A PHYLOGENETIC CLASSIFICATION OF WATERFOWL (AVES: ANSERIFORMES), INCLUDING SELECTED FOSSIL SPECIES

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Abstract

A summary classification of 175 modern species and 30 well-represented fossil forms of waterfowl (Aves: Anseriformes) is presented, based on a series of phylogenetic (cladistic) analyses of the group using morphological characters (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b). The proposed classification includes a superordinal grouping with the Order Galliformes, and subdivides the Anseriformes into two suborders (Anhimae and Anseres), two superfamilies (Anseranatoidea and Anatoidea), and five families (Anhimidae, Anseranatidae, †Presbyornithidae, †Cnemiornithidae, and Anatidae). Among the latter, the Anatidae is the largest and comprises six subfamilies: Dendrocygninae (comprising two tribes and two genera), Dendrocheninae (two genera), Anserinae (four tribes, nine genera), Stictonetinae (one genus), Tadorninae (four tribes, 15 genera), and Anatinae (five tribes, 31 genera). The classification also incorporates: phylogenetic inferences and associated taxonomic decisions subsequent to the preliminary work by Livezey (1986a); corrections of classifications included with the earlier analyses; recognition of two species of comb-duck (Sarkdiornis); and provisional partitions of several problematic species groups (Branta canadensis, Merganetta armata, and Somateria mollissima). Also included are a concise historical review of the classification of the order, an assessment of the relative support documented for the taxonomic groups defined within the classification, and suggestions for future investigations.

Introduction

Brief History of Classification

Early Treatises.—The first comprehensive classification of waterfowl was that by Willughby and Ray (1676), in which known members of the Anseriformes were segregated from other aquatic birds (e.g., Sphenisciformes, some Rallidae, some Charadriiformes). This classification was a largely dichotomous scheme in which the Anseriformes were defined as swimming birds having webbed feet, short legs, and with toes arranged three forward and one (free) digit oriented backward; most members were defined further by the possession of a broad bill, the sole exception being the separately grouped, narrow-billed Smew (Sarkdiornis) and mergansers (Lophodytes, Mergus). Within the larger group, Willughby and Ray (1676) partitioned members into the larger “goose-kind” (typified by the swans and true geese) and the smaller “duck-kind”; the latter group was subdivided further into the diving species or “sea-ducks” (typified by shelducks, eiders, scoters, goldeneyes, and scaup) and the “pond-ducks” (including the typical dabbling ducks).

The classification by Linnaeus (1758) was fundamental in the application of a binomial taxonomy. With respect to the waterfowl, however, Linnaeus (1758) adopted the primary segregation of mergansers proposed by Willughby and Ray (1676), although he placed the two groups adjacently within the eclectic “genus”
Anseres together with a number of taxa currently assigned to other taxonomic orders. Linnaeus (1758) sorted the other 39 recognized taxa among groups characterized as having bills with “humped” bases (swans, shelducks, and scoters), bills having sides of the base equal (most anatids), variably recurved wings (miscellaneous domestic ducks), or crests (including American Wood Duck [Aix sponsa] and Tufted Duck [Aythya fuligula]).

Finding the scheme by Linnaeus (1758) impractical, Brisson (1760) proposed an alternative in which 26 orders of birds were distinguished on the basis of an enlarged suite of characters. The resultant classification was the first in which the typical waterfowl (here including the mergansers) were segregated from all other birds in a single higher taxon; the poorly known screamers were classified apart from other waterfowl, as they would be until the study by Parker (1863). Brisson (1760) divided the group into three subgroups, termed genera: “Merganseris” (mergansers), “Anserinum” (geese, swans, some sheldgeese, and the Common Eider [Somateria mollissima]), and “Anatinum” (other ducks).

The classification of waterfowl by Buffon (1784, 1786) represented, at best, stasis in the classificatory history of waterfowl. Moreover, Buffon (1784, 1786) obscured the foregoing advancements by segregating the mergansers from other ducks (placing them adjacent to the loons), and simply listing (essentially in order of decreasing size, without indicating explicit subgroupings) the species of waterfowl within a diverse series of avian taxa; most of the latter taxa corresponded to higher groups currently considered taxonomic families. The absence of an obvious classificatory structure in the works by Buffon prompted Pennant (1786) to prepare an index to the series that corresponded with his own, earlier classification (Pennant, 1781).

Latham (1785) closely followed the classification by Linnaeus (1758) with respect to the waterfowl; however, although he retained a separate “genus” for the mergansers, he placed them immediately before the “genus” for the ducks, geese, and swans. Bonnaterre (1791) included waterfowl among a number of other aquatic groups and some shorebirds in his fifth class of genera; the mergansers were listed before other ducks, geese, and swans, immediately following the skimmers (Charadriiformes: Rynchopidae). Illiger (1811) advanced the concept of the taxonomic family as a natural group of genera, and united the ducks, geese, and swans within the single family “Lamellosodentati,” with the single exception of assigning the Cape Barren Goose (Cereopsis novaehollandiae) to the “Grallatores.” A series of largely derivative works by Merrem (1813), Cuvier (1817), Vieillot (1818), and Temminck (1820) followed, most perpetuating the fundamental division between mergansers and other waterfowl first formalized by Wilughby and Ray (1676). Leach (1820) prepared the first classification of birds in which family names were based on type genera and were derived using the suffix “-idae,” although whether the work meets all formal criteria of publication for purposes of seniority of family-group taxa remains a point of controversy (Bock, 1994; Olson, 1995).

Vigors (1825a) presented a quinarian arrangement of avian orders, the fifth of which comprised the waterfowl or Natatores. This division was partitioned further into five subgroups: (1) geese and swans, (2) Cereopsis, (3) dabbling ducks (Dendrocygna and other ducks lacking a lobed hallux), (4) mergansers, and (5) eiders and pochards. The singular placement of the poorly known Cereopsis as “transitional” between geese and ducks presumably stemmed in part from the earlier lapse by Illiger (1811). In a companion work, Vigors (1825b) provided a more
detailed classification of waterfowl, in which the waterfowl were restricted to the Family Anatidae of the Order Natatorios, the latter also including four other families of water birds; the Anatidae were subdivided into the subfamilies Anserina (geese, including Plectropterus), Cereopsina (Cereopsis), Anatina (shelducks and dabbling ducks), and Cygnina (swans), as well as an unnamed subfamily for the seaducks (tentatively including Mergus), pochards, and stiff-tailed ducks.

Subsequent classifications of waterfowl based on quinarian or related perspectives include those by Yarrell (1827) and Swainson (1837). Classifications by Lesson (1828, 1831) were quinarian at least at ordinal and subordinal levels, within which he included waterfowl as a single family in an order including most aquatic birds (e.g., loons, grebes, penguins, alcids, and pelecaniforms). Lesson (1828) placed Cereopsis immediately following the typical geese, but later he (1831) listed the genus immediately before them. In both works, however, Lesson (1828, 1831) included Mergus as the last member of the ducks.

Eyton (1838) held strong biblical beliefs and considered higher classification to be a largely arbitrary exercise, but nonetheless prepared a classification of waterfowl based on anatomical characters (including osteological) comprising six subfamilies: Plectropterinae (including modern genera Anseranas and Plectropterus), Anserinae (Cereopsis, Branta, Anser, Coscoroba, Cygnus, Sarkidornis, Alloochen, Chloephaga, Tadorna [part], and Nettapus), Anatinae (Dendrocygna, Tadorna [part], Malacorhynchus, Cairina, Aix, Anas, and Marmaronetta), Fuligulinae (Tachyeres, Rhodonessa, Netta, Atyña, Polylecta, Somateria, Histrionicus, Camptorhynchus, Melania, and Bucephala), Erismaturinae (Thalassornis, Oxyura [including Nomonyx], and Biziura), and Merginae (Mergellus and Mergus [including Lophodytes]). Eyton (1869) later produced an abridged version of this classification. Subsequent classificatory proposals by Gray (1841, 1871), Reichenbach (1849–1850), Bonaparte (1856), Baird et al. (1860), Sclater and Salvin (1876), Sclater (1880), Stejneger (1885), and Lydekker (1891), although not individually influential, contributed to the systematics of Anseriformes a number of minor taxonomic refinements and family-group names.

Fürbringer (1888) prepared a monumental summary of the comparative anatomy of birds, within which he delineated a number of taxonomic groups. In this scheme, the screamers were segregated from typical waterfowl, and within the latter the mergansers were considered distinct from other members. Although no classification of waterfowl was presented, the anatomical monograph by Parker (1890) contributed substantially to the osteological evidence for natural groups of Anseriformes. The syntheses by Gadow (1892, 1893) were important for the assessment of anatomical differences in a systematic context, but the included classifications of the waterfowl were rudimentary and accompanied by little explicit justification.

The most important systematic treatment of waterfowl to appear in the late 19th century was that by Salvadori (1895). Drawing largely from Sclater and Salvin (1876) and Sclater (1880), Salvadori (1895) arranged the waterfowl (Order Chenomorphae, here including the screamers and flamingos) in three couplets of suborders and families, the third (Anatidae) comprising 11 subfamilies. Salvadori (1895) formally grouped eight genera under the subfamilial taxon Plectropterinae, a group later to be modified for reference to the “perching ducks.” Salvadori (1895) also taxonomically distinguished the true geese (Anser and Branta) from the superficially similar sheldgeese (Chloephaga and Cyanochen) and Maned
Duck (Chenonetta), and grouped together three peculiar genera adapted to lotic habitats (Hymenolaimus, Salvadorina, and Merganetta).

Based on an anatomical study of the whistling ducks (Dendrocygna), Shufeldt (1914) altered the classification of the genus by Salvadori (1895) in elevating the genus to subfamilial rank. In his classic four-volume work, Phillips (1922, 1923, 1925, 1926) largely followed the subfamilial classification proposed by Shufeldt (1914), with most deviations from that scheme resulting from the deletion of "geese" (e.g., Cyanochen, Chenonetta) from this series dedicated to the "ducks." Among the important intuitions expressed by Phillips (1922) were the heterogeneity of the "perching ducks," the distinctness of the shelducks from the typical dabbling ducks, and intermediacy of Heteronetta between the surface-feeding and diving ducks.

In the first volume of the renowned "Check-list of Birds of the World," Peters (1931) classified waterfowl (including the screamers) in a single order comprising two couplets of suborders and families; the Anatidae were subdivided into ten subfamilies. The arrangement of genera among the latter resembled that by Salvadori (1895), but Peters (1931) made a number of changes, including the grouping of Plectropterus with Anseranas, the movement of some sheldgeese into the subfamily including the true geese, and the dismantling of the subfamily of "perching ducks." In a compilation of fossil birds, Lambrecht (1933) recognized ten subfamilies of the Anatidae; important deviations from contemporary arrangements included the essentially reversed sequence of subfamilies (Merginae first, Cygninae last) and inclusion of Nettapus with pochards in the Nyrocinæ. Kuroda (1939) primarily followed the classification by Salvadori (1895).

Delacour, the Ethological Tradition, and Contemporary Works. — Inspired by the seminal ethological works of Heinroth (1911) and the ongoing behavioral analyses by Lorenz (1941), Delacour (1936, 1938) began a series of works on the systematics of Anseriformes primarily based on behavioral patterns. In a landmark work, Delacour and Mayr (1945) presented what was to become the most influential classification of waterfowl of the 20th century. The key innovation of the classification by Delacour and Mayr (1945) was the delineation of tribes within subfamilies; the resultant scheme (Table 1) divided waterfowl (screamers excluded) into two subfamilies, Anserinae (true geese, swans, and allies) and Anatinae (true ducks and allies). This classification was followed, with only minor changes, in a subsequent series of monographs (Delacour, 1954, 1956, 1959, 1964). Notable revisions in the latter series included the movement of Anseranas from the Cairinini to a monotypic subfamily; and the erection of the Tribe Somateriini for the eiders, after Humphrey (1958).

During this period, Boetticher (1929, 1936–1938, 1937, 1942, 1943, 1950, 1952) presented a number of intuitive evolutionary trees for selected subgroups of waterfowl based on anatomical and behavioral similarities, and proposed a series of increasingly detailed and hierarchically complex classifications. In a final synthesis, Boetticher (1952) presented a classification of waterfowl (excluding screamers) comprising two families, Anseranatidae (Anseranas) and Anatidae (other taxa). The Anatidae was divided into two subfamilies, Anserinae (subdivided into two tribes comprising four "sections" and five genera) and Anatinae (subdivided into seven tribes comprising 16 "sections" and 36 genera); in addition, subgenera were given parenthetically and selected groups of species encompassing several subgenera were indicated by brackets.

As part of a remarkably long series of works in which a number of innovative
Table 1.—Classification of modern genera of Anatidae (Anseriformes exclusive of Anhimidae) proposed by Delacour and Mayr (1945). Genera are listed in the sequence used in the original work; those enclosed in brackets were annotated by Delacour and Mayr (1945) as “aberrant.”

| I. Subfamily Anserinae | II. Subfamily Anatinae |
|------------------------|------------------------|
| 1. Tribe Anserini      | 1. Tribe Tadornini     | 2. Tribe Anatini     | 3. Tribe Aythyini  | 4. Tribe Cairinini | 5. Tribe Mergini | 6. Tribe Oxyumini | 7. Tribe Merganetti |
| Branta                 | Lophonetta             | Anas*                | Netta              | Amazonetta        | Somateria*        | Oxyura*           | Merganetta         |
| Dendrocygna            | Tadorna                | [Hymenolaimus]       | Aythya             | Cheronetta        | Camptorhynchos    | Biziura           |                   |
| Anser                  | Alophoench             | [Malacorhynchos]     | Aix                | Melanitta         | Histrionicus       |                   |                   |
| Cygnus                 | Neoochen               | [Rhodonetta]         | Nettapus           | Histrionicus       |                   |                   |                   |
| Coscoroba              | Cyanochen              | [Stictonetta]        | Sarkidiornis       | Clangula           |                   |                   |                   |
|                        | Chloephaga             |                        | Cairina*           | Bucephala          |                   |                   |                   |
|                        | [Cereopsis]            |                        | Plectopterus       | Mergus*            |                   |                   |                   |
|                        | [Tachyeres]            |                        |                   |                   |                   |                   |                   |

* Includes Salvadorina, Marmaronetta, Callonetta, Speculanas, and Mareca.
* Includes Polysticta.
* Includes Nemonyx.
* Includes Pteronetta
* Includes Mergellus and Lophodytes.
anatomical and numerical characters were described, Verheyen (1953, 1955) proposed a novel classification of waterfowl. The idiosyncratic nature of the scheme by Verheyen (1953, 1955), in which the Anseriformes (exclusive of the screamers, Anhimae) were divided into four suborders (Anseres, Anseranates, Dendrocygnes, and Anates), 14 families (including monotypic Coscorobidae and Stictonettidae), and a number of tribes and informal groups, led to only a very limited acceptance by other systematists.

The utilization of osteological characters as a basis for the classification of waterfowl was advanced significantly by Woolfenden (1961). The summary classification proposed by Woolfenden (1961) largely followed that used by Delacour (1954, 1956, 1959), but with the following notable exceptions: Anseranas was segregated as a monotypic family; the swans (Coscoroba, Cygnus, and Olor), typical geese (Anser and Branta), and Cape Barren Goose were placed in separate tribes within the Anserinae; the Tribe Cairinini or “perching ducks” was dismantled, Plectropterus being assigned to the Tadornini and the remaining taxa to the Anatini; the eiders were returned to the seaducks (Mergini); and the aberrant Rhodonessa and Merganetta were moved from the Anatini to the Aythyini and the monotypic Merganettini, respectively.

The use of ethological phenetics for the estimation of the relationships of waterfowl became the primary focus of the research program of Johnsgard (1960a, 1961a, 1961b, 1962, 1965a, 1965b, 1968, 1978), and formed the basis for the second edition of Peter’s “Checklist” by Johnsgard (1979). The classification of waterfowl presented in the “Checklist” did not include tribal taxa, but indicated most of the corresponding divisions at subfamilial rank and the sequence and content of genera agree with the earlier schemes by Johnsgard (1965a, 1978). Widely adopted classificatory revisions made by Johnsgard (1961a, 1965a, 1978, 1979) include: placement of Thalassornis as a close relative of Dendrocygna; inclusion of Stictonetta among the Anserinae; confirmation of the Tadorninae, including Tadornaes, as distinct from the true geese and other ducks; placement of Marmaronetta as transitional between dabbling ducks and pochards; and opposition to the removal of the eiders (Somateria and Polysticta) from the seaducks (Mergini) by Humphrey (1958) and Delacour (1959). The systematic assessments by Johnsgard, like those of Delacour and Mayr (1945) and Delacour (1954, 1956, 1959), also considered capacity for interspecific hybridization to be indicative of close phylogenetic relationship (e.g., Johnsgard, 1960b, 1968; Gillham and Gillham, 1996). The study of interspecific hybrids in waterfowl has a long history (e.g., Phillips, 1915, 1928; Sibley, 1957; Johnsgard, 1960b, 1963; Scherer and Hilsberg, 1982), and the view that loss of capacity for hybridization is critical to speciation is related to the “recognition concept” of species (McEvey, 1993; Lambert and Spencer, 1995).

Brodkorb (1964) and Howard (1964) independently provided comprehensive, taxonomically arranged listings of fossil waterfowl. An original contribution to the systematics of waterfowl was the classification by Wolters (1976), one marked by narrowly delimited genera and an unusual attention to lesser taxonomic ranks. The classification by Delacour and Mayr (1945), as revised by Delacour (1954, 1956, 1959) and Johnsgard (1965a, 1978, 1979), was adopted with few or no refinements by Blake (1977), Cramp and Simmons (1977), Todd (1979, 1996), Brown et al. (1982), the American Ornithologists’ Union (1983), Marchant and Higgins (1990), and Carboneras (1992). The tradition of phenetic comparisons of behavioral patterns as a basis for the systematics of waterfowl continues to the
present day (e.g., Eldridge, 1979, 1985; Fullagar and Carbonell, 1986; Fullagar et al., 1990; Young, 1995), in spite of the advantages of applying phylogenetic methods for behavior-based reconstructions (de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996).

Classifications Based on Molecular Studies.—The first biochemically based assessments of the relationships of Anseriformes were not phylogenetic (sensu cladistic), and pose the same methodological difficulties as intuitive reconstructions based on comparative behavior. Regardless of the analytical details—including underlying data, metrics employed, presentation of dendrograms, or partial agreement among phenetic arrangements or between phenograms and phylogenetic trees (Scherer and Sontag, 1986; Bledsoe and Raikow, 1990)—patterns of overall similarity (or disimilarity) are not reliable estimators of phylogenetic relationships (Wiley, 1981). Nonphylogenetic, molecular comparisons involving waterfowl include: qualitative comparisons of proteins (Sibley, 1960; Sibley and Ahlquist, 1972; Brush, 1976), immunological comparisons (Bottjer, 1983), phenetic studies based on electrophoresis (Numachi et al., 1983; Patton and Avise, 1985; Oates and Principato, 1994), quantitative phenetics of uropygial lipids (Jacob and Glaser, 1975; Jacob, 1982; Jacob and Hoerschelmann, 1993), and restriction-site analysis of mitochondrial and nuclear DNA (Kessler and Avise, 1984, 1985; Tuohy et al., 1992). Although generalizations about these studies are problematic because of the diversity of methodologies and taxonomic representations upon which the inferences were based, several consistent patterns emerged (reviewed by Scherer and Sontag, 1986): *Anseranas* is markedly distinct from other waterfowl, swans and true geese are more similar to each other than to other anatids, and the true ducks (Anatini, Aythyini, Mergini, and Oxyurini) tend to be more similar to each other than to other anatids.

The most widely publicized DNA-based research program to date was that by Sibley and colleagues, using DNA hybridization (Sibley and Ahlquist, 1990). Unfortunately, this technique, like those summarized above, is phenetic and therefore subject to groupings distorted by autapomorphy, unequal rates of evolution, sympleiomorphy, or (as with any method of reconstruction) homoplasy (Cracraft, 1987a; Houde, 1987; Sarich et al., 1989; Springer and Krajeski, 1989; Sheldon and Bledsoe, 1993). Assertions that DNA hybridization, properly applied, can provide distance measures that transcend the inherent analytical shortcomings of phenetic estimates (e.g., Bledsoe and Sheldon, 1990; Sheldon, 1994; Sheldon et al., 1995) have not been substantiated. In addition, the application of this technique by Sibley and Ahlquist (1990) was criticized on other methodological grounds, including sparse data matrices, unspecified transformations of data, and suboptimal clustering algorithms (Lewin, 1988a, 1988b; Cracraft, 1992a; Lanyon, 1992; Mindell, 1992).

Classifications stemming from this work (Sibley et al., 1988; Sibley and Monroe, 1990, 1993) were based only loosely on the published trees (Siegel-Causey, 1993), and those for the Anseriformes were extended far beyond the 13 species (representing Anhimia, Chauna, Anseranas, Dendrocygna, Branta, Cygnus, Aix, Anas, Melanitta, and Oxyura) actually sampled by Sibley and Ahlquist (1990). Consequently, several unusual aspects of their proposed classification—including the merging of true geese, sheldgeese, shelducks, and some “perching” ducks in the single Tribe Anserini, or the inclusion of pochards and seaducks with dabbling ducks in the Tribe Anatini—were made without justification. The basis for the classification by Sibley and Monroe (1990) is undermined further by the subjective placements of most of the sampled taxa within the trees, necessitated by the sparsity of the distance matrix and the
asymmetry of comparisons; these empirically unsupported placements include those for *Dendrocygna, Branta, Cygnus*, and *Oxyura* (Lanyon, 1992). The supplement prepared by Sibley and Monroe (1993) included only two important classificatory revisions for the waterfowl: adoption of the taxonomic sequence for the Anatini proposed by Livezey (1991), and return of *Heteronetta* to the stiff-tailed ducks.

Reanalysis of the data compiled by Sibley and Ahlquist (1990) by Harshman (1994) confirmed only the basal position of *Anseranas* with respect to other waterfowl. A concurrent study using DNA hybridization by Madsen et al. (1988) suffered from comparable limitations of taxonomic sampling as well as unfavorable properties of summary metrics; the analysis indicated patterns of similarity largely congruent with traditional perceptions of relationships, with the exception of a comparatively basal placement of *Oxyura*, an inference shared by Sibley and Ahlquist (1990).

To date, the only published cladistic reconstructions of relationships of waterfowl using molecular data are those by Sraml et al. (1996) and Mindell et al. (1997); the first of these studies was based on sequence data from cytochrome *b* and the second from 12S rDNA. The study by Sraml et al. (1996) was severely limited both with respect to the taxa included and the sampling of the gene; the latter deficiency underlies the poor support of nodes in the resultant trees. The reconstruction by Mindell et al. (1997), to the extent possible given the limited number of anseriform taxa represented, is consistent with that presented here (Fig. 1) with the exception of the placement of *Anseranas* as the sister group of the Anhimidae; counter evidence for the latter grouping is presented by Livezey (1997a).

An ongoing analysis by Harshman (personal communication) using cytochrome *b* represents a significant improvement in both taxonomic and genomic sampling, and preliminary indications are that greater resolution and support of nodes was achieved. The relationships indicated in the analysis by Harshman (personal communication) contrast markedly with the poorly resolved groupings suggested by Sraml et al. (1996) and show substantial agreement with those proposed by Livezey (1986a) and Mindell et al. (1997). Reconstructions by Harshman (personal communication) that differ from those summarized in this classification include: the position of *Coscoroba* and *Cereopsis* as sister genera; the *Oxyurini* as sister group to the Tadorninae and Anatinae (the latter groups being merged); and unexpected difficulties in topological placements of *Nettapus*, some *Cairina*, and the bizarre *Biziura*.

The provision of sequence data for a number of Anseriformes and outgroups (Galliformes) makes possible the direct comparison of comparable phylogenetic (cladistic) hypotheses based on independent morphological and molecular data, and hopefully will contribute toward a consensus concerning the relative merit of congruence across analyses, trees based on combined data, and attendant issues of character weighting (morphological versus molecular characters, transversions versus transitions in sequence data), rooting of trees, and the statistical attributes of diverse types of data (Neff, 1986; Wheeler, 1986; Sanderson and Donoghue, 1989; Swofford, 1991; Chippindale and Wiens, 1994; Omland, 1994; de Queiroz et al., 1995; Hillis et al., 1996). Only with empirical assessments of this kind can systematics move away from speculation and prejudice (e.g., Sibley and Ahlquist, 1987, 1990; Monroe, 1989; Hedges and Sibley, 1994; Sibley, 1994) and toward reconstructive methods and hypotheses that incorporate the maximal phylogenetic information from all available data (Hillis, 1987; Cracraft and Mindell, 1989; Moritz and Hillis, 1990; Eernisse and Kluge, 1993; Patterson et al., 1993; Avise, 1996; Hillis et al., 1996).
Fig. 1.—Tree summarizing the phylogenetic relationships among genera of Anseriformes reflected in the proposed classification; halftone lines indicate provisional groupings or placements. Analyses upon which the classification is based include the original genus-level analysis of the order (Livezey, 1986a), as well as works specific to included subgroups (most to species level), indicated by circled numbers by corresponding nodes in the tree: (1) Livezey (1997a); (2) Livezey (1989a, 1996a); (3) Livezey (1995a); (4) Livezey (1996a); (5) Livezey (1986b, 1986c, 1989a, 1996b); (6) Livezey (1997a); (7) Livezey (1995b); (8) Livezey (1990, 1991, 1993a, 1996b); (9) Livezey (1996c); and (10) Livezey (1989b, 1993b, 1995c).
Proposed Phylogenetic Classification

General Objectives.—The primary objective of this paper is to summarize in a single classification the findings of a series of works on the systematics of Recent Anseriformes (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b) using phylogenetic (cladistic) methods (Hennig, 1966; Wiley, 1981). A graphical summary of the genus-level phylogenetic inferences of these works is depicted in Figure 1. This classification is proposed in the hope that it will provide a constructive, evolutionary framework for the study of waterfowl, an aspiration contrary to the conservative view in which “standard taxonomic sequences” are to be insulated from classificatory revisions (Mayr, 1989; Bock, 1990; Mayr and Bock, 1994). The notion that stability of taxonomic sequences is of greater importance than the communication of current opinions on phylogeny, combined with an abiding pessimism regarding the likelihood of accurate phylogenetic reconstructions or classifications, reached an extreme in the recommendation that ornithologists adopt an alphabetical sequence of taxa (species within genera, genera within subfamilies, and so on) as a global standard (Moreau, 1961; Lack, 1967, 1968). Ironically, the proposed imposition of stability on the dynamic changes in accepted systematic relationships would exacerbate the mistaken notion that the phylogeny of the Class Aves is well known (e.g., Ricklefs, 1980).

Revisions and Corrections.—This classification incorporates a number of changes in phylogenetic inferences made since the original, preliminary work by Livezey (1986a), together with changes since Livezey (1989a). In addition, this final synthesis is updated by provisional species-level revisions of several problematic modern genera of waterfowl (e.g., Sarkidiornis, Merganetta), discussions of taxonomically vexing “species groups” (e.g., Branta canadensis), and preliminary placements of well-represented fossil taxa. Also included are two decisions subsequent to earlier phylogenetic works on the groups concerned (Livezey, 1996b, 1997a) to elevate taxa from subgeneric to generic rank (Casarca, Aristonetta), to better represent inferred phylogenetic relationships in the classification. This summary classification also incorporates the correction of several errors of authorship in preceding classifications (Livezey, 1995b, 1995c, 1996b, 1996c; Table 2) and generic seniority (Livezey, 1996c), clarifies adoption of subgenera of Dendrocygna under the principle of first reviser (Livezey, 1995a), and coordinates subtribal names in accordance with the recommendations of the International Commission on Zoological Nomenclature (1985).

Methods

Phylogenetic Classification

The construction of classifications based on explicit phylogenetic hypotheses follows the principles outlined by Wiley (1981), with the exception that normal taxa are used for fossils and annotated by a dagger (†), as opposed to the use of “plesion.” The dagger is restricted to fossil taxa (i.e., extinct forms known only from subfossil and fossil remains), and is not used to indicate species extirpated in modern times (e.g., Camptorhynchus labradorius). These conventions include the use of sequencing three or more taxa of the same rank (in order of increasing close relationship) within a single higher taxon to avoid the unwieldy proliferation of ranks to maintain a strictly dichotomous classificatory scheme. Where such sequences of taxa of equal rank are of indeterminate relationship, the defining,
Table 2.—Compilation of modern family-group taxa used in the proposed classification and corresponding authors, with comparison of original ranks of these group names and the first use of these names at the rank used in the present work.

| Current family-group taxon | Author of senior family-group taxon | Original rank of family-group taxon | First designation of taxon at current taxonomic rank |
|---------------------------|-------------------------------------|------------------------------------|-----------------------------------------------------|
| Superfamily Anseranatoidea | Sclater, 1880                       | Subfamily                          | Sibley et al., 1988                                 |
| Superfamily Anatoidea      | Leach, 1829                         | Family                             | Livezey, 1997                                      |
| Family Anhimidae           | Stejneger, 1885                     | Family                             | —                                                   |
| Family Anseranatidae       | Sclater, 1880                       | Subfamily                          | Stejneger, 1885                                   |
| Family Anatidae            | Leach, 1829                         | Family                             | —                                                   |
| Subfamily Dendrocygnina    | Reichenbach, 1849–1850              | Family                             | —                                                   |
| Subfamily Anserinae        | Vigors, 1825b                       | Subfamily                          | —                                                   |
| Subfamily Stictonettina    | Boetticher, 1950                    | Subtribe                           | Wolters, 1976                                      |
| Subfamily Tadorninae       | Reichenbach, 1849–1850              | Subfamily                          | —                                                   |
| Subfamily Anatinai         | Leach, 1820                         | Family                             | Swainson, 1837                                     |
| Tribe Dendrocygni          | Reichenbach, 1849–1850              | Family                             | Delacour and Mayr, 1945                            |
| Tribe Thalassornithini     | Livezey, 1986                       | Subfamily                          | Livezey, 1995                                      |
| Tribe Cereopsini           | Vigors, 1825b                       | Subfamily                          | Boetticher, 1942                                   |
| Tribe Anserini             | Vigors, 1825b                       | Subfamily                          | Delacour and Mayr, 1945                            |
| Tribe Cygnini              | Vigors, 1825b                       | Subfamily                          | Delacour and Mayr, 1945                            |
| Tribe Merganettinna        | Bonaparte, 1853                     | Subfamily                          | Delacour and Mayr, 1945                            |
| Tribe Plectopterini        | Eyton, 1838                         | Subfamily                          | Livezey, 1996                                      |
| Tribe Tadorninae           | Reichenbach, 1849–1850              | Subfamily                          | Delacour and Mayr, 1945                            |
| Tribe Malacorhynchini      | Boetticher, 1950                    | Tribe                              | —                                                   |
| Tribe Anatinai             | Leach, 1820                         | Family                             | Delacour and Mayr, 1945                            |
| Tribe Aythyini             | Delacour and Mayr, 1945             | Tribe                              | —                                                   |
| Tribe Mergini              | Rafinesque, 1815; or Swainson, 1831| Subfamily                          | Delacour and Mayr, 1945                            |
| Tribe Oxyurini             | Phillips, 1926                      | Subfamily                          | Delacour and Mayr, 1945                            |
| Subtribe Coscorobina       | Boetticher, 1936–1938               | Subfamily                          | Boetticher, 1952                                   |
| Subtribe Cygnina           | Vigors, 1825b                       | Subfamily                          | Boetticher, 1952                                   |
| Subtribe Chloephagina      | Boetticher, 1942                    | Tribe                              | Boetticher, 1952                                   |
| Subtribe Tadorninae        | Reichenbach, 1849–1850              | Subfamily                          | Boetticher, 1952                                   |
| Subtribe Cairinina         | Boetticher, 1936–1938               | Subfamily                          | Boetticher, 1952                                   |
| Subtribe Nettapodina       | Bonaparte, 1856                     | Subfamily                          | Livezey, 1991                                      |
| Subtribe Anatinai          | Leach, 1820                         | Family                             | Boetticher, 1952                                   |
| Subtribe Marmaroneettina   | Livezey, 1996                       | Subtribe                           | —                                                   |
| Subtribe Rhodonesina       | Boetticher, 1950                    | Tribe                              | Boetticher, 1952                                   |
| Subtribe Aythyina          | Delacour and Mayr, 1945             | Tribe                              | Boetticher, 1952                                   |
| Subtribe Somaterina        | Reichenbach, 1849–1850              | Subfamily                          | Boetticher, 1952                                   |
| Subtribe Margina           | Rafinesque, 1815; or Swainson, 1831| Subfamily                          | Boetticher, 1952                                   |
| Subtribe Heteronettina     | Boetticher, 1950                    | Tribe                              | Boetticher, 1952                                   |
| Subtribe Oxyurina          | Phillips, 1926                      | Subfamily                          | Boetticher, 1952                                   |

- Taxa given "section" endings of -eae, conventional for botanical tribe; Bonaparte (1853, 1856), Boetticher (1942), and Boetticher (1950) treated these as equivalent to tribes (i.e., as primary subdivisions of subfamilies), but Boetticher (1952) later explicitly treated these as partitions of tribes.
- Original derivation of subfamily (Thalassornithinae) incorrect; emended by Livezey (1989a).
- Originally used as subfamily of Family Erismatiuridae, comprising Merganetta and the stiff-tailed ducks, therefore approximately equivalent to a tribe in the current sense.
- First treated at tribal rank (Cairinini) by Delacour and Mayr (1945).
- Original ending of -eae retained by Livezey (1991, 1995b), coordinated herein with conventional ending of -ina for subtribes.
next-higher taxon is annotated sedis mutabilis; where groups of taxa are of uncertain monophyly, the defining taxon is annotated incertae sedis. Higher-order taxa were based largely on published synonymies and classifications (Boetticher, 1942, 1950, 1952; Brodkorb, 1964; Wolters, 1976; Bock, 1994). Within the limits of these conventions, the classification was constructed to: (1) conform with existing nomenclatural codes for availability and seniority of taxa; (2) reflect the maximal number of hierarchical ranks and areas of uncertainty inferred in the companion phylogenetic analyses; and (3) avoid, where content-neutral, the proposal of new ranks or binomial combinations. Complete literature references are not provided for each author-year citation given for taxa in the classification, but instead are limited to direct citations of publications in the narrative parts of the text, as well as in tables, figure legends, and appendices. The English name for a higher taxon is not given where this simply would repeat that of the next-lower, included taxon.

Species Limits

The identification of the working units in phylogenetic analyses, i.e., the delimitation of species, is a critical and problematic part of any systematic study. The prospects of achieving a species-level classification satisfactory to all is as unlikely for the Anseriformes as for any vertebrate order. The controversy and conflicting paradigms that attend such taxonomic decisions in waterfowl is exemplified by the continuing controversy involving the species-level delimitations within the mallard (Anas platyrhynchos) group (Yamashina, 1948; Johnsgard, 1961c, 1967; Aldrich and Baer, 1970; Williams and Roderick, 1973; Heusmann, 1974; Braithwaite and Miller, 1975; Morgan et al., 1976; Hubbard, 1977; Brodsky and Weatherhead, 1984; Haddon, 1984; Gillespie, 1985; Ankney et al., 1986, 1987; Ankney and Dennis, 1988; Bélanger et al., 1988; Brodsy et al., 1988; Hepp et al., 1988; Avise et al., 1990; Hitchmough et al., 1990; Livezey, 1991, 1993a; Browne et al., 1993; Reichel and Lemke, 1994; Rhymer et al., 1994).

In this work, the Anseriformes are classified to species level, with included subspecies indicated for polytypic species. In delimiting species-level taxa, my approach is simply to distinguish the terminal taxa that differ in at least one of the characters analyzed. This practice represents a practical application of the phylogenetic species concept in the context of morphological characters (Cracraft, 1983, 1987b, 1988, 1992b, McKittrick and Zink, 1988; Nixon and Wheeler, 1990; Davis and Nixon, 1992; Zink and McKittrick, 1995), which approximates in many such cases the lineages that are distinguished under the evolutionary species concept (Wiley, 1978; Frost and Hillis, 1990; Frost and Kluge, 1994). In some cases these terminal taxa correspond to conventional subspecies (e.g., within Somateria mollissima), whereas in others the working taxa include two or more recognized subspecies (e.g., even a narrowly delimited Anas platyrhynchos includes conboschias). However, this analytical extrapolation does not necessarily represent a recommendation to the ornithological community at large or the bird-watching public that these lineages be elevated uncritically to species status in checklists, field guides, and popular books. Instead, recognition of taxa at species rank in this classification represents a compromise based primarily on the practicalities of phylogenetic reconstruction and secondarily on the goal of conserving taxonomically the maximal amount of demonstrated evolutionary divergence between sister lineages. Characters used in provisionally delimiting taxa within species groups
not subjected to formal analysis in previous works (Branta canadensis, Sarkidiornis melanotos, and Merganetta armata) are given in the Appendix.

**Fossil Taxa**

In spite of persistent methodological shortcomings of many paleornithological reconstructions (see general critiques by Cracraft, 1979, 1980), paleontological finds continue to offer significant new insights into the phylogeny and biogeography of waterfowl. Paleontologically facilitated advances in our understanding of waterfowl include an enhanced appreciation of insular endemism (Olson and James, 1991), one likely to undergo further refinements with continued study of subfossil anseriforms in New Zealand (P. R. Millener, personal communication), Madagascar (S. M. Goodman, personal communication), and smaller Pacific islands (cf. Derscheid, 1939), as well as the paleontological documentation of former continental distributions of modern tribes (e.g., Nearctic tadornines; Ross, 1935; Brodkorb, 1964; Howard, 1964). Consequently, an effort was made to include well-represented fossil anseriforms in the classification, either on the basis of formal phylogenetic analyses (e.g., Livezey and Martin, 1988; Livezey, 1989a, 1996a, 1997b) or on diagnoses based on synapomorphies inferred from analyses of modern representatives (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b).

A number of fossil taxa, however, lacked material adequate for phylogenetic assignment and were omitted from the classification, including: Paranyroca magna (Miller and Compton, 1939), Romainvillia stehlini (Lebedinsky, 1927), Eonesa anaticula (Wetmore, 1938), Cygnopterus affinis (Van Beneden, 1883), Cygnopterus alphonsii (Cheneval, 1984), Cygnus senckenbergi (Lambrecht, 1931), Cygnanser csakvarenisis (Lambrecht, 1933), Paracygnus plattensis (Short, 1969), Presbychen abavus (Wetmore, 1930), Heterochen pratensis (Short, 1970), Eremonchen russelli (Brodkorb, 1961), Brantadoma robusta (Short, 1970), Ocyplenessa Shotwelli (Brodkorb, 1961), and Aldabranas cabri (Harrison and Walker, 1978). Also excluded are a number of fossil taxa assigned to Dendrocycna, Anser, Branta, Cygnus, Anas, and Aythya, most of which is inadequately represented for confident assignment to genus (Brodkorb, 1964; Howard, 1964), although published descriptions indicate that some excluded taxa classified as Branta or Cygnus may be accurate at least to tribal level.

An indication of the poor diagnosibility of European fossils assigned to anseriform genera during the late 19th and early 20th centuries is provided by Milkovský (1992), in which 13 fossil anseriform taxa were reclassified as follows: Aves, incertae sedis (two); families in orders other than the Anseriformes (two); Anseriformes, incertae sedis (one); Anatidae, incertae sedis (one); Aythyni, incertae sedis (one); referral to a genus in another tribe of Anatidae, some merely confirming earlier reclassifications by others (four); referral to a genus in the same tribe of Anatidae (one); and retention in the original genus (one). Most assignments of fossils from the Oligocene or Miocene to modern genera (e.g., Anas and Aythya) probably represent misclassifications of at least subfamilial scale (Brodkorb, 1962; Livezey and Martin, 1988). Some taxa assigned to Cygnus (Northcote, 1982, 1988, 1992) and “Anas” (Newton and Gadow, 1893; Wetmore, 1960; Olson and Jouventin, 1996) were represented by sufficient material for approximate placements. Several taxa of fossil ducks from Australia were synonymized with modern species by Olson (1977a), whereas the validity and generic assignments
of two distinctive New Zealand fossil taxa were confirmed (Olson, 1977b). The position of "Mergus" miscellus described by Alvarez and Olson (1978), if inclusion within the Mergini is justified, remains unclear and the taxon is not included in this classification (Livezey and Martin, 1988).

**PHYLOGENETIC CLASSIFICATION OF ANSERIFORMES**

**Superorder Galloanserimorphae** (Sibley et al., 1988).—Fowl

**Order Anseriformes** (Wagler, 1831).—Waterfowl

**Suborder Anhimae** Wetmore and Miller, 1926

**Family Anhimidae** Stejneger, 1885.—Screamers

Genus *Anhima* Brisson, 1760

*Anhima cornuta* (Linnaeus, 1766).—Horned Screamer

Genus *Chauna* Illiger, 1811.—Crested screamers

*Chauna chavaria* (Linnaeus, 1766).—Northern Crested Screamer

*Chauna torquata* (Oken, 1816).—Southern Crested Screamer

**Suborder Anseres** Wagler, 1831.—True waterfowl

**Superfamily Anseranatoidea** (Sclater, 1880)

**Family Anseranatidae** (Sclater, 1880)

Genus *Anseranas* Lesson, 1828

*Anseranas semipalmata* (Latham, 1798).—Magpie Goose

**Superfamily Anatoidea** (Leach, 1820).—True waterfowl

†**Family Presbyornithidae** Wetmore, 1926

Genus *Presbyornis* Wetmore, 1926

*Presbyornis perventus* Wetmore, 1926

†**Family Cnemiornithidae** Stejneger, 1885

Genus *Cnemiornis* Owen, 1865.—New Zealand geese

*Cnemiornis calcitrans* Owen, 1866.—South Island Goose

*Cnemiornis gracilis* Forbes, 1892.—North Island Goose

**Family Anatidae** Leach, 1820.—Typical waterfowl

**Subfamily Dendrocygninae** Reichenbach, 1849—1850.—Whistling-ducks and allies

**Tribe Dendrocygnini** (Reichenbach, 1849—1850).—Whistling-ducks

Genus *Dendrocygna* Swainson, 1837

Subgenus *Lamprocygna* Boetticher, 1949

*Dendrocygna viduata* (Linnaeus, 1766).—White-faced Whistling-Duck

*Dendrocygna autumnalis* (Linnaeus, 1758).—Black-bellied Whistling-Duck (includes *fulgens* Friedmann, 1947)

Subgenus *Dendrocygna* Swainson, 1837

Infragenus *Nesocygna* Boetticher, 1949
Dendrocygna guttata Schlegel, 1866.—Spotted Whistling-Duck
Dendrocygna arborea (Linnaeus, 1758).—West Indian Whistling-Duck
Infragenus Dendrocygna Swainson, 1837; sedis mutabilis
Dendrocygna bicolor (Vieillot, 1816).—Fulvous Whistling-Duck
Dendrocygna eytoni (Eyton, 1838).—Plumed Whistling-Duck
Dendrocygna arcuata (Horsfield, 1824).—Wandering Whistling-Duck (includes australis Reichenbach, 1849–1850; and pygmaea Mayr, 1945)
Dendrocygna javanica (Horsfield, 1821).—Lesser Whistling-Duck

Tribe Thalassornithini (Livezey, 1986)
Genus Thalassornis Eyton, 1838
Thalassornis leuconotus Eyton, 1838.—White-backed Duck (includes insularis Richmond, 1897)

†Subfamily Dendrocheninae Livezey and Martin, 1988
Genus Dendrochen Miller, 1944
Dendrochen robusta Miller, 1944
Genus Mionetta Livezey and Martin, 1988 b
Mionetta blanchardi (Milne-Edwards, 1863)

Subfamily Anserinae Vigors, 1825.—Geese and swans

Tribe Cereopsini (Vigors, 1825)
Genus Cereopsis Latham, 1801
Cereopsis novaehollandiae Latham, 1801.—Cape Barren Goose

Tribe Anserini (Vigors, 1825).—True geese; sedis mutabilis
Genus Anser Brisson, 1760.—Pale-breasted geese
Subgenus Anser Brisson, 1760
Anser cygnoides (Linnaeus, 1758).—Swan Goose
Anser fabalis (Latham, 1787).—Bean Goose c
Anser (f.) fabalis (Latham, 1787).—Taiga Bean Goose (includes middendorffii Severtsov, 1873; and johanseni Delacour, 1951)
Anser (f.) serrirostris Swinhoe, 1871.—Tundra Bean Goose (includes rossicus Buturlin, 1933)
Anser brachyrhynchus Baillon, 1834.—Pink-footed Goose
Anser anser (Linnaeus, 1758).—Greylag Geese
Anser (a.) anser (Linnaeus, 1758).—Western Greylag Goose
Anser (a.) rubrirostris Swinhoe, 1871.—Eastern Greylag Goose
Anser albifrons (Scopoli, 1769).—Greater White-
fronted Goose (includes gambeli Hartlaub, 1852; frontalis Baird, 1858; flavirostris Dalgety and Scott, 1948; and elgasi Delacour and Ripley, 1975)

*Anser erythropus* (Linnaeus, 1758).—Lesser White-fronted Goose

Subgenus *Chen* Boie, 1822

*Anser indicus* (Latham, 1790).—Bar-headed Goose

*Anser canagicus* (Sevastianov, 1802).—Emperor Goose

*Anser caerulescens* (Linnaeus, 1758).—Snow Goose (includes atlanticus [Kennard, 1927])

*Anser rossii* Cassin, 1861.—Ross’s Goose

†Genus *Geochen* Wetmore, 1943

*Geochen rhuax* Wetmore, 1943.—Large Hawaiian Goose

Genus *Branta* Scopoli, 1769.—Brant (dark-breasted) geese

Subgenus *Leucoblepharon* Baird, 1858; sedis mutabilis

*Branta canadensis*-group (Linnaeus, 1758); sedis mutabilis.—Canada Goose

*Branta (c.) canadensis* (Linnaeus, 1758).—Atlantic Canada Goose (includes interior Todd, 1938)

*Branta (c.) moffitti* Aldrich, 1946.—Giant Canada Goose (includes maxima Delacour, 1951)

*Branta (c.) leucopareia* Brandt, 1836.—Aleutian Canada Goose (includes asiatica Aldrich, 1946)

*Branta (c.) hutchinsii* (Richardson, 1832).—Lesser Canada Goose (includes parvipes [Cassin, 1852])

*Branta (c.) occidentalis* (Baird, 1858).—Dusky Canada Goose (includes fulva Delacour, 1951)

*Branta (c.) minima* Ridgway, 1885.—Cackling Canada Goose (includes taverneri Delacour, 1951)

†*Branta hylobadistes* Olson and James, 1991.—Greater Nene

*Branta sandvicensis* (Vigors, 1834).—Lesser Nene

Subgenus *Branta* Scopoli, 1769

*Branta bernicla* (Linnaeus, 1758).—Dark-bellied Brant (includes nigricans [Lawrence, 1846]; and orientalis Tugarinov, 1941)

*Branta hrota* (Müller, 1776).—Pale-bellied Brant

Subgenus *Leucopareia* Reichenbach, 1853

*Branta leucopsis* (Bechstein, 1803).—Barnacle Goose

*Branta ruficollis* (Pallas, 1769).—Red-breasted Goose

**Tribe Cygnini** (Vigors, 1825).—Swans

**Subtribe Coscorobina** (Boetticher, 1936–1938)

Genus *Coscoroba* Reichenbach, 1853
Coscoroba coscoroba (Molina, 1782). — Coscoroba Swan

Subtribe Cygnina (Vigors, 1825). — Typical swans

Genus *Cygnus* Bechstein, 1803

Subgenus *Chenopis* Wagler, 1823. — Austral swans

*Cygnus atratus* (Latham, 1790). — Black Swan

† *Cygnus summnerensis* (Forbes, 1890). — New Zealand Swan

*Cygnus melanocoryphus* (Molina, 1782). — Black-necked Swan

Subgenus *Cygnus* Bechstein, 1803

*Cygnus olor* (Gmelin, 1789). — Mute Swan

† *Cygnus equitum* Bate, 1916. — Dwarf Maltese Swan

Subgenus *Olor* Wagler, 1832. — Tundra swans

† *Cygnus falconeri* Parker, 1865. — Giant Maltese Swan

*Cygnus buccinator* (Richardson, 1831). — Trumpeter Swan

*Cygnus columbianus* (Ord, 1815). — Whistling Swan

*Cygnus bewickii* (Yarrell, 1830). — Bewick’s Swan

*Cygnus cygnus* (Linnaeus, 1758). — Whooper Swan

† Tribe Thambetochenini Livezey, 1996. — Moa-nalos

Genus *Chelychelynechen* Olson and James, 1991

*Chelychelynechen quassus* Olson and James, 1991. — Turtle-billed Moa-nalo

Genus *Ptaiochen* Olson and James, 1991

*Ptaiochen pau* Olson and James, 1991. — Short-billed Moa-nalo

Genus *Thambetochen* Olson and Wetmore, 1976

*Thambetochen chauliodus* Olson and Wetmore, 1976. — Greater Moa-nalo

*Thambetochen xanion* Olson and James, 1991. — Oahu Moa-nalo

Subfamily Stictonettinae (Boetticher, 1950)

Genus *Stictonetta* Reichenbach, 1853

*Stictonetta naevosa* (Gould, 1841). — Freckled Duck

Subfamily Tadorninae Reichenbach, 1849–1850. — Shelducks and allies

Tribe Merganettini (Bonaparte, 1853). — Torrent-ducks and allies

Genus *Hymenolaimus* Gray, 1843

*Hymenolaimus malacorhynchos* (Gmelin, 1789). — Blue Duck

Genus *Tachyeres* Owen, 1875. — Steamer-ducks

*Tachyeres patachonicus* (King, 1831). — Flying Steamer-Duck

*Tachyeres pteneres* (Forster, 1844). — Magellanic Flightless Steamer-Duck

*Tachyeres brachypterus* (Latham, 1790). — Falkland Flightless Steamer-Duck
Tachyeres leucocephalus Humphrey and Thompson, 1981.—White-headed Flightless Steamer-Duck
Genus Merganetta Gould, 1842.—Torrent-ducks
Merganetta armata-group Gould, 1841; sedis mutabilis
Merganetta (m.) armata Gould, 1841.—Southern Torrent-Duck
Merganetta (m.) turneri Sclater and Salvin, 1869.—Turner’s Torrent-Duck
Merganetta (m.) garleppi Berlepsch, 1894.—Bolivian Torrent-Duck (includes berlepschi Hartert, 1909)
Merganetta (m.) leucogenis (Tschudi, 1843).—Peruvian Torrent-Duck
Merganetta (m.) colombiana Des Murs, 1845.—Colombian Torrent-Duck

Tribe Plectropterini (Eyton, 1838).—Pied shelducks
Genus Plectropterus Stephens, 1824
Plectropterus gambensis (Linnaeus, 1766).—Spur-winged Goose (includes niger Sclater, 1877)
Genus Sarkidiornis Eyton, 1838.—Comb-ducks
Sarkidiornis melanotos (Pennant, 1769).—Gray-sided Comb-Duck
Sarkidiornis sylvicola Ihering and Ihering, 1907.—Black-sided Comb-Duck

†Tribe Euryanatini (Livezey, 1989)
Genus Euryanas Oliver, 1930
Euryanas finschi (Van Beneden, 1875).—Finsch’s Duck

Tribe Tadornini (Reichenbach, 1849–1850).—True shelducks and sheldgeese

Subtribe indeterminate
†Genus Centrornis Andrews, 1897
Centrornis majori Andrews, 1897.—Greater Madagascan Sheldgoose
†Genus Anabernicula Ross, 1935.—Pygmy sheldgeese
Anabernicula minuscula Wetmore, 1924
Anabernicula gracilenta Ross, 1935
Anabernicula oreonensis Howard, 1964

Subtribe Chloephagina (Boetticher, 1942).—Sheldgeese
Genus Cyanochen Bonaparte, 1856
Cyanochen cyanopterus (Rüppell, 1845).—Blue-winged Sheldgoose
Genus Alopochen Stejneger, 1885; sedis mutabilis
Alopochen aegypticus (Linnaeus, 1766).—African Sheldgoose
†Alopochen sirabensis (Andrews, 1897).—Lesser Madagascan Sheldgoose
†Alopochen mauritianus (Newton and Gadow, 1893).—Mauritius Sheldgoose
Genus *Neochen* Oberholser, 1918
  *Neochen jubata* (Spix, 1825).—Orinoco Sheldgoose
  †*Neochen pugil* (Winge, 1887).—Greater Orinoco Sheldgoose
Genus *Chloephaga* Eyton, 1838.—Neotropical sheldgeese
Subgenus *Oressochen* Bannister, 1870
  *Chloephaga melanoptera* (Eyton, 1838).—Andean Sheldgoose
Subgenus *Chloephaga* Eyton, 1838.—Patagonian sheldgoose; sedis mutabilis
Infragenus *Chloephaga* Eyton, 1838
  *Chloephaga picta* (Gmelin, 1789).—Upland Sheldgoose (includes *leucoptera* [Gmelin, 1789])
Infragenus *Taenidiestes* Reichenbach, 1853
  *Chloephaga hybrida* (Molina, 1782).—Kelp Sheldgoose (includes *malvinarum* Phillips, 1916)
Infragenus *Chloetropus* Bannister, 1870.—Hooded sheldgoose
  *Chloephaga poliocephalus* Sclater, 1857.—Ashy-headed Sheldgoose
  *Chloephaga rubidiceps* Sclater, 1860.—Ruddy-headed Sheldgoose
Subtribe *Tadornina* (Reichenbach, 1849–1850).—Shelducks
  †Genus *Pachyanas* Oliver, 1955
    *Pachyanas chathamica* Oliver, 1955.—Chatham Island Shelduck
Genus *Tadorna* Oken, 1817.—Banded shelducks
  *Tadorna tadorna* (Linnaeus, 1758).—Red-billed Shelduck
  *Tadorna radjah* (Lesson, 1828).—Radjah Shelduck (includes *raftergum* Hartert, 1905)
Genus *Casarca* Bonaparte, 1838.—Unbanded shelducks
Subgenus *Casarca* Bonaparte, 1838.—Reddish shelducks
  *Casarca ferruginea* (Pallas, 1764).—Ruddy Shelduck
  *Casarca cana* (Gmelin, 1789).—Cape Shelduck
Subgenus *Pseudotadorna* Kuroda, 1917.—Blackish shelducks
  *Casarca tadornoides* (Jardine and Selby, 1828).—Australian Shelduck
  *Casarca variegata* (Gmelin, 1789).—Paradise Shelduck
  *Casarca cristata* (Kuroda, 1917).—Crested Shelduck
Subfamily *Anatinae* (Leach, 1820).—True ducks; sedis mutabilis
  Tribe *Malacorhynchini* (Boetticher, 1950); incertae sedis
Genus *Malacorhynchus* Swainson, 1831.—Pink-eared ducks
  *Malacorhynchus membranaceus* (Latham, 1801).—Australian Pink-eared Duck
†Malacorhynchus scarletti Olson, 1977.—New Zealand Pink-eared Duck
Genus Salvadorina Rothschild and Hartert, 1894
Salvadorina waigiensis Rothschild and Hartert, 1894.—Salvadori’s Duck

Tribe Anatini (Leach, 1820).—Surface-feeding ducks; incertae sedis

Subtribe Cairinina (Boetticher, 1936–1938).—Long-billed wood ducks
Super genus Cairina Fleming, 1822.—Greater wood ducks
Genus Cairina Fleming, 1822.—Muscovy ducks
Cairina moschata (Linneaus, 1758).—Muscovy Duck
Cairina scutulata (Müller, 1842).—White-winged Duck
Genus Pteronetta Salvadori, 1895
Pteronetta hartlaubi (Cassin, 1859).—Hartlaub’s Duck
Super genus Aix Boie, 1828
Genus Aix Boie, 1828.—Northern wood ducks
Aix sponsa (Linneaus, 1758).—American Wood Duck
Aix galericulata (Linneaus, 1758).—Mandarin Duck

Subtribe Nettapodina (Bonaparte, 1856).—Stout-billed wood ducks
Genus Chenonetta Brandt, 1836
Chenonetta jubata (Latham, 1801).—Maned Duck
Genus Nettapus Brandt, 1836.—Pygmy-geese
Subgenus Nettapus Brandt, 1836
Nettapus auritus (Boddaert, 1783).—African Pygmy-goose
Subgenus Cheniscus Eyton, 1838.—Pale-rumped pygmy-geese
Nettapus coromandelianus (Gmelin, 1789).—Cotton Pygmy-goose (includes albipennis Gould, 1842)
Nettapus pulchellus (Gould, 1842).—Green Pygmy-goose

Subtribe Anatina (Leach, 1820).—Dabbling ducks
Super genus Amazonetta Boetticher, 1929.—Micro-teal
Genus Amazonetta Boetticher, 1929
Amazonetta brasiliensis (Gmelin, 1789).—Brazilian Teal (includes ipecutiri [Vieillot, 1816])
Genus Callonetta Delacour, 1936
Callonetta leucophrys (Vieillot, 1816).—Ringed Teal
Super genus Lophonetta Riley, 1914
Genus Lophonetta Riley, 1914
Lophonetta specularioides (King, 1828).—Crested Duck (includes alitricola Ménégaux, 1909)
Genus *Speculanas* Boetticher, 1929
*Speculanas specularis* (King, 1828).—Bronze-winged Duck

Supergenus *Anas* Linnaeus, 1758.—True dabbling ducks

Genus indeterminate
†*“Anas” theodori* Newton and Gadow, 1893.—Mauritius Duck
†*“Anas” pachyscelus* Wetmore, 1960.—Bermuda Duck
†*“Anas” marecula* Olson and Jouventin, 1996.—Amsterdam Island Duck

Genus *Mareca* Stephens, 1824.—Wigeons

Subgenus *Notonetta* Roberts, 1922
*Mareca capensis* (Gmelin, 1789).—Cape Teal

Subgenus *Chaulelasmus* Bonaparte, 1838.—Gadwalls
*Mareca strepera* (Linnaeus, 1758).—Common Gadwall
*Mareca couesi* (Streets, 1876).—Washington Island Gadwall

Subgenus *Eunetta* Bonaparte, 1856
*Mareca falcata* (Georgi, 1775).—Falcated Duck

Subgenus *Mareca* Stephens, 1824.—Typical wigeons
*Mareca sibilatrix* (Poeppig, 1829).—Chiloé Wigeon
*Mareca penelope* (Linnaeus, 1758).—Eurasian Wigeon
*Mareca americana* (Gmelin, 1789).—American Wigeon

Genus *Anas* Linnaeus, 1758.—Typical dabbling ducks; sedis mutabilis

Subgenus *Anas* Linnaeus, 1758.—Mallards
Infragenus *Melananas* Roberts, 1922
*Anas sparsa* Eyton, 1838.—African Black Duck (includes *leucostigma* Rüppell, 1845)

Infragenus *Anas* Linnaeus, 1758.—Northern mallards; sedis mutabilis
*Anas rubripes* Brewster, 1902.—American Black Duck
*Anas platyrhynchos* Linnaeus, 1758.—Mallard (includes *conboschas* Brehm, 1831)
*Anas fulvigula* Ridgway, 1874.—Mottled Duck (includes *maculosa* Sennett, 1889)
*Anas diazi* Ridgway, 1886.—Mexican Duck
*Anas wyvilliana* Sclater, 1878.—Hawaiian Duck
*Anas laysanensis* Rothschild, 1892.—Laysan Duck
*Anas oustaleti* Salvadori, 1894.—Marianas Duck

Infragenus *Polionetta* Oates, 1899.—South Pacific mallards
*Anas luzonica* Fraser, 1839.—Philippine Duck
*Anas superciliosa* Gmelin, 1789.—Pacific Gray
Duck (includes pelewensis Hartlaub and Finsch, 1872; and rogersi Mathews, 1912)  
*Anas poecilorhyncha* Forster, 1781.—Indonesian Spot-billed Duck (includes haringtoni Oates, 1907)  
*Anas zonorhyncha* Swinhoe, 1866.—Chinese Spot-billed Duck  
Infragenus Afranas Roberts, 1922.—African mallards  
*Anas undulata* Dubois, 1839.—Yellow-billed Duck (includes rueppelli Blyth, 1855)  
*Anas melleri* Sclater, 1865.—Meller’s Duck  
Subgenus Spatula Boie, 1822.—Blue-winged ducks  
Infragenus Pterocyanea Bonaparte, 1841.—Blue-winged teal  
*Anas discors* Linnaeus, 1766.—Blue-winged Teal  
*Anas cyanoptera* Vieillot, 1816.—Cinnamon Teal (includes orinomus [Oberholser, 1906]; septentrionalium Snyder and Lumsden, 1951; tropica Snyder and Lumsden, 1951; and borreroi Snyder and Lumsden, 1951)  
Infragenus Spatula Boie, 1822.—Shovelers  
*Anas smithii* Hartert, 1891.—Cape Shoveler  
*Anas platalea* Vieillot, 1816.—Red Shoveler  
*Anas rhynchotis* Latham, 1802.—Australasian Shoveler (includes variegata [Gould, 1856])  
*Anas clypeata* Linnaeus, 1758.—Northern Shoveler  
Subgenus Nesonetta Gray, 1844.—Australasian teal  
Infragenus Virago Newton, 1872.—Gray teal; sedis mutabilis  
*Anas bernieri* Hartlaub, 1860.—Madagascan Teal  
*Anas gibberifrons* Müller, 1842.—Indonesian Gray Teal  
*Anas gracilis* Buller, 1869.—Australasian Gray Teal (includes remissa Ripley, 1942)  
*Anas albogularis* (Hume, 1873).—Andaman Teal  
Infragenus Nesonetta Gray, 1844.—Reddish teal  
*Anas castanea* (Eyton, 1838).—Chestnut Teal  
*Anas chlorotis* Gray, 1845.—Brown Teal  
*Anas aucklandica* Gray, 1844.—Auckland Islands Teal  
*Anas nesiotis* (Fleming, 1935).—Campbell Island Teal  
Subgenus Dafila Stephens, 1824.—Pintails  
Infragenus Paecilonitta Eyton, 1838.—Pale-cheeked pintails  
*Anas bahamensis* Linnaeus, 1758.—White-cheeked Pintail (includes rubirostris Vieillot, 1816; and galapagensis [Ridgway, 1889])  
*Anas erythrorhyncha* Gmelin, 1789.—Red-billed Pintail
Infragenus *Dafilonettion* Boetticher, 1937.—Speckled teal
  *Anas flavirostris* Vieillot, 1816.—Yellow-billed Teal (includes *oxyptera* Meyen, 1834)
  *Anas andium* (Sclater and Salvin, 1873).—Andean Teal (includes *altipetens* [Conover, 1941])
Infragenus *Dafila* Stephens, 1824.—Brown pintails
  *Anas georgica* Gmelin, 1789.—Brown Pintail (includes *spinicauda* Vieillot, 1816; and *niceforoi* Wetmore and Borrero, 1946)
  *Anas acuta* Linnaeus, 1758.—Northern Pintail
  *Anas eatoni* (Sharpe, 1875).—Eaton’s Pintail (includes *drygalskii* Reichenow, 1904)

Subgenus *Querquedula* Stephens, 1824.—Holarctic teal
Infragenus *Querquedula* Stephens, 1824
  *Anas querquedula* Linnaeus, 1758.—Garganey Teal
Infragenus *Nettion* Kaup, 1829.—Green-winged teal
  *Anas formosa* Georgi, 1775.—Baikal Teal
  *Anas crecca* Linnaeus, 1758.—Eurasian Green-winged Teal (includes *nimia* Friedmann, 1948)
  *Anas carolinensis* Gmelin, 1789.—American Green-winged Teal

Subgenus *Punanetta* Bonaparte, 1856.—Spotted teal
Infragenus *Punanetta* Bonaparte, 1856.—Pale-cheeked teal
  *Anas versicolor* Vieillot, 1816.—Silver Teal (includes *fretensis* King, 1831)
  *Anas puna* Tschudi, 1844.—Puna Teal
Infragenus *Micronetta* Roberts, 1922
  *Anas hottentota* Eyton, 1838.—Hottentot Teal

**Tribe Aythyini** Delacour and Mayr, 1945.—Pochards

**Subtribe Marmaronettina** (Livezey, 1996)
  **Genus** *Marmaronetta* Reichenbach, 1853
    *Marmaronetta angustirostris* (Ménétriers, 1832).—Marbled Duck

**Subtribe Rhodonessina** (Boetticher, 1950).—Stem pochards
  **Genus** *Netta* Kaup, 1829
    Subgenus *Netta* Kaup, 1829
      *Netta rufina* (Pallas, 1773).—Red-crested Pochard
    Subgenus *Rhodonessa* Reichenbach, 1853
      *Netta caryophyllacea* (Latham, 1790).—Pink-headed Pochard
  **Genus** *Metopiana* Bonaparte, 1856
    Subgenus *Metopiana* Bonaparte, 1856
      *Metopiana peposaca* (Vieillot, 1816).—Rosy-billed Pochard
    Subgenus *Phaeoaythia* Delacour, 1937
      *Metopiana erythrophthalma* (Wied, 1832).—Southern Pochard (includes *brunnea* [Eyton, 1838])
Subtribe Aythyina (Delacour and Mayr, 1945).—True pochards
Genus Aristonetta Baird, 1858.—Red-headed pochards
Aristonetta valisineria (Wilson, 1814).—Canvasback
Aristonetta americana (Eyton, 1838).—Redhead
Aristonetta ferina (Linnaeus, 1758).—Eurasian Pochard
Genus Aythya Boie, 1822.—Typical pochards
Subgenus Nyroca Fleming, 1822.—White-eyed pochards
Aythya australis (Eyton, 1838).—Australian White-eyed Pochard (includes extima Mayr, 1940)
Aythya innotata (Salvadori, 1894).—Madagascan White-eyed Pochard
Aythya nyroca (Güldenstädt, 1770).—Ferruginous White-eyed Pochard
Aythya baeri (Radde, 1863).—Siberian White-eyed Pochard
Subgenus Aythya Boie, 1822.—Scaup
Aythya novaeseelandiae (Gmelin, 1789).—New Zealand Scaup
Aythya collaris (Donovan, 1809).—Ring-necked Scaup
Aythya fuligula (Linnaeus, 1758).—Tufted Scaup
Aythya marila (Linnaeus, 1761).—Greater Scaup (includes mariloides [Vigors, 1839])
Aythya affinis (Eyton, 1838).—Lesser Scaup

Tribe Mergini (Rafinesque, 1815; alternatively, Swainson, 1831).—Seaducks
Subtribe Somaterina (Reichenbach, 1849–1850).—Eiders
Genus Polysticta Eyton, 1836
Polysticta stelleri (Pallas, 1769).—Steller’s Eider
Genus Somateria Leach, 1819.—Greater eiders
Subgenus Lampronetta Brandt, 1847
Somateria fischeri (Brandt, 1847).—Spectacled Eider
Subgenus Somateria Leach, 1819
Somateria spectabilis (Linnaeus, 1758).—King Eider
Somateria mollissima-group (Linnaeus, 1758).—Common Eider
Somateria (m.) v-nigrum Gray, 1855.—Pacific Eider
Somateria (m.) borealis (Brehm, 1824).—Northern Eider
Somateria (m.) dresseri Sharpe, 1871.—Canada Eider (includes sedentaria Snyder, 1941)
Somateria (m.) mollissima (Linnaeus, 1758).—European Eider (includes islandica Brehm, 1831; and faeroeensis Brehm, 1831)
†Subtribe Chendytina, new taxon

Genus Chendytes Miller, 1925
  Chendytes lawi Miller, 1925
  Chendytes milleri Howard, 1955

Subtribe Mergina (Rafinesque, 1815; alternatively, Swainson, 1831).—Typical seaducks

Supergenus Histrionicus Lesson, 1828
  Genus Histrionicus Lesson, 1828
    Histrionicus histrionicus (Linnaeus, 1758).—Harlequin Duck
  Genus Camptorhynchus Bonaparte, 1838
    Camptorhynchus labradorius (Gmelin, 1789).—Labrador Duck
  Genus Melanitta Boie, 1822.—Scoters and allies
    Subgenus Melanitta Boie, 1822.—White-marked scoters
      Melanitta perspicillata (Linnaeus, 1758).—Surf Scoter
      Melanitta fusca (Linnaeus, 1758).—Velvet Scoter
      Melanitta deglandi (Bonaparte, 1850).—White-winged Scoter (includes stejnegeri [Ridgway, 1887])
    Subgenus Oidemia Fleming, 1822.—Black scoters
      Melanitta nigra (Linnaeus, 1758).—Eurasian Black Scoter
      Melanitta americana (Swainson, 1832).—American Black Scoter
  Supergenus Mergus Linnaeus, 1758.—Mergansers and allies
    Genus Clangula Leach, 1819
      Clangula hyemalis (Linnaeus, 1758).—Long-tailed Duck
    Genus Bucephala Baird, 1858.—Goldeneyes
      Subgenus Bucephala Baird, 1858
        Bucephala albeola (Linnaeus, 1758).—Bufflehead
      Subgenus Glaucomictes Stejneger, 1885
        Bucephala clangula (Linnaeus, 1758).—Common Goldeneye (includes americana [Bonaparte, 1838])
        Bucephala islandica (Gmelin, 1789).—Barrow’s Goldeneye
    Genus Mergellus Selby, 1840
      Mergellus albellus (Linnaeus, 1758).—Smew
    Genus Lophodytes Reichenbach, 1853
      Lophodytes cucullatus (Linnaeus, 1758).—Hooded Merganser
    Genus Mergus Linnaeus, 1758.—Typical mergansers
      Subgenus Promergus Mathews and Iredale, 1913
        Mergus australis Hombron and Jacquinot, 1841.—Auckland Islands Merganser
      Subgenus Prister Heine, 1890
Mergus octosetaceus Vieillot, 1817.—Brazilian Merganser
Subgenus Mergus Linnaeus, 1758.—Greater mergansers
Mergus merganser Linnaeus, 1758.—Common Merganser (includes orientalis Gould, 1845; and americanus Cassin, 1852)
Mergus serrator Linnaeus, 1758.—Red-breasted Merganser (includes schoelieri Salomonsen, 1949)
Mergus squamatus Gould, 1864.—Chinese Merganser

Tribe Oxyurini (Phillips, 1926).—Stiff-tailed ducks and allies
Subtribe Heteronettina (Boetticher, 1950)
Genus Heteronetta Salvadori, 1865
Heteronetta atricapilla (Merrem, 1841).—Black-headed Duck

Subtribe Oxyurina (Phillips, 1926).—Stiff-tailed ducks
Supergenus Nomonyx Ridgway, 1880
Genus Nomonyx Ridgway, 1880
Nomonyx dominicus (Linnaeus, 1766).—Masked Duck
Supergenus Oxyura Bonaparte, 1828.—Typical stiff-tailed ducks
Genus Oxyura Bonaparte, 1828.—Ruddy (blue-billed) ducks
Subgenus Oxyura Bonaparte, 1828
Oxyura jamaicensis (Gmelin, 1789).—Northern Ruddy Duck (includes rubida Wilson, 1814)
Subgenus Cerconectes Wagler, 1832; sedis mutabilis
Oxyura ferruginea (Eyton, 1838).—Peruvian Ruddy Duck
Oxyura vittata (Philippi, 1860).—Argentine Ruddy Duck
Oxyura australis Gould, 1836.—Blue-billed Duck
Oxyura maccoa (Eyton, 1836).—Maccoa Duck
Oxyura leucocephala (Scopoli, 1769).—White-headed Duck
Genus Biziura Stephens, 1824.—Musk-ducks
Biziura lobata (Shaw, 1796).—Australian Musk-Duck
†Biziura delautouri Forbes, 1892.—New Zealand Musk-Duck

^ Adoption by Livezey (1995a) of two of four subgenera of Dendrocygna erected by Boetticher (1949) was performed under the Principle of First Reviser (International Commission on Zoological Nomenclature, 1985: Article 24).

^ Several other fossil taxa from the Miocene may be assignable to Mionetta (Livezey and Martin, 1988; see also Cheneval, 1987), including: Anas[?] consobrina Milne-Edwards, 1867; and Anas[?] natator Milne-Edwards, 1867.
Partition of complex into orange-billed, taiga-breeding form and largely black-billed, tundra-breeding form is provisional.

Position tentative, genus may be synonymous with Branta (Livezey, 1996a).

Probably includes several phylogenetic species; one geo-phenotypic partitioning of subspecific taxa is shown (Livezey, 1996a).

Relationships among some Cygnus not resolved (Livezey, 1996a), and Maltese fossil swans provisionally placed based on Northcote (1982, 1988, 1992).

 Provisionally placed based on Livezey (1989a).  
Position of tribe provisional (Livezey, 1996a).

Based on Livezey (1986b) and Livezey and Humphrey (1992).

Genus may comprise 3–5 sibling species; weak support for segregating the three southern forms from the two northern forms.

Tribal taxon for this genus in Livezey (1986a), Sarkidiornini, was incorrectly derived and should have been Sarkidiornithini (the same change in stem would apply to corresponding subtribal name); authorship for the family-group name is Oberholser, 1918 (Sarkidiornithinae).

 Provisionally placed based on Livezey (1989a) and subsequent assessments of related genera (Livezey, 1996b).

Provisionally placed based on codings of characters for limited fossil elements (unpublished data).

 Relationships among C. hybrida, C. picta, and the sister species C. poliocephala and C. rubidiceps unresolved (Livezey, 1997a).

Generic assignment based on codings of characters for limited fossil elements (unpublished data) and/or published descriptions.

 Relationships among tribes in Subfamily Anatinae not resolved (Livezey, 1996b).

Composition of tribe and its inclusion in Subfamily Anatinae provisional (Livezey, 1996b).

Monophyly of the Tribe Anatini not confirmed (Livezey, 1996b).

Generic placement within supergenus not possible based on available specimens.

Recognition of species provisional (Livezey, 1993a).

Relationships and species status of included taxa unresolved (Livezey, 1991); A. wyvilliana and A. laysanensis assignable to Horizonetta Oberholser, 1917.

 Possibly of hybrid origin (Yamashina, 1948; Ripley, 1957; Livezey, 1991), and evidently extinct (Reichel and Lemke, 1994).

Subgeneric assignment tentative (Livezey, 1991).

Segregation of A. gracilis from A. gibberifrons at species level follows osteological evidence presented by Ripley (1942), Mees (1982), and Parker et al. (1985).

Correction of mistaken attribution of seniority to Rhodonessa by Livezey (1996c).

Relationships between the sister species A. nyroca and A. baeri and other white-eyes remain unresolved (Livezey, 1996c).

May comprise two or more sibling species (Livezey, 1995c); it is recommended minimally that v-nigrum be segregated.

Position of genus provisional (Livezey, 1993b).

 Provisionally includes sibling species from the Chatham Islands and South Island, New Zealand (Livezey, 1995c).
Oxyura (J.) andina Lehmann, 1946 (Colombian Ruddy Duck) is provisionally considered here to pertain to hybrid progeny of O. (J.) jamaicensis and O. ferruginea (Livezey, 1995b).

**DISCUSSION**

**Points of Consensus and Controversy**

**Graded Classes of Support.**—In order to provide an assessment of the relative empirical support of taxonomic groupings defined in the classification, I discuss below selected taxa under five provisional classes based on the evidence presented in the associated analyses (Livezey, 1986a, 1986b, 1986c, 1989a, 1989b, 1990, 1991, 1993a, 1993b, 1995a, 1995b, 1995c, 1996a, 1996b, 1996c, 1997a, 1997b) and a familiarity with the underlying characters. The lists are not intended to be exhaustive, and therefore interpretations of support may not be given for some taxa of interest; for such groups, the reader is invited to examine the original analyses.

**Practically Unassailable.**—Among the higher taxonomic groups for which I consider that monophyly has been established beyond a reasonable doubt are: Order Anseriformes, Suborder Anhimae, Suborder Anseres, Superfamily Anatoidea (including Presbyornis), and Family Anatidae. The monophyly of many polytypic genera also has been established using a variety of characters; these genera include Chauna, Cygnus, Tachyeres, Somateria, Mergus, and Oxyura (sensu stricto).

**Strongly Supported.**—Contrary to the arguments of Feduccia (1980, 1996), Olson and Feduccia (1980), and Olson (1985), the position of the Galliformes as the sister order of the waterfowl is supported by substantial evidence from both morphological and molecular studies (Livezey, 1997b), therefore justifying the Superorder Galloanserimorphae. Monophyly has been well demonstrated for the node uniting the subfamilies Tadorninae and Anatinia, as well as those defining the Tribe Thamboetochemini, Subtribe Tadornina, Subtribe Aythyina, Subtribe Oxyurina, and Supergenus Mergus. Strong support also is known for several polytypic genera, including Dendrocygna, Somateria, the subgenus Olror, as well as a number of species groups (Chloephaga poliocephala and C. rubidiceps; Bucephala clangula and B. islandica).

**Moderately Supported.**—Adequate but suboptimal support attends a number of inferred groups of Anseriformes. These include the tribes Cygnini, Mergini, and Oxyurini; Subtribe Somaterina; genera Chloephaga, Aristonetta, Melanitta, Bucephala, Oxyura; Subgenus Nyroca; and a number of species groups (Casarca tadornoides and C. variegata; Aythya fuligula, A. affinis, and A. marila; Somateria exclusive of fischeri).

**Weakly Supported.**—Marginally supported nodes and associated taxonomic groups include the subfamilial position of the tribes Thamboetochemini (Anserinae or Tadorninae) and Malacorhynchini (Tadorninae or Anatinae), monophyly of the Subfamily Dendrocygnine and the subtribes Chloephagina and Mergina, the node uniting Mergellus with its sister genus, monophyly of the genera Anser and Bran- ta, and monophyly of a number of subgenera and species groups in most anatid tribes (especially within the Dendrocygningar, Anserini, Tadornini, Anatini, Aythynini, and Oxyurini). Also, for reasons detailed elsewhere (Livezey, 1996c), the position of Aythya collaris within the Subtribe Aythyina remains problematic. Finally, the positions of many fossil taxa remain tentative, notably those of Eu- ryanas, Centrornis, Anabernicula, and Pachyanas.

**Unresolved.**—Monophyly of the subfamilies Tadorninae and Anatinia has not
been demonstrated; provisional support for the naturalness of these two groups hinges on ancillary analytical methods, e.g., weighting of osteological characters more heavily than those of plumages (Livezey, 1996b). No single, empirically preferable reconstruction is available for the phylogenetic relationships among members of the following groups: Olor group of swans, tribes within the Tadorninae, tribes within the Anatinae, and subtribes within the Anatini. Also unresolved are: the subgeneric placement of Anas bernieri (Anatini), relationships within the subgenus Nyroca (Aythyini), the sister group of Oxyura jamaicensis, and relationships among several members of the Anas platyrhynchos group (Anatini). Also, relationships within Branta canadensis, Merganetta armata, and Somateria mollissima, three taxa traditionally considered monospecific but possibly comprising several species, require concerted reassessment.

**Future Directions**

Much remains to be done concerning the study of the evolution of waterfowl, and these understudied topics include more than confirmatory systematic investigations and attention to areas of poor resolution. In addition to the use of this classification for organizational purposes (e.g., Madge and Burn, 1988) and the refinement of the consensus concerning the phylogeny of Anseriformes (e.g., Christidis and Boles, 1994), it is hoped that the preceeding classification will facilitate the use of the underlying phylogenetic hypothesis for comparative study. Appropriate topics for such explorations, some of which have been examined already in a phylogenetic context, include: nest parasitism (Eadie et al., 1988; Rohwer and Freeman, 1989), parental care (Johnsgard and Kear, 1968; Kear, 1970; Scott and Clutton-Brock, 1989), natal vocalizations (Kear, 1968), parameters of reproduction (Rohwer, 1988), morphological convergence (Faith, 1989), brood amalgamation (Beauchamp, 1997), evolutionary patterns in flightlessness and ontogeny (Livezey and Humphrey, 1986; Livezey, 1989b, 1990, 1993a, 1993b, 1995a, 1995b), historical biogeography (Livezey, 1991, 1996a, 1997a), and diel activity patterns (McNeil et al., 1992).

Courtship behavior, one of the first behavioral aspects of waterfowl to be subjected to intense study (Lorenz, 1941; Delacour and Mayr, 1945; Johnsgard, 1961a, 1965a; Johnsgard and Carbonell, 1996), especially merits reassessment within a phylogenetic context. Indeed, behavioral characters merit consideration as characters in primary phylogenetic reconstruction (de Queiroz and Wimberger, 1993; Wimberger and de Queiroz, 1996), although problems of homology, inadequate data for many species, and variation among studies in the treatment of rare or infrequent behavioral patterns render suspect any analyses based uncritically on the ethological literature (e.g., Irwin, 1996). Myriad other aspects of the evolution of waterfowl await study, and as the availability of quantitative methods for phylogenetic assessments improves (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Martins and Hansen, 1996; Ridley and Grafen, 1996), the revelation of patterns extendable to fossil taxa and other avian groups can be expected in the near future.
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APPENDIX

Characters Used in Preliminary Analyses of Miscellaneous Genera and Species Groups

Branta canadensis Complex

A tentative partitioning of the complex into five geographically integritous, phenotypically congruent forms is adopted, based on three external characters:

1. Body size (mean mass, kg), ordered: (a) small, 1.5–2.0 (other Branta spp., B. [c.] minima, B. [c.] hutchinsii); (b) medium, 2.1–3.9 (all other B. canadensis); (c) large, 4.0–5.2 (B. [c.] moffitti, B. [c.] maxima).

2. Brown color of ventrum: (a) pale (all others); (b) dark (B. [c.] minima, B. [c.] occidentalis, B. [c.] fulva).

3. Narrow white collar at base of neck: (a) typically absent (other Branta); (b) typically present (B. [c.] leucopareia, including “asiatica”). Note: also occurs uncommonly to rarely in B. (c.) taverneri and B. (c.) minima; possibly treat as intermediate state or polymorphism.

Sarkidiornis Complex

Two allopatric species are recognized based on color of contrasting, uniformly dark sides and flanks.

1. Sides and flanks: (a) gray (S. melanotos); (b) black (S. sylvicola).

Merganetta Complex

Five diagnosable, parapatric taxa are tentatively recognized. Provisional diagnostic characters (for adult males) include:

1. Black suborbital stripe (adult males): (a) absent (other Merganetta); (b) present (M. armata).

2. Contrastingly black chin and throat (adult males): (a) absent (other Merganetta); (b) present (M. armata).

3. Venter, contrastingly black color (adult males, ordered): (a) absent (other
Merganetta [berlepschi variable]); (b) present, confined to breast (M. armata); (c) present, including entire ventrum (M. turneri).

4. Ground color of venter, rusty color (adult males): (a) absent (Merganetta colombiana and M. leucogenis); (b) present (other Merganetta [very dark in turneri, berlepschi]).

5. Mantle, at least lateral margins (adult males): (a) black and white striped (others, including Merganetta armata, M. garleppi [intermediate, variable]); (b) black and brown striped (M. leucogenis, M. colombiana, M. turneri).

6. Mantle, medial portion, black color (adult males): (a) absent (other Merganetta); (b) present (M. turneri, M. leucogenis).
Livezey, Bradley C. 1997. "A phylogenetic classification of waterfowl (Aves: Anseriformes), including selected fossil species." *Annals of the Carnegie Museum* 66(4), 457–496. https://doi.org/10.5962/p.215141.