

A PHYLOGENETIC ANALYSIS OF RECENT ANSERIFORM GENERA USING MORPHOLOGICAL CHARACTERS

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ABSTRACT.—A phylogenetic analysis of all Recent genera of the Anseriformes using 120 morphological characters supports much of the current consensus regarding intraordinal relationships. I found that (1) *Anseranas* should be placed in a monotypic family; (2) *Dendrocygna*, *Thalassornis*, geese and swans, and *Stictonetta* are paraphyletic to the rest of the Anatidae; (3) *Cereopsis* is the sister group to *Anser* and *Branta*, and *Coscoroba* is the sister group to *Cygnus* and *Olor*; (4) *Plectropterus* is the sister group to the Tadorninae (shelducks) and the Anatinae (typical ducks); (5) the shelducks are monophyletic and include *Sarkidiornis* (provisionally), *Malacorhynchus*, *Hymenolaimus*, *Merganetta*, and *Tachyeres*; (6) the tribe "Cairinini" ("perching ducks") is an unnatural, polyphyletic assemblage and is rejected; (7) the dabbling ducks (including the smaller "perching ducks") comprise an unresolved, probably paraphyletic group; (8) tribal monophyly of the pochards (including *Marmaronetta* and *Rhodonessa*), sea ducks (including the eiders), and stiff-tailed ducks (including *Heteronetta*) is confirmed; and (9) the retention of *Mergellus* and resurrection of *Nomonyx* are recommended based on clarifications of intratribal relationships. Problematic groups, effects of homoplasy, phenetic comparisons, life-history correlates, biogeographic patterns, and fossil species are discussed, and a phylogenetic classification of Recent genera is proposed. Received 18 November 1985, accepted 2 April 1986.

THE order Anseriformes is considered to comprise the families Anhimidae (2 genera, 3 species) and Anatidae (approximately 43 genera and 150 species). The family Anatidae is undoubtedly one of the best-studied groups of birds, owing largely to the historical importance of waterfowl for hunting (Weller 1964a), domestication (Delacour 1964a), and aviculture (Delacour 1964b).

The classification of the Anatidae proposed by Delacour and Mayr (1945) has been followed, with only minor revisions, in recent decades (e.g. Delacour 1954, 1956, 1959, 1964c; Johnsgard 1961a, 1962, 1965a, 1978, 1979; Woolfenden 1961; Frith 1967; Bellrose 1976; Palmer 1976; A.O.U. 1983; Bottjer 1983; Scott 1985). Perhaps the most innovative aspect of this system (inspired by the works of Salvadori 1895; Phillips 1922, 1923, 1925; and Peters 1931) was the erection of "tribes," groups of genera that were considered to be closely related within the subfamilies of the Anatidae. These tribes became the primary focus of subsequent works on anatid classification, many of which addressed the tribal assignments of problematic genera (e.g. Humphrey and Butsch 1958; Johnsgard 1960a, 1961b; Humphrey and Ripley

1962; Davies and Frith 1964; Raikow 1971; Kear and Murton 1973). Most authors assumed the validity of the tribes and used them as working units in phylogenetic analyses of the family (e.g. Johnsgard 1961a, Bottjer 1983). A few workers named additional tribes (Moynihan 1958, Delacour 1959, Woolfenden 1961, Weller 1968b) or attempted to test the naturalness of those originally proposed (Cotter 1957, Woolfenden 1961, Brush 1976).

Behavioral characters have been accorded considerable weight in classifications of waterfowl. Delacour and Mayr (1945) based their revision on characters they considered to be "non-adaptive," including behavioral displays, nesting and feeding habits, and selected morphological characters (e.g. posture, body proportions, head shape, syringeal bulla). Reliance on comparative ethology in anatid systematics was furthered by the studies of Lorenz (1951-1953), McKinney (1953), and Myres (1959) and was increased significantly by Johnsgard (1960a-c, 1961a-d, 1962, 1964, 1965a, b, 1966a, b, 1967, 1978), whose work was largely ethological and influenced profoundly by that of Delacour (1954, 1956, 1959, 1964c). This emphasis, work on interspecific hybridization

(Sibley 1957; Gray 1958; Johnsgard 1960d, 1963), and study of plumage patterns of downy young (Delacour 1954, 1956, 1959; Frith 1955, 1964b; Kear 1967) were prompted in part by the opportunity to observe waterfowl in avicultural collections.

Other data used in the classification of waterfowl include syringeal anatomy (Humphrey 1955, 1958; Johnsgard 1961e), cytogenetics (Yamashina 1952), serology (Cotter 1957, Bottjer 1983), osteology (DeMay 1940, Verheyen 1955, Humphrey and Butsch 1958, Woolfenden 1961, Humphrey and Ripley 1962, Raikow 1971), feather lice (Timmermann 1963), eggshell structure (Tyler 1964), egg-white proteins (Sibley 1960, Sibley and Ahlquist 1972), feather proteins (Brush 1976), myology (Zusi and Bentz 1978), lipids from the uropygial gland (Jacob and Glaser 1975, Jacob 1982), and mitochondrial DNA (Kessler and Avise 1984).

These studies, with the possible exceptions of those by Lorenz (1953) and Kessler and Avise (1984), estimated the evolutionary relationships of groups by assessments of overall similarities; no attempts were made to determine primitive conditions or to distinguish shared primitive characters from shared derived characters ("special" similarity). Moreover, the "evolutionary trees" presented in most of these works lack references to the specific characters used to support the branching patterns (e.g. Delacour and Mayr 1945; Johnsgard 1961a, 1978; Woolfenden 1961).

I performed a phylogenetic (cladistic) analysis of Recent genera of Anseriformes using 120 morphological characters. I present a hypothetical evolutionary tree for the order, consider the taxonomic implications, and discuss selected life-history and biogeographic correlates and the classification of selected fossil species. Many of the characters were described first in the pioneering work of Woolfenden (1961), to whom I dedicate this paper.

METHODS

Taxa and specimens.—Both genera of Anhimidae and all Recent genera of Anatidae were studied. I analyzed separately several subgenera (sometimes considered genera), including *Olor*, *Lophonetta*, *Pteronetta*, *Amazonetta*, *Callonetta*, *Mergellus*, *Lophodytes*, and *Nomonyx*. Several other "subgenera" were found to be identical to the taxa with which they generally are merged and are not labeled separately in the trees:

Casarca (= *Tadorna*), *Metopiana* (= *Netta*), *Oidemia* (= *Melanitta*), and *Charitonetta* (= *Bucephala*). For *Anas*, species from several subgenera were examined: Mallard (*Anas platyrhynchos*), Northern Pintail (*A. acuta*), American Wigeon (*A. americana*), Green-winged Teal (*A. crecca*), and Northern Shoveler (*A. clypeata*). Other species of *Anas* were studied for certain characters. Salvadori's Duck [*Anas (Salvadorina) waigiensis*], provisionally assigned to *Anas* but considered problematic by some (Mayr 1931, Kear 1975), was not included because no skeletal specimens were available (Wood et al. 1982). Except for *Rhodonessa* (monotypic, probably extinct; one complete skeleton) and *Campptorhynchus* (monotypic, extinct; casts of two partial skeletons), all genera analyzed were represented by at least two complete skeletons. For all polytypic genera at least two species were studied, and a number of the common, diverse, or problematic genera were represented by large series.

For *Campptorhynchus*, character states for unavailable elements either were assumed provisionally (for characters invariant within the anatines) or coded as "missing." Assumption of anatine characters for *Campptorhynchus* is conservative (cf. Humphrey and Butsch 1958, Zusi and Bentz 1978) and did not alter its position in the resultant tree (compared with analyses without this assumption), but permitted more efficient computation of trees and a shorter final solution.

Analysis of characters.—For the phylogenetic analysis presented, 120 characters were used (Appendix 1); a majority of the osteological characters were described in Woolfenden (1961) and illustrated in Howard (1929). Some characters were rejected because variation prevented even modal state assignments for some genera or because discrete states could not be distinguished.

Sources for data on the postcranial skeleton were Wetmore (1951), Rand (1954), Verheyen (1955), Woolfenden (1961), Humphrey and Clark (1964), and Raikow (1971). Additional sources were (by anatomical region): integument and molt (DeMay 1940, Siegfried 1970, Palmer 1976), trachea and syrinx (Wetmore 1926; Niethammer 1952; Wolff and Wolff 1952; Humphrey 1955, 1958, unpubl. data; Humphrey and Butsch 1958; Johnsgard 1961b, e; Humphrey and Ripley 1962; Humphrey and Clark 1964; Weller 1968b), and skull (Abbott 1938, Harrison 1958, Raikow 1970a, Olson and Feduccia 1980a). I included only qualitative characters because the polarities and states of mensural characters are especially difficult to determine. Each character is an anatomical trait for which two or more discrete character states were defined.

Derivation of trees.—Polarities of each character (primitive states) were determined by comparison with outgroups—*Burhinus* and *Larus* (Charadriiformes), *Ortalis* and *Meleagris* (Galliformes), *Ciconia*

(Ciconiiformes), and *Phoenicopterus* (Ciconiiformes or Charadriiformes)—each of which has been proposed as closely related to the Anseriformes (Delacour and Mayr 1945; Delacour 1954; Mainardi 1962; Simonetta 1963; Sibley et al. 1969; Sibley and Ahlquist 1972; Brush 1976; Feduccia 1977, 1978; Olson and Feduccia 1980a, b; Olson 1985). Generally, the galliforms were most useful for establishing polarities. Outgroups were used to construct a hypothetical ancestor (a vector of primitive character states) for the Anseriformes, which was used to root the evolutionary tree; the primitive condition of nine characters could not be determined and were coded as missing (Appendix 1). Transformation series were treated as linear unless they appeared to be nonlinear or problematic; the latter were treated as unordered (Appendix 1). The syringeal bulla was given a weight of 2 because it is a locomotion-independent character complex involving enlargement, symmetry, and fenestration; all other characters were assigned unit weight.

The logic and terminology of phylogenetic analysis are discussed in Wiley (1981). The tree was derived using the PAUP program (Swofford 1984), a program that seeks trees of maximum parsimony (i.e. requires the least number of character-state changes; see Kluge 1984) and that permits the examination of series of "equally short" trees. The large size of the data set prohibited an exhaustive search *guaranteed* to find the shortest tree(s), but two thorough methods—alternate and global branch swapping—were employed and produced identical topologies.

A data matrix for all outgroups and the Anseriformes and a list of specimens examined are available from the author on request.

RESULTS

General findings.—Of 50 equally short trees examined that resulted from minor changes in character distributions, only three distinct topologies were found. The tree illustrated (Fig. 1) has the topology of 46 of these trees (consistency index = 0.59). Two trees reversed the order of branching of *Thalassornis* with the geese and swans, and two others altered relationships in the goldeneye-merganser clade (*Bucephala*, *Mergellus*, *Lophodytes*, *Mergus*).

Anhimids and Anseranas.—Monophyly of the Anhimidae and the waterfowl and the early branching of *Anseranas* were confirmed (Fig. 2). The "primitive" status of *Anseranas* has been recognized widely (Miller 1919; Boetticher 1943; Delacour 1954; Johnsgard 1961c, e, 1962, 1978, 1979; Woolfenden 1961; Olson and Feduccia 1980a). Notable exceptions were the placement of *Anseranas* with the superficially similar *Plec-*

tropterus (Peters 1931, Delacour and Mayr 1945) and the proposition that *Anseranas* is an aberrant "true goose" (Davies and Frith 1964, Frith 1967). Both the anhimids and *Anseranas* have undergone substantial autapomorphic change since divergence, much of which is unique in the order.

Geese, swans, and proto-ducks.—I found that the "Anserinae," as currently defined (e.g. Johnsgard 1978), is paraphyletic to the rest of the family (Fig. 2), in contrast to the monophyly depicted by Delacour and Mayr (1945), Boetticher (1952), and Woolfenden (1961). Johnsgard (1961a, e) depicted the group as paraphyletic to the "Anatinae," but later (1978) diagrammed it as monophyletic, as did Bellrose (1976). These variations, however, may reflect different approaches to tree construction as much as changing perceptions of relationships.

The branching sequence (Fig. 2) differs from conventional schemes (Johnsgard 1967, 1978; Kear 1967; Raikow 1971; Brush 1976) in that *Dendrocygna* and *Thalassornis* are not sister genera but instead comprise a grade. In an equally parsimonious topology, *Thalassornis* diverged immediately after the goose-swan branch. Most of the 13 autapomorphies in *Thalassornis* represent adaptations for diving and include several convergences with diving ducks in other clades. Until the works of Johnsgard (1967) and Raikow (1971), *Thalassornis* was considered to be an aberrant stiff-tailed duck and allied with *Oxyura* (e.g. Peters 1931; Delacour and Mayr 1945; Delacour 1959, 1964c), a treatment repeated recently (Howard and Moore 1984, Scott 1985).

Ten character changes confirmed the monophyly of the geese and swans (Fig. 2), as hypothesized by most authorities in recent decades (Delacour and Mayr 1945; Delacour 1954; Johnsgard 1961a, e, 1965a, 1978; Woolfenden 1961; Bottjer 1983). Also, there is a sister-group relationship between *Coscoroba* and the "typical" swans (*Cygnus*, *Olor*; 6 characters) and between *Cereopsis* and the "typical" geese (*Anser*, *Branta*; 2 characters). My analysis demonstrated monophyly of *Olor*, but no apomorphies distinguished *Cygnus* from the common ancestor of *Cygnus* and *Olor* (Fig. 2); hence, the topology of *Cygnus* remains unresolved. The generic monophyly of *Anser* and *Branta* also was not established. Traditionally, *Coscoroba* and *Cereopsis* have been considered to be either "links"

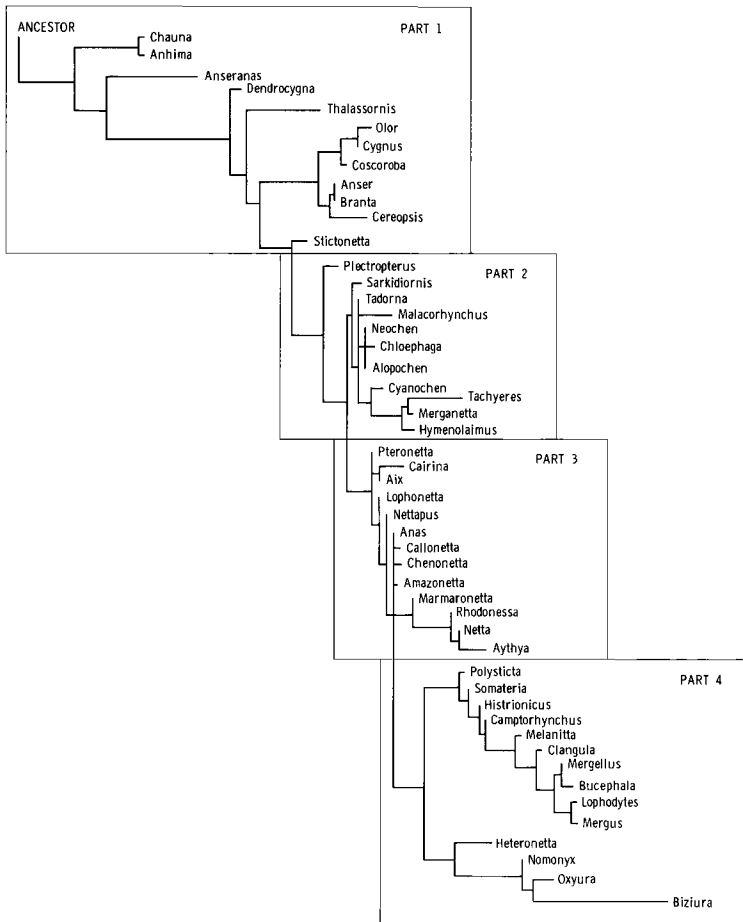


Fig. 1. Phylogenetic tree of Recent anseriform genera and selected subgenera based on 120 morphological characters listed in Appendix 1. Lengths of horizontal lines correspond to the number of character changes (apomorphies) in the lineages. Sections of the tree are detailed in Figs. 2-5.

between tribes, early branches from the common ancestor to the "true" geese and swans, or, for *Cereopsis*, an aberrant shelduck or the sole member of a separate tribe (Peters 1931; Delacour and Mayr 1945; Delacour 1954, 1964c; Johnsgard 1961a, e, 1978; Woolfenden 1961; Frith 1967; Kear and Murton 1973; Bottjer 1983).

My analysis showed *Stictonetta* to be the last branch in the grade of waterfowl with reticulate tarsi (Figs. 1 and 2). *Stictonetta long* was believed to be an aberrant member of the shelducks (near *Tadorna*; Peters 1931, Boetticher 1952) or the dabbling ducks (e.g. *Anas*; Delacour and Mayr 1945; Delacour 1956, 1964c). Based on anatomical comparisons, however, other workers suggested that the genus was de-

rived from an earlier "anserine" branch of the Anatidae (Verheyen 1955; Johnsgard 1960c, 1961a, b, 1962, 1965a, b, 1978; Woolfenden 1961; Frith 1964a, b, 1967; Brush 1976; Olson and Feduccia 1980a).

Plectropterus and the shelducks.—I found that *Plectropterus* is not related closely to the "perching ducks" (e.g. *Sarkidiornis*, *Cairina*, and *Nettapus*) as generally recognized since Delacour and Mayr (1945). Instead, *Plectropterus* is the earliest branch of the waterfowl with scutellate tarsi, and lacks five synapomorphies uniting more-derived members of the family (Fig. 3). Woolfenden (1961) concluded that *Plectropterus* was most similar osteologically to the shelducks, and Tyler (1964) found that egg-

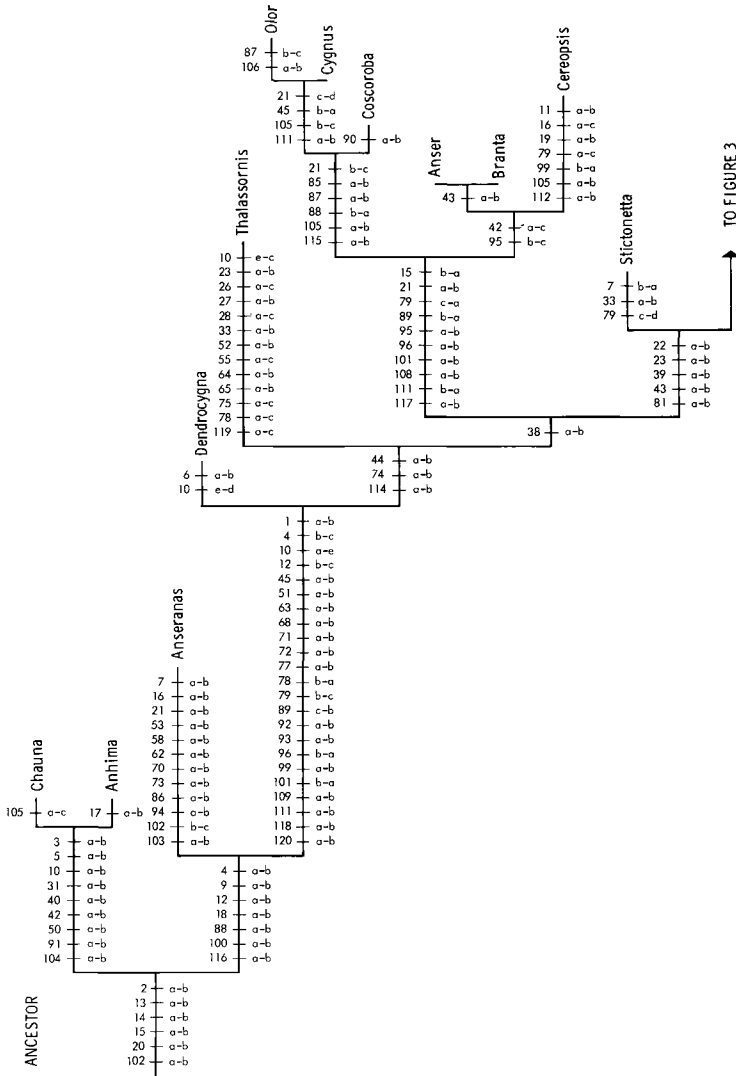


Fig. 2. Detailed diagram of Part 1 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1.

shells of *Plectropterus* were intermediate between those of anserines and shelducks in structure. Bottjer (1983) found that *Plectropterus* differed greatly from other "perching ducks" serologically but attributed the result to experimental error.

My analysis supports the monophyly of the shelducks, although only by a single, possibly convergent character; further study may show the shelducks to be a grade of relatively primitive ducks. The clade includes a polytomy in-

volving *Tadorna*, *Malacorhynchus*, and two clades containing three genera each (Fig. 3). I found *Malacorhynchus* to be a highly derived shelduck; this genus has been assigned most frequently to the dabbling ducks (e.g. Delacour 1956, Woolfenden 1961, Frith 1967, Johnsgard 1978), although Frith (1955) noted that the pattern of its downy young differed greatly from those of *Anas* and Brush (1976) found that *Malacorhynchus* was distinctly different from *Anas* in its feather proteins. A single synapomorphy

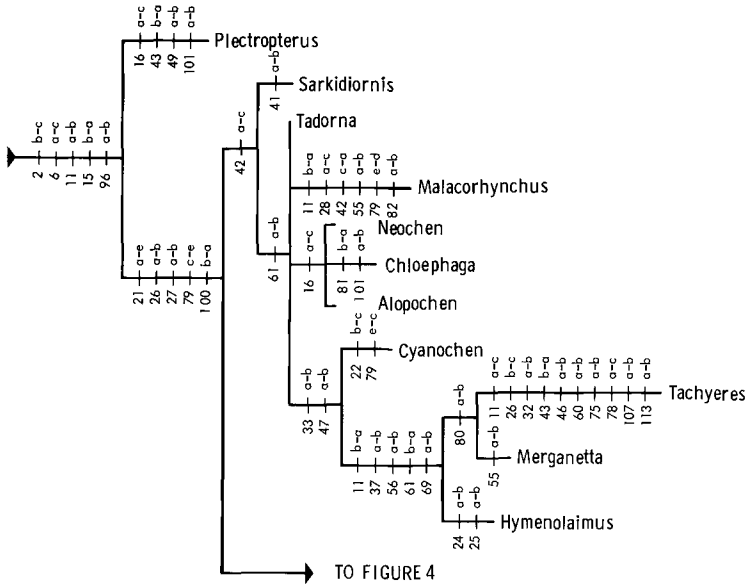


Fig. 3. Detailed diagram of Part 2 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Graphical proximity of branches within the polytomy in the shelducks does *not* reflect relatedness.

of the skull supports the monophyly of the three genera of "sheldgeese"—*Alopochen*, *Chloephaga*, and *Neochen* (Fig. 3).

The Comb Duck (*Sarkidiornis melanotos*), traditionally placed in the "Cairinini" (Delacour and Mayr 1945, Johnsgard 1978), appears to be an early branch of the shelducks. However, three humeral characters that were important in distinguishing the "anserines" and shelducks from the "anatines" [capital shaft ridge (character 22), deltoid crest (25), and external tuberosity (32)] were of equivocal or "intermediate" condition in this species. In addition, the enlarged, uniquely distally directed metacarpal I of *Sarkidiornis*, a character complex herein considered to incorporate two aspects [orientation (41) and length (42)], proved difficult to characterize. Perhaps *Sarkidiornis* branched immediately before *Cairina* or, alternatively, after *Plectropterus* but before the divergence of the shelducks from other "anatines."

Three problematic genera—*Hymenolaimus*, *Merganetta*, and *Tachyeres*—comprise a highly derived clade of shelducks (Figs. 1 and 3). Several of the characters uniting these genera are evidently related to diving and are shared by

diving ducks in other clades (see Discussion). *Hymenolaimus* and *Merganetta* have been treated as allied either with the shelducks, "perching ducks," or as exceptional, possibly primitive dabbling ducks (Delacour and Mayr 1945, 1946; Delacour 1956; Ripley 1957; Johnsgard 1965a, 1966a). Some workers placed *Merganetta* in its own tribe, *Merganettini* (Woolfenden 1961; Kear and Steel 1971; Kear 1972, 1975; Brush 1976; Johnsgard 1978). My analysis does not support the suggestion (Olson and Feduccia 1980a: 22) that "... the typical members of the 'subfamily' Anserinae and the typical members of the 'subfamily' Anatinae are more closely related to one another than to *Stictonetta*, *Malacorhynchus*, or *Merganetta*."

The third and most derived member of this clade is *Tachyeres* (Fig. 3), a neotropical genus generally placed in the shelducks or in a separate tribe allied with the shelducks (Delacour 1954; Moynihan 1958; Johnsgard 1965a, 1978; Weller 1976; but see Ripley 1957, Woolfenden 1961). Like all shelducks, *Merganetta* and *Tachyeres* show an enlargement of metacarpal I (adorned with keratin spurs in *Merganetta*) that is sexually dimorphic and age related (Weller 1968a, Livezey unpubl. data). *Cyanochen* is hy-

pothesized to be the sister genus to the *Hymenolaimus-Merganetta-Tachyeres* clade, although this relationship is supported by only two synapomorphies. Bottjer (1983) suggested that *Cyanochen* may have branched before the other shelducks.

“Perching” ducks and “dabbling” ducks.—The sister group to the shelducks comprises four groups (Fig. 1): a poorly resolved grade of “perching” and “dabbling” genera (*Pteronetta*, *Cairina*, *Aix*, *Lophonetta*, *Nettapus*, *Anas*, *Callonetta*, *Chenonetta*, and *Amazonetta*), which in turn gave rise to the pochards and independently to the sea ducks and stiff-tailed ducks. The first group (Fig. 4), henceforth termed “dabbling ducks,” is a paraphyletic group of genera previously allocated to either the “Anatini” or the “Cairinini” (Delacour and Mayr 1945; Delacour 1956; Johnsgard 1960c, d, 1961a, e, 1962, 1965a, 1978).

The polyphyletic character of the “Cairinini” was inferred by Woolfenden (1961). The tribe has been recognized by subsequent workers in spite of the equivocal allocation of several genera (e.g. *Callonetta* and *Amazonetta*; Johnsgard 1960a, 1965a, 1978), the widely recognized heterogeneity of its members in behavior, morphology, and biochemistry (Johnsgard 1960c, 1961a, 1962, 1965a, 1978; Woolfenden 1961; Tyler 1964; Brush 1976; Bottjer 1983), the lower incidence of interspecific hybridization within the tribe than between its members and those of other tribes (Johnsgard 1960d), and the conspicuous lack of a single character (or combination of characters) that uniquely distinguishes its members from other anatines. Johnsgard (1965a, 1978) admitted that retention of the tribe was partly a taxonomic convenience to avoid creation of “a comparatively large tribe” (1978: xxi) and omitted it as a suprageneric taxon in his latest list (Johnsgard 1979).

The genera of dabbling ducks (on the basis of three variable multistate characters) form a grade from relatively primitive (e.g. *Cairina*, *Lophonetta*) to more-derived forms (e.g. *Anas*, *Callonetta*). A single osteological synapomorphy supports a close relationship between *Cairina* and *Aix* (Fig. 4), a relationship suggested previously by karyotypic and serological comparisons (Yamashina 1952, Cotter 1957, Bottjer 1983).

Pochards.—The pochards are a monophyletic group in an unresolved polytomy that involves

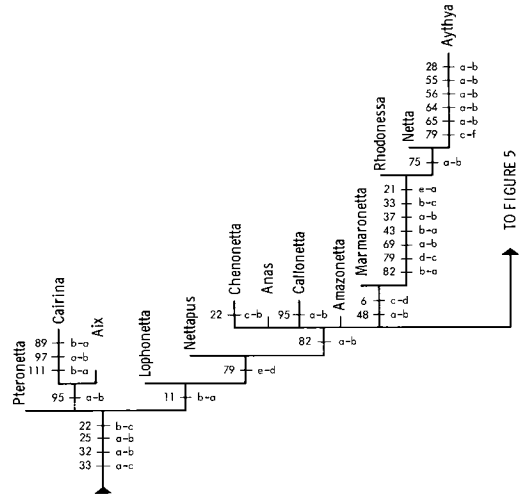


Fig. 4. Detailed diagram of Part 3 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Graphical proximity of branches within the polytomy in the dabbling ducks does not reflect relatedness.

Anas, *Callonetta*, *Chenonetta*, *Amazonetta*, and the sea ducks and stiff-tailed ducks (Fig. 4), suggesting that the pochards arose independently of other diving ducks. I found that *Rhodonessa* is the sister group to *Netta* and *Aythya*, which agrees with most studies (Verheyen 1955; Johnsgard 1961a, e, 1962, 1978, 1979; Woolfenden 1961; Humphrey and Ripley 1962; Brush 1976) since Delacour and Mayr (1945, 1946) and Delacour (1956) provisionally placed *Rhodonessa* in the dabbling ducks. *Marmaronetta*, a genus believed to “link” the Anatini with the pochards but retained within the Anatini (Johnsgard 1961a, b, e, 1978; Delacour 1964c; Brush 1976), is supported in my study as the sister genus to the pochards by two osteological synapomorphies (Fig. 4). This relationship is corroborated by the secondary loss of metallic coloration in the speculum (Delacour and Mayr 1946).

Sea ducks.—The sea ducks comprise a monophyletic group related to the stiff-tailed ducks, although this relationship is supported by only a few, possibly convergent characters related to diving (Fig. 5). My result contradicts the previously proposed close relationship between sea ducks and “perching ducks” (Delacour and Mayr 1945, Delacour 1959, Bottjer 1983). With

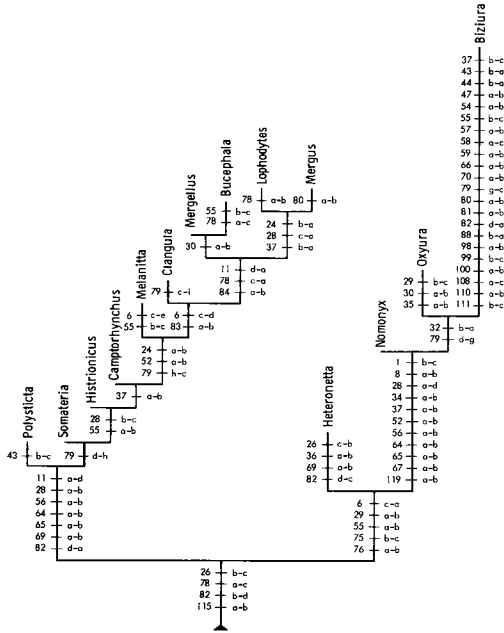


Fig. 5. Detailed diagram of Part 4 of the phylogenetic tree of the Anseriformes shown in Fig. 1. Characters are listed in Appendix 1. Placement of *Camptorhynchus* is tentative.

the possible exception of a few workers who advocated (largely on the retention of primitive *Anas*-like characters) the tribal separation of the eiders (*Somateria* and *Polysticta*) from the other sea ducks (Humphrey 1955, 1958; Delacour 1959; Brush 1976; Todd 1979), the monophyly of the sea ducks has not been questioned recently (e.g. Johnsgard 1960b, 1961a, e, 1964, 1978; Woolfenden 1961; Bottjer 1983).

The proposed sequences of genera within the group has varied (e.g. Delacour and Mayr 1945; Delacour 1959; Johnsgard 1960b, 1961a, 1965a, 1978, 1979). My analysis (Fig. 5) indicates that *Polysticta*, *Somateria*, *Histriornis*, and *Camptorhynchus* comprise a less specialized, basal grade of genera retaining primitive, unfenestrated syringeal bullae. This series of genera gives rise to a well-supported clade of, in order of increasing relatedness, *Melanitta*, *Clangula*, and the goldeneye-merganser clade. The eiders (*Polysticta*, *Somateria*) appear to be paraphyletic to the other sea ducks; this paraphyly is supported only weakly, and downy patterns suggest that the eiders may be monophyletic (see Discussion). Placement of *Camptorhynchus* must re-

main tentative because of the limited material available. Humphrey and Butsch (1958) placed *Camptorhynchus* after *Melanitta* but before *Clangula*, and Zusi and Bentz (1978) allied the genus with eiders, evidently on the basis of shared primitive characters. The very close relationship of goldeneyes and mergansers has had unanimous support in recent decades (e.g. Delacour and Mayr 1945; Boetticher 1952; Humphrey 1955; Delacour 1959; Myres 1959; Johnsgard 1960b, d, 1961a, 1978; Brush 1976).

This analysis shows the Smew (*Mergellus albellus*) to be either the sister genus to *Bucephala* (Fig. 5) or the sister group to the *Lophodytes-Mergus* clade. The former topology is corroborated by the relatively high frequency of *Mergellus* × *Bucephala* hybrids in the wild (Phillips 1925, Ball 1934, Gray 1958, Nilsson 1974, Johnsgard 1978). Previous workers either listed the Smew between the goldeneyes (*Bucephala*) and the mergansers (*Mergus*, *Lophodytes*) as a monotypic genus (Peters 1931, Woolfenden 1961, A.O.U. 1983), or merged it (with *Lophodytes*) into *Mergus* (Delacour and Mayr 1945; Boetticher 1952; Humphrey 1955; Delacour 1959, 1964c; Johnsgard 1960c, 1961a, d, 1965a, 1978, 1979).

Stiff-tailed ducks.—My study supports the monophyly of the stiff-tailed ducks, wherein *Heteronetta* is the sister genus to the more typical members (Fig. 5). The position of the clade as closely related to the sea ducks and highly derived (especially *Biziura*) agrees with recent orderings of genera by taxonomists (e.g. Johnsgard 1979) but disagrees with suggestions of a pre-dabbling duck (Raikow 1970b, Johnsgard 1978) or pre-shelduck (Johnsgard 1965b, Bottjer 1983) origin for the group. A few workers have expressed doubts about the relationships of *Heteronetta* (Johnsgard 1960c, Brush 1976), and others accepted the relationship between *Heteronetta* and other stiff-tailed ducks but suggested that the genus be accorded tribal rank (Weller 1967, 1968b; Rees and Hillgarth 1984).

My analysis shows that the Masked Duck [*Nomonyx (Oxyura) dominica*] is the sister group to the highly derived *Oxyura-Biziura* clade (Fig. 5), i.e. *Oxyura* is related more closely to *Biziura* than to the very similar *Nomonyx*. This topology is supported as well by the derived loss of a speculum in *Oxyura* and *Biziura*, which is retained in *Nomonyx* (Delacour 1959). This finding supports the resurrection of *Nomonyx* as advocated by Woolfenden (1961), a recom-

mendation rejected by Delacour (1964c), Johnsgard (1967), and most subsequent workers. I did not examine skeletons of all species of *Oxyura*, so monophyly of the genus was not established with certainty.

DISCUSSION

Diving habit and homoplasy.—Considerable homoplasy (convergence) of characters is shown in the tree (Figs. 1–5) and by the consistencies of characters (Appendix 1). The majority of the convergences are associated with adaptations for diving, and most involve the leg elements (characters 52, 55, 56, 64, 65, 69, 75), pelvis (119), and skeletal pneumaticity (28, 78). These features tend to co-occur, especially within elements. Convergence between *Thalassornis* and the stiff-tailed ducks is particularly pervasive (Figs. 2 and 5). It appears, however, that the moderately large number of characters included in this analysis reduced the impact of such homoplasy on the resultant tree, although deletions or heavy weighting of selected characters can produce topological changes. For example, because of a number of diving-related homoplasies, postulation of the *Hymenolaimus-Merganetta-Tachyeres* clade as the sister group to the sea ducks and stiff-tailed ducks is only slightly less parsimonious than the topology presented (Fig. 1). Similarly, heavier weighting of appendicular characters places *Heteronetta* as the sister group to both the sea ducks and other stiff-tailed ducks.

Patterns of downy young.—Although an analysis of downy patterns for the entire order is not possible at present, a cladistic reevaluation of the downy young illustrated in Delacour (1954, 1956, 1959) permits an independent test of two parts of my phylogenetic hypothesis (using *Anas* as the outgroup). Patterns in downy stiff-tailed ducks agree well, wherein (1) *Heteronetta* retains virtually all dabbling-duck characters; (2) *Nomonyx*, *Oxyura*, and *Biziura* share a synapomorphic, dark cheek stripe; (3) *Oxyura* and *Biziura* are united by the derived loss of the pale supraorbital stripe; and (4) *Biziura* shares a loss of dorsal and wing spotting with the Peruvian Ruddy Duck (*O. ferruginea*) and dark cheeks with the Australian Blue-billed Duck (*O. australis*). Patterns of downy Mergini also are informative: (1) eiders retain the supraorbital stripe of dabblers but, in contrast to

osteological evidence, appear monophyletic in their dusky undersides, obsolete dorsal spots, and dark cheeks; (2) other Mergini lack the supraorbital stripe and dorsal spotting of the dabbling ducks (loral spot and vestigial back spots retained in *Histrionicus*); (3) *Melanitta* and its sister genera are synapomorphic in their dark breast bands, a character secondarily lost in *Mergus*; (4) the Black Scoter (*Melanitta nigra*) and Surf Scoter (*M. perspicillata*) are united by the derived darkening of the lower breast and belly; (5) *Bucephala*, *Mergellus*, *Lophodytes*, and *Mergus* share a reversal in (presence of) dorsal spotting; (6) obscured (*Lophodytes*) to dark (*Mergus*) cheeks unite the mergansers; and (7) *Mergus* is derived further in the anteriorly incomplete breast band and pale suborbital stripe.

Similarity vs. relatedness.—Recognition of the different types of character change is important in light of the conspicuously unequal rates of morphological evolution in different lineages, e.g. autapomorphies of *Branta* vs. *Cereopsis* (Fig. 2) and *Oxyura* vs. *Biziura* (Fig. 5). The inadequacy of simple distance techniques was demonstrated using these data through a comparison of phylogenetic relationships with "path lengths" or patristic distances. Selected results were: (1) *Anseranas* is roughly equidistant from the anhimids and other anatids [corroborated immunologically by Bottjer (1983)], but is the sister group to the latter (Fig. 2); (2) *Thalassornis* is most similar to *Dendrocygna* but is more closely related to other anatids, excluding *Anseranas* (Fig. 2); (3) *Heteronetta* appears "nearer" to *Anas* than to *Oxyura*, a member of the sister group of *Heteronetta* (Figs. 4 and 5); and (4) because of autapomorphies in *Oxyura*, *Biziura* is phenetically "closer" to *Nomonyx* than it is to its sister genus *Oxyura* (Fig. 5).

Life-history correlates.—Diving, at least as an escape behavior, occurs throughout the order except in the anhimids and possibly *Anseranas* (Johnsgard 1962, Todd 1979). Groups that routinely dive for food are fewer, but occur in six lineages throughout the family (Weller 1964b): *Dendrocygna*, *Thalassornis*, *Hymenolaimus-Merganetta-Tachyeres*, pochards, sea ducks, and stiff-tailed ducks.

Perching habit, the probably primitive character used traditionally to define the polyphyletic "perching ducks," occurs in many genera, including *Anseranas*, *Dendrocygna*, *Plectropterus*, *Sarkidiornis*, *Tadorna*, *Malacorhynchus*, *Cairina*, *Aix*,

Chenonetta, *Rhodonessa*, and *Amazonetta* (Ali 1960, Johnsgard 1978, Todd 1979). A related trait (also used to justify the "Cairinini"), nesting in tree cavities, occurs in *Dendrocygna*, some shelducks (*Sarkidiornis*, *Neoche*, *Alopochen*, *Tadorna*, *Malacorhynchus*), a number of dabbling ducks (e.g. *Aix*, some *Anas*), and some sea ducks (*Histrionicus*, *Bucephala*, *Mergellus*, *Lophodytes*, *Mergus*).

Use of terrestrial cavities for nesting also occurs in some shelducks (*Tadorna*, *Hymenolaimus*, *Merganetta*, *Tachyeres*), in some *Anas*, and in the sea ducks cited above (Hobbs 1957, Warham 1959, Johnsgard 1962, Johnson 1963, Weller 1964c, Kear 1970, Moffett 1970, Humphrey and Livezey 1985). Other species nest on the ground or over water (Weller 1964c, Kear 1970). Only the Black-headed Duck (*Heteronetta atricapilla*) is an obligate nest parasite, although infrequent nest parasitism occurs in a number of other genera including *Dendrocygna*, *Branta*, *Anas*, *Aythya*, and *Mergus* (Weller 1959, 1968b). Although ground nesting appears to be primitive for the order (Johnsgard 1965a, Kear 1970), nesting habit is probably unreliable for intraordinal phylogenetic inferences. Clutch size, proportion of yolk in eggs, incubation period, parental carrying of young, and sexual dimorphism also appear to be quite plastic (Johnsgard 1961f, 1966b; Lack 1967, 1968, 1974; Johnsgard and Kear 1968; Kear 1970; Livezey and Humphrey 1984).

Selected reproductive characteristics, however, show distinct primitive-to-derived sequences (Kear 1970). Most change near the divergence of the goose-swan clade but may be confounded by an evolutionary trend toward reduced body size: (1) nest bowl unlined vs. lined with down (secondarily lost in stiff-tailed ducks); (2) biparental nest construction, incubation, and attendance of young vs. female alone responsible; and (3) brooding period and pair bond long ("anserines," roughly 6 months) vs. moderately long (shelducks, roughly 4 months) vs. comparatively short (dabblers and divers, less than 2 months). Participation of males in brood rearing is variable within *Anas*, however, wherein several neotropical species are characterized by protracted, perhaps permanent pair bonds (Johnsgard 1978).

Biogeographic patterns.—Despite the early acknowledgment of the diversity of "aberrant and primitive" genera in Australia (Delacour and

Mayr 1945: 51), most previous biogeographers contended that the Anseriformes originated in the Northern Hemisphere, probably the Palearctic (Howard 1950, Weller 1964d). Although the fossil record of waterfowl is more complete for the Northern Hemisphere (Howard 1964), early forms are known from both hemispheres, and the apparent disparity in representation probably reflects intensity of paleontological research. The only essentially northern groups are *Olor*, *Anser-Branta*, *Cyanochen*, *Rhodonessa*, and the sea ducks; genera that have roughly equal distributions in both hemispheres are *Cygnus*, *Tadorna*, *Alopochen*, *Anas*, *Netta*, *Aythya*, and *Oxyura*. The remaining 20 genera are limited to or most speciose in the Southern Hemisphere, and, with the anhimids, include most of the early branches in the order. Furthermore, the earliest branches (Fig. 2) in the swan and goose clades are genera limited to the Southern Hemisphere. The numerous holarctic species of *Anas*, *Aythya*, and the sea ducks (Weller 1964d) may represent radiations hastened by widespread glaciations (cf. Ploeger 1968). Consequently, I agree with Cracraft (1980) that the Anseriformes probably originated in the Southern Hemisphere.

Taxonomic implications.—The tribes of Anatidae originally proposed by Delacour and Mayr (1945) were defined primarily in terms of genera of the Northern Hemisphere. Although most tribes were assigned members from both hemispheres, only the monotypic "Merganetini" was limited to the Southern Hemisphere. A number of "aberrant" southern genera were sorted tentatively among these tribes: *Anseranas* and *Plectropterus* to the Cairinini; *Cereopsis*, *Tachyeres*, and *Lophonetta* to the Tadornini; *Stictonetta*, *Malacorhynchus*, and *Hymenolaimus* to the Anatini; and *Thalassornis* to the Oxyurini. Since then four of these genera have been placed in their own subfamilies or tribes, one has been moved to another subfamily, and the others have remained problematic (Wolfenden 1961, Johnsgard 1978). Several findings in my study involve these genera, and suggest a revision of the classification of waterfowl (Appendix 2).

The dabbling ducks are paraphyletic and should be considered a phylogenetically unresolved group. I therefore place these genera in a provisional taxon, the "Anatini" (Appendix 2). If paraphyly of this group is corroborated by further work, the erection of addition-

al tribes corresponding to the branches in the grade would be warranted.

Classification of fossil groups.—Several early fossils can be classified tentatively on the basis of published descriptions (Howard 1964). *Romainvillia* (upper Eocene or lower Oligocene), *Cygnopterus* (upper Oligocene), and *Paranyroca* (lower Miocene) possess the primitive procoracoidal foramen (character 92) retained among Recent genera only by anhimids and *Anseranas*. Conformation of the tarsometatarsal trochlea (68) indicates that at least *Romainvillia* and *Paranyroca* are derived with respect to *Anseranas*, and the hypotarsus (72) of *Paranyroca* shows it to be more primitive than *Dendrocygna*. Accordingly, these fossils should be listed after *Anseranas* and before *Dendrocygna* and sequenced (provisionally by epoch of occurrence) as *Romainvillia*, *Cygnopterus*, and *Paranyroca*; the fossils may be given familial names or be designated "plesions" (Wiley 1981) at familial rank. Phylogenetic reappraisals of several other fossil Anseriformes [e.g. *Anas(?) blanchardi*, the tadornines *Anabernicula* and *Brantadorna*, and *Chendytes*; Howard 1964], and the probable anseriform *Presbyornis* (Olson and Feduccia 1980a), should provide minimum ages of branch points in the phylogeny.

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APPENDIX 1

The 120 characters used in this analysis are listed below and are numbered and grouped anatomically. Character states are lettered and correspond to the character changes in Figs. 2-5. Plesiomorphic (primitive) conditions generally are designated "a" and derived character states are ordered alphabetically thereafter (implying a linear transformation series); characters followed by a "U" were analyzed as unordered. Characters for which the primitive state was not determined are marked with "U*." Characters judged to be unusually variable, generally necessitating determinations of modal conditions, are indicated with a "V." Taxa with problematic state determinations are listed in parentheses after the corresponding character. Consistency indices (CI) follow each character. Anatomical terminology follows Howard (1929) and Woolfenden (1961) unless annotated otherwise.

Integument

1. Molt of remiges: (a) sequential; (b) synchronous, once annually; (c) synchronous, twice annually. (Variable in Phoenicopteridae; Sileo et al. 1977.) CI = 1.0.
2. Tarsal sheath: (a) scutellate anteriorly and posteriorly; (b) reticulate anteriorly and posteriorly; (c) scutellate anteriorly (at least distally) and reticulate posteriorly. CI = 1.0.
3. Spongy subcutaneous layer: (a) absent; (b) present. CI = 1.0.
4. Interdigital webbing of feet (excluding hallux): (a) lacking (slight webbing in anhimids); (b) incomplete (semipalmate); (c) complete (incised in *Cereopsis* and *Branta sandwicensis*). CI = 1.0.
5. Apterium: (a) present; (b) obsolete. CI = 1.0.

Trachea

6. Bulla ossea of males (U, weight = 2): (a) not enlarged; (b) symmetrically enlarged; (c) asymmetrically enlarged, unfenestrated;

(d) asymmetrically enlarged, fenestrated; (e) enlargement reduced and symmetrical, or obsolete. (*Thalassornis*, *Malacorhynchus*, *Nettapus*.) CI = 0.67.

7. Extrasternal, subdermal looping of trachea in males (U*): (a) present; (b) absent. CI = 0.33.
8. Inflatable tracheal air sacs: (a) absent; (b) present. CI = 1.0

Skull

9. Occipital fontanelles: (a) absent; (b) present. CI = 1.0.
10. Lacrymals (U): (a) not fused to skull; (b) fused to skull dorsally, small, nonpneumatic; (c) fused dorsally, moderately thick, long, ventrally directed (lacking flange), nonpneumatic; (d) fused to skull dorsally, and (typically) also fused to postorbital process, slightly pneumatic; (e) fused dorsally, of variable shape and pneumaticity, posteroventrally directed, often with flanged ventral terminus. CI = 1.0.
11. Supraorbital process (U; best developed in adult males): (a) absent or small, straight, essentially coplanar with dorsal surface of skull; (b) large, flat, medially appressed to dorsal margin of orbit; (c) large, thick, rugose, dorsolaterally directed; (d) long, slender, dorsally directed, often curved. (*Aythya*, *Bucephala albeola*.) CI = 0.38.
12. Anterior terminus of premaxillae: (a) strongly ventrally hooked, typically pointed; (b) strongly ventrally hooked, moderately rounded; (c) not ventrally hooked (directed anteriorly), rounded, spatulate. CI = 1.0.
13. Bill lamellae: (a) absent; (b) present. (Nonhomologous lamellae in flamingos, vestigial in anhingids; Olson and Feduccia 1980a.) CI = 1.0.
14. Retroarticular processes of mandible: (a) lacking, small, or recurved and rounded; (b) recurved, pointed, and bladeliike. CI = 1.0.
15. Quadrate, lateral view: (a) not squarish, with variably deeply curved dorsal margin between orbital and otic processes; (b) squarish, with dorsal margin straight. CI = 0.33.
16. Frontonasal region of skull (U): (a) essentially continuous with profile defined by premaxillae and frontals; (b) enlarged into conspicuous, laterally compressed, dorsal prominence (larger in males); (c) with rounded, pneumatic swelling (especially in adult males). CI = 0.50.
17. Frontals: (a) without dorsally directed hornlike prominence; (b) with small, ossified "horn" on midline. CI = 1.0.
18. Pterygoid-palatine articulation: (a) a simple abutment; (b) a ball-and-socket arrangement involving two extensions of the pterygoid. CI = 1.0.
19. Dorsum of upper bill in region of external nares: (a) essentially continuous with curvature of skull to somewhat convex; (b) substantially dorsally bowed. CI = 1.0.
20. Basipterygoid processes: (a) lacking or (in Galliformes) present but without basal supports; (b) present, lipped, almost pedicellate. CI = 1.0.

Vertebrae

21. Number of cervical vertebrae (U, V): (a) 17; (b) 18-20; (c) 21; (d) 22-25; (e) 16. (Some Tadorninae.) CI = 0.67.

Humerus

22. Capital shaft ridge: (a) prominent and directed toward head; (b) prominent and directed toward external tuberosity; (c) obsolete proximally or absent completely. (*Sarkidiornis*, *Cyanochen*, *Hymenolaimus*, *Chenonetta*.) CI = 0.50.
23. Capital groove: (a) short, essentially directed distally; (b) extending laterally toward external tuberosity, undercutting head. (*Thalassornis*.) CI = 0.50.
24. Proximo-anconal region: (a) variably rounded by shaft; (b) traversed by a deep, uninterrupted trenchlike depression from under head to internal edge immediately distal to bicipital crest. CI = 0.33.
25. Deltoid crest (V): (a) margin rounded, laterally flaring, concave anconally; (b) margin angular or squared, depressed around shaft toward palmar side, convex anconally. (*Sarkidiornis*, *Hymenolaimus*.) CI = 0.50.
26. Surface of attachment for anterior articular ligament: (a) not ele-

vated, essentially parallels shaft; (b) elevated, angled distally; (c) elevated, angled medially. CI = 0.40.

27. Internal tuberosity: (a) proximally rotated, exposing completely the pneumatic foramen in anconal view, lacking a distinct, distally directed prominence; (b) produced distally so as to largely or completely obscure pneumatic foramen in anconal view, typically with prominent, distally directed point. CI = 0.50.
28. Pneumatic fossa (U): (a) open, usually containing numerous bony struts; (b) closed by bony shell except for a small central opening; (c) completely closed; (d) closed but perforated by numerous small holes. (*Lophodytes*.) CI = 0.43.
29. Attachment site of *M. latissimus dorsi posterioris*: (a) well medial to external edge of pectoral attachment; (b) in line with outer edge of pectoral attachment, on anconal surface of shaft; (c) in line with outer edge of pectoral attachment, on raised ridge. CI = 1.0.
30. Distal portion of anconal surface of bicipital crest: (a) poorly developed or shelllike; (b) produced medially with distinct proximal cuplike depression, visible as translucent window in palmar view. CI = 0.50.
31. Distal terminus of deltoid crest: (a) essentially continuous with lateral edge of shaft; (b) produced into prominent tuberosity on palmar surface of shaft. CI = 1.0.
32. External tuberosity: (a) prominent, buttressed, typically with attachment site elevated, parallel to shaft, not sloping away with anconal surface of deltoid crest; (b) reduced, lacking buttress, with attachment site sloping and essentially flush with anconal surface of deltoid crest. (*Stictonetta*, *Sarkidiornis*, *Cyanochen*, *Merganetta*, *Oxyura*.) CI = 0.33.
33. Relative anconal heights of ectepicondyle and entepicondyle: (a) ectepicondyle distinctly higher than entepicondyle; (b) condyles essentially equally high; (c) ectepicondyle lower than entepicondyle. (*Hymenolaimus*.) CI = 0.40.
34. Pit for attachment of *M. flexor carpi ulnaris*: (a) prominent; (b) reduced to obsolete. CI = 1.0.
35. External condyle and brachial depression (palmar side, distal end): (a) separated by smooth strip of bone; (b) connected by rounded ridge. CI = 1.0.
36. Attachment site for external head of triceps: (a) immediately distal to head, typically in excavation under head; (b) displaced distally on lobe of bone and obscures external terminus of capital groove. CI = 1.0.

Carpometacarpus

37. Distal end of internal rim of carpal trochlea (external view): (a) with prominent swelling; (b) without prominent swelling; (c) deeply excavated. (*Marmaronetta*, *Hymenolaimus*, *Clangula*, *Mergellus*, *Heteronetta*.) CI = 0.33.
38. External rim of carpal trochlea: (a) essentially continuous, unnotched; (b) with prominent notch distally. CI = 1.0.
39. Dorsal surface of metacarpal II: (a) flattened proximally (can appear angular); (b) rounded proximally. CI = 1.0.
40. Tuberosity of metacarpal II: (a) small; (b) prominent, spurred. CI = 1.0.
41. Angle of process of metacarpal I: (a) perpendicular to or proximally directed relative to shaft; (b) angled distally. (*Plectropterus*.) CI = 1.0.
42. Process of metacarpal I (U): (a) not enlarged, length less than width of trochlea; (b) an enlarged, pointed spur, longer than width of trochlea; (c) enlarged, blunt, typically with rugose-capped spur, longer than width of trochlea. (*Plectropterus*, *Hymenolaimus*, *Lophonetta*.) CI = 0.50.
43. Attachment site of *M. extensor metacarpi ulnaris* (Zusi and Bentz 1978; "flexor" of Woolfenden 1961) (U, V): (a) completely proximal to proximal fornx of metacarpal II and III: (b) opposite, at least partly, fornx; (c) completely distal to fornx. (*Tachyeres*.) CI = 0.29.
44. Lower proximal surface of metacarpal III: (a) ungrooved, rounded; (b) distinctly grooved. CI = 0.50.
45. Facets for digits II and III (U*): (a) facet for digit III extending farther distally than facet for digit II; (b) facets essentially equal in distal extent. CI = 0.33.
46. Cuneiform fossa: (a) shallow to moderately deep; (b) deep, rounded, ovate, with distinct rim. CI = 1.0.

APPENDIX 1. Continued.

47. Distal portion of internal rim of carpal trochlea: (a) of uniform thickness with proximal portion; (b) distinctly thickened. CI = 0.50.
48. Internal rim of carpal trochlea (posterior view): (a) in line with internal margin of shaft; (b) sharply deflected laterally. (*Callonetta*.) CI = 1.0.

Radial carpal

49. Size and shape: (a) small, short, and blunt; (b) elongated into large pointed spur. CI = 1.0.

Appendicular pneumaticity

50. Distal alar and pelvic elements: (a) essentially nonpneumatic; (b) pneumatic with one or more large foramina. CI = 1.0.

Femur

51. Head, relative to plane of external surface of shaft: (a) oriented posteriorly; (b) perpendicular. CI = 1.0.
52. Anterior extent of trochanter: (a) relatively great, such that anterior-posterior depth of trochanter substantially exceeds depth of head; (b) reduced, such that depth of trochanter only equals that of head. CI = 0.33.
53. Distal extent of internal condyle: (a) distinctly less than that of external condyle; (b) equal to that of external condyle. CI = 1.0.
54. Rotular depression: (a) shallow to moderately deep, margin relatively indistinct; (b) deep, distinctly bordered proximally. CI = 1.0.
55. Curvature of shaft, lateral view (U): (a) straight to slight; (b) moderate; (c) strong, subangular. CI = 0.22.
56. Popliteal fossa: (a) shallow; (b) deep, typically pitted. CI = 0.25.
57. Lobe at midpoint of posterior surface of shaft: (a) not prominent; (b) prominent. CI = 1.0.
58. Posterior intermuscular line (U): (a) relatively distinct, following internal edge of shaft; (b) relatively distinct, swings laterally toward trochanter; (c) indistinct. CI = 1.0.
59. Internal edge of distal end of shaft: (a) smoothly curving and continuous with proximal portion; (b) leveled by raised ridge to internal condyle. CI = 1.0.
60. Posterior intermuscular line: (a) distinguishable only as fine etching; (b) forming overhanging ridge proximally. CI = 1.0.

Tibiotarsus

61. Proximal articulating surface: (a) in line with shaft, squares with distal condyles; (b) strongly rotated counterclockwise about shaft (proximal view). CI = 0.50.
62. Rim of internal condyle: (a) distinctly notched; (b) lacking notch. CI = 1.0.
63. Inner cnemial crest: (a) not deflected laterally; (b) laterally deflected. CI = 1.0.
64. Anterior extent of condyles: (a) internal distinctly greater than external; (b) approximately equal. (*Aythya*.) CI = 0.25.
65. Inner cnemial crest: (a) lacking distinct ridge extending distally along anterior surface of shaft; (b) continued by distinct ridge distally along anterior surface of shaft to point well beyond proximal terminus of fibular crest. CI = 0.25.
66. Internal condyle, posterior view: (a) with relatively rounded internal edge; (b) flared, with squared medial edge. CI = 1.0.
67. External ligamental prominence: (a) essentially continuous with curvature of shaft; (b) produced laterally, ridgelike. CI = 1.0.

Tarsometatarsus

68. Trochlea for digit II: (a) approximately equal to trochlea for digit IV in distal extent; (b) proximal to trochlea for digit IV. CI = 1.0.
69. Anterior (of two) ligamental passages between trochlea for digits III and IV (in distal wall of distal foramen) (V): (a) obscured from view anteriorly by bone; (b) largely or completely exposed anteriorly because of reduction of bony covering. CI = 0.25.
70. Internal calcaneal ridge of hypotarsus: (a) slightly to moderately exceeds other calcaneal ridges in posterior extent; (b) greatly exceeds other (more external) calcaneal ridges. CI = 0.50.
71. Facet for metatarsal I: (a) deep; (b) obsolete. CI = 1.0.

72. Calcaneal ridges of hypotarsus: (a) 2, lateral to midline of shaft, bordered medially by depression (deep in *Anseranas*); (b) 3 or 4, situated on midline of shaft, without depression on internal margin. CI = 1.0.
73. Wing on trochlea for digit II: (a) not prominent medially; (b) medially prominent, thickened. CI = 1.0.
74. Groove in trochlea for digit II: (a) absent; (b) present, but posterior terminus of groove variable in extent. CI = 1.0.
75. Anterior extent of internal and external ridges of shaft: (a) essentially equal, no twisting of shaft about its long axis; (b) internal ridge less prominent anteriorly than external, becoming flush with shaft immediately distal to proximal foramen, associated with moderate twisting of shaft; (c) internal edge of shaft depressed below level of shaft anteriorly, associated with strong twisting of shaft. (*Hymenolaimus*, *Merganetta*, *Amazonetta*.) CI = 0.33.
76. External margin of shaft: (a) concave (in anterior profile), curving smoothly to external surface of trochlea for digit IV; (b) essentially straight, trochlea for digit IV internally deflected. CI = 1.0.
77. Posterior opening of distal foramen: (a) directed posteriorly, flush with surface of shaft; (b) directed distoposteriorly, recessed in depression immediately proximal to symphysis of trochlea for digits III and IV. (*Anseranas*.) CI = 1.0.

Sternum

78. Pneumatic foramen (U*): (a) open, ovoid; (b) pitted, largely occluded by medial bar; (c) closed (sometimes marked by small depression). CI = 0.25.
79. Ventral manubrial region (U*, V): (a) keel-like, laterally compressed medial flange; (b) thick medial wedge; (c) lacking median protuberance(s); (d) long, peglike spine; (e) small lump; (f) a pair of small pointed prominences separated at midline by a deep excavation, typically with an ovoid pit at base; (g) a wide, moderately long, dorsoventrally compressed flange; (h) a pair of points partially separated by a shallow midline excavation; (i) a small, unforked, dorsoventrally compressed flange. (*Cyanochen*, *Hymenolaimus*, *Cairina*, *Lophonetta*, *Chenonetta*, *Polysticta*.) CI = 0.50.
80. Carina (keel) shape, lateral profile: (a) well developed, ventral margin curved throughout length; (b) reduced, ventral margin essentially straight for posterior half. CI = 0.33.
81. Posterior-lateral processes (U*): (a) extend well posterior to post-pectoral line of sternal plate; (b) approximately equal to post-pectoral line in posterior extent. CI = 0.33.
82. Dorsal manubrial region (U, V): (a) rounded notch; (b) rounded notch with small point on midline; (c) rounded notch with moderately large point on midline; (d) even shelf. (*Malacorhynchus*, *Hymenolaimus*, *Marmaronetta*, *Callonetta*.) CI = 0.43.
83. Abdominal plate (dense, symmetrical extension of sternal plate posterior to both post-pectoral line and posterior-lateral processes): (a) absent; (b) present. CI = 1.0.
84. Sternal notches (posterior margin of plate medial to posterior-lateral processes): (a) typically open posteriorly; (b) typically closed posteriorly, forming fenestrae. CI = 1.0.
85. Xiphial area: (a) posterior margin approximately straight or concave; (b) with medial, irregularly shaped, roughly circular extension of thin bone (anterior to posterior-lateral processes). CI = 1.0.
86. Costal margin: (a) comprises less than half of basin length; (b) comprises more than half of basin length. CI = 1.0.
87. Carina: (a) lacking pneumatic foramen in anterior margin, apparently solid; (b) with small pneumatic foramen in anterior edge, but carina uninflated, (c) hollow, containing loop of trachea, with large pneumatic foramen in anterior edge. CI = 1.0.
88. Intermuscular line: (a) angles medially to carinal base well anterior to posterior edge of plate; (b) extends posteriorly to posterior margin of plate. CI = 0.33.
89. Foramina of basin (U*): (a) limited to midline and anterior margin; (b) essentially absent; (c) present on anterior margin, midline, and scattered across plate (often among transverse bony striations). CI = 0.50.
90. Midpoint of coracoidal sulcus: (a) solid; (b) having oval pneumatic foramen. CI = 1.0.

Costae

91. Uncinate processes: (a) present; (b) absent. CI = 1.0.

Coracoid

92. Procoracoidal foramen: (a) present (variable in *Chauna*); (b) absent. CI = 1.0.
93. Pneumatic foramen on dorsal surface anterior to sternal facet: (a) present; (b) absent. CI = 1.0.
94. Dorsal sternal facet: (a) with anterior border essentially smoothly curving; (b) with prominent circular internal lip. CI = 1.0.
95. Brachial tuberosity (U): (a) essentially without foramina under posterior edge; (b) with small foramina under posterior edge; (c) with small foramina, typically contained within larger foramina, under posterior edge. CI = 0.50.
96. Depression on ventral surface anterior to sternal facet (U*): (a) present, typically deep; (b) absent. (*Anseranas*.) CI = 0.25.
97. Furcular facet: (a) with posterior margin complete or slightly reduced; (b) posterior margin deeply notched. CI = 1.0.
98. Angle of head: (a) coplanar to slightly ventral to plane of blade; (b) distinctly ventral to plane of blade. CI = 1.0.
99. Sternocoracoidal process: (a) wide, long, and rounded flange, extending farther laterally than sternal facet; (b) variably shaped, rounded or angular process, approximately equal to sternal facet in lateral extent; (c) long pointed process, extending farther laterally than sternal facet. CI = 0.67.
100. Ventral (external) sternal facet (V): (a) anterior margin moderately raised or continuous with blade; (b) anterior margin with distinct buttress. CI = 0.33.

Furculum

101. Coracoidal tuberosities (U*): (a) present; (b) obsolete. CI = 0.25.
102. Furcular process: (a) a flattened point; (b) variable, but reduced, essentially continuous with curvature of clavicles; (c) swollen truncate lobe. CI = 1.0.
103. Clavicular symphysis: (a) without foramina; (b) with medial foramina. CI = 1.0.
104. Clavicles: (a) roughly circular in cross-section; (b) distinctly flattened antero-posteriorly. CI = 1.0.
105. Lateral surfaces of clavicles: (a) smooth, unperforated; (b) with depressions containing several small foramina; (c) with depression containing large pneumatic foramen. CI = 0.50.
106. Region of clavicular symphysis: (a) a continuous smooth curve; (b) markedly extended posterodorsally, forming a U-shaped accommodation for tracheal loop and associated modification of carina. CI = 1.0.

Scapula

107. Coracoidal articulation: (a) flush with blade; (b) base protruding ventrally as rounded hump. CI = 1.0.
108. Taper (profile) of blade (U): (a) of uniform width or tapering continuously throughout length; (b) width maximal at midpoint; (c) width maximal at terminus. (*Cygnus, Olor*.) CI = 1.0.
109. Coracoidal articulation: (a) equal to acromion in proximal extent; (b) distinctly distal to acromion. CI = 1.0.
110. Internal surface, immediately posterior to glenoid facet: (a) essentially smooth; (b) having deep depression. CI = 1.0.
111. Anterior edge (U*): (a) containing pneumatic fossa; (b) without pneumatic fossa. (*Cairina*.) CI = 0.25.
112. Dorsal surface of neck: (a) marked by single distinct raised attachment scar; (b) marked by two prominent raised attachment scars. CI = 1.0.

Pelvis

113. Preacetabular iliac fossa: (a) smoothly curved surface; (b) containing a deep, irregularly shaped depression. CI = 1.0.
114. Caudal margin: (a) ischium extending well caudad to ilium; (b) variable, but ischium and ilium roughly equal in caudal extent, forming an obliquely sloping margin, with elements typically separated posteriorly by a distinct notch. CI = 1.0.
115. Body of pubis (V): (a) concave dorsally (rarely almost straight); (b) convex dorsally. CI = 0.50.
116. Orientation of postschiac pubis: (a) directed posteriorly; (b) directed ventrally. CI = 1.0.
117. Shape of postschiac pubis: (a) of uniform width or evenly widening caudally; (b) widened into roughly circular flange, especially extensive anteroventrally. CI = 1.0.

118. Dorsolateral crests: (a) distinct to caudal margin of pelvis; (b) becomes obsolete cranial to caudal margin. CI = 1.0.
119. Anterior terminus of shield (posterior terminus of fusion of median dorsal ridge): (a) cranial to acetabula; (b) essentially coincident with acetabula; (c) well caudad to acetabula. CI = 0.67.
120. Recessus iliacus (Baumel 1979; a pneumatic pocket at caudal terminus of renal depression): (a) present; (b) absent. CI = 1.0.

APPENDIX 2. A Linnean classification of the Recent genera of Anseriformes. I follow the conventions of Wiley (1981), with the exception of the provisional recognition of the paraphyletic "Anatini" (annotated *incertae sedis*). I have retained, where possible, the names and taxonomic ranks of previous classifications. Names of subtribes are given endings of -eae after the names for the "sections" of Boetticher (1952) and are derived from the oldest included genus. *Sedis mutabilis* follows taxa in which the order of included groups is unresolved. * = two subfamilies may be in reverse order; ** = subtribes possibly are sister groups; *** = probable sister groups.

Order Anseriformes
Suborder Anhimae
Family Anhimidae
Genus <i>Anhima</i>
Genus <i>Chauna</i>
Suborder Anseres
Family Anseranatidae
Genus <i>Anseranas</i>
Family Anatidae
Subfamily Dendrocygninae
Genus <i>Dendrocygna</i>
Subfamily Thalassorninae*
Genus <i>Thalassornis</i>
Subfamily Anserinae*
Tribe Anserini
Genus <i>Cereopsis</i>
Genus <i>Anser</i>
Genus <i>Branta</i>
Tribe Cygnini
Genus <i>Coscoroba</i>
Genus <i>Cygnus</i>
Genus <i>Olor</i>
Subfamily Stictonettinae
Genus <i>Stictonetta</i>
Subfamily Plectropterinae
Genus <i>Plectropterus</i>
Subfamily Tadorninae
Tribe Sarkidiornini
Genus <i>Sarkidiornis</i>
Tribe Tadornini <i>sedis mutabilis</i>
Subtribe Tadorneae
Genus <i>Tadorna</i>
Subtribe Malacorhyncheae
Genus <i>Malacorhynchus</i>
Subtribe Chloephageae <i>sedis mutabilis</i>
Genus <i>Alopochen</i>
Genus <i>Neochen</i>
Genus <i>Chloephaga</i>
Subtribe Cyanocheae**
Genus <i>Cyanochen</i>
Subtribe Merganettae**
Genus <i>Hymenolaimus</i>

APPENDIX 2. Continued

Genus *Merganetta*
 Genus *Tachyeres*
 Subfamily Anatinae
 [Tribe] "Anatini" *incertae sedis*
 Genus *Pteronetta*
 Genus *Cairina*
 Genus *Aix*
 Genus *Lophonetta*
 Genus *Nettapus*
 Genus *Anas*
 Genus *Callonetta*
 Genus *Chenonetta*
 Genus *Amazonetta*
 Tribe Aythyini
 Genus *Marmaronetta*
 Genus *Rhodonessa*
 Genus *Netta*
 Genus *Aythya*

APPENDIX 2. Continued

Tribe Mergini
 Genus *Polysticta*
 Genus *Somateria*
 Genus *Histrionicus*
 Genus *Camptorhynchus*
 Genus *Melanitta*
 Genus *Clangula*
 Genus *Bucephala****
 Genus *Mergellus****
 Genus *Lophodytes*
 Genus *Mergus*
 Tribe Oxyurini
 Genus *Heteronetta*
 Genus *Nomonyx*
 Genus *Oxyura*
 Genus *Biziura*
