initiated by factors such as flooding rains and drought (specially in Aust.). Many austral ducks exploit seasonally persistent or occasional, extremely propitious conditions by responding with an extended breeding season. In reality, most are seasonal breeders but productivity of some will vary greatly according to rainfall and flooding; most notable with many species in Aust. For further details see Fullagar *et al.* (1988).

Wide range in diet, from totally vegetable to totally animal, and in feeding habits, from terrestrial grazing to bottom diving; correlated with conspicuous adaptations in structure of bill, musculature of head, length of neck, and in general proportions of body. Terminology of feeding methods in species accounts mainly after Sziji (1965) and Bauer & Glutz (1968, 1969); see also Olney (1963). Typical filtering action of most members of the order, described earlier, best termed 'suzzling'. Most species gregarious, feeding, loafing, roosting, and travelling in cohesive flocks, integrated by calls and special pre-flight signals. Generally solitary breeders nesting in concealed sites, though some species colonial, either habitually or, more often, as alternative to dispersed nesting, usually in protected areas such as islands. Degree of territorialism when breeding and relation between territory and nestsite vary between species and larger taxa; some strictly territorial; others occupy wholly or largely undefended home-ranges. Monogamous pair-bond in most species but much variation between taxonomic groups in duration of bond and degree of male promiscuity (if any). Social systems and displays correlated with formation and maintenance of pairs; complex (see classic work of Lorenz 1951-53) and largely dissimilar in six sub-families (see below). Copulation on water in all species (except some Anserinae and Tadorninae), typically with male grasping female's nape in bill. Vocalizations varied but generally simple (mainly honks, grunts, guacks, coos, and whistles); often different between sexes when linked with anatomical differences in vocal apparatuses (syringeal bullae). Non-vocal sound-signals produced in some species. Calls of downy young are: (1) Contact or Greeting Call (also termed Pleasure and Contentment Call) and (2) Distress Call (see Kear 1968). Comfort-behaviour well known. Bathing frequent and elaborate. Typically performed while swimming in water too deep for standing; involves head-dipping, wing-thrashing, somersaulting, and diving. Followed by oiling (with use of bill and head) and preening. Full description of comfort movements, the behaviour patterns of shaking, stretching, preening, bathing and related activities given by McKinney (1965). The diagrams (Figs 1 to 14) based on those from McKinney illustrate most of these actions, all of which are common to all wildfowl. Some essentially aquatic species (genera Thalassornis, Oxyura and Biziura) have other, slightly specialized, preening and shaking actions peculiar to them because they are performed on water. No elaborate thermoregulatory responses except erection of feathers. Other behavioural characters are: (1) direct head-scratching; (2) resting, often on one leg, with head



Figs 1–14. Comfort movements of Anatidae (based on Grey Teal): (1a-c) Body-shake; (2) Wing-shake; (3a-c) Swimming-shake; (4) Head-shake; (5) Head-flick; (6) Tail-wag; (7) Foot-shake; (8a,b) Wing-shuffle and tail-fan; (9a) Wing-and-leg Stretch; (9b) Both-wing Stretch; (10) Foot-pecking; (11) Bill-cleaning; (12a-e) Head-dipping; (13a,b) Wing-thrashing (14a-f) Somersaulting.

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turned back and bill inserted in scapulars on same side as lifted leg (Heinroth & Heinroth 1954), latter being characteristically stowed away in waterproof flank 'pocket'.

Breeding strictly seasonal in boreal, migratory species and populations; less so or opportunistic at warmer latitudes. For most wildfowl, censuses of breeding numbers extremely difficult. Although breeding habitat and nest-sites show considerable diversity, nests usually placed over water or on or near ground. Well hidden in vegetation or sometimes concealed in other dark places such as burrows and tree holes (or nest-boxes); some species also use old nests of other birds or cliff ledges. Often near water but some species may at times nest far away from it. Nests made only of vegetation, or other materials, within reach of sitting bird, using side-building method (see Harrison 1967). In spite of limited scope of this method materials are often collected from large area by repeated movements of this form. Nest usually lined with down plucked from female's belly (often cryptic and grown specially for this purpose). Value of down for insulation and for concealing nest examined for arctic geese by Thompson & Raveling (1988). Eggs, large, immaculate; surfaces greasy. Clutches often large. Regulation of clutch-size in Anatidae has been the subject of much investigation in n. hemisphere (Rohwer 1984, 1988), but has received little attention in s. Proximate (physiological and psychological [Lack 1974]) factors that may regulate clutch-size include availability of food, condition of birds, weather, age or experience of the breeding birds, ability to incubate, and, of the female, to acquire resources for production of eggs, time of breeding, hormonal levels and interactions between two or more of these (Bengston 1971; Johnsgard 1973; Braithwaite 1977; Ankney & MacInnes 1978; Drent & Daan 1980; Duncan 1987; Ankney & Afton 1988; Kingsford 1989; Briggs 1990). Ultimate (evolutionary [Lack 1974]) factors that may regulate clutch-size are availability of food, condition of birds, length of breeding season, weather, predation and viability of eggs, ability to incubate and rear brood, time of breeding, trade-offs between annual reproductive effort and residual reproductive value, and interactions between two or more of these (Williams 1966; Lack 1967; Ryder 1970; Johnsgard 1973; Braithwaite 1977; Pellis & Pellis 1982; Toft et al. 1984; Lessells 1986; Arnold et al. 1987; Briggs 1990). Both proximate and ultimate factors can act together to influence clutch-size. Eggs laid at intervals of 24 h in most species but longer in some. Clutch covered by down in most species during recess of adult. Some species may lay some or all of their eggs in nests of other anatids; such nest-parasitism may reach significant proportions in some populations, especially of pochards (Aythya) and stiff-tails (Oxyura and Stictonetta but not Biziura); only one species (Black-headed Duck Heteronetta atricapilla) obligate parasite. In some species, two or more females may lay at same site, at extreme producing 'dump' of eggs without incubating them. Most species single-brooded but many will re-nest if eggs lost. Multiple clutches more common in austral species. Except some species of Anserinae, incubation by female; starts with last egg; so hatching synchronic. No true brood-patches (Skutch 1976). Displaced eggs retrieved if within reach of sitting bird, using bill. Eggshells left in nest. Downy young typically led, but not carried, to water after leaving nest but see Sowls (1955) and Johnsgard & Kear (1968) for exceptional carrying of eggs, shells and young. Young feed themselves in all species except Musk Duck Biziura lobata, but some food provided indirectly in earlier stages by a few Anserinae and Anatinae (Kear 1970). Establish recognition of own species by special imprinting upon parent's calls and image during brief critical period; exceptionally (e.g. during experiments) may become imprinted on wrong species or even inanimate objects (Heinroth 1911; Lorenz 1935; Hess 1957; Boyd & Fabricius 1965; Schutz 1965). Incubation and fledgling periods vary, correlated with latitude at which breeding takes place; shorter in boreal migratory species nesting in high latitudes with short summer season.

Term 'waterfowl' used in North America to describe the group is restricted by 'wildfowl' in English with 'waterfowl' having wider meaning. Further special terminology (Hardy 1952) includes 'cob' and 'pen' to distinguish male from female in swans; male goose and male duck referred to as 'gander' and 'drake' respectively but female in both best called 'hen' to avoid confusion with group names. Young swan is a 'cygnet'; young goose a 'gosling' and young duck 'duckling'. 'Whiffling' is the term used to describe the deliberate loss of height in flight by alternate side-slipping and even rolling onto the back; a practice most characteristically adopted by many geese when descending rapidly. Collective names include 'herd' for flock of swans and 'gaggle' (on the ground) or 'skein' (flying) for geese. Less well known are 'dropping' for shelduck; 'spring' for a flight of teal and 'paddling' for duck on water. 'Flapper' is used to describe young wild duck. Some of these terms are elegant but are regrettably falling into disuse.

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Sub-family ANSERINAE swans and geese

Largest wildfowl. Tarsi reticulated in front. Twenty-four species in three genera of swans: Cygnus; extralimital Coscoroba (South America); and Olor (tundra swans, Holarctic); most with all-white plumage. Cygnus includes: Mute Swan C. olor (introduced) and Black Swan C. atratus (Aust., introduced NZ) and Black-necked Swan C. melanocoryphus (extralimital South America). Olor includes four largely allopatric forms of n. Arctic swans. Two main genera of geese: 'grey' geese Anser (nine species); 'black' geese Branta (five species). Aberrant Cereopsis (Cape Barren Goose, Aust.).

Bills of swans and geese, strong; adapted for grazing, especially in more terrestrial geese in which lamellae take form of varying number of horny 'teeth' especially along edges of upper mandible. No iridescent plumage coloration, pied pattern on wing, or contrastingly coloured tertials. Plumages of geese combine mostly grey, brown, or black with white. Especially in *Anser*, neck feathers of geese arranged in vertical furrows. Vocal apparatus in both sexes a simple tympaniform membrane where bronchi join trachea; in some swans trachea convoluted inside sternum. Lores naked in adult *Cygnus* and *Olor*. Bill and feet, usually bright pink or orange-yellow in *Coscoroba* and *Anser*, dark slate or black in *Branta* and bi-coloured in *Cereopsis*; prominent yellow-green cere covering base of bill in *Cereopsis*; in *Cygnus* and *Olor*, bill usually black with orange, yellow or red; feet, dark. Webs between front toes reduced in terrestrial *Cereopsis* and Hawaiian Goose *B. sandvicensis*. During post-breeding moult, male and female of mated pair normally shed flight-feathers and become flightless at different times. In at least some *Cygnus* and *Olor*, male first to moult, followed by female when male flying again or nearly so (Kear 1970). Downy young simply patterned with varying shades of white, grey, olive-yellow or brown. *Cereopsis* shows most striking pattern of downy young.

Largely Holarctic; four species native in s. hemisphere (two in our region). Most prefer cool or cold regions but generally stop short at ice or deep snow. Large aquatic and terrestrial herbivores; no more than marginally marine (except Brent Goose *B. bernicla* notably) and avoid most deep or fast-flowing waters. Many attached to grasslands and other areas of low, non-woody vegetation in high to mid-latitudes, from tundra to steppe, stopping short at deserts and mountains and most avoiding dense tall vegetation. Vigilant and wary; when breeding, favour sites that are inaccessible (islands and cliff ledges) or eminences commanding wide views over open country. Strong fliers. Most boreal swans and geese highly migratory (in w. Palaearctic, *C. olor* partial exception). Moultmigration restricted to non-breeders (i.e. mainly immatures); breeding males remain with mates and families, moulting during breeding cycle. In *Olor*, non-breeders tend to unite near breeding areas; in *Anser* and *Branta*, move northwards; most Holarctic species to tundra and forest tundra. Normal migration often at high altitudes, day and night; traditional halting places used on way (Hochbaum 1955).

Essentially vegetarian, feeding in shallow water and on land, mainly on grasses (including grain in some species) and aquatic and marsh plants. Cygnus and Olor mainly underwater grazers, neck-dipping and up-ending with frequent foot-paddling (O. cygnus); will also graze on land. Anser, Branta and Cereopsis mainly specialized terrestrial grazers while walking, also probing and digging, sometimes in soft mud; will also feed in water by up-ending, etc. Except C. olor partly, often highly gregarious at all times when not breeding, typically in flocks composed of pairs and family parties. Pre-flight signals largely Bill-lifting (C. olor, C. atratus), Head-bobbing (Olor), lateral Head-shaking (Anser), or Head-tossing (some Branta); usually reinforced by vociferous calls. When breeding, often loosely colonial (at times with small territories) at protective sites, especially in Anser and Branta: Cereobsis typically on coastal islands. Cygnus and Olor mostly with well-dispersed nests (in large territories), though C. atratus often, and C. olor sometimes, colonial. Strong, strictly monogamous long-term pair-bonds, of indefinite duration. Also strong family bonds, between parents and young, and between siblings. No communal courtship. Most important display in formation and maintenance of pair-bond, mutual Triumph Ceremony usually with characteristic calls; especially in geese, often initiated by male after attack on rival. Also performed at times by members of same family group. Unlike most Anatinae, little ritualization of comfortbehaviour especially in heterosexual situations though some movements (e.g. Body-shake, Wing-flap) used in threat by some species. Copulation typically while swimming on water except in Coscoroba (in shallows) and B. sandvicensis, Cereopsis (on land). Pre-copulatory display consists of mutual Head-dipping, female eventually assuming Prone-posture. In mutual post-copulatory display, pair rise in water to greater or lesser extent in most species; posture and movements varying in Cygnus and Olor, similar in all Anser and Branta, ended by bathing and wing-flapping. Elaborate nest-relief ceremony claimed in C. atratus; needs confirming. Though varying degrees of reliance on visual displays, vocalizations generally play key role in most species for individual recognition and cohesion of flock. Voice considerably reduced in C. olor; used generally at close quarters and not for example for territorial advertisement as in Olor and some other Cygnus; far-carrying, non-vocal throbbing sound from wings replace flight-calls of others. Voice loud but rather unspecialized in rest; quite powerful, sonorous, and often musical in Olor (in which sometimes used in duet), and honking in Coscoroba, Cereopsis, Anser, and

Branta. Apparent greater noisiness of last two genera in part related to almost continuous vocal activity of larger, close-knit flocks outside breeding season; but vocabulary of calls also larger than in *Cygnus* and *Olor*, especially in *Anser*. Calls closely similar in both sexes, though sometimes differ in pitch. In addition to usual calls of most Anatidae, downy young also have distinctive **Sleepy-calls**, given when nestling down before sleeping, also at times while feeding (Kear 1970). When threatened at close quarters, all species hiss freely. Comfort-behaviour and other behavioural characters much as in other anatidae, but bathing often spectacular with somersaulting and kick-diving.

Seasonal breeding in most; in Arctic species, highly synchronized laying periods. Nests on ground in open or in vegetation, usually near water but can be distant. Lined with down, though considerably less in Cygnus and Olor than in Anser and Branta (and most other Anatidae). Built by both sexes in Cygnus and Olor though female does larger share. Eggs white, creamy white, or pale green; smooth or with chalky covering. Clutches usually 4-7 (1-14); smaller in high-latitude forms, which do not lay replacements. Sometimes multi-brooded in C. atratus. Eggs laid at intervals of 1-2 days. Incubation by both sexes in C. atratus; in others, male may cover eggs only during laying or recess of female. Male often mounts guard at various distances from nest, especially in Anser and Branta. Incubation periods 29-36 days (swans), 24-30 days (geese) (Kear 1970). Downy young tended by both parents, but brooded only by female. In Cygnus and Olor, adults indirectly provide some food in early stages (plucking underwater vegetation and foot-paddling), young taking it from surface; in all Cygnus small young also habitually carried on back. Brood aggressively defended from predators; deferment of wing moult by one of pair in most or all species (see above) ensures that one parent always able to protect young. Fledging periods relatively short in high arctic breeders, long in temperate species. Distraction-display by both sexes, in form of 'injuryfeigning' or 'injury-flight' also recorded in some Anser and Branta and in Cereopsis, but apparently lacking in Cygnus and Olor (see Hebard 1960). Young stay with parents after fledging at least through first autumn, in most through first winter, and into spring migration in some, at least in n. species; may reunite with them at end of one or more subsequent breeding seasons. Mature at 2-3 years.

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Cygnus olor Mute Swan

COLOUR PLATE FACING PAGE 1196

Anas olor Gmelin, 1789, Syst. Nat. 1: 502; based on the 'Mute Swan' of Latham, 1785, Gen. Syn. Birds 3: 436, and Pennant, 1785, Arctic Zool.: 543 — Russia, Siberia, Persico etiam littori maris Caspii.

The scientific name is simply of two Latin words for 'swan'. MONOTYPIC

FIELD IDENTIFICATION Length 130–160 cm; wingspan 240 cm; weight: males 11.8 kg, females 9.7 kg. Very large wholly white, long-necked swan with orange bill and black knob on forehead. Female smaller; immature brown-grey with knobless bill. Fleshy black knob of male enlarges in breeding season, but no seasonal plumages.

DESCRIPTION ADULT MALE Plumage wholly white. Iris, brown. Bill, orange with black base and fleshy knob on forehead. Lores, bare, black. Legs and feet, black (rarely pale grey or grey-pink). ADULT FEMALE. Like male, but bill and iris paler. DOWNY YOUNG. Wholly light grey (rarely white). Bill, blue-grey. Iris, black-brown. Legs and feet, bluegrey (pale grey or grey pink in white morph — retained into adulthood). IMMATURE. Wholly pale grey-brown. Iris, brown. Bill, knobless, grey-pink (changes to orange in first year). Skin at base of bill and lores, black. Legs and feet, grey-black.

SIMILAR SPECIES None; unmistakable on ground and in air.

Seen singly or in pairs on ornamental lakes, rivers, also small numbers on some small wetlands, streams and sea coasts of NZ. Popular ornamental bird and readily adapts to artificial waters and hand-feeding. On water, wings often carried partly raised; feeds by up-ending or plucking vegetation from beneath or on surface; also feeds on land. On land, walks with slow, clumsy waddle. Pugnacious, territorial; in aggressive posture, wings somewhat raised or arched, neck bent backwards in strong curve. When swimming have jerky, surging progress, paddling with both feet at same time. Flight strong, direct with loud, penetrating rhythmic whistle of wings; take flight from water with some difficulty with loud pattering of feet on water. Not mute as name implies but generally silent; both sexes occasionally snort and give hoarse muted trumpetings during social displays at breeding sites; also loud hisses in these circumstances and when threatened. Downy young give soft peeping calls, sometimes repeated as short trill pee-pee-pee-pip.



GENERAL No detailed studies of Mute Swans, feral or ornamental, made in A'asia; much information available extralimitally (e.g. BWP). The following is a general statement of what is known within our region.

AUST. History of introduction has not been recorded (see Long 1981). At present, apparently one small (c. 20 birds) feral population at Northam Weir on the Avon R., WA (Masters & Milhinch 1974); previously, a small, possibly controlled, population on L. Leake, Tas.; birds released there about 1944 but since captured and removed (Green 1977; Sharland 1981; P.J. Fullagar). At Northam Weir, birds generally sedentary but with some local movements within c. 15 km (Masters & Milhinch 1974). Breeding has been reported at Coolbellup, WA (Serventy & Whittell 1967). From time to time, single birds or few together reported (Frith 1982) such as on Lachlan R., NSW and elsewhere but no exact knowledge, even of birds held on ornamental lakes. No further information.

Introduced from Britain in 1866 and later (Thom-NZ son 1922), becoming established chiefly at L. Ellesmere and Canterbury, SI. Has spread or also been introduced elsewhere, so that present population of <200 birds, mostly at L. Ellesmere and N. Canterbury, occurs in districts of Auckland, Hawke's Bay, Wellington and Taranaki, NI, and Dunedin, SI (NZ Atlas). Inhabit terrestrial wetlands, coastal lagoons, and lakes, usually with thick emergent fringing vegetation; also on artificial and ornamental waters. Apparently sedentary. No information on diet. Nest in territorial pairs, aggressively defending feeding areas and nest-sites. Breeding areas on L. Ellesmere small, with nests only few metres apart, separated by dense patches of Typha. Breeding starts usually in Sept. at L. Ellesmere. Nests, massive heaps or mats of Typha leaves. Eggs, dull greenish white; 3-13 recorded in nests. Incubation by female alone; incubation period c. 35 days. Cygnets, precocial, nidifugous, downy when small; guarded by both parents for about 5 months before fledging. No information on social organization and behaviour, breeding success or other aspects of life-history in A'asia.

PLUMAGES Few skins examined; this based partly on BWP and Palmer (1976).

ADULT Definitive basic. Attained between first summer of second calendar year, and second winter. First breeding at 2–4 years in males, 2–3 in females (BWP). Entirely white. Ferrous staining sometimes causes rust-red (–) markings on crown and, to a lesser extent, on neck, belly and rest of head. Longest scapulars parallel-sided and broad, with almost square tips.

DOWNY YOUNG Pale, slightly brownish grey, darkest on back, merging to white underparts and foreneck. Sometimes small grey-black (82) patch in front of eye, absent in larger chicks. Unlike cygnets of Black Swan Cygnus atratus, lores completely feathered, lacking narrow strip of black skin between bill and eye. Feathering encroaches further on culmen than on other parts of bill.

JUVENILE HEAD AND NECK, grey brown (-), paler on chin and foreneck; feathering sparse on lores. UPPER-PARTS. Feathers tipped light grey-brown (119C); white bases are exposed in lower mantle, back and rump, giving mottled appearance. Scapulars narrow and tapering, becoming wider in subsequent plumages. UPPERWING. Coverts pale grey to white, suffused light grey-brown (c119C) on tips and outer webs. Remiges whitish with light grey-brown (c119C) suffusion on tips and outer webs; shafts brown (c23). TAIL, white, with light grey-brown (c119D) tinge strongest on outer webs. UNDERPARTS. Flanks and sides of breast, light grey-brown (119C), merging to pale grey-brown (c119D or paler) on rest of underparts. Axillaries white. UNDERWING, white.

FIRST WINTER AND SUMMER Basic 1 (and possibly other plumages, See Moults). HEAD AND NECK. New feathers, attained in autumn on crown and nape, dark brown (c121) with narrow white tips; 'later on, wholly white' (BWP). Rest of head and neck, white. Juvenile feathers at base of upper mandible not replaced, and wear off during winter. Body mottled brown, becoming off white as white feathers emerge on mantle, scapulars and flanks from autumn to spring, and brown edges of most remaining feathers wear off. Juvenile flight feathers, and most of wing-coverts and tail retained.

SECOND WINTER Some birds in Palaearctic have brown (-) spots on shafts near tips of primaries, or brown-tipped feath-

ers or shaft-streaks on head, rump, scapulars or outer median coverts (BWP).

BARE PARTS

ADULT Iris, black-brown (119); described as hazel in BWP. Bare triangle between eye and bill, and knob above base of upper mandible, grey-black (82) to black-brown. Knob (male) enlarged in spring, when it encroaches on culmen, and almost reaches end of nostrils; smaller outside breeding seasons, and in females. Both mandibles have narrow black (89) nails and tomia; base of interramal region, and narrow strip of skin running from nares to knob, grey-black (82). Rest of upper mandible, orange (light 116) with pink (3) to pinkorange (106) tinge near tip. Rest of lower mandible, off-white, grading to pale orange (c106) near end. Bill, more vivid orange in breeding season (Palmer 1976; BWP). Feet and legs, greyblack (82).

DOWNY YOUNG Iris, black-brown. Bill, greyblack (82); feet and legs, dark grey (83) to grey-black.

JUVENILES Bill, dark grey (-), passing through shades of pinkish brown before adult colour attained in first winter. Early changes in bill colour not closely correlated with age (Palmer 1976).

MOULTS

ADULT POST-BREEDING Pre-basic. Timing assumed to be similar to Black Swan Cygnus atratus, with non-breeders undergoing main moult Oct.-Dec., and breeders a month or two later (M.J. Williams). Complete, flight feathers simultaneous. Flightless for 3–4 weeks (Ginn & Melville 1983), but primaries not full grown in males for 66–67 days, in females 60 days (Mathiasson 1973, where also information on growth rates of primaries). Breeding females moult when cygnets small, males when female almost able to fly again. After wing complete, body moult continues (BWP).

POST-JUVENILE According to BWP, starts shortly after fledging; feathers of nape and crown first, followed by rest of neck and head, upper mantle, shorter scapulars and some feathers of sides of body in autumn. Most of mantle, scapulars, sides of body, breast and some central rectrices with their coverts renewed by time complete summer moult begins in second calendar year, with sequence as adult. This sequence inconsistent with that given by Palmer (1976), who said that Basic 1 plumage, comprising all feathering but wing, acquired in a span of 2–3 weeks, about 4.5 months after hatching. BWP's assertion that crown and nape become white in first winter and summer (brown in first autumn) suggests that crown and nape feathers are replaced twice before juvenile wing is replaced.

MEASUREMENTS, WEIGHTS No data from A'asian birds (see BWP).

STRUCTURE Wing, long, pointed. Eleven primaries, p11 minute, p9 and p8 longest, about equal; p10 14-25 shorter, p7 4-14, p6 50-65, p1 210-240. Outer web of p9-p7 and inner p10-p8 emarginated. Tail, rather long, wedge-shaped; 20-24 feathers. Bill, fairly long, with narrow nail and conspicuous bare knob at base of culmen in adult, far smaller in juvenile. Middle toe longest, outer toe *c*. 97%, inner *c*. 80%, hind *c*. 24%. DIR

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Mute Swan *Cygnus olor* 1. Adult male 2. Adult female 3. Juvenile 4. Downy young 5. Adult male

Black Swan *Cygnus atratus* 6. Adult 7. Juvenile 8. Downy young 9. Adult 10. Juvenile

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