A PHYLOGENETIC REASSESSMENT OF THE TADORNINE–ANATINE DIVERGENCE (AVES: ANSERIFORMES: ANATIDAE)

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ABSTRACT

Phylogenetic analysis of eight problematic genera of waterfowl (Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus, and Salvadorina) and representatives of other tadornine genera and anatine tribes was undertaken using 114 morphological characters (39 skeletal, four tracheal, 11 natal, and 60 of the definitive integument) and a variety of weighting schemes, in an attempt to clarify relationships in the most poorly understood segment of the phylogeny of Anseriformes (Livezey, 1986a). Under equal weighting of characters, 40 equally parsimonious trees were found that shared the following findings: (1) a sister-group relationship of Stictonetta to a clade comprising the Tadorninae and Anatinae; (2) a sister-relationship between Plectropterus and Sarkidiornis; (3) monophyly of the typical shelducks and sheldgeese (Tadorna, Cyanochen, Alopochen, Neochen, and Chlorophaga); (4) monophyly of Hymenolaimus, Tachyeres, and Merganetta; and (5) a sister-relationship between Salvadorina and Malacorhynchus. An analysis wherein skeletal characters were given twice the weight of other character groups resulted in four shortest trees which, in addition to the findings under equal weighting, indicated that: (1) Plectropterus + Sarkidiornis represent the sister-group of the typical shelducks and sheldgeese; (2) a sister-relationship between the clade comprising Hymenolaimus, Tachyeres, and Merganetta and the preceding clade, collectively constituting the “tadornine” clade; and (3) a sister-relationship between Malacorhynchus + Salvadorina and an “anatine” clade comprising the remaining tribes and subtribes (Cairinae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini). An analysis in which skeletal, tracheal, natal, and definitive characters were assigned weights of four, three, two, and one, respectively, produced identical results to the preceding weighting scheme. Successive weighting by rescaled consistency indices produced two shortest trees that resembled those found under the two preceding protocols except: (1) the Mergini were placed as the sister-group of the “tadornine” clade defined above; and (2) the Cairinae (Cairina, Pteronetta, and Aix) were placed as the sister-group to Plectropterus + Sarkidiornis. Based on the comparative strengths of hypothesized homologies of skeletal characters and assessments of topological support (including bootstrapping, decay indices, and near-shortest trees) for all weighting schemes, a conservative classification was based on the a priori weighting schemes favoring skeletal characters. Maps of selected ecomorphological attributes on this phylogenetic tree revealed several distinct evolutionary trends, but incompletely resolved relationships among these diverse genera and within suprageneric taxa limited inferences. Additional promising areas for anatomically based systematic study are identified, and the need for continued cladistic study of this poorly resolved but topologically critical segment of the phylogeny of Anseriformes is emphasized.

INTRODUCTION

Greater diversity of opinion has attended the classification of the following eight southern-hemisphere genera of waterfowl than in any assemblage of similar size in the Anseriformes: Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus, and Salvadorina (Table 1). Early taxonomists typically included these genera within larger, more-familiar groups of waterfowl on the basis of superficial comparisons and very limited material (Eyton, 1838; Gray, 1841, 1871; Bonaparte, 1856; Sclater, 1880; Salvadori, 1895; Phillips 1922, 1923, 1925, 1926).

In recent decades, taxonomic classifications of the Freckled Duck (Stictonetta
Table 1.—A century of taxonomic classifications of eight taxonomically problematic genera of Anatidae.

| Genus          | Phillips (1922–1925) | Peters (1931) | Anaitae, between Casarca and Tadorna. |
|---------------|----------------------|---------------|----------------------------------------|
| Stictonetta   | Anatiniae, between Mar-maronetta and Heteronetta. | Anatiniae, between Anas and Heteronetta. |
| Plectropterus  | Plectropterineae, before Cairina and Sarkidiornis. | Plectropterineae, before Cairina and Sarkidiornis. |
| Sarkidiornis   | Plectropterineae, between taxa currently merged into Cairina. | Plectropterineae, between taxa currently merged into Cairina. |
| Hymenolaimus  | Merganettinae, between Salvadorina and Merganetta. | Merganettinae, between Salvadorina and Merganetta. |
| Tachyeres     | Fuligulinae, between Aythya and Bucephala. | Fuligulinae, between Aythya and Bucephala. |
| Merganetta     | Merganettinae, with Salvadorina and Hymenolaimus. | Merganettinae, with Salvadorina and Hymenolaimus. |
| Malacorhynchus | Anatiniae, between Anas (part) and Marmaronetta. | Anatiniae, between Anas (part) and Aix. |
| Salvadorina    | Merganettinae, with Hymenolaimus and Merganetta. | Merganettinae, with Hymenolaimus and Merganetta. |

* a Generic taxa used by author(s) are replaced by currently accepted synonyms.
* b Johnsgard (1979) listed no tribes within subfamilies.
* c Salvadorina merged with Anas by author.
* d Skeletal specimens of Salvadorina not examined by Woolfenden (1961).

naevosa) have included placements as: an aberrant dabbling duck (Delacour, 1938; Delacour and Mayr, 1945) or shelduck (Boetticher, 1942, 1952); the sole member of a tribe or higher taxon closely related to the true geese (Verheyen, 1953, 1955; Frith, 1964a, 1964b, 1965, 1967; Johnsgard, 1978); a very primitive sister-group of the majority of modern ducks, geese, and swans (Frith, 1967; Olson and Feduccia, 1980; Madsen et al., 1988; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990); or as both very primitive and a close relative of the stiff-tailed ducks (Fullagar et al., 1990; Marchant and Higgins, 1990). Also, assignments of single species to monogeneric higher taxa has led to the phylogenetically misleading conclusion that each has, like Stictonetta, “no near living relatives” (e.g., Johnsgard, 1978:xx) or “is not closely related to any other tribe” (e.g., Edkins and Hansen, 1972:105). However, under an assumption of the monophyly of the biota of the earth, any species is the sister-group (i.e., closest relative) of some other group of organisms. At present, there is a consensus among most systematists that Stictonetta should be excluded from the true ducks (Anatinae), although other details of its relationships within the Anseriformes remain in dispute (Wolters, 1976; Johnsgard, 1979; Livezey, 1986a; Madsen et al., 1988; Sibley and Monroe, 1990).

The Spur-winged Goose (Plectropterus gambensis) and Comb Duck (Sarkidiornis melanotus), traditionally considered to be members of an assemblage termed the “perching ducks,” or formally the Subfamily Cairininae or Tribe Cairinini (e.g., Delacour, 1938, 1959, 1964; Delacour and Mayr, 1945; Boetticher,
Table 1.—Extended.

| Delacour and Mayr (1945) | Boetticher (1952) | Delacour (1954–1959) |
|--------------------------|-------------------|---------------------|
| Anatinae, Anatini, as “aberrant.” | Anatinae, Tadornini, in monotypic “section.” | Anatinae, Anatini, after Hymenolaimus, and Merganetta. |
| Anatinae, Cairinini, after Sarkidiornis and Cairina. | Anatinae, Cairinini, before Cairina and Sarkidiornis. | Anatinae, Cairinini, after Sarkidiornis and Cairina. |
| Anatinae, Cairinini, between Nettapus and Cairina. | Anatinae, Cairinini, between Cairina and Nettapus. | Anatinae, Cairinini, between Nettapus and Cairina. |
| Anatinae, Anatini, as “aberrant.”  | Anatinae, anatini, after Malacorhyncha. | Anatinae, Anatini, between Malacorhyncha and Merganetta. |
| Anatinae, Tadornini, as “aberrant.” | Anatinae, Tachyonini, monogenic. | Anatinae, Tadornini, after Lophoneta. |
| Anatinae, Meganettini (monotypic), after Oxyurini. | Anatinae, Oxyurini, after Heteronetta. | Anatinae, Anatini, between Hymenolaimus and Stictonetta. |
| Anatinae, Anatini, as “aberrant.” | Anatinae, Anatini, before Hymenolaimus. | Anatinae, Anatini, between Rhodonessa and Hymenolaimus. |
| Anatinae, Anatini, merged with Anas. | Anatinae, Anatini, between taxa currently merged into Anas. | Anatinae, Anatini, merged with Anas. |

1952; Johnsgard, 1965a, 1978), were reassigned to a monotypic subfamily (Plectropterinae) and the shelducks (Tadorninae), respectively, by Livezey (1986a). Similarly, steamer-ducks (Tachyeres spp.; Livezey and Humphrey, 1992) and the Torrent Duck (Merganetta armata), for which persistent doubts concerning phylogenetic relationships were finessed by some through allocations to monotypic tribes (Delacour and Mayr, 1945; Verheyen, 1953; Johnsgard, 1965a, 1978), also were included in the poorly resolved Tadorninae by Livezey (1986a).

The Blue Duck (Hymenolaimus malacorhynchos) and the Pink-eared Duck (Malacorhynchos membranaceus), traditionally considered to be aberrant members of the dabbling ducks (Delacour, 1938; Delacour and Mayr, 1945; Boetticher, 1952; Delacour, 1956; Johnsgard, 1965a, 1965b, 1978, 1979; Kear and Steel, 1971; Sibley and Monroe, 1990), were included as well among the tadornines by Livezey (1986a). However, Olson and Feduccia (1980:22) suggested that Malacorhynchos, together with Stictonetta and perhaps Merganetta, were “primitive relics of an early anatid radiation and may be only distantly related to the remainder of the Anatidae.” Salvadori’s Duck (Salvadorina waigiuensis), for which skeletal and tracheal specimens were not available in the analysis performed by Livezey (1986a), also has been classified in recent decades as an unusual member of the dabbling ducks, and often merged with the genus Anas (Mayr, 1931; Delacour and Mayr, 1945; Delacour, 1956; Johnsgard, 1965a, 1978, 1979). Subsequent behavioral comparisons (Kear, 1975) and limited osteological data (Mlčkovský, 1989), however, indicate that the species may be more closely related to other waterfowl variably specialized for lotic habitats (Merganetta and Hymenolaimus) or to the unique Malacorhynchos. Based in large part on these data, Livezey (1991) tentatively included the genus among the shelducks and allies.
Table 1.—Continued.

| Genus            | Woolfenden (1961)                        | Johnsgaard (1965) | Wolters (1976)                  |
|------------------|------------------------------------------|-------------------|--------------------------------|
| Stictonetta      | Anserinae, Dendrocygnini (not examined).  | Anserinae, Stictonettini (monotypic), after Anserini.       | Stictonettinae (monotypic), between Dendrocygninae and Anseri-|
|                  |                                          |                   | nae. Plectropterinae (monotypic), between Tadorninae and   |
| Plectropterus    | Anatinae, Tadornini, before Chloephaga and Cyanochen. | Anatinae, Cairinini, before Cairina and Sarkidiornis.       | Anatinae, before Cairina and Pteronetta.                    |
| Sarkidiornis     | Anatinae, Anatini, before Pteronetta and Cairina. | Anatinae, Cairinini, between Cairina and Pteronetta.        | Anatinae, before Cairina and Pteronetta.                    |
| Hymenolaimus     | Anatinae, Anatini, between Malacorhynchus and Tachyeres. | Anatinae, Anatini, before Merganetta and Anas.               | Anatinae, between Malacorhynchus and Tachyeres.             |
| Tachyeres        | Anatinae, Anatini, after Malacorhynchus and Hymenolaimus. | Anatinae, Tachyerini, between Tadornini and Cairinini.      | Anatinae, between Hymenolaimus and Marmornetta.            |
| Merganetta       | Anatinae, Merganettini, monotypic.        | Anatinae, Anatini, between Hymenolaimus and Anas.           | Anatinae, between Lophonetta and Salvadorina.               |
| Malacorhynchus   | Anatinae, Anatini, between Salvadorina and Hymenolaimus. | Anatinae, Anatini, between Anas and Marmornetta.            | Anatinae, between Salvadorina and Hymenolaimus.            |
| Salvadorina      | Anatinae, Anatini, between Anas and Malacorhynchus. | Anatinae, Anatini, as monotypic subgenus of Anas.           | Anatinae, between Merganetta and Malacorhynchus.          |

(Tadorninae). Thirteen representative classifications of these eight genera spanning the last century are summarized in Table 1.

Woolfenden (1961) presented the first study of the comparative osteology of waterfowl from the perspective of (phenetic) assessments of relationships. Livezey (1986b) presented a species-level phylogenetic analysis of Tachyeres based on morphological comparisons, one which compared favorably with an assessment of genetic distances in the group (Corbin et al., 1988) and biochemical patterns in secretions from the uropygial glands (Livezey et al., 1986). Other contributions to the knowledge of the anatomy of these genera include, by genus: Stictonetta (Campbell, 1899; Frith, 1964b; Olson and Feduccia, 1980), Plectropterus (Rand, 1954; Möller, 1969), Sarkidiornis (Garrod, 1875), Hymenolaimus (Kear and Burton, 1971), Tachyeres (Livezey and Humphrey, 1986, 1992), Merganetta (Niehammer, 1952; Weller, 1968; Raikow, 1970), Malacorhynchus (Frith, 1955, 1967), and Salvadorina (Rothschild, 1895; Mayr, 1931; Kear, 1975; Mlíkovský, 1989). Tyler (1964) included several of these genera in a comparison of the microanatomy of anseriform egg shells. Fossils assignable to any of these eight genera are limited to Pleistocene material of Sarkidiornis and subfossil material of Malacorhynchus (Brodkorb, 1964; Howard, 1964a; Olson, 1977, 1985; Worthy, 1995).
Phylogenetic analyses using molecular characters are considered by some to hold potential for especially reliable inferences of phylogeny, but an assumption of inherent superiority lacks empirical support (Hillis, 1987; Sanderson and Donoghue, 1989; Moritz and Hillis, 1990). Moreover, comparisons of studies based on molecular and morphological data, even where fundamentally phenetic methodologies were applied, share broad areas of agreement (e.g., Bledsoe and Rai-kow, 1990; Omland, 1994; see also Swoford, 1991). Unfortunately, most of the larger studies of Anseriformes employing molecular techniques included none of the eight genera considered here (Kessler and Avise, 1984; Patton and Avise, 1985; Scherer and Sontag, 1986). Numachi et al. (1983) included but a single member of this group of genera, Sarkidiornis, precluding any tests of relationships among members. Bottjer (1983) included Plectropterus and Sarkidiornis in his immunological comparisons; one especially distinctive finding was the low similarity between Plectropterus and the “perching ducks” Cairina, Chenonetta, and Aix. The electrophoretic comparisons of egg-white proteins by Sibley and Ahl-quist (1972:fig. 10–12) included Plectropterus, Sarkidiornis, Hymenolaimus, and Malacorhynchus, but not even a phenetic analysis of the intriguing patterns was presented. Other molecular analyses including two or more of these taxa also were phenetic in methodology, and therefore any inferred associations represent
assessments of overall similarity rather than direct indications of phylogenetic relationship (Jacob and Glasser, 1975; Brush, 1976; Jacob, 1982; Jacob and Hoerschelmann, 1993). Of the latter, the comparisons of feather proteins by Brush (1976) included six of the eight genera of interest here, but the resultant banding patterns proved difficult to interpret phylogenetically and rendered tribal assignments problematic for *Stictonetta, Hymenolaimus, Merganetta*, and *Malacorhynchus*.

The analyses by Sibley and Ahlquist (1990) using DNA hybridization, and the related classification (Sibley et al., 1988; Sibley and Monroe, 1990), also lacked any samples from these eight genera. The placement of *Stictonetta* by Madsen et al. (1988) in an analysis of 13 species of Anseriformes using DNA hybridization must be viewed with caution in light of criticisms of this general methodology (Cracraft, 1987; Houde, 1987; Sarich et al., 1989; Springer and Krajewski, 1989), poor representation of taxa, and unfavorable metric properties evident in the comparisons.

The primarily osteological study by Livezey (1986a) remains the only work in which even a majority of these problematic “tadornine” genera were analyzed. However, support for inferences in the topological vicinity of the divergence of the “shelducks” (Tadorninae) and the “surface-feeding ducks” (Anatinae) in the preliminary analysis by Livezey (1986a), should be considered tentative. This assessment stems from several concerns: (1) the polychotomous topology depicted for the genera included in the tadornines (Livezey, 1986a:fig. 1, 3); (2) the limited numbers of characters supporting groupings within this segment of the tree, e.g., those uniting *Cyanochen* with *Hymenolaimus, Merganetta*, and *Tachyeres*; (3) the impossibility of an assessment of support (e.g., bootstrapping of characters or consideration of suboptimal topologies) or the treatment of polymorphic character states at the time of the analysis; (4) three characters used by Livezey (1986a) to support clades in the tadornines—characters 15, 33, and 61—were judged unreliable for these taxa based upon further study (Livezey, unpublished data); (5) several of the characters of the pelvic limb (including characters 56 and 69) show significant homoplasy evidently associated with diving habit (Livezey, 1986a; Faith, 1989), therefore groups united in part by these characters (e.g., *Hymenolaimus, Tachyeres*, and *Merganetta*) merit confirmation; and (6) the profound limitations of software and computing platform increased the likelihood of suboptimal solution sets (e.g., retention of more than 50 trees in memory for this data set typically caused a “crash” of the analysis).

Livezey (1986a) indicated several areas of poor resolution and marginal support in the resultant phylogenetic hypothesis, and subsequent study discovered alternative solutions to at least the basal segment of the tree (Livezey, 1989). In addition, reanalysis of the original data matrix compiled by Livezey (1986a) using improved versions of analytical software discovered multiple, slightly shorter alternative trees including several distinct topologies (J. Harshman, personal communication), the majority of which were the result of poorly resolved relationships in the vicinity of the divergence of “tadornine” and “anatine” genera. With respect to the eight genera of concern here, these alternative trees shared the following elements: (1) paraphyly of *Stictonetta* and *Plectropterus* to “tadornine” and “anatine” genera (as inferred by Livezey, 1986a); and (2) placement of *Malacorhynchus, Blue-winged Sheldgoose* (*Cyanochen cyanopterus*), true shelducks (*Tadorna*) and other sheldgeese (*Alopochen, Neochen*, and *Chloephaga*), *Sarki-
diornis, and the clade comprising Hymenolaimus, Merganetta, and Tachyeres as paraphyletic to the genera included in the Anatinae by Livezey (1986a).

Contradictory assessments of relationships in this group of genera “transitional” between the anseriform subfamilies Tadorninae and Anatinae, as well as shortcomings in analyses to date, justify a renewed effort to recover phylogenetic structure in this important group of waterfowl. Because of the phylogenetically central position of these genera, i.e., their topological proximity to the divergences of the tribes of the Anatinae (Livezey, 1986a, 1991), a study of this kind provides an opportunity to assess available morphological evidence concerning the relationships among the anatine tribes as well. This paper, one of a series of finer-scale analyses of the major subparts of the phylogeny of waterfowl (Livezey, 1991, 1995a, 1995b, 1995c, in press a, in press b, in press c), presents a phylogenetic analysis of the eight aforementioned genera and representatives of related tribes, using an enlarged set of morphological characters and improved analytical algorithms. This analysis is followed by ancillary considerations of morphological evolution, phylogenetic patterns of behavior and ecology, implications for historical biogeography, and promising areas for future study for this most challenging aspect of the phylogeny of Anseriformes.

**MATERIALS AND METHODS**

**Taxonomy**

**Composition of the Ingroup.**—Determination of the broad limits of the comparatively derived members of the Anseriformes, based on the cladistic analyses by Livezey (1986a, 1995a, in press c), conservatively included representatives of all groups exclusive of the screamers (Anhimidae), Magpie Goose (Anseranatidae: Anseranas semipalmata), whistling ducks and allies (Dendrocygninae), and true geese and swans (Anserinae). Comparisons included representatives of all taxa included in the eight genera of primary interest—Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, Tachyeres, Merganetta, Malacorhynchus, and Salvadorina. Representatives of other “tadornine” genera (Cyanoochen, Alopochen, Neoochen, Chlorocepha, and Tadorna), also were included, which were inferred to constitute a monophyletic group in this series of phylogenetic analyses (Livezey, in press a). The Cape Barren Goose (Cereopsis novaehollandiae), considered by some to be an aberrant sheldgoose or an evolutionary “link” between the true geese and the sheldgeese (Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1961a, 1978; Woolfenden, 1961; Frith, 1967; Kear and Murton, 1973), is excluded from this study on the basis of its inclusion among the true geese and swans (Livezey, 1986a, 1989, in press c).

Also included are “basal” representatives (see below for methods of characterization) of the major clades of Anatinae: three subtribes of dabbling ducks or Anatini (Cairineae, Nettapodeae, and Anataeae; Livezey, 1991), as well as the pochards (Aythyini; Livezey, in press b), seaducks (Mergini; Livezey, 1995b), and stiff-tailed ducks (Oxyurini; Livezey, 1995c). Inclusion of the separate subtribes of Anatini defined by Livezey (1991) in the analysis was necessitated by variation among the subgroups in characters determined to be informative as well among “tadornine” genera. Under the taxonomy proposed by Livezey (1991), the three subtribes of Anatini comprise the following genera: Cairineae (Cairina, Pteronetta, and Aix), Nettapodeae (Chenonetta and Nettapus), and Anataeae (Amazonetta, Callonetta, Lophonetta, Speculanas, Mareca, and Anas).
Composition of Included Genera.—Five of the eight genera of primary interest in this analysis are considered to comprise single species by most taxonomists: Stictonetta, Plectropterus, Sarkidiornis, Hymenolaimus, and Merganetta (e.g., Delacour and Mayr, 1945; Delacour, 1954, 1956, 1959; Johnsgard, 1961a, 1965a, 1965b, 1978, 1979; Wolters, 1976). Segregation of Salvadori’s Duck in the genus Salvadorina (Woolfenden, 1961; Kear, 1975; Wolters, 1976; Mlíkovský, 1989; Sibley and Monroe, 1990; Livezey, 1991), instead of inclusion of the species within Anas (e.g., Delacour and Mayr, 1945; Boetticher, 1952; Delacour, 1956; Johnsgard, 1965a, 1978), delimits another monotypic genus in this group.

Two of these purportedly monotypic genera—Sarkidiornis and Merganetta—include two or more qualitatively distinct taxa that might be accorded species rank. For example, in light of plumage differences and geographical isolation (Madge and Burn, 1988), partitioning of Sarkidiornis into a nominate African species S. melanotus and a Neotropical species S. sylvicola is consistent with both the emphasis of the “minimal diagnosable unit” under the phylogenetic species concept, and the requirements of distinct historical “identities” and independent evolutionary “tendencies” and “fate” under the evolutionary species concept (Wiley, 1978; Cracraft, 1983, 1988; McKitrick and Zink, 1988; Frost and Hillis, 1990). In practice, application of the phylogenetic species concept can approximate the lineages conceptualized under the evolutionary species concept (Frost and Kluge, 1994). Numerous synapomorphies demonstrate the monophyly of Sarkidiornis (see beyond), however, and the included species were identical for the characters coded here; therefore the species-level taxonomy of the genus is not germane to this analysis. Similarly, substantial support for monophyly of Merganetta (see beyond) and identical states of analyzed characters render inconsequential any species-level interpretation one might impose on this poorly understood complex of three to six recognized forms for purposes of this analysis (Conover, 1943; Delacour, 1956; Johnsgard, 1978; Madge and Burn, 1988). The steamer-ducks (Tachyeres) are treated as a single generic taxon for this analysis; the genus comprises four confusingly similar species (Livezey and Humphrey, 1992), is demonstrably monophyletic (Livezey, 1986a, 1986b, present study), members of the genus were identical for included characters, and the phylogeny of included taxa has been examined elsewhere (Livezey, 1986b; Corbin et al., 1988).

The Spur-winged Goose (Plectropterus gambensis) currently is considered to comprise two poorly differentiated subspecies (northern, comparatively pale gambensis and southern, comparatively dark niger) having a broad area of intergradation; the two forms are considered as a single analytical taxon here (Delacour, 1959; Johnsgard, 1978; Brown et al., 1982; Madge and Burn, 1988). No diagnosable populations have been detected within the other four critical genera—Stictonetta, Hymenolaimus, Malacorhynchus, and Salvadorina (Delacour, 1956, 1959; Johnsgard, 1978, 1979).

Specimens and Related Data

Specimens Examined.—Study skins of adult birds were compared for determination of plumage pattern and general structure of the externum in the collections of several major museums, most importantly the National Museum of Natural History and the American Museum of Natural History. Colors of the irides, bill, tarsi, and feet of adults also were characterized using study skins, but colors
of unfeathered integument are not always reliably coded using dried specimens; consequently, colors of soft parts were confirmed using published descriptions (see below), notes on specimen labels, photographs of living individuals, and direct observation of living birds in avicultural collections or in the wild. Plumage patterns of downy young, specimens of which are comparatively rare in museum collections, were ascertained by comparisons of study skins (including an important collection at the Wildfowl and Wetlands Trust) and fluid-preserved specimens.

Prepared skeletal specimens of adults were used for osteological comparisons. Numbers of prepared skeletons available varied significantly among taxa. Large series of skeletons (100 or more) were available for several groups (Tachyeres, Anas), whereas fewer than five were available for several others (Hymenolaimus, Merganetta); at least five skeletons were studied for other taxa, with the exception of Salvadorina (for which no complete skeletal specimen exists). Tracheal characters were determined using ossified elements in skeletal specimens and complete tracheae removed from fluid-preserved specimens (some previously mounted and dried).

**Published Data.**—Published descriptions and illustrations of adult and subadult plumages supplemented data collected from direct study (Conover, 1943; Delacour, 1954, 1956, 1959, 1964; Johnsgard, 1965a, 1978; Weller, 1968; Todd, 1979; Humphrey and Livezey, 1982; Madge and Burn, 1988; Marchant and Higgins, 1990; Hoyo et al., 1992). Preliminary study of variation in natal plumages was accomplished using the illustrations and descriptions of downy young provided by Delacour and Mayr (1945, 1946), Delacour (1954, 1956, 1959, 1964), Frith (1955, 1964b), Pengelly and Kear (1970), Kear (1972, 1975), and Humphrey and Livezey (1985). Variation and alternative interpretations of skeletal characters, most of which were based on my earlier analyses (Livezey, 1986a, 1989, 1991), were made using the works by Shufeldt (1909), Verheyen (1953), Rand (1954), Woolfenden (1961), Humphrey and Clark (1964), Cracraft (1968), Weller (1968), Möller (1969), and Raikow (1970). The few skeletal characters determinable for Salvadorina were coded using the descriptions of a few elements by Mayr (1931) and Mlíkovský (1989). Additional information on the tracheal anatomy of waterfowl was taken from Yarrell (1827), Garrod (1875), Campbell (1899), Mayr (1931), Niethammer (1952), Johnsgard (1961b, 1971), and Humphrey and Clark (1964).

**Definition of Characters**

**Theory and Objectives.**—Characters used in this phylogenetic analysis are distinct morphological features, hypothesized to be homologous (de Pinna, 1991; Lipscomb, 1992; Hall, 1994), that comprise two or more states within the ingroup or differ between the ingroup and outgroups. Of the states defined, one is hypothesized as the primitive or plesiomorphous state based on outgroup comparisons (see below), and the other(s) as the derived or apomorphic state(s). Definition of characters and included states are essential to any cladistic analysis, but recognition of homology and description of the implicit distinctions between states remain the most challenging and influential aspect of phylogenetic inference (Pogue and Mickevich, 1990).

Given that shared derived characters (synapomorphies) constitute the only empirical support for the delimitation of hierarchically nested sets of closest relatives (clades), the primary objective of character analysis is the discovery of such
Changes in states (transformation series) germane to the group of interest. Autapomorphies, character changes that are unique to terminal taxa, cannot contribute to the resolution of such groupings of included taxa (Wiley, 1981), although such differences traditionally have been accorded considerable weight in previous attempts at classification (e.g., Delacour, 1954; Johnsgard, 1961a, 1965a, 1978). However, autapomorphies of the key eight genera of interest were included in this analysis for several reasons: (1) inclusion of autapomorphic divergence in cladistically based phylograms can provide insights into relative evolutionary rates, (2) autapomorphic characters of polytypic genera also are synapomorphic for included members, and (3) autapomorphic divergence can be depicted in phylogenetic trees independently of the character changes supporting topological structure and associated summary statistics.

Characters Defined.—A total of 114 morphological characters were defined for this analysis: 39 characters of the skeleton, four of the trachea and syrinx, 11 of the natal plumage, and 60 of the definitive plumage and soft parts (Appendix 1). Most skeletal characters were adapted from those described by Livezey (1986a), with lesser numbers from Livezey (1989, 1991); for this analysis, states of these characters were restricted to those represented by the ingroup. This more detailed consideration of tracheosyringeal anatomy obviated the ad hoc weighting of the single (composite) syringeal transformation series defined in the analysis by Livezey (1986a).

Behavioral patterns, especially courtship displays, have received considerable study in waterfowl (Delacour and Mayr, 1945; Delacour, 1954, 1956, 1959; Johnsgard, 1960a, 1961a, 1962, 1965a, 1978). Such ethological data have provided insights into phylogenetic relationships of waterfowl (e.g., Johnsgard, 1961a) and have been shown to be comparable in consistency to morphological and molecular characters (de Queiroz and Wimberger, 1993). Formal inclusion of such data in the phylogenetic analysis, however, was precluded by numerous missing data, problems of coding behavioral characters termed "rare" or "uncommon" in a discrete scheme, and questions of homology and polarity not addressable from published descriptions.

Each character was coded for the 19 members of the ingroup and a hypothetical "ancestor" (see below), producing a data matrix of dimension 20 × 114 (Appendix 2). Missing data were as follows: 28 entries for skeletal characters of Salvadorina were coded as "missing"; two natal characters for the "hypothetical ancestor" were coded as "missing," indicating an unknown polarity; and one entry for character 44, three entries for character 46, single entries for characters 47 and 48, and two entries for character 77 were treated as "missing" because of problematic comparability of states. In total, there were 38 matrix entries coded as "missing" (1.7% of matrix). The impact of missing data on phylogenetic inference has been considered by Nixon and Davis (1991) and Platnick et al. (1991). Fourteen characters were "multistate" (i.e., included two or more derived states), of which two (characters 29 and 78) were ordered, i.e., a particular ordination of derived states was considered more probable on structural or developmental grounds (Wilkinson, 1992). Analytical implications of multistate characters and ordering attract continuing controversy and empirical study (Hauser and Presch, 1991; Mickevich and Lipscomb, 1991; Lipscomb, 1992; Barriel and Tassy, 1993; Slowinski, 1993). Consequently, an assessment of the analytical impact of these two orderings was made by comparison with analyses in which all characters were treated as unordered.
Characterization of Generic Vectors.—Coding of states for characters found to be uniform among members of genera was straightforward. Most character states for the “typical” tadornines—Cyanochen, Alopecochen, Neoochen, Chloephaga, and Tadorna—were based largely on a separate species-level analysis (Livezey, in press a). Several characters for the polyspecific genera in this group (Chloephaga, Tadorna) varied among species. Similarly, character states for the “composite” vectors for the seven major subgroups of Anatinae, where invariant within groups, were made on the basis of the present study or taken from Livezey (1991). Where determinable on the basis of distribution of states within the species-level analyses of these genera (Livezey, 1991, 1995b, 1995c, in press b), the “basal” state (therefore presumptive locally ancestral state) was used to characterize the genus in this analysis. Where variation and distribution of states within a genus precluded such a determination, the state was coded as polymorphic (character 4 for Cairineae, character 8 for the genera of Tadornini, character 82 for Anateae, and character 91 for Nettapodeae).

Determination of Basal Polarities

Outgroup Comparisons.—Basal polarities of characters, i.e., the states of characters judged to be ancestral for the ingroup under analysis, were inferred by reference to outgroups (Watrous and Wheeler, 1981; Maddison et al., 1984), as opposed to ontogenetic criteria (de Queiroz, 1985; Mabee, 1989; Wheeler, 1990; Williams et al., 1990). Based on the analysis by Livezey (1986a), the most informative outgroups for study were the taxa of Anseriformes paraphyletic to the clade comprising Stictonetta, Plectropterus, Tadorninae, and Anatinae. Characters were compared against representative members of each of the subfamilies and tribes, with primary exemplars given in parentheses: Anseranatinae (Anseranas semipalmata), Dendrocygninae (Dendrocygna autumnalis and Thalassornis leucopterus), and Anserinae (Cereopsis novaehollandiae, Branta canadensis, Anser anser, Coscoroba coscoroba, and Cygnus olor). Character states that were found in successive outgroups were considered plesiomorphous and used to define the states presumed to be ancestral for the ingroup.

Hypothetical Ancestor.—A hypothetical ancestor, the set of character states judged to be primitive based on outgroup comparisons, was used to root the phylogenetic tree(s). This method provided a single, simple root for the ingroup without explicitly including representative outgroup taxa in this study, thereby avoiding ancillary analytical digressions concerning relationships among outgroups, considered elsewhere (Livezey, 1986a, 1989, 1995a, in press c; Livezey and Martin, 1988). Monophyly of the ingroup under study here was demonstrated by Livezey (1986a), and is further substantiated in the present analysis if one or more unambiguous synapomorphies for the taxa exclusive of the hypothetical ancestor are discovered; a less stringent criterion is a basal branch with positive length.

Derivation of Trees

Global Parsimony and Search Algorithms.—Phylogenetic reconstruction was based on the cladistic principle of grouping taxa on the basis of shared derived characters (synapomorphies), and the set of trees that accomplished this with a minimum number of hypothesized character transformations in the entire tree was sought (i.e., in accordance with the criterion of global parsimony). This approach
was first formulated by Hennig (1966) and has been reviewed by Wiley (1981) and Wiley et al. (1991). Exhaustive searches of all possible trees were prohibited by the size of the data matrix; use of the branch-and-bound algorithm, a method guaranteed to discover all most-parsimonious trees (Hendy and Penny, 1982), also was not practical for a problem of this moderately large size (Swafford, 1993). Consequently, topological searches were undertaken using global branch swapping (a heuristic technique), the retention of ten trees at each step, using options for both simple and random order of entry of taxa (ten replications), and the retention of multiple equally parsimonious trees throughout the search. Also, three alternative branch-swapping methods (nearest-neighbor interchanges, tree-bisection-reconnection, and subtree-pruning-regrafting) were used to avoid local optima or “islands” of suboptimal topologies (Maddison, 1991; Page, 1993).

Several summary statistics were used to quantify the evidence supporting phylogenetic trees (Kluge and Farris, 1969; Farris, 1989): total tree length; consistency index, both including (CI) and excluding uninformative characters (CI*); homoplasy index, both including (HI) and excluding uninformative characters (HI*); retention index (RI); and rescaled consistency index (RC). All phylogenetic analyses were performed using the software PAUP version 3.1 (Swafford, 1993) and MacClade version 3.0 (Maddison and Maddison, 1992) on a Macintosh Quadra 800.

**Weighting of Characters.** — In addition to the equal (unit) weighting of characters employed in the baseline analyses, several alternative weighting schemes were used. Use of differential weighting in phylogenetic analysis remains controversial (Neff, 1986; Wheeler, 1986; Chippindale and Weins, 1994), but was included here to explore the impact of preconceived and post facto inferences concerning relative reliability of different character types. Two a priori differential weighting schemes were used: (1) “two-group” scheme—skeletal characters, considered here to be evolutionarily more conservative than more-superficial morphological features based on studies by Livezey (1986a, 1991, 1995a, 1995b, 1995c, in press a, in press b, in press c), were given a weight of two whereas other character groups were given a weight of one; and (2) “four-group” scheme—in which skeletal, tracheal, natal integumentary, and definitive integumentary characters were given weights of four, three, two, and one, respectively. Weighting of skeletal characters over those of the integument in this analysis was prompted further by the marginal confidence held in the homologies and the comparatively greater difficulties of variation and sexual dimorphism in several plumage characters included here (Appendix 1). Finally, I employed an a posteriori weighting method—successive weighting (Farris, 1969; Carpenter, 1988)—in which characters are iteratively reweighted (base weight of 2) on the basis of rescaled consistency indices of characters.

**Consensus Trees.** — Where multiple, equally parsimonious trees were discovered using the same set of analytical options, two consensus methods were employed to summarize graphically the topological regions given support by the set of shortest trees: strict consensus trees (showing only those nodes shared by all equally parsimonious trees; Sokal and Rohlff, 1981) and majority-rule consensus trees (Margush and McMorris, 1981). The utility of consensus trees does not enjoy unanimous recognition (e.g., Barrett et al., 1991), and it has been shown that such summary trees are seldom interpretable in the same ways as the actual trees from which they are compiled (Swafford, 1991; Wiley et al., 1991). Accordingly, con-
sensus methods were used simply to summarize areas of congruence among equally parsimonious trees.

Assessment of Support

**Bootstrapping of Characters.**—Standard summary statistics (e.g., consistency index) are flawed measures of empirical support for phylogenetic trees, because most are conditional in part on the number of taxa analyzed (Brooks et al., 1986; Archie, 1989a, 1989b, 1990; Sanderson and Donoghue, 1989; Faith and Cranston, 1991; Meier et al., 1991). Consequently, stability of nodes in minimal-length trees in this analysis was assessed using bootstrapping, although the limitations of this method in phylogenetic contexts remain controversial (Carpenter, 1992; Davis, 1993; Hillis and Bull, 1993; Penny et al., 1994). Applications involved generating 100 bootstrapped replicates using the same heuristic methods employed in the primary analyses, and summarizing those branches robust to this procedure through majority-rule consensus trees. The nature of the characters analyzed violates the assumption of statistical independence required for the bootstrapped percentages to be viewed as statistically rigorous levels of confidence (Felsenstein, 1985a; Sanderson, 1989), therefore the procedure was employed here as one of several quantitative indices to empirical support for branches (Bremer, 1994).

**Phylogenetic "Signal" and Suboptimal Trees.**—One measure of the phylogenetic "signal" of a data set is the skewness statistic for the distribution of resultant tree lengths (Hillis, 1991; Huelsenbeck, 1991; Hillis and Huelsenbeck, 1991; Källersjö et al., 1992). Exhaustive generation of tree lengths was not feasible for a data set of this size, therefore the skewness statistics ($g_1$) for random samples of 1000 trees (excluding the hypothetical ancestor) under each of the three a priori weighting schemes were calculated as an index to "phylogenetic signal" (Archie and Felsenstein, 1993). Values of $g_1$, however, provide poorly focused indices to phylogenetic informativeness, distributional characteristics of $g_1$ remain poorly known, and values can be subject to significant bias (Källersjö et al., 1992).

An alternative measure of support proposed by Bremer (1988), later dubbed the "decay index" by Donoghue et al. (1992), is the relative stability of nodes with respect to increased homoplasy (sensu lato, including both convergence and reversals). Specifically, the "decay index" for a given node is the minimal number of additional steps in tree length at which topologies not supporting the node are discovered. Estimates of the "decay index" were made for selected clades found to be robust under bootstrapping and various weighting regimes using exclusionary constraints in heuristic searches in PAUP.

**Topologically Constrained Analyses.**—The impact of particular topological constraints on the lengths of the shortest trees permissible for this matrix (i.e., the increases in total length) were estimated by performing searches constrained to preserve the specific phylogenetic relationship in question (while allowing topological modifications in other parts of the tree to accommodate this constraint). These comparisons were especially useful in quantifying the sacrifices in parsimony required to accommodate previously proposed phylogenetic relationships or traditional classifications in terms of the present data set.

**Phylogenetic Classification**

A Linnean classification, which incorporated inferred phylogenetic information while minimizing disruption of existing taxonomy, was prepared using the meth-
ods described by Wiley (1979, 1981) and Wiley et al. (1991). These methods include the use of the “sequencing convention” to avoid daunting numbers of taxonomic ranks, annotation of taxa in unresolved polytomes as *sedis mutabilis*, and identification of possibly paraphyletic or polyphyletic taxa through annotation as *incertae sedis*. Taxa applied to higher taxonomic categories follow standard requirements of availability and seniority (International Commission of Zoological Nomenclature, 1985), based on published synonymies and classifications (Phillips, 1922, 1923, 1925, 1926; Boetticher, 1942, 1952; Wolters, 1976).

Comparative Analyses

**General Objectives.**—Phylogenetic hypotheses provide an opportunity to examine the history of evolutionary change in selected life-historical parameters (Eldredge and Cracraft, 1980; Felsenstein, 1985b; Brooks and McLennan, 1991; Harvey and Pagel, 1991). In this study, a number of ecomorphological attributes not amenable to discrete coding and determination of homology were compiled and mapped *a posteriori* onto phylogenetic trees (Maddison, 1989; Mickevich and Weller, 1990) using MacClade 3.01 (Maddison and Maddison, 1992). Similar phylogenetic mapping was employed in analyses of other anseriform groups (Livezey, 1995a, 1995b, 1995c, in press a, in press b, in press c).

Detailed comparisons of the effects of different optimizations on the traces of attributes—e.g., ACCTRAN (length-neutral favoring of reversals over parallelisms) and DELTRAN (length-neutral favoring of parallelisms over reversals)—were not performed because no justification was evident for favoring one method over another. Moreover, two alternative character optimizations—Dollo optimization, in which it is required that each derived state is uniquely derived (Farris, 1977; Maddison et al., 1984), and the related option of irreversibility of character change (Sanderson, 1993)—were considered inappropriate for this analysis. However, regions of the trees in which ambiguity of traces occurred are shown as “equivocal” (Maddison and Maddison, 1992). Quantitative methods for analysis of characters with respect to a phytogeny (e.g., Coddington, 1988, 1994; Pagel and Harvey, 1988; Grafen, 1989, 1992; Pagel, 1994), including the preliminary methods for tracing continuous characters permitted by MacClade, were not used primarily because of the inclusion of a number of higher taxa (e.g., Cairineae, Anateae) in the analyses that contain species exhibiting a diversity of states for the parameters of interest as well as poor resolution in parts of the phylogeny (see beyond).

Attributes mapped include body mass (unweighted mean of sexes), mean clutch size, mean egg mass, relative clutch mass (mean mass of clutch divided by mean female body mass), preferred nest site (terrestrial or cavity), perching habit, relative frequency of diving, and period of activity (diurnal, crepuscular, or nocturnal). Data for these mapped attributes were taken from unpublished records associated with specimens and from the literature (Niethammer, 1953; Delacour, 1954, 1955, 1956, 1959; Scott, 1954; Hallstrom, 1956; Hobbs, 1957; Warham, 1959; Johnsgard, 1960a, 1961a, 1962, 1965a, 1965b, 1978; Schönwetter, 1961; Johnson, 1963; Weller, 1964a, 1964b, 1964c, 1976; Frith, 1967; Kear, 1970, 1975; Moffett, 1970; Siegfried, 1979; Clark, 1980; Wilson and Wilson, 1980; Brown et al., 1982; Humphrey and Livezey, 1982, 1985; Livezey and Humphrey, 1984a, 1984b; Eadie et al., 1988; Livezey, 1988; Madge and Burn, 1988; Rohwer, 1988; Marchant and Higgins, 1990; Triggs et al., 1991, 1992; Williams, 1991; McNeil et al., 1992; Dunning, 1993).
RESULTS

Shortest Trees

Characters Weighted Equally. —Forty most-parsimonious trees were found using equal weighting of characters, each having length 215, consistency index (CI) of 0.670 (0.543 excluding uninformative characters, CI*), homoplasy index (HI) of 0.367 (0.479 excluding uninformative characters, HI*), retention index (RI) of 0.641, and rescaled consistency index (RC) of 0.430. The skewness statistic (g1) for the unweighted matrix, based on 1000 randomly generated trees, was −0.612; this figure is substantially more negative than that expected for random data.

A strict consensus tree of the 40 topologies revealed only broad inferences shared by the “simplest” interpretations of the equally weighted characters (Fig. 1): (1) monophyly of the taxa analyzed exclusive of Stictonetta; (2) a sister relationship between Plectropterus and Sarkidiornis; (3) monophyly of the typical shelducks and sheldgeese (Tadorna, Cyanochen, Alopochen, Neoochen, and Chlorophaga), with intergeneric relationships as inferred by Livezey (1996a); (4) monophyly of Hymenolaimus, Tachyeres, and Merganetta, wherein the last two genera are sister-groups; and (5) a sister relationship between Salvadorina and Malacorhynchus. The solution set was unchanged if all characters were analyzed as unordered.

A majority of the shortest trees (Fig. 2) indicated the following additional phylogenetic structure: (1) a sister relationship between Plectropterus + Sarkidiornis and the clade comprising the typical shelducks and sheldgeese (39 of 40 trees); (2) a sister relationship between the preceding two clades and that comprising Hymenolaimus, Tachyeres, and Merganetta (38 of 40 trees); and (3) monophyly of the six taxa of “typical” anatines (Cairineae, Nettapodeae, Anataeae, Aythyini, Mergini, and Oxyurini), within which the three subtribes of Anatini defined by Livezey (1991) are monophyletic and the two subtribes of smaller “perching ducks” are sister-groups.

Comparative Consistencies. —Mean consistency indices for informative characters under equal weighting were: skeletal, 0.63 (n = 27; range, 0.33–1.00); tracheal, 0.75 (n = 2; range, 0.50–1.00); natal, 0.62 (n = 10; range, 0.20–1.00); and definitive integument, 0.64 (n = 27; range, 0.25–1.00). Consistency indices varied among the 40 trees, as a result of differences of single steps, in eight skeletal characters (characters 5, 10, 11, 21, 24, 25, 30, 35), one natal character (46), and ten characters of the definitive integument (55, 56, 91, 93, 95–100).

“Two-Group” Weighting. —A heuristic search employing the “two-group” a priori weighting scheme, within which skeletal characters were given a weight of two and all others retained weights of one, discovered four shortest trees sharing the following summary statistics: length = 290, CI = 0.676 (CI* = 0.554), HI = 0.372 (HI* = 0.474), RI = 0.674, and RC = 0.455. The skewness statistic (g1) for the “two-group” matrix, based on 1000 randomly generated trees, was −0.584. The four topologies differed only in the relationships inferred among the six taxa of “typical” anatines. A strict consensus tree of these four shortest topologies (Fig. 3) confirmed the phylogenetic structure shared by a majority of the trees found under equal weighting (Fig. 2), with the following additional resolutions: (1) the clade comprising Salvadorina and Malacorhynchus is inferred to be the sister-group of the six taxa of “typical” Anatinae; and (2) within the latter, the Mergini and Oxyurini are inferred to be sister tribes. A majority-rule consensus tree of the topologies under “two-group” weighting revealed that three of the
Fig. 1.—Strict consensus tree of 40 equally parsimonious trees for 19 taxa of Anatidae under equal weighting of characters.
Fig. 2.—Majority-rule consensus tree of 40 equally parsimonious trees for 19 taxa of Anatidae under equal weighting of characters. Percentages of these 40 trees in which each branch was conserved are shown.
Fig. 3.—Strict consensus tree of four equally parsimonious trees for 19 taxa of Anatidae, wherein skeletal characters were given a weight of two and all other characters a weight of one ("two-group" weighting scheme).
four shortest trees confirmed the sister relationship between the Anateae and the two, generically restricted subtribes of "perching ducks," Cairininae and Nettapodeae (Fig. 4). This solution set is topologically identical to that based on an analysis in which all characters were treated as unordered.

Numbers of unambiguous character changes supporting each branch in the first of the four most-parsimonious trees varied from the single synapomorphy uniting Salvadorina and Malacorhynchus with the "typical" anatines, to the seven uniting Hymenolaimus, Tachyeres, and Merganetta (Fig. 5); identities of supporting characters are shown in Figure 6. As in all the weighting schemes for these taxa, the most prominent component of differentiation among taxa was autapomorphy, which does not contribute to resolution of phylogenetic relationships. The topological variants within the Anatinae differed primarily in the transformations inferred for characters 46, 56, and 99 (Appendices 1, 2).

"Four-Group" Weighting.—Under the "four-group" weighting scheme, wherein weights of 4, 3, 2, and 1 were applied to characters of the skeleton, trachea, natal integument, and definitive integument, respectively, a single most-parsimonious tree was found. The skewness statistic ($g_4$) for the "four-group" matrix, based on 1000 randomly generated trees, was -0.588. The topology of this tree was identical to the first of the four shortest trees recovered under the "two-group" weighting scheme (Fig. 5, 6), and had the following summary statistics: total length = 476, CI = 0.676 (CI* = 0.559), HI = 0.378 (HI* = 0.471), RI = 0.691, and RC = 0.468. Analysis using the same weighting scheme but in which all characters were treated as unordered resulted in a single tree that differed in only two topological features: (1) Plectropterus was placed as the sister-group to all included taxa but Stictonetta (as in Livezey, 1986a); and (2) the Cairineae was placed as the sister-group to other Anatinae, including Salvadorina + Malacorhynchus.

Successive Weighting.—Using the equally weighted data matrix as a starting point (admitting 40 shortest trees), two successive reweightings of the characters (base weight 2, using RC) recovered, respectively, eight and two trees of equal length; these two trees were resistant to additional reweighting cycles. Both trees had the following summary statistics: length = 230; CI = 0.857 (CI* = 0.703); HI = 0.178 (HI* = 0.315); RI = 0.828; and RC = 0.709. The skewness statistic ($g_4$) for 1000 randomly generated trees based on the successively weighted matrix was -0.772.

A strict consensus tree of these two solutions differed from those for the shortest trees derived using a priori weighting schemes in two important ways (Fig. 7): (1) placement of the Mergini as the sister-group of all taxa exclusive of Stictonetta and the clade comprising Salvadorina, Malacorhynchus, Nettapodeae, Anateae, Aythyini, and Oxyurini (a placement made on first iteration); and (2) placement of the Cairineae as the sister-group of the clade comprising Plectropterus and Sarkidiornis (placement made on the second iteration). The interrelated effects of reweighting on the distributions of character changes in the trees are difficult to interpret, but examination of supporting characters indicates that comparatively few characters underlie these two divergent inferences. Topologically identical series of solutions were found using successive weighting of unordered characters.

The position of the Mergini reflects, at least in part, shared changes in characters 95 (lobation of hallux), 98 (ground color of secondary remiges), and 99 (color of wing linings). The position of the Cairineae in the successive weighting analysis evidently stems from a number of characters that members of the subtribe
Fig. 4.—Majority-rule consensus tree of four equally parsimonious trees for 19 taxa of Anatidae, wherein skeletal characters were given a weight of two and all other characters a weight of one ("two-group" weighting scheme). Percentages of these four trees in which each branch was conserved are shown.
shared with *Plectropterus, Sarkidiornis*, or (less commonly) both genera: characters 5 (processus supraorbitalis), 10 (spina externa sterni), 64 (unfeathered facial region), 93 (coloration of tertials), 96 (black dorsal color), and 99 (color of wing linings). Of the characters primarily involved in these two inferences, one posed difficulties in codings for several taxa (character 99) and only three achieved a CI of 1.00 (characters 5, 10, and 96). In addition, most of the foregoing characters suffered declines in consistency with the inclusion of more genera of waterfowl or species-level codings (Livezey, 1991, 1995b, in press a) of magnitudes in excess of those typically associated with the inclusion of additional taxa (Sanderson and Donoghue, 1989).

**Support for Branches**

Bootstrapping of Characters.—Under equal weighting of characters, a majority-rule consensus tree of 100 bootstrapped replicates conserved only the nine clades shared by all 40 shortest trees (Fig. 1); support for these branches ranged from 56% for the four genera of sheldgeese to 99% for the ingroup exclusive of *Stictonetta* (Fig. 8). Identical groups were preserved in a majority-rule consensus tree of 100 bootstrapped replicates under the “two-group” weighting scheme, with only minor differences in percentages (Fig. 9). A majority-rule consensus tree of 100 bootstrapped replicates under the “four-group” weighting scheme retained the same groupings with the exception of that uniting *Salvadorina* with *Malacorhynchus* (Fig. 10). Bootstrapping after two iterations of successive
weighting produced a majority-rule consensus tree topologically identical to those derived from bootstrapping under equal weighting or "two-group" weighting (Fig. 8, 9), with the exception of the placement of the Cairineae as sister-group of Plectropterus and Sarkidiornis, a grouping retained in only 59% of the replicates (Fig. 11).

Near-shortest Trees.—Under equal weighting, numbers of equally parsimonious trees increased precipitously with admission of suboptimal solutions; retention of trees having only two additional steps resulted in the discovery of over 3500 trees (Table 2). Subjecting the matrix to "two-group" weighting lowered the numbers of topologies of near-minimal lengths considerably, and "four-group" weighting further narrowed the solution sets at near-minimal lengths (Table 2). Tallies of near-minimal tree lengths under successive weighting resembled those for the "four-group" weighting scheme (Table 2).

Bremer or "Decay" Indices.—Stability of several clades common to most weighting schemes or consensus techniques with respect to additional homoplasy (i.e., suboptimal tree lengths) was measured using Bremer or "decay" indices. Monophyly of the ingroup exclusive of Stictonetta was resistant to increased homoplasy under all weighting schemes, e.g., requiring an additional six steps under equal weighting to disrupt the clade (Table 3). The clade comprising Hymenolaimus, Tachyeres, and Merganetta showed moderately high resistance to increased homoplasy, an integrity that was magnified under regimes that weighted skeletal characters highly (Table 3). Three other recurrent clades—typical shelducks and sheldgeese, Plectropterus + Sarkidiornis, and Malacorhynchus + Salvadorina—required only one to three additional steps before alternative arrangements were admissible under most weighting regimes (Table 3).

Ecomorphological Evolution

Morphological Attributes.—For purposes of a posteriori mapping, the first of the four shortest trees derived using "two-group" weighting of characters was used (Fig. 5, 6), a tree sharing most of the well-supported elements common to trees based on other analyses (Fig. 1–4, 7–11). In spite of the generalizations necessary for coding parameters for genera and higher taxa in the ingroup, broad evolutionary patterns in body mass, sexual size dimorphism, and sexual dichromatism were evident. Body mass appears to have undergone a substantial decrease in the common ancestor of the ingroup, although the ancestral state of this attribute is questionable; significant, subsequent increases in body mass characterize three clades: Sarkidiornis + Plectropterus, the sheldgeese, and Tachyeres (Fig. 12A). Uncertainty in the states of associated stems makes the homology of the large body masses of the first two clades indeterminate.

Patterns of sexual size dimorphism within the ingroup shows a similar pattern to that evident in body mass, although increases in the former include Tadorna (indicating homology in the increase in a clade comprising seven genera), Merganetta (interpretable as homologous to that in Tachyeres), and the Cairineae (Fig. 6.—Detailed phylogenetic tree, one of four equally parsimonious trees for 19 taxa of Anatidae under the "two-group" weighting scheme, showing the characters unambiguously supporting each branch. Character numbers correspond to those used in the character descriptions (Appendix 1) and data matrix (Appendix 2).
Fig. 7.—Strict consensus tree of the two shortest phylogenetic trees for 19 taxa of Anatidae converged upon after three successive reweightings of characters based on rescaled consistency indices, using equal initial weights and a base for reweighting of two.

12B). The moderately high dimorphism of the Cairineae is more parsimoniously interpreted under the alternative position of this group, as sister-group to Sarkidiornis and Plectropterus, supported by successive weighting (Fig. 7, 11).

Sexual dichromatism manifested evolutionary patterns completely distinct from those for sexual size dimorphism (Fig. 12C). Comparatively minor, quantitative dichromatism appears to have evolved independently in Sarkidiornis, Tachyeres, and basal Anateae; this intermediate state evidently gave rise to pronounced, qualitative dichromatism in a number of more-derived members of the latter subtribe (Livezey, 1991). Distinct, qualitative sexual dichromatism appears to have evolved in four other lineages independently: Chloephaga, Tadorna, Merganetta, and the remaining taxa of "typical" Anatinae (Fig. 12C).

Parameters of Reproduction.—Polygyny without establishment of significant pair-bonds, inferred to be derived in this group of Anseriformes, is shared by the clade comprising Plectropterus and Sarkidiornis and the Cairineae (Fig. 12D). Among Anseriformes, parental investment by males is inversely correlated with sexual size dimorphism (Sigurjónsdóttir, 1981), an attribute that was especially high in these three taxa (Fig. 12B; Livezey and Humphrey, 1984a). The association between paternal investment and sexual dichromatism in waterfowl is less clear (Johnsgard, 1962; Scott and Clutton-Brock, 1989). Sexual dichromatism in Anseriformes has traditionally been interpreted in terms of isolating mechanisms among closely related species (e.g., Sibley, 1957; Johnsgard, 1960a, 1963), a perspective of questionable utility among these diverse taxa showing little or no
Fig. 8.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under equal weighting of characters.
Fig. 9.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under "two-group" weighting.
Fig. 10.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates under “four-group” weighting.
Fig. 11.—Majority-rule consensus trees for 19 taxa of Anatidae of 100 bootstrapped replicates for matrix subjected to successive weighting (see text for details).
Table 2.—Numbers of trees of minimal and near-minimal lengths under three a priori and one successive weighting schemes for 19 generic, subtribal, and tribal taxa of Anatidae.

| Weighting scheme | Minimal length (m) | m   | m + 1 | m + 2 | m + 3 | m + 4 |
|------------------|--------------------|------|-------|-------|-------|-------|
| Unit (equal)      | 215                | 40   | 488   | 3503  | —     | —     |
| “Two-group”       | 290                | 4    | 34    | 148   | 657   | —     |
| “Four-group”      | 476                | 1    | 9     | 28    | 114   | 425   |
| Successive       | 230                | 2    | 8     | 36    | 188   | 673   |

tendency toward hybridization (Scherer and Hilsberg, 1982) and in light of conceptual difficulties with this emphasis (Livezey, 1991, 1995b).

Preferred nest site appears to have undergone two independent shifts to cavities, in *Tadorna* and (within the context of this particular tree, homologously) in the Cairinae and Nettapodeae (Fig. 12E). Modal clutch size varied greatly in this group (Fig. 12F), and states of terminal taxa rendered hypotheses of states indeterminate for most stems and characterization of the Anateae, Mergini, Oxyurini, and Aythyini problematic. Suggested evolutionary changes in this parameter are (Fig. 12F): (1) an increase in the ancestor of the ingroup; (2) several increases within the shelducks and sheldgeese; (3) decreases, possibly homologous, in *Hymenolaimus* and *Merganetta*; and (4) increases, interpretable as homologous within the context of this particular tree, in the Cairinae and Nettapodeae.

Mean egg masses (g) for the eight key genera of the ingroup were: *Stictonetta* (66), *Plectropterus* (131), *Sarkidiornis* (65), *Hymenolaimus* (73), *Merganetta* (62), *Tachyeres* (115–167), *Malacorhynchus* (31), and *Salvadorina* (57). Egg mass is generally correlated with body mass in the ingroup, making a mapping of this parameter largely redundant with that presented for body mass (Fig. 12A). Explicit mapping of relative clutch mass also proved intractable for these taxa because of variation in the three parameters composing this ratio (female body mass, egg mass, clutch size), some of which are poorly known for some genera. In addition, generalizing this ratio for the tribal and generic vectors also proved problematic; the range of values within several subtribal and tribal taxa encompassed a greater range than all eight of the genera of primary interest combined. Estimates for relative clutch masses (percentages of female body mass, largely based on Rohwer, 1988) for the key ingroup genera were as follows: *Stictonetta* (55), 
Plectropterus

Table 3.—Bremer or “decay” indices for selected clades within 19 generic, subtribal, and tribal taxa of Anatidae under three a priori and one successive weighting schemes. Percentage of minimal total tree length represented by each index is given in parentheses to facilitate comparisons across weighting schemes.

| Clade                        | Weighting scheme |
|------------------------------|------------------|
|                              | Equal | Two-group | Four-group | Successive |
| **Tadorninae + Anatinae**     | 6 (2.8)| 7 (2.4)   | 8 (1.7)    | 6 (2.6)    |
| **Tadornina**                | 1 (0.5)| 2 (0.7)   | 3 (0.6)    | 1 (0.4)    |
| **Plectropterus + Sarkidiornis** | 3 (1.4)| 5 (1.7)   | 5 (1.1)    | 5 (2.2)    |
| **Hymenolaimus + Tachyeres + Merganetta** | 3 (1.4)| 4 (1.4)   | 20 (4.2)   | 9 (3.9)    |
| **Malacorhynchus + Salvadorina** | 2 (0.9)| 4 (1.4)   | 1 (0.2)    | 2 (0.9)    |

* Includes all taxa analyzed herein except hypothetical ancestor and *Stictonetta*.

* Includes *Cyanoche, Alopochen, Neochen, Chloephaga, and Tadorna.*
Fig. 12.—Mapping of eight ecomorphological attributes on the first of four minimal-length trees recovered under “two-group” weighting of characters (Appendices 1, 2): A—body mass, B—sexual size dimorphism, C—sexual dichromatism, D—mating system, E—typical nest site, F—clutch size, G—paternal attendance of broods, and H—diving habit. The tree shown is topologically identical to the single shortest tree found under the “four-group” weighting scheme, in which a soft polytomy involving the taxa Aythyini, Oxyurini, Mergini, Cairineae, Nettapodeae, and Anateae is depicted as resolved.
In addition to the three taxa in which polygyny is typical (Plectropterus, Sarkidiornis, and Cairineae), a derived loss of paternal attendance of broods is characteristic of the Aythyini, Mergini, and Oxyurini; variation within the Anateae in...
this attribute necessitated coding the taxon as polymorphic (Fig. 12G). Within the phylogenetic hypothesis used as a basis for mapping, the simplest evolutionary pattern suggested is a loss of paternal attendance in the ancestor of the “typical” Anatinae, with subsequent, independent reversals in the Nettapodeae and some Anateae.
Ecological Trends.—Most ecological attributes successfully mapped in other anseriform groups (Livezey, 1995b, 1995c, in press a, in press b, in press c) remain too poorly known for the key genera under study here, and furthermore were variable within the higher taxa included in this analysis. These inadequately documented attributes include: diel pattern, in which most species are probably
crepuscular, but some like marine *Tachyeres* are influenced by tides (Livezey, 1988; McNeil et al., 1992); diet, in which most species probably feed on both plants and invertebrates, rarely vertebrates; aquatic habitat, in which all species are primarily freshwater except most *Tachyeres*, some *Tadorna*, some *Chloephaga*, and most Mergini; nest parasitism, which is probably infrequent in most ingroup taxa as in most Anseriformes (Rohwer and Freeman, 1989); formation of crèches (Eadie et al., 1988); parental carrying of young (Johnsgard and Kear, 1968) through the air (reported in *Sarkidiornis*, *Tadorna*, *Alopochen*, *Chloephaga*, and some members of the *Cairineae*, *Anateae*, Mergini, and Oxyurini) or on water (reported in *Salvadorina*, and some members of *Chloephaga*, the Mergini and Oxyurini); and migratory habit, wherein most species show variable seasonal movements, with the notable exceptions being sedentary *Hymenolaimus* and *Merganetta*, and flightless species of *Tachyeres*.

Diving habit is characteristic of four taxa in this analysis, evidently representing either: (1) three or four convergent acquisitions, the interpretation most consistent with most described evolutionary scenarios (Delacour and Mayr, 1945; Johnsgard, 1978; Faith, 1989); or (2) a single derivation in the ancestor of the *Tadorninae* and *Anatinae* followed by three independent losses (Fig. 12H). Possible homoplasy in several morphological characters related to diving habit or its loss (e.g., characters 38, 41), both having locally high consistencies but showing global homoplasy (Livezey, 1986a; Faith, 1989), might compromise their utility for phylogenetic inference (especially with respect to *Hymenolaimus*, *Merganetta*, and *Tachyeres*). Several of these diving-related characters are coded for this analysis as lacking for tribes in which a majority of the members possess the trait (Aythyini, Mergini, Oxyurini), because the absence of the character in basal members of each tribe indicates the character was acquired independently in more-derived members of these groups (Livezey, 1995b, 1995c, in press b).

**DISCUSSION**

**Phylogenetic Inferences**

**Points of Concern.**—With the exception of the support for the monophyly of the ingroup exclusive of *Stictonetta* (i.e., *Tadorninae* + *Anatinae*), most members of the ingroup are characterized more by unique divergence than nested, unifying characters. For example, *Merganetta* and *Tachyeres* are inferred to be sister-genera on the basis of two unambiguous synapomorphies, whereas the genera are themselves supported by 15 and 13 autapomorphies, respectively (Fig. 6). In part because of concerns regarding possible homoplasy stemming from convergent life histories, I remain somewhat suspicious with respect to the clade comprising *Hymenolaimus*, *Merganetta*, and *Tachyeres*, in part because of the possible effects of “long-branch attraction” (see below). However, there are seven unambiguous characters that support this clade (Fig. 6), the grouping is comparatively robust with respect to weighting schemes (Table 3; Fig. 1–11), and there is a significant sacrifice of parsimony (Table 4) required to accommodate the positions of these genera proposed by Johnsgard (1965a, 1978, 1979).

The position of the *Cairineae* remains a challenging problem; this group comprises three genera and five species traditionally included among the “perching ducks” (e.g., Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1961a, 1965a, 1978, 1979), but was inferred by Livezey (1991) to be the sister-group of a clade comprising the *Nettapodeae* and *Anateae*. In this study, most weighting schemes
Table 4.—Minimal numbers of additional steps required to preserve previously hypothesized taxonomic grouping among 19 generic, subtribal, and tribal taxa of Anatidae, under three a priori and one successive weighting schemes. Percentage of minimal total tree length represented by each index is given in parentheses to facilitate comparisons across weighting schemes.

| Taxonomic group | Equal | Two-group | Four-group | Successive |
|-----------------|-------|-----------|------------|------------|
| Tribe Cairinini\(^a\) | 2 (0.9) | 6 (2.1) | 12 (2.5) | 3 (1.3) |
| Subfamily Anatinae\(^b\) | 10 (4.7) | 18 (6.2) | 31 (6.5) | 18 (7.8) |
| Subfamily Anatinae\(^c\) exclusive of Hymenolaimus | 2 (0.9) | 6 (2.1) | 12 (2.5) | 5 (2.2) |
| Tree based on Johnsgard (1961a, 1978)\(^d\) | 36 (16.7) | 62 (21.4) | 117 (24.6) | 58 (25.2) |
| Tree depicted by Livezey (1986a:fig. 1)\(^e\) | 16 (7.4) | 19 (6.6) | 29 (6.1) | 43 (18.7) |
| Sicutonetta + Oxyurini\(^f\) | 7 (3.3) | 16 (5.5) | 31 (6.5) | 9 (3.9) |

\(^a\) Of the taxa defined herein, includes Plectropterus, Sarkidiornis, Cairinieae, and Nettapodeae; Amazonetta and Callonetta, included in this tribe by Johnsgard (1978), are here included as basal members of the Anataceae (Livezey, 1991).

\(^b\) Includes Plectropterus, Sarkidiornis, Hymenolaimus, Merganetta, Malacorhynchus, Salvadorina, Cairinieae, Nettapodeae, Anataceae, Aythyni, Mergini, and Oxyurini (Johnsgard, 1965a, 1978, 1979).

\(^c\) Conservative reconstruction of phylogenetic diagrams depicted by Johnsgard (1961a, 1978) as permitted using the present taxonomic units (Fig. 13).

\(^d\) Constraint follows Livezey (1986a:fig. 1), except Anatinae simplified to polytomy involving Salvadorina (missing taxon), Cairinieae, Nettapodeae, Anataceae, Aythyni, and Mergini + Oxyurini.

\(^e\) Grouping followed by Marchant and Higgins (1990).

either: (1) failed to establish the higher-order relationships of this taxon (Fig. 1, 8–10); or (2) placed the Cairinieae as the sister-group to the Nettapodeae (contra Livezey, 1991) with or without indicating a sister-relationship of the latter to the Anataceae (Fig. 2–6). Under “four-group” weighting, the alternative treatment of two ordered characters as unordered alone resulted in the placement of the Cairinieae as the sister-group of other Anatinae, along with an associated placement of Plectropterus as sister-group of Tadorninae + Anatinae. Under successive weighting, the Cairinieae were inferred to be the sister-group of the “tadornine” clade comprising Plectropterus and Sarkidiornis (Fig. 7, 11); this was the only significant discrepancy between the findings of a priori and successive weighting schemes that were robust to bootstrapping. Pending further study, I recommend tentatively retaining the Cairinieae, Nettapodeae, and Anataceae as subtribes of the Anatini (as in Livezey, 1991), while noting the likely monophyly of the first two subtribes (contra Livezey, 1991) and the less well-supported alternative placement of the Cairinieae (apart from the Nettapodeae) with Plectropterus and Sarkidiornis (contra Livezey, 1986a, 1991).

One analytical artifact of parsimony analysis is “long-branch attraction” or the tendency for branches showing many character changes to be joined under certain analytical circumstances (Felsenstein, 1978; Huelsenbeck and Hillis, 1993; Penny et al., 1994; Hillis, 1995; Huelsenbeck, 1995). Three couplets of taxa united in this analysis might be vulnerable to this artifact (Fig. 6): (1) Plectropterus and Sarkidiornis, (2) Merganetta and Tachyeres (perhaps also including Hymenolaimus), and (3) Malacorhynchus and Salvadorina. The extent to which these groupings were fostered by “long-branch attraction” cannot be tested at present, but the possibility should be considered in any assessment of these groupings of problematic genera.
Apparent intertribal relationships within the Anatinae indicated in this analysis are among the weakest aspects of the study. None of the weighting schemes provided well-supported resolution of relationships among the Cairininae, Nettapodeae, Anateae, Aythyini, Mergini, and Oxyurini (Fig. 8–11). A sister-group relationship between the Mergini and Oxyurini was indicated in a number of the shortest topologies recovered (Fig. 3–6), an inference based on a single apomorphy related to the diving-related modification of the pelvic girdle and very possibly convergent (Appendix 1). The agreement between this inference and that indicated in the single tree depicted by Livezey (1986a) provides no independent confirmation because both studies shared most osteological characters, and furthermore supplementary analysis of the matrix used by Livezey (1986a) revealed that other arrangements were equally parsimonious (J. Harshman, personal communication).

Comparison with Previous Studies.—Congruence among independent studies is an important component of the assessment of phylogenetic reconstruction (Mickevich and Johnson, 1976; Mickevich, 1978; Hillis, 1987, 1995; Miyamoto and Fitch, 1995). Unfortunately, little phylogenetic work has been performed for the taxa of concern here, a deficiency particularly marked for molecular data and which significantly limits the comparisons that are possible. Support in this analysis for a clade comprising Plectropterus and Sarkidiornis as the sister-group of the four genera of “typical” shelducks and sheldgeese (Fig. 2–6) represents a significant departure from the position inferred for Plectropterus by Livezey (1986a). This revised inference, however, is consistent with the close relationship between these genera proposed by most recent workers (Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1961a, 1965a, 1978, 1979). However, available evidence confirms the polyphyletic nature of the “Tribe Cairinini” as generally constituted (comprising nine genera and 13 species; e.g., Johnsgard, 1965a, 1978).

The close relationships inferred among the genera Hymenolaimus, Tachyeres, and Merganetta (Fig. 1–11) are consistent with several other anatomical and behavioral characteristics. All three are extremely territorial, even by tadornine standards, and this pugnacity is shown by both sexes (Wright, 1965; Kear and Steel, 1971; Kear, 1972; Weller, 1976; Eldridge, 1985, 1986a, 1986b; Livezey and Humphrey, 1985; Veltman and Williams, 1990). Also, in all three genera, territorial combat often involves blows using the variably developed metacarpal wing-knobs (Kear and Steel, 1971; Weller, 1968; Livezey and Humphrey, 1985; Eldridge, 1986b). In part because of inadequately defined states and a paucity of comparative data, no consistent indications of phylogenetic relationships are indicated by courtship displays and other ritualized behaviors in these three genera (Moynihan, 1958; Johnsgard, 1961a, 1965a, 1966; Eldridge, 1979, 1985, 1986a).

The inferred positions of Salvadorina and Malacorhynchus, found herein to be sister-genera and together composing the sister-group of “typical” Anatinae under the two a priori weighting schemes (Fig. 1–11), represent significant departures from that inferred for Malacorhynchus by Livezey (1986a) or those assumed for Salvadorina by Livezey (1986a, 1991). The present hypothesis seems intuitively consistent with the “subfamilial intermediacy” implied by the placements of these genera as tadornine or as basal, “aberrant” anatines (Delacour and Mayr, 1945; Delacour, 1959; Johnsgard, 1965a, 1965b, 1978) and is consistent with skeletal similarities noted by Mlikovsky (1989). This analysis indicates that the characters shared between Salvadorina and the genera Hymenolaimus and Merganetta cited by Kear (1975) are either plesiomorphous or homoplasious; however, the rec-
ommendation by Kear (1975) that *Salvadorina* be recognized as a genus distinct from *Anas* is supported. The territorial behavior of *Salvadorina* (Hallstrom, 1956; Kear, 1975)—shared by the two aforementioned genera, most Tadorninae, and some basal Anatini—also appears to be locally plesiomorphous. Although Kear (1975) reported that *Salvadorina* uses wing knobs in combat, the presence of "true" calcar alae (character 30) in this genus is unlikely based on examination of skin specimens (Appendices 1, 2).

Searches under topological constraints (Table 4) were employed to provide quantitative assessments of the "penalties" (minimal increases in total tree length) of preserving groupings suggested by other classifications and hypotheses. To preserve as monophyletic the traditionally constituted "perching ducks" (assuming no specific topology within the group) requires, depending on weighting scheme, an additional 2–12 steps (1–3% increase in total length; Table 4). Constraining the analyses to preserve as monophyletic the Anatinae as traditionally constituted (e.g., Johnsgard, 1965a, 1978, 1979), without assuming any constraints regarding topology within the subfamily, requires an additional 10–31 steps or 5–8% increase in tree length (Table 4). Exclusion of *Hymenolaimus* from this group revealed that a majority of the additional steps were attributable to the classification of this genus alone (Table 4). Analyses constrained to preserve all of the intergeneric relationships depicted by Johnsgard (1961a, 1978), graphically summarized in Figure 13, indicated that 36–117 additional steps were required using the present data matrix, representing an increase in total tree length of 17–25% (Table 4). A similar constrained analysis determined that the tree depicted by Livezey (1986a), to the level of detail permitted by taxa analyzed in both studies,
would require 16–43 extra steps (6.1–18.7% increase in total length), depending on weighting scheme (Table 4).

A sister-relationship between Stictonetta and the Oxyurini (cf. Fullagar et al., 1990; Marchant and Higgins, 1990), without assuming any specific placement of the composite group within the tree, requires a minimum of 7–31 additional steps, a 3–7% increase in total tree length (Table 4). Movement of Stictonetta with the Oxyurini (cf. Marchant and Higgins, 1990) to the position proposed for the latter by Sibley and Monroe (1990)—as sister-group of all Anseriformes exclusive of Anhimidae, Anseranas, Dendrocygna, and Thalassornis—requires several steps in addition to those required simply to link the Oxyurini with Stictonetta (Livezey, in press c).

Proposed Classification of Modern Members

Subfamilial Taxa.—Based on the phylogenetic inferences using the weighting schemes considered to favor the most reliable characters (conservatively summarized in Fig. 3, preferred variant shown in Fig. 4), I recognize three subfamilies within the present group of 19 taxa (Appendix 3): Stictonettinae (monotypic, Stictonetta naevosa), Tadorninae (three modern tribes, ten modern genera), and Anatinae (five modern tribes, one new, and one incertae sedis). This subfamilial taxonomy differs from that proposed by Livezey (1986a) in the inclusion of Plectropterus, formerly a monotypic subfamily Plectropterinae Gray, 1840, as a tribe (with Sarkidiornis) in the Tadorninae (Appendix 3).

Tribes of Tadorninae.—The Tadorninae here reconstructed (Fig. 3–6), comprise three tribes (Appendix 3): Tribe Merganettini, comprising Hymenolaimus, Tachyeres, and Merganetta; Tribe Plectropterini, comprising Plectropterus and Sarkidiornis; and Tribe Tadornini, comprising the subtribes Chlorophageae (Cyanochen, Alopochen, Neochen, Chloephaga) and Tadornae (Tadorna). Differences from the generic classification given by Livezey (1986a) include: (1) inclusion of Plectropterus (formerly a separate subfamily) with Sarkidiornis (formerly a separate tribe) as sister-groups in a single tribe of the Tadorninae; (2) monophyly of the Tadornini, in which the subtribe Tadornae (comprising Tadorna) is the sister-group of the sheldgeese (formerly subtribes Cyanocheneae and Chlorophageae; Livezey, in press a); and (3) exclusion of Malacorhynchus from the subfamily. Furthermore, contrary to the provisional allocation by Livezey (1991), Salvadorina is not included in the Tadorninae.

Tribes of Anatinae.—Five modern tribes are recognized in this subfamily (Appendix 3), in which the order of all but the first is unresolved, hence the subfamily is annotated sedis mutabilis (Fig. 3, 4): Tribe Malacorhynchini, new taxon, comprising Malacorhynchus and Salvadorina; Tribe Anatini, incertae sedis, tentatively comprising three subtribes Cairineae, Nettapodeae, and Anateae (Livezey, 1991); Tribe Aythini (Livezey, in press b); Tribe Mergini (Livezey, 1995b); and Tribe Oxyurini (Livezey, 1995c). Generic composition of the Aythini, Mergini, and Oxyurini remains unchanged from that proposed by Livezey (1986a), and the provisional generic composition of the Anatini advocated here follows that proposed by Livezey (1991). Provisional retention of the three subtribes of the Anatini recognized by Livezey (1991) is recommended, in part, to avoid the confusion that would stem from applying the tribal taxon “Cairinini,” traditionally including nine genera and 13 species, to a restricted group comprising only the Cairineae (three genera, five species) and Nettapodeae (two genera, four species), and excluding Plectropterus, Sarkidiornis, Amazonetta, and Callonetta.
Biogeographical Patterns

Biogeographical patterns in this region of the phylogeny of Anseriformes are complicated by the broad but different distributional patterns shown by several taxa (e.g., Anataeae, Aythyini, and Oxyurini). Furthermore, comparisons with the distributional limits of tribes given by Weller (1964d) are problematic because of important differences in the composition of tribes (especially Cairinini, Anatini) defined in this study and those used by Weller (1964d). In spite of these difficulties, the frequency of predominantly southern-hemisphere genera in these taxa (Stictonetta, Plectropterus, Sarkidiornis, most Tadornini, Hymenolaimus, Tachyeres, Merganetta, Salvadorina, Malacorhynchus), as well as the southern distributions of basal members of the Anatini (Livezey, 1991) and Oxyurini (Livezey, 1995c), corroborate the hypothesis of southern origins for the Stictonettinae, Tadorninae, and Anatinae. This inference is consistent with a larger hypothesis of a southern-hemispheric origin for the Anseriformes (Livezey, 1986a, 1989).

The sister-relationship inferred for Merganetta and Tachyeres (Fig. 1–11) is at least consistent with the Neotropical distributions of the genera (Delacour, 1954, 1959). Similarly, the distributional limits of another counterintuitive pair of genera inferred to be sister-groups, Salvadorina and Malacorhynchus, is geographically “parsimonious” given the Australasian distributions of the two genera (Delacour, 1959).

Several fossil taxa assignable to this region of the anseriform phylogeny also indicate the predominantly southern-hemisphere distributions of the member taxa. The peculiar genus Euryanas finschi from New Zealand (Van Beneden, 1875, 1876; Oliver, 1930, 1945) was most parsimoniously placed as the sister-group of the present ingroup exclusive of Stictonetta in an earlier, more-limited analysis (Livezey, 1989). Another subfossil endemic of New Zealand, Pachyanas chathamica (Oliver, 1955), also appears to belong to the Tadornini (unpublished study of material recently collected by P. Millener). Other fossil taxa assignable to the Tadornini include the Madagascan genera Centrornis (Andrews, 1897) and Chenalopex (Andrews, 1897; Brodkorb, 1964), and the Nearctic genera Anabernicula (Ross, 1935; Howard, 1946, 1964a, 1964b; Short, 1970) and Brantadorna (Howard, 1963).

Directions for Future Study

A number of aspects of anseriform phylogeny remain poorly understood, and a majority of these involve the relationships among the taxa analyzed in the present analysis (Fig. 1–11). This state of affairs is ironic, given that the original motivation for the earlier analysis (Livezey, 1986a), which formed the basis for this and other species-level studies, was the placement of the genus Tachyeres among the Tadorninae and Anatinae. This situation is particularly vexing in that these poorly resolved segments of the phylogeny of waterfowl include those among most tribes of the Anatinae, the largest subfamily in the order and one of particular importance for comparative studies (Sigurjonsdottir, 1981; Faith, 1989; Scott and Clutton-Brock, 1989). Poor resolution, combined with a great diversity of physical and ecological characters among genera in the vicinity of the “tadornine–anatine divergence,” rendered many ecomorphological parameters all but incomparable in this study (Fig. 12 and associated text).

In order to resolve the phylogenetic relationships that remain resistant to analysis, characters (morphological, molecular, or behavioral) of intermediate evolu-
tionary conservatism are needed. Characters of greatest utility would be those which are less conservative than those uniting the Tadorninae and Anatinae, but more conservative than those accumulating as autapomorphies in the present analysis (some of which are useful, however, as synapomorphies for polytypic genera). Morphological systems deserving of particular attention in this regard are accessible only using anatomical (fluid-preserved) specimens, however, and therefore will not be useful for the placement of fossil taxa in this region of the anseriform phylogeny. These systems include the anatomical details of tracheal and syringeal myology and osteology, cranial and pelvic myology, pteryography, and buccolingual integument.

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APPENDIX 1

Character Descriptions

Characters are numbered continuously through skeletal, tracheal, natal, and definitive subgroups. Characters for which polarity remains undetermined are indicated by asterisks. Consistency indices (CI) listed are those associated with trees derived under equal weighting of characters; ranges of indices are given for those characters in which CIs varied among equally parsimonious trees.
Skeleton.—Those adapted from Livezey (1986a) are revised to include only relevant states and to assume local polarity. Synapomorphies for genera within subtribes of Anatini from Livezey (1991), as well as tribal synapomorphies for Aythyini (Livezey, in press b), Mergini (Livezey, 1995a), and Oxyurini (Livezey, 1995b), are not included. Characters 15, 33, and 61 from Livezey (1986a), and character 156 from Livezey (1991) are excluded as unreliable for these groups. States for Salvadorina are unknown except as determined from skin specimens, Mayr (1931), and Mlikovsky (1989). Nomenclature follows Baumel and Witmer (1993).

1. Maxilla, typical shape: (a) not “subconical”; (b) “subconical,” with essentially straight culmen (Alopochen intermediate, variable, sexually dimorphic). Note—see Fig. 14. CI = 0.50.

2. Maxilla and (to lesser degree) mandibula, distinct recurvature: (a) absent, (b) present (Stictonetta extreme, T. tadorna most conspicuous of genus). CI = 0.50.

3. Maxilla and mandibula, distally spatulate conformation: (a) absent, (b) present (Malacorhynchus; convergent state in subgenus Spatula of Anas). (Livezey 1991: character 157.) Note—see Fig. 15. CI = 1.00.

4. Cranium, os lacrimale, processus supraorbitalis and os frontale, margo lateralis, prominent enclosed foramen (not to be confused with minute, largely occluded foramina neurovascularia): (a) absent, (b) present (Alopochen variable, obscured in adult males), (a/b) polymorphic (derived state in Cairina). CI = 1.00.

5. Cranium, os lacrimale, processus supraorbitalis: (a) essentially lacking or small, straight, and coplanar with dorsal surface of skull; (b) comparatively large, flat, often triangular in dorsal aspect, appressed to laterodorsal margin of orbit; (c) large, thick, rugose, dorsolaterally prominent; (d) long, slender, dorsally prominent. (Livezey 1986a: character 11.) Note—state “b” affected in appearance by
Fig. 15.—Mandibulae of selected genera of Anatidae, ventral views: A—Hymenolaimus malachorhynchos (KUMNH 55871), B—Malacorhynchus membranaceus (UMMZ 204434).

variably developed sulcus glandulae nasalis in some genera; this and other aspects of os lacrimale in Stictonetta confounded by unique synostosis of processus orbitalis with dorsally ossified Membrana jugolacrimale. CI = 0.75–1.00.

6. Cranium, ossa frontales, pneumatic dorsal convexity (males): (a) absent; (b) present, rounded, confined to region immediately caudal to zona flexoria craniofacialis; (c) present, variably produced into two-parted prominence, the more-caudal one bilaterally compressed and interorbital in position. Note—revised state for Cyanochen based on examination of skins, few skeletons available inadequate for diagnosis of this variably developed, sexually dimorphic character; see Möller (1969) and Livezey (in pressa, in pressc). (Livezey, 1986a.character 16, revised, corrected.) CI = 1.00.

7. Cranium, basis cranii, lamina parasphenoidalis: (a) rounded; (b) distinctly convex ventrally, with prominent medial ridge (Anateae). (Livezey, 1991:character 155.) CI = 1.00.

8. Vertebrae cervicales, modal number: (a) 17; (a/b) polymorphic, 16–17; (b) 16. (Livezey, 1986a.character 21, revised.) CI = 0.86.

9. Sternum, corpus sterni, foramen pneumaticum: (a) present, (b) absent. (Livezey, 1986a.character 78.) CI = 0.50.

10. Sternum, rostrum sterni, spina externa: (a) lateromedially compressed flange (ancestor); (b) elongate, peg-like spine; (c) small or obsolete. (Livezey, 1986a.character 79, revised significantly.) CI = 0.50–0.67.

11. Sternum, rostrum sterni, spina interna: (a) absent; (b) present, small. (Livezey, 1986a.character 82 [incorrect for Chenonetta]; Livezey, 1991:character 151.) CI = 0.33–1.00.
12. Sternum, carina sterni, margo ventralis, profile in lateral view: (a) distinctly convex throughout length, (b) essentially straight for caudal half. (Livezey, 1986a: character 80.) Cl = 1.00.

13. Sternum, trabecula lateralis: (a) essentially equal in caudal extent to caudal terminus of linea intermusculus, (b) extend well caudad to caudal terminus of linea intermusculus. (Livezey, 1986a: character 81, revised.) Cl = 1.00.

14. Furcula, extremitas omalis claviculae, processus acrocoracoideus: (a) present, although of variable conspicuousness; (b) obsolete. (Livezey, 1986a: character 101.) Cl = 0.50.

15. Furcula, extremitas sternalis claviculae, apophysis furculae: (a) present, (b) obsolete. Note—see Woolfenden (1961), Mlikovsky (1989). Cl = 0.33.

16. Scapula, extremitas cranialis scapulae, tuberculum coracoideum: (a) coplanar with corpus scapulae, margo ventralis; (b) protrusive, distinctly ventral to corpus scapulae, margo ventralis. (Livezey, 1986a: character 107.) Cl = 1.00.

17. Coracoideum, extremitas omalis coracodei, processus acrocoracoideus, subtending pneumatic depression: (a) absent, (b) present. (Livezey, 1986a: character 95, Livezey, 1991: character 154.) Cl = 1.00.

18. Scapula, extremitas cranialis scapulae, tuberculum coracoideum: (a) present, (b) obsolete. Note—see Rand (1954). Cl = 1.00.

19. Scapula, extremitas cranialis scapulae, facies articularis cranialis, cristae deltopectoralis: (a) prominent, (b) not prominent, buttressed. (Livezey, 1986a: character 100.) Cl = 0.50.

20. Humerus, extremitas proximalis, facies caudalis immediately distal to capitulum: (a) variably convex; (b) with transverse trench-like depression, distinctly concave. (Livezey, 1986a: character 24.) Cl = 1.00.

21. Humerus, extremitas proximalis, crista deltopectoralis: (a) margo dorsocranialis prominent, rounded, facies caudalis concave; (b) margo dorsocranialis angular, facies caudalis convex. (Livezey, 1986a: character 25.) Cl = 0.25–0.50.

22. Humerus, extremitas proximalis humeri, tuberculum ventrale: (a) comparatively proximal, exposing fossa pneumotricipitalis in caudal view; (b) comparatively distal, largely or completely obscuring fossa pneumotricipitalis in caudal view. (Livezey, 1986a: character 26.) Cl = 0.50.

23. Humerus, extremitas proximalis humeri, fossa pneumotricipitalis, foramen pneumaticum: (a) present, (b) absent. (Livezey, 1986a: character 28.) Cl = 1.00.

24. Humerus, extremitas proximalis humeri, tuberculum dorsale: (a) prominent, buttressed; (b) not prominent, buttressed. (Livezey, 1986a: character 32.) Cl = 0.25–0.33.

25. Humerus, corpus humeri, margo caudalis (“capital shaft ridge”): (a) prominent, proximally directed toward caput humeri; (b) prominent, proximally directed toward tuberculum dorsale; (c) obsolete. (Livezey, 1986a: character 22, ordering not assumed.) Cl = 0.40–0.67.

26. Humerus, extremitas distalis humeri, tuberculum supracondylare ventrale: (a) not elevated, essentially coplanar with corpus humeri; (b) elevated, angled distally; (c) elevated, angled medially. (Livezey, 1986a: character 26.) Cl = 0.50.

27. Os carpi radiale: (a) not modified into spur, (b) modified into spur. (Livezey, 1986a: character 49.) Note—see Rand (1954). Cl = 1.00.

28. Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum dorsalis, distal terminus, prominent swelling: (a) present, (b) absent. (Livezey, 1986a: character 37.) Cl = 1.00.

29. Carpometacarpus, extremitas proximalis carpometacarpi, processus flexo-
rius, orientation relative to shaft (ordered): (a) perpendicular to or proximally directed, (b) slightly distally directed, (c) distinctly distally directed. (Livezey, 1986a:character 41, revised.) CI = 1.00.

30. Carpometacarpus, extremitas proximalis carpometacarpi, os metacarpale alulare, processus extensorius, enlargement into “spur” (calcar alae): (a) absent; (b) present, especially prominent in adult males. (Livezey, 1986a:character 42.) CI = 0.33–0.50.

31. Carpometacarpus, extremitas proximalis carpometacarpi, fovea carpalis caudalis: (a) present but comparatively shallow; (b) present, comparatively deep, distinctly ovate. (Livezey, 1986a:character 46.) CI = 1.00.

32. Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum ventralis: (a) of uniform depth, (b) distinctly thickened proximally. (Livezey, 1986a:character 47.) CI = 0.50.

33. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, impressio m. extensor metacarpi ulnaris, position relative to synostosis metacarpali proximalis: (a) opposite, at least partly; (b) completely proximal. (Livezey, 1986a:character 43, revised.) CI = 0.50.

34. Illium, ala preacetabularis ili, facies dorsalis, fossa iliaca dorsalis: (a) presenting smooth, only moderately concave surface; (b) containing deep, irregularly shaped depression. (Livezey, 1986a:character 113.) CI = 1.00.

35. Pubis, scapus pubis: (a) concave dorsally, (b) convex dorsally. (Livezey, 1986a:character 115.) CI = 0.50–1.00.

36. Femur, corpus femoris, craniocaudal curvature (lateral perspective): (a) absent or slight, (b) moderate. (Livezey, 1986a:character 55.) CI = 0.50.

37. Femur, corpus femoris, facies caudalis, linea intermuscularis caudalis: (a) present but not prominent; (b) prominent, produced into overhanging ridge proximally. (Livezey, 1986a:character 60.) CI = 1.00.

38. Femur, extremitas distalis femoris, fossa poplitea: (a) shallow, (b) deep. (Livezey, 1986a:character 56.) CI = 1.00.

39. Tarsometatarsus, corpus tarsometatarsi, facies dorsalis, margo medialis, dorsal prominence relative to margo lateralis: (a) essentially equal, (b) distinctly less prominent. (Livezey, 1986a:character 75.) CI = 1.00.

Trachea (Fig. 16).—Pertain to males. Nomenclature follows King (1989, 1993). (Livezey, 1986a:7 incorrect for Stictonetta, excluded.)

40. Asymmetrical bulla syringealis: (a) absent, (b) present (Malacorhynchus vestigial). (Livezey, 1986a:character 6, revised.) CI = 0.50.

41. Syrinx, narrow constriction between tympanum and bulla: (a) absent, (b) present. Note—see Garrod (1875). CI = 1.00.

42. Bulla syringealis (if present), fenestrae: (a) absent; (b) present, but relatively prominent, widely distributed; (c) present, small, few, confined to craniolateral margin. CI = 1.00.

43. Bilobate bulbus trachealis: (a) absent; (b) present, males. Note—see Campbell (1899). CI = 1.00.

Natal Integument (Fig. 17).

44. Ground color of venter*: (a) yellow, (b) dusky, (c) white, (x) basal state not determinable (Mergini). Note—polarity difficult, see Livezey, 1991:character 121. CI = 0.50.
45. Dark, vertical supraorbital stripe: (a) absent, (b) present. CI = 0.50.
46. Dark auricular spot: (a) absent, (b) present, (x) noncomparable. CI = 0.20–0.250.
47. Pale scapular spots*: (a) absent, (b) present, (x) unknown or basal state not determinable. CI = 0.33.
48. Pale rump spots*: (a) absent, (b) present (Hymenolaimus rufous), (x) unknown or basal state not determinable. CI = 1.00.
49. Dorsal scapular and rump spots (if present): (a) separate, (b) confluent. CI = 0.33.
50. Pale, medial mantle stripe: (a) absent, (b) present. CI = 1.00.
51. Foot color: (a) gray(ish), (b) bright yellow or orange. CI = 1.00.
52. Dusky, oblique facial stripes: (a) absent, (b) present. Note—intraspecifically variable. CI = 1.00.
53. Sharp, dark preorbital (loral) stripe: (a) present, (b) absent (Cairineae excluding Pteronetta). (Livezey, 1991:character 107.) CI = 0.33.
54. Broad, pale supraorbital stripe, continuing caudoventrally around dark orbital patch along sides of neck: (a) absent, (b) present. CI = 1.00.

Definitive Integument.—Character 101 of Livezey (1991) was deemed not reliably characterized at this scale and excluded. Redundant synapomorphies for anatine tribes (see other works), as well as characters defining clades within genera of Tadornini (Livezey, in press a) or clades within Tachyeres (Humphrey and Livezey, 1985; Corbin et al., 1986; Livezey, 1986a; Livezey and Humphrey, 1992), also were excluded.

55. Rectrices: (a) not as follows (including narrow elongate tails of Merganetta, Salvadorina); (b) long and broad, typically extending beyond feet in prepared skin specimens. (Livezey, 1991:character 1.) CI = 0.50–1.00.
56. Dark, variably extensive postorbital stripe (juvenal and definitive basic plumages of both sexes, as well as definitive alternate of females in some): (a) absent, (b) present (possibly excluding micro-teal, *Heteronetta*). (Livezey, 1991: character 128.) Cl = 0.50–1.00.

57. Black, lateromedially compressed comb-like crista cariosa on culmen: (a) absent, (b) present. CI = 1.00.

58. Sharp, black speckling of white face: (a) absent (but see *Cairina scutulata*), (b) present. CI = 1.00.

59. Narrow, black shoulder marks at cranial margin of darkened sides: (a) absent, (b) present (obscured in *S. sylvicola*). CI = 1.00.

60. Lesser dorsal wing coverts, contrasting pale (typically white) color: (a) absent (*Plectopterus* nonhomologous, see character d8), (b) present. CI = 0.33.

61. Lesser dorsal wing coverts, contrasting pale color (if present): (a) white, (b) blue. CI = 1.00.

62. Cranialmost lesser dorsal wing coverts, contrastingly white producing narrow white leading edge of wing: (a) absent, (b) present. CI = 1.00.

63. Jagged, black coloration on sides: (a) absent, (b) present. CI = 1.00.

64. Bare, variably colored facial region (from bill to eye to auricular region, including ramal and interramal areas of mandibles) in males: (a) absent, (b) present. CI = 0.50.

65. Single, bare, fleshy-red patches on sides of neck of adult males: (a) absent, (b) present. CI = 1.00.

66. Crista nuchalis pennarum of black-tipped, white feathers from corona to base of neck: (a) absent, (b) present. CI = 1.00.

67. Sides of head and neck, variable suffusion with yellowish buff: (a) absent, (b) present. CI = 1.00.

68. Undertail coverts, variable suffusion with yellowish buff: (a) absent, (b) present. CI = 1.00.

69. Well-defined single black lines from sides of rump extending ventrally and demarcating the belly from the undertail coverts: (a) absent, (b) present. CI = 1.00.

70. Well-developed tomial flaps of maxilla, opposed by lateral extensions of mandibular: (a) absent, (b) present (*Malacorhynchus* extreme). CI = 0.50.

71. Maxilla and mandibula, narrow, submerging conformation: (a) absent, (b) present. CI = 1.00.

72. Mandibular rami, lateral compression defining long, very narrow interramal region: (a) absent, (b) present. CI = 1.00.

73. Black-and-white scalloping on sides and flanks: (a) absent, (b) present (terminal white band narrower in *Salvadorina*). CI = 1.00.

74. Sharply defined gray-and-chestnut breast and sides, contrasting sharply with white venter: (a) absent, (b) present. CI = 1.00.

Fig. 17.—Facial patterns of natal plumages of the Freckled Duck and selected genera of Anatidae, lateral views: A— *Stictonetta naevosa* (AUM 0.60097), B— *Plectopterus gambensis* (ROM 91832), C— *Sarkidiornis melanotus* (AMNH 731312), D— *Hymenolaimus malacorhynchos* (WWT 2359), E— *Tachyeres patachonicus* (USNM 48560), F— *Merganetta (armata) turneri* (FMNH 208125), G— *Malacorhynchus membranaceus* (WWT 3572), H— *Salvadorina waigiuensis* (based on Kear, 1975:fig 2; see also Delacour, 1956:pl. XXIII).
75. Narrow white barring of mantle: (a) absent, (b) present (comparatively extensive, including entire dorsum in Salvadorina). CI = 1.00.
76. Narrow white terminal white tips of secondary remiges: (a) absent, (b) present. CI = 1.00.
77. Sharply defined black scalloping on otherwise white wing linings, extending to axillars: (a) absent, (b) present (marks on axillars of Salvadorina tending to spotting). CI = 1.00.
78. Modal number of pairs of rectrices (ordered): (a) five, (b) six, (c) seven, (d) nine. CI = 0.75.
79. Rectrices: (a) not elongate, narrow; (b) elongate, narrow. Note—see character 55. CI = 0.50.
80. Black-and-white barring of rump: (a) absent, (b) present. CI = 0.50.
81. Leg color: (a) black or gray, (b) yellow, (c) red. CI = 0.50.
82. Bill color (breeding males): (a) gray; (b) pinkish white; (c) orange or red, including pink and coral; (d) yellow; (a/c) polymorphic (Anateae). CI = 0.67.
83. Wing linings, fine vermiculations: (a) absent, (b) present. CI = 1.00.
84. Major secondary coverts tipped with narrow white(ish) bars, producing cranial border to speculum (if any): (a) absent (Malacorhynchus, caudal only; T. radjah, broad, not homologous), (b) present (Anateae, excluding microteal). CI = 0.33.
85. Rufous underparts (females): (a) absent, (b) present. CI = 1.00.
86. Bifurcating, black, postorbital stripe: (a) absent, (b) present. CI = 1.00.
87. Tarsus, dorsal surface: (a) reticulate, (b) scutellate. CI = 1.00.
88. Wing spurs, prominent claws: (a) absent, (b) present. CI = 1.00.
90. Uniformly gray dorsal wing coverts: (a) absent, (b) present. CI = 1.00.
91. Rump, ground color: (a) brown(ish); (b) black; (c) uniformly gray; (d) white; (a/b) polymorphic, black or brown. CI = 0.57–0.67.
92. Dorsal chestnut wash: (a) absent, (b) present. CI = 0.33.
93. Uniformly black tertials (in some extending to scapulars or entire dorsum): (a) absent, (b) present. CI = 0.25–0.33.
94. Demarcation of color between neck and breast: (a) absent, (b) present. Note—see Livezey (in press a). CI = 0.50.
95. Lobation of hallux, and enlargement of subungual lobes in other digits: (a) absent (including basal Aythyini, Oxyurini), (b) present. CI = 0.33–0.50.
96. Dorsum entirely glossy black: (a) absent, (b) present. CI = 0.50–1.00.
97. Dorsum, iridescent greenish (to purplish) color on dark dorsum of wings: (a) absent; (b) present, including all of dorsal surface of wing except distal primaries and (in some) leading edge; (c) present, limited to secondary coverts (Cairineae in part, Nettapodeae variable); (d) present, limited to secondary remiges (Chloephageae variable). CI = 0.75–1.00.
98. Secondary remiges, ground color: (a) brown(ish), (b) iridescent greenish black (including tribes in which border produces speculum), (c) largely white, (d) gray. CI = 0.43–0.60.
99. Wing linings: (a) grayish brown, in some mottled with whitish (Malacorhynchus white with brown bars); (b) “pure” white; (c) black; (d) gray. CI = 0.43–0.60.
100. Pedal unguis: (a) not strongly developed, curved; (b) strongly developed, curved, subraptorial. CI = 0.50–1.00.
101. Unguis of pedal digit III: (a) not qualitatively distinct from other digits;
(b) distinctly broadened with marked concavity on plantar surface, medially displaced with enlarged lobate cutaneous pad enclosed in plantar cavity. CI = 1.00.

102. Interdigital webs of pedal digits, deep incisura: (a) absent, (b) present. CI = 1.00.

103. Bill lamellae, extreme ventral elongation and increase in number: (a) absent, (b) present. CI = 1.00.

104. Bill lamellae, confinement to proximal half of maxilla: (a) absent, (b) present. CI = 1.00.

105. Dark crown and nape band: (a) absent, (b) present. Note—possibly related to brown head of Salvadorina. CI = 1.00.

106. White terminal tail band formed by narrow pale tips of rectrices: (a) absent, (b) present. CI = 1.00.

107. Dark periorbital patch: (a) absent, (b) present. CI = 1.00.

108. Small pink postorbital spot: (a) absent, (b) present. CI = 1.00.

109. Contrastingly buffy undertail coverts: (a) absent, (b) present. CI = 1.00.

110. Head and neck contrastingly dark grayish black: (a) absent, (b) present. CI = 1.00.

111. Uniformly blue-gray ground color of body plumage: (a) absent, (b) present. CI = 1.00.

112. Reddish brown mottling of breast, mantle, and wing linings: (a) absent, (b) present. CI = 1.00.

113. Scapulars, vexilla externum with contrasting, narrow, black margins: (a) absent, (b) present. CI = 1.00.

114. Venter boldly striped (adult males): (a) absent, (b) present. CI = 1.00.

**Attributes For Mapping**

(primitive states in boldface)

A. Body mass (g, ordered): (a) <500, (b) 500–1500, (c) 1500–2500, (d) >2500.

B. Sexual size dimorphism (ratio, ordered): (a) 1.05–1.20, (b) 1.21–1.40, (c) >1.40.

C. Sexual dichromatism: (a) absent (others); (b) rudimentary, confined to quantitative differences in coloration of plumage and rhamphotheca (Anateae included here on the basis of states in basal members); (c) pronounced, involving distinct qualitative differences in pattern; (b/c) two states of almost equal frequency among members (Cairina and Pteronetta, b; Aix, c).

D. Mating system: (a) monogamy, (b) serial polygyny.

E. Typical nest site: (a) terrestrial (including over water), (b) cavity.

F. Clutch size (median, ordered): (a) 3–5, (b) 6–8, (c) 9–11.

G. Paternal attendance of broods: (a) typical (including poorly known Nettapus), (b) atypical.

H. Diving habit: (a) not developed, (b) developed (including only moderately specialized Salvadorina).
### Data Matrix

Matrix of 114 morphological characters (numbered, described in Appendix 1) used in the phylogenetic analysis of *Stictonetta*, genera of “tadornines,” clades of “anatines,” and a hypothetical ancestor, followed by eight attributes mapped *a posteriori* (lettered A–H). Skeletal characters are labelled “s1” to “s39,” tracheal characters “t1” to “t4,” natal characters “n1” to “n11,” and those of definitive integument “d1” to “d60.” States are coded as lower-case letters, and questions marks (coded as “x” in Appendix 1) signify undetermined states.

| Taxon         | Character 1 | Character 2 | Character 3 | Character 4 | Character 5 | Character 6 | Character 7 | Character 8 | Character 9 | Character 10 | Character 11 | Character 12 | Character 13 | Character 14 | Character 15 |
|---------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|--------------|--------------|--------------|--------------|--------------|
| 1  Ancestor   | a           | a           | a           | a           | a           | a           | a           | a           | a           | a            | a            | a            | a            | a            | a            |
| 2  Stictonetta| a           | b           | a           | a           | a           | a           | a           | b           | a           | a            | a            | a            | a            | a            | a            |
| 3  Plectopterus| a           | a           | a           | a           | b           | c           | a           | a           | a           | a            | a            | a            | b            | a            | a            |
| 4  Sarkidiornis| a           | a           | a           | a           | b           | a           | b           | a           | c           | a            | a            | a            | a            | a            | a            |
| 5  Cyanochen   | b           | a           | a           | b           | b           | a           | a           | b           | a           | c            | a            | a            | a            | b            | a            |
| 6  Aloporchon  | b           | a           | a           | b           | b           | a           | b           | a           | c           | a            | a            | b            | b            | b            | a            |
| 7  Neochon     | b           | a           | a           | b           | b           | b           | a           | b           | a           | a            | b            | b            | a            | a            | b            |
| 8  Chlorophaga | b           | a           | a           | b           | b           | b           | a           | b           | a           | a            | b            | b            | a            | a            | b            |
| 9  Tadorna     | b           | b           | a           | a           | b           | a           | a           | a           | a           | a            | a            | b            | a            | a            | b            |
| 10 Hymenolaimus| a           | a           | a           | a           | a           | b           | a           | c           | a           | a            | a            | b            | b            | a            | a            |
| 11 Tachyeres   | a           | a           | a           | a           | a           | b           | b           | c           | a           | b            | b            | a            | a            | b            | a            |
| 12 Merengnetta | a           | a           | a           | a           | a           | b           | a           | b           | c           | a            | b            | b            | a            | a            | a            |
| 13 Salvadorina | a           | a           | a           | a           | a           | b           | a           | b           | b           | c            | a            | a            | a            | b            | a            |
| 14 Malacorychus| a           | a           | b           | b           | b           | b           | b           | b           | b           | c            | a            | a            | a            | b            | a            |
| 15 Carinae     | a           | a           | a           | a           | a           | b           | b           | b           | b           | b            | a            | a            | a            | b            | a            |
| 16 Netopodeae  | a           | a           | a           | a           | a           | b           | b           | a           | b           | a            | a            | a            | a            | b            | a            |
| 17 Anatae      | a           | a           | a           | a           | a           | b           | b           | a           | b           | b            | a            | a            | a            | a            | b            |
| 18 Athyymi     | a           | a           | a           | a           | a           | a           | a           | a           | b           | b            | a            | a            | a            | a            | b            |
| 19 Mergini     | a           | a           | a           | a           | a           | a           | a           | b           | b           | a            | a            | a            | a            | b            | a            |
| 20 Oxyurini    | a           | a           | a           | a           | a           | a           | b           | a           | b           | a            | a            | a            | a            | a            | a            |

| Taxon         | Character 16 | Character 17 | Character 18 | Character 19 | Character 20 | Character 21 | Character 22 | Character 23 | Character 24 | Character 25 | Character 26 | Character 27 | Character 28 | Character 29 | Character 30 |
|---------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| 1  Ancestor   | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            | a            |
| 2  Stictonetta| a            | b            | a            | a            | a            | a            | a            | a            | b            | a            | a            | a            | a            | a            | a            |
| 3  Plectopterus| a           | a           | a           | a           | a           | a           | a           | b           | a           | b            | a            | a            | b            | a            | a            |
| 4  Sarkidiornis| a           | a           | a           | b           | a           | b           | a           | b           | a           | b            | a            | a            | b            | a            | a            |
| 5  Cyanochen   | b           | a           | a           | b           | b           | a           | a           | b           | a           | b            | a            | a            | b            | a            | a            |
| 6  Aloporchon  | b           | a           | a           | a           | a           | b           | b           | a           | b           | a            | a            | b            | b            | a            | a            |
| 7  Neochon     | b           | a           | a           | b           | b           | b           | a           | b           | c           | a            | b            | b            | a            | c            | a            |
| 8  Chlorophaga | b           | a           | a           | b           | b           | b           | a           | a           | b           | b            | a            | a            | b            | b            | b            |
| 9  Tadorna     | b           | b           | a           | a           | b           | a           | a           | a           | a           | a            | a            | b            | a            | a            | b            |
| 10 Hymenolaimus| a           | a           | a           | a           | a           | b           | a           | b           | c           | a            | b            | b            | a            | a            | b            |
| 11 Tachyeres   | a           | a           | a           | a           | a           | b           | b           | b           | b           | a            | a            | b            | b            | a            | a            |
| 12 Merengnetta | a           | a           | b           | b           | b           | a           | a           | b           | b            | a            | b            | b            | a            | b            | a            |
| 13 Salvadorina | a           | a           | a           | a           | a           | b           | a           | b           | c           | a            | a            | a            | a            | b            | a            |
| 14 Malacorychus| a           | a           | a           | a           | a           | a           | a           | a           | a           | b            | a            | b            | a            | a            | a            |
| 15 Carinae     | a           | a           | a           | a           | a           | a           | b           | b           | b           | b            | a            | a            | a            | b            | a            |
| 16 Netopodeae  | a           | a           | a           | a           | a           | b           | b           | a           | b           | a            | b            | c            | b            | a            | a            |
| 17 Anatae      | a           | a           | a           | a           | a           | b           | b           | a           | b           | a            | b            | c            | b            | a            | a            |
| 18 Athyymi     | a           | a           | a           | a           | a           | a           | a           | b           | b           | a            | a            | b            | c            | a            | a            |
| 19 Mergini     | a           | a           | a           | a           | a           | a           | a           | b           | b           | b            | c            | a            | a            | c            | a            |
| 20 Oxyurini    | a           | a           | a           | a           | a           | a           | b           | a           | b           | a            | b            | c            | b            | a            | a            |
| Taxon          | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 |
|---------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1 Ancestor    | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 2 Stictonetta | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | b  | b  | a  |
| 3 Plectropterus| a  | a  | b  | a  | a  | a  | a  | a  | b  | b  | c  | a  | a  | a  |
| 4 Sarkidiornis | a  | a  | a  | a  | a  | a  | a  | a  | b  | b  | a  | a  | a  | a  |
| 5 Cyanophen    | a  | b  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 6 Alopochen    | a  | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 7 Neochen      | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 8 Chlorophaga  | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 9 Tadorna      | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 10 Hymenolaimus| a  | b  | a  | a  | a  | a  | a  | b  | a  | b  | a  | a  | c  | b  |
| 11 Tachyeres   | b  | b  | b  | b  | a  | a  | b  | b  | b  | b  | a  | a  | c  | b  |
| 12 Meraganeta  | a  | b  | a  | a  | a  | b  | a  | b  | a  | b  | a  | a  | c  | b  |
| 13 Salvadorina | ?  | ?  | ?  | ?  | ?  | ?  | ?  | ?  | b  | a  | a  | a  | c  | a  |
| 14 Malacorhynchus | a  | a  | a  | a  | b  | a  | a  | b  | a  | a  | a  | c  | a  |
| 15 Cairineae   | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 16 Nettapodeae | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 17 Anateae     | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | a  | a  | c  | a  |
| 18 Athyini     | a  | a  | a  | a  | a  | a  | a  | a  | b  | a  | b  | a  | c  | a  |
| 19 Mergini     | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  | a  | ?  | a  |
| 20 Oxyurini    | a  | a  | a  | a  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  |

| Taxon          | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
|---------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| 1 Ancestor    | a  | ?  | ?  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 2 Stictonetta | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 3 Plectropterus| a  | b  | b  | a  | a  | a  | b  | a  | a  | a  | a  | a  | a  | a  | a  |
| 4 Sarkidiornis | a  | b  | b  | a  | a  | a  | b  | a  | a  | a  | b  | b  | a  | a  | a  |
| 5 Cyanophen    | b  | b  | b  | a  | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  |
| 6 Alopochen    | b  | b  | b  | b  | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  |
| 7 Neochen      | b  | b  | b  | b  | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  |
| 8 Chlorophaga  | b  | b  | b  | b  | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  |
| 9 Tadorna      | b  | b  | b  | b  | a  | a  | a  | a  | b  | a  | a  | a  | b  | a  | a  |
| 10 Hymenolaimus| a  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 11 Tachyeres   | b  | b  | b  | b  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 12 Meraganeta  | b  | b  | b  | b  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 13 Salvadorina | b  | b  | b  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 14 Malacorhynchus | b  | b  | b  | b  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
| 15 Cairineae   | b  | b  | b  | b  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  | a  |
## APPENDIX 2—Continued.

| Taxon                        | Character | Character |
|------------------------------|-----------|-----------|
|                              | 61        | 62        |
|                              | d7        | d8        |
| 1 Ancestor                   | a         | a         |
| 2 Stictonetta                | a         | a         |
| 3 Plectropterus              | b         | b         |
| 4 Sarkidiornis               | a         | a         |
| 5 Cyanochel                  | b         | a         |
| 6 Alopochen                  | a         | a         |
| 7 Neocen                      | a         | a         |
| 8 Chlorophaga                | a         | a         |
| 9 Tadorna                    | a         | a         |
| 10 Hymenolaimus              | a         | a         |
| 11 Tachyeres                 | a         | a         |
| 12 Mergeria                  | a         | a         |
| 13 Salvadornia               | a         | a         |
| 14 Malacorhynchus            | a         | a         |
| 15 Cairineae                 | a         | a         |
| 16 Nettapodeae               | a         | a         |
| 17 Anateae                   | a         | a         |
| 18 Aythyni                   | a         | a         |
| 19 Mergini                   | a         | a         |
| 20 Oxyurini                  | a         | a         |

| Taxon                        | Character | Character |
|------------------------------|-----------|-----------|
|                              | 76        | 77        |
|                              | d22       | d23       |
| 1 Ancestor                   | a         | c         |
| 2 Stictonetta                | a         | a         |
| 3 Plectropterus              | a         | c         |
| 4 Sarkidiornis               | a         | c         |
| 5 Cyanochel                  | a         | c         |
| 6 Alopochen                  | a         | c         |
| 7 Neocen                      | a         | c         |
| 8 Chlorophaga                | a         | c         |
| 9 Tadorna                    | a         | c         |
| 10 Hymenolaimus              | a         | c         |
| 11 Tachyeres                 | a         | d         |
| 12 Mergeria                  | a         | a         |
| 13 Salvadornia               | b         | b         |
| 14 Malacorhynchus            | b         | b         |
| 15 Cairineae                 | a         | c         |
| 16 Nettapodeae               | a         | c         |
| 17 Anateae                   | a         | c         |
| 18 Aythyni                   | a         | c         |
| 19 Mergini                   | a         | c         |
| 20 Oxyurini                  | a         | c         |
### Character

| Taxon | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 |
|-------|----|----|----|----|----|----|----|----|----|-----|-----|-----|-----|-----|-----|-----|
| 1     | a  | a  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 2     | a  | a  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 3     | b  | a  | b  | a  | a  | b  | b  | b  | b  | a   | b   | a   | a   | a   | a   | a   |
| 4     | b  | a  | b  | a  | a  | b  | b  | c  | b  | a   | a   | a   | a   | a   | a   | a   |
| 5     | c  | a  | a  | a  | a  | a  | a  | d  | b  | b   | a   | a   | a   | a   | a   | a   |
| 6     | b  | b  | b  | b  | a  | a  | a  | d  | b  | b   | a   | a   | a   | a   | a   | a   |
| 7     | b  | b  | b  | b  | a  | a  | d  | c  | c  | a   | a   | a   | a   | a   | a   | a   |
| 8     | d  | a  | a  | b  | a  | a  | d  | c  | b  | a   | a   | a   | a   | a   | a   | a   |
| 9     | b  | b  | b  | b  | a  | a  | d  | b  | b  | a   | a   | a   | a   | a   | a   | a   |
| 10    | c  | a  | a  | a  | b  | a  | a  | d  | a  | b   | a   | b   | a   | a   | a   | a   |
| 11    | c  | a  | a  | a  | b  | a  | a  | c  | d  | a   | a   | a   | a   | a   | a   | a   |
| 12    | c  | a  | a  | a  | b  | a  | a  | b  | d  | a   | a   | a   | a   | a   | a   | a   |
| 13    | c  | a  | a  | a  | b  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 14    | d  | a  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 15    | b  | b  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 16    | a/b| a  | a  | a  | a  | a  | a  | c  | b  | c   | a   | a   | a   | a   | a   | a   |
| 17    | a  | a  | a  | a  | a  | a  | a  | a  | b  | c   | a   | a   | a   | a   | a   | a   |
| 18    | a  | a  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |
| 19    | a  | a  | a  | a  | b  | a  | a  | b  | b  | a   | a   | a   | a   | a   | a   | a   |
| 20    | a  | a  | a  | a  | a  | a  | a  | a  | a  | a   | a   | a   | a   | a   | a   | a   |

### Character

| Taxon | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | 119 | 120 | 121 | 122 |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| 1     | a   | a   | a   | a   | a   | a   | a   | a   | c   | a   | a   | a   | a   | a   | a   | a   | a   |
| 2     | a   | a   | a   | a   | a   | a   | a   | a   | a   | b   | a   | a   | a   | a   | a   | a   | a   |
| 3     | a   | a   | a   | a   | a   | a   | a   | d   | c   | a   | b   | a/b | b   | b   | a   | a   | a   |
| 4     | a   | a   | a   | a   | a   | a   | a   | a   | c   | b   | b   | a/b | c   | b   | c   | b   | a   |
| 5     | a   | a   | a   | a   | a   | a   | a   | a   | a   | c   | c   | a   | a   | a   | b   | a   | a   |
| 6     | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | c   | b   | a   | a   | a   | a   | a   |
| 7     | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | b   | a   | a   | a   | a   | a   | a   |
| 8     | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | c   | a/b | c   | a   | b   |
| 9     | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 10    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 11    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 12    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 13    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 14    | b   | b   | b   | b   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 15    | a   | a   | a   | a   | a   | a   | a   | b/c | b/c | b/c | b/c | b/c | b/c | b/c | b/c | b/c | b/c |
| 16    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 17    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 18    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 19    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
| 20    | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   | a   |
Appendix 3
Classification

Formation and hyphenation of English group names follow conventions of Parkes (1978); capitalization of those for *Sarkidiornis*, *Tachyeres*, and *Merganetta* indicate currently recognized or tentatively proposed polytypy.

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

**Suborder Anseres Wagler, 1831.**

**Family Anatidae Vigors, 1825.**

Subfamily Stictonettinae Wolters, 1976.

- Genus *Stictonetta* Reichenbach, 1853.—Freckled Duck.

Subfamily Tadorninae Reichenbach, “1850.”—Shelducks and allies.

- Tribe Merganettini Delacour and Mayr, 1945.
  - Genus *Hymenolaimus* Gray, 1843.—Blue Duck.
  - Genus *Tachyeres* Owen, 1875.—Steamer-ducks (see Livezey and Humphrey, 1992).
  - Genus *Merganetta* Gould, 1842.—Torrent-ducks.

- Tribe Plectropterini, new taxon.
  - Genus *Plectropterus* Stephens, 1824.—Spur-winged Goose.
  - Genus *Sarkidiornis* Eyton, 1838.—Comb-ducks.

- Tribe Tadornini Delacour and Mayr, 1945 (see Livezey, in press a).
  - Subtribe Chloephageae Boetticher, 1942.
    - Genus *Cyanochen* Bonaparte, 1856.
    - Genus *Alopochen* Stejneger, 1885.
    - Genus *Neochen* Oberholser, 1918.
    - Genus *Chloephaga* Eyton, 1838.
  - Subtribe Tadornaeae Boetticher, 1942.
    - Genus *Tadorna* Oken, 1817.

Subfamily Anatinae Swainson, 1837, *sedis mutabilis.*—Dabbling ducks and allies.

- Tribe Malacorhynchini, new taxon.
  - Genus *Malacorhynchus* Swainson, 1831.—Pink-eared Duck.
  - Genus *Salvadorina* Rothschild and Hartert, 1894.—Salvadori’s Duck.

- Tribe Anatini Delacour and Mayr, 1945; *incertae sedis* (see Livezey, 1991).

- Tribe Aythyini Delacour and Mayr, 1945 (see Livezey, in press c).

- Tribe Mergini Delacour and Mayr, 1945 (see Livezey, 1995b).

- Tribe Oxyurini Delacour and Mayr, 1945 (see Livezey, 1995c).
Livezey, Bradley C. 1996. "A phylogenetic reassessment of the tadornine-anatine divergence (Aves: Anseriformes: Anatidae)." Annals of the Carnegie Museum 65(1), 27–88. https://doi.org/10.5962/p.215133.

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