A PHYLOGENETIC ANALYSIS AND CLASSIFICATION OF RECENT DABBLING DUCKS (TRIBE ANATINI) BASED ON COMPARATIVE MORPHOLOGY

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ABSTRACT.—Cladistic analysis of 157 characters of definitive plumages and soft parts, natal plumages, tracheae, and nontracheal skeletons of 59 Anatini (*sensu* Livezey 1986) provided a phylogenetic hypothesis of high consistency (CI = 0.71, excluding unique autapomorphies) and resolution (tree completely resolved except for two nested trichotomies, a trichotomy within the northern-hemisphere mallards, and the tentative placements of two poorly known species of *Anas*). Major phylogenetic inferences (lists of three or more taxa are in order of increasing relatedness) include the following: (1) monophyly of the tribe is weakly demonstrated; (2) the tribe comprises three subtribes—Cairineae (*Cairina, Pteronetta, Aix*), Nettapodeae (*Chenonetta, Nettapus*), and Anateae (all other genera); (3) subtribe Anateae comprises three "supergenera" (each comprising two genera)—*Amazonetta* (*A. brasiliensis* and *Callonetta leucophrys*), *Lophonetta* (*L. specularioides* and *Speculanas specularis*), and *Anas* (genera *Mareca* and *Anas*); (4) the genus *Mareca* or wigeons includes six species—*capensis, strepera, falcata, sibilatrix, penelope,* and *americana;* and (5) the large genus *Anas* comprises two weakly supported subgroups or cohorts, the first of which includes two subgenera (mallards [*Anas*] and blue-winged ducks [*Spatula*]) and the second includes four subgenera (Australasian teal [*Nesonetta*], pintails [*Dafila*], Holarctic teal [*Querquedula*], and spotted teal [*Punanetta*]). Other findings include that a sister-relationship exists between *Anas sparsa* and other mallards, that subgroups of the "true" mallards are largely congruent with biogeographic subdivisions (northern-hemispheric, African, and South Pacific), that the four species of shoveler are monophyletic, that a sister-relationship between the speckled teals (*flavirostris* and *andium*) and brown pintails (*georgica, acuta,* and *eatoni*) exists, and that *A. querquedula* is the sister-group to the green-winged teals (*formosa, crecca,* and *carolinensis*) and not closely related to the blue-winged ducks. Supplementary data and related theory indicated that (1) interspecific interfertility is a poor indicator of relationship, (2) the phylogenetic species concept provided the most practical definition of terminal taxa, (3) a majority of groups within the Anatini originated in the southern hemisphere, (4) body size, sexual size dimorphism, and egg size are strongly constrained phylogenetically, whereas sexual dichromatism and clutch size are less predictable, (5) biparental attendance of broods is primitive within Anatini, and (6) characters of definitive plumages, natal plumages, tracheae, and skeletons had similar consistencies but attained maximal utility at different levels within the phylogeny, which indicates different rates of character evolution within the tribe. *Received 19 July 1990, accepted 4 December 1990.*

TRIBE Anatini (dabbling ducks; *sensu* Livezey 1986) comprises all typical surface-feeding ducks and the smaller "perching ducks," which were formerly grouped under the tribal name "Cairinini" (Delacour and Mayr 1945) or included in the subfamily Plectropterinae (Phillips 1922). These are perhaps the most familiar waterfowl and together include roughly one third of the extant species of Anseriformes. Bock and Farrand (1980) listed *Anas* as one of the largest avian genera, yet they conservatively recognized only 36 species. Current taxonomic groupings within the Anatini, like other subgroups of waterfowl, derive principally from the classic work by Delacour and Mayr (1945) and, to a lesser extent, earlier investigations (Salvadori 1895; Phillips 1922, 1923, 1925, 1926; Peters 1931; Kuroda 1939; and Boetticher 1942). The taxonomy and inferred evolutionary "affinities" of dabbling and perching ducks proposed by Delacour and Mayr (1945), based on comparisons of behavioral and external similarities, were expanded by Delacour (1954, 1956, 1959, 1964). Subsequent research on the systematics of dabbling ducks used comparisons of behavior and morphology (e.g. Boetticher 1952; Lorenz 1941, 1951–1953; Johnsgard 1960a, b, 1961a, b, 1962, 1965; Kaltenhauser 1971; Scherer and Hilsberg 1982) and largely confirmed the phenetic groupings defined by Delacour and

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Mayr (1945). Important changes proposed at two major taxonomic levels included the relationships of several problematic species to the tribe, and relationships among the species within the Anatini.

Most of the taxonomic revisions recommended subsequent to Delacour and Mayr's (1945) proposal pertained to generic or tribal membership. Johnsgard (1960c) determined that the Ringed Teal (*"Anas" leucophrys*) differed sufficiently from typical *Anas* to be returned to the monotypic genus *Callonetta*. In a comprehensive study of waterfowl osteology, Woolfenden (1961) recommended that the "perching ducks" (Tribe Cairinini, *sensu* Delacour and Mayr 1945, but exclusive of *Plectropterus*) be merged into the "dabbling ducks" (Tribe Anatini). Johnsgard proposed to re-assign the Pink-headed Duck (*Rhodonessa caryophyllacea;* 1961a) and Marbled Teal (*Marmaronetta* [*Anas*] *angustirostris;* 1961c) to the pochards (Tribe Aythyini). Johnsgard (1961a) also advocated the inclusion of the Crested Duck (*Lophonetta specularioides*) within the Anatini rather than among the shelducks (Tribe Tadornini) as proposed by Delacour and Mayr (1945). Salvadori's Duck (*Salvadorina* [*Anas*] *waigiuensis*) was included in *Anas* by Delacour and Mayr (1945), but earlier authors placed it in a separate subfamily Merganettinae with *Merganetta* (Salvadori 1895, Phillips 1926), and others retained it as a monotypic genus of problematic relationships (Mayr 1931, Peters 1931, Kear 1975). Several other species included as aberrant members of the Anatini by Delacour and Mayr (1945) subsequently have had varied taxonomic treatments. These include the Blue Duck (*Hymenolaimus malacorhynchos*), Pink-eared Duck (*Malacorhynchus membranaceus*), and Freckled Duck (*Stictonetta naevosa*). *Hymenolaimus* was studied in detail (Kear 1972), and *Stictonetta* was later removed from the Anatinae on the basis of morphological and behavioral comparisons (see Johnsgard 1960a, 1961a, 1962). The unique Torrent Duck (*Merganetta armata*) was placed in the monospecific tribe Merganettini (Delacour and Mayr 1945) but considered to be closely related to *Anas* (Niethammer 1952). *Merganetta* was included by Delacour (1956) and Johnsgard (1961a, 1965) within the Anatini, although Johnsgard (1978) later returned it to its own tribe. Eldridge (1979) concluded that *Merganetta* is most similar ethologically to Tadorninae.

These taxonomic revisions were adopted in large part by Johnsgard (1979) in the latest edition of the "Checklist of Birds of the World," although tribes within the Anatinae were omitted. In a recent phylogenetic analysis of Recent genera of Anseriformes, Livezey (1986) concluded that (1) *Stictonetta* and *Plectropterus* are representatives of monotypic, pre-anatine branches of subfamilial rank, (2) *Sarkidiornis, Malacorhynchus, Hymenolaimus,* and *Merganetta* are unusual members of the Tadorninae, (3) *Marmaronetta* and *Rhodonessa* are members of the Aythyini, and (4) the relationships among the remaining members of Cairinini and Anatini could not be determined from osteology and therefore were merged into the single, possibly paraphyletic tribe Anatini. Livezey (1986) omitted *Salvadorina* from this analysis, but Mlíkovský (1989) reexamined the partial skeletons of *S. waigiuensis* described by Mayr (1931) and concluded that the species may be more closely related to *Hymenolaimus* and *Malacorhynchus* than to *Anas*.

Relationships among dabbling ducks, particularly within the genus *Anas*, have received comparatively little study. Special attention was given relationships within *Anas* (Delacour and Mayr 1945; Lorenz 1951–1953; Johnsgard 1961a, 1965). These studies were based largely on comparisons of behavior (and to a lesser extent, plumage) and none attempted to compile comparative data for even a majority of species. All (except perhaps Lorenz 1951–1953) were phenetic in nature (i.e. groupings of species were based on assessments of overall similarity irrespective of possible polarities of characters). A pronounced "tradition" of taxonomic sequences of dabbling ducks developed (benchmark works include Salvadori 1895; Phillips 1922–1926; Peters 1931; Delacour and Mayr 1945; Johnsgard 1961a, 1979), which reflected a consensus of roughly "primitive-to-advanced" intratribal relationships. These classifications primarily reflect changing taxonomic conventions and secondarily indicate differences in perceptions of relationships among Anatini. Variations in species names aside, important trends include a reduction in numbers of species of Anatini (*sensu* Livezey 1986, excluding *Salvadorina*) recognized (65 by Salvadori 1895, 64 by Phillips 1922–1926, 60 by Peters 1931, 46 by Delacour and Mayr 1945 and by Johnsgard 1961a); a reduction in number of genera recognized (17 by Salvadori 1895, 10 by Phillips 1922–1926, 13 by Peters 1931, 7 by Delacour and

Mayr 1945, and 8 by Johnsgard 1961a); and an increase in the numbers of presumed "natural" groups within *Anas*, a change that largely reflected the "Groups 1-14" of Delacour and Mayr (1945) and the clusters depicted by Johnsgard (1961a) or considered "superspecies" by Johnsgard (1979).

Molecular studies of Anseriformes have contributed significant, largely confirmational information on probable relationships (Scherer and Sontag 1986). A number of biochemical studies have included more than one species of Anatini. Among these are compositional comparisons of uropygial secretions (Jacob and Glaser 1975, Jacob 1982); electrophoretic studies of proteins from a diversity of tissues (Sibley and Ahlquist 1972, Brush 1976, Numachi et al. 1983, Oates et al. 1983, Patton and Avise 1985); immunological comparisons of blood plasma (Bottjer 1983); restriction endonuclease analysis of mitochondrial DNA (Kessler and Avise 1984, Avise et al. 1990); and DNA hybridization (Madsen et al. 1988). None of these studies, however, included samples from >14 species of *Anas* or >19 species of Anatini (*sensu* Livezey 1986), few considered problematic species, and none employed cladistic methodologies. Branching diagrams in these studies usually were based on simple UPGMA clustering of taxa based on pairwise distances. For the resultant branching diagrams to represent phylogenetic relationships, such clustering algorithms require the additional assumption of equal rates of molecular evolution in all lineages (Wiley 1981, Hillis 1987). Moreover, some of the studies were hampered by (1) small numbers of loci compared (e.g. 10 loci in Numachi et al. [1983] and 26 in Patton and Avise [1985]), (2) data matrices that lack substantial proportions of pairwise distances and have undesirable metric properties (Madsen et al. 1988), (3) a substantial dependence on traditional classifications in investigational design and inferences (Bottjer 1983, Patton and Avise 1985), or (4) a reliance on traditional, phenetic classifications of fossil species for estimates of divergence times and evolutionary rates (Patton and Avise 1985, Madsen et al. 1988).

I present a phylogenetic (cladistic) analysis of the Anatini from 157 polarized characters of the skulls, syringeal bullae, natal plumages, definitive plumages, and soft parts of 59 taxa. I discuss relative consistencies and evolutionary rates of character groups, ecological and biogeographical correlates, and relationships of traditionally problematic taxa and closely related tribes, and I propose an annotated Linnean classification of the Anatini.

MATERIALS AND METHODS

Taxa included.—All 88 specific and subspecific taxa of Recent Anatini were included for analysis as members of the ingroup, although skin specimens of downy young, tracheae, and (especially) skeletons were not available for all taxa. For the derivation of trees, I combined taxa with identical character-states, which reduced the number of analytical units to 59. These analytical combinations merged taxa typically considered to be subspecies. I defined *subspecies* for practical purposes as lineages that differed only *quantitatively* (often in intensity of plumage colors or size) from conspecific taxa. These differences probably reflect spatially separated samples of clinal variation. This practice produced the nontraditional combination of *Anas fulvigula* and *A. diazi* (while maintaining the *qualitatively* distinguishable *A. platyrhynchos* and *A. rubripes*), and the elevation to species rank of a number of taxa commonly treated as subspecies (*A. wyvilliana, A. laysanensis, A. oustaleti, A. zonorhyncha, A. albogularis, A. chlorotis, A. eatoni, A. andium, A. carolinensis,* and *A. puna*). Several other taxa are either of problematic tribal assignment (e.g. *Salvadorina, Merganetta*) or are "basal," Anatini-like members of other tribes of Anatinae (e.g. *Polysticta, Marmaronetta, Heteronetta*) and were included for ancillary comparisons. These latter genera and several others (*Sarkidiornis, Tadorna, Somateria*) were included as members of the outgroup for determination of polarities.

Specimens examined.—I examined study skins of downy young (mostly age-class Ia, brightly patterned with no plumaceous feathers) and adults, skeletal material (particularly skulls), and syringeal bullae (most mounted with tracheae) of all species of Anatini except for the following: *Anas oustaleti* (downy young not examined, but described by Phillips [1923]), *A. chlorotis* and *A. aucklandica* (downy young not examined, but described and illustrated in Delacour [1956, 1964]); *A. melleri* (skeleton and syrinx not available), *A. albogularis* (skeleton and syrinx not available), and *A. bernieri* (skeleton, syrinx, and downy young not known). I included a series of study skins of adults of all species, and for a majority of species, samples of three or more were studied for characters of the skull, trachea, and natal plumage. The collections of study skins of adults and downy young at the National Museum of Natural History (NMNH) and American Museum of Natural History (AMNH), and the skeletal collections at the NMNH and the University of Kansas Museum of Natural History (KUMNH), were especially important. I received a generous loan of skins of downy young and mounted tracheae from the Wildfowl Trust (WT), Slimbridge, England.

Analysis of some characters was facilitated by study of several published references: Phillips (1922–1926), Delacour and Mayr (1945), Delacour (1956, 1964), Ripley (1957a, b), Huey (1961), Woolfenden (1961), Johnsgard (1965, 1978), Oring (1968), Palmer (1976), Soothill and Whitehead (1978), Todd (1979), Weller (1980), Hosking and Kear (1985), Madge and Burn (1988). Data on body mass, sexual dimorphism, distributions, and reproductive parameters were compiled from these references and others listed by Livezey (1990).

Definition and analysis of characters.—A total of 157 characters that had two or more discrete states were included in the analysis (Appendix 1). Based on outgroup comparisons, I divided characters into a single primitive state (for the Anatini) and one or more derived states. To confirm the monophyly of terminal taxa, representative autapomorphies were compiled (but not included in the analysis; a list is available from the author on request). Key references for character descriptions were as follows: Humphrey and Parkes (1959) for definitive plumages, Humphrey and Clark (1964) and Warner (1971) for the syrinx, and Butendieck and Wissdorf (1982) for the skull. Several skeletal characters given by Woolfenden (1961) for subgroups of the Anatini (especially *Amazonetta* and *Callonetta*) were excluded because of intraspecific variation and problematic definition of states. Behavioral characters of Anatini have been studied intensely (Delacour and Mayr 1945; Lorenz 1951-1953; McKinney 1953, 1965; Delacour 1956; Johnsgard 1961a, 1962, 1965), but they were excluded because of difficulties in definition of character states and numerous missing data.

Derivation of phylogenetic trees.—Searches for most-parsimonious topologies (trees requiring the fewest character changes) were made with "global" branch-swapping algorithms with "MULPARS" (MAXTREE = 250) in the PAUP program (Swofford 1985). Both procedures search for the "shortest" tree(s) possible and permit the storage of a number of equally parsimonious topologies, but neither *guarantees* the determination of the shortest possible tree(s). Exhaustive search algorithms (e.g. branch-and-bound) were not employed because of the prohibitively great computational expenditure necessitated by data sets of this size. The 16 multistate characters (those with two or more derived states) were analyzed as unordered, with the exception of the meristic, ordinal counts of rectrices (character 27). To find preliminary topologies within reasonably short computing times, I replaced several unknown syringeal character states in *A. bernieri* with those shared by other Australian teal (*A. gibberifrons, A. castanea, A. chlorotis,* and *A. aucklandica*); similarly, several natal character states of *A. bernieri* were hypothesized to be those shared by *A. gibberifrons* and *A. albogularis.* I also described the topological differences of subsequent analysis with missing-data codes replaced. All characters were assigned unit weight. Trees were rooted using an "hypothetical ancestor" (vector of plesiomorphous character states), which was prepared from polarities inferred from outgroup comparisons. (See Appendix 3 for an annotated data matrix.) Theory and methodological rationales for phylogenetic analysis are given by Wiley (1981) and Swofford (1985). All computations were made on the IBM mainframe computer at the University of Kansas.

Phylogenetic classification.—The hierarchical groupings within phylogenetic trees can be summarized in Linnean classifications (Wiley 1981). Parageneric taxa—supergenera, subgenera, and infragenera—were erected as needed to conserve phylogenetic information and based on synonomies presented by Phillips (1923), Brodkorb (1964), and Wolters (1976).

RESULTS

Trees found.—Under the constraint of character states hypothesized (as detailed above) in the Madagascan Teal (*A. bernieri*), inferred trees had consistency indices of 0.71 and lengths of 250 (inclusion of representative autapomorphies inflated the consistency index by 0.05). Only three unresolved sections of the phylogeny were indicated (Fig. 1). The first poorly resolved segment involved the relationships among three subgenus-groups in the genus *Anas* (*sensu stricto*). Three topological variants were found: (1) the groups (*Nesonetta, Dafila,* and *Punanetta-Querquedula*) as a trichotomy; (2) *Dafila* as the sister-group to a clade that comprises *Dafila* and *Punanetta-Querquedula;* and (3) *Punanetta-Querquedula* as the sister-group to a clade composed of *Dafila* and *Nesonetta.* The second poorly resolved section involved the relationships among four entities: the poorly known *A. bernieri;* the relatively similar *A. gibberifrons* and *A. albogularis;* and a resolved clade that includes *A. castanea, A. chlorotis,* and *A. aucklandica* (Fig. 1). Four equally parsimonious topological variants were found for these four groups: (1) *A. bernieri, A. albogularis,* and *A. gibberifrons* composing a grade paraphyletic to the "reddish teal" (*A. castanea, A. chlorotis,* and *A. auklandica*); (2) *A. bernieri* as the sister-group to a trichotomy involving *A. albogularis, A. gibberifrons,* and the clade of "reddish teal"; (3) a trichotomy involving *A. bernieri,* a clade of *A. albogularis* and *A. gibberifrons,* and the clade of "reddish teal"; and (4) *A. bernieri* as the sister-group to *A. gibberifrons* + *A. albogularis,* and together these three as the sister-group to the "reddish teal." Given the poor resolution of these two segments of the tree, the included relationships are considered indeterminate and depicted as trichotomies (Fig. 1). The third poorly resolved segment involved two nested trichotomies including *A. diazi*, *A. fulvigula*, and the clade composed of *A. platyrhynchos* and its Pacific relatives (Fig. 1). All other parts of the phylogeny in the constrained analysis were invariant.

Replacement of the hypothesized character states in *A. bernieri* with missing-data codes resulted in 81 trees (CI = 0.715), in which *A. bernieri* is associated with the "first cohort," either as a monotypic branch of a trichotomy with or as the sister-group to the other two member clades. This placement was based entirely on the questionably homologous reddish foot-color of *A. bernieri*. If this character is coded as not homologous to the orange feet of mallards and shovelers, then *A. bernieri* was placed with equal parsimony in a diversity of "basal" positions among the subgenera throughout the genus *Anas*. Exclusive of *A. bernieri* and the two trichotomies described above, the tree based on the unconstrained analysis (Fig. 1) was invariant.

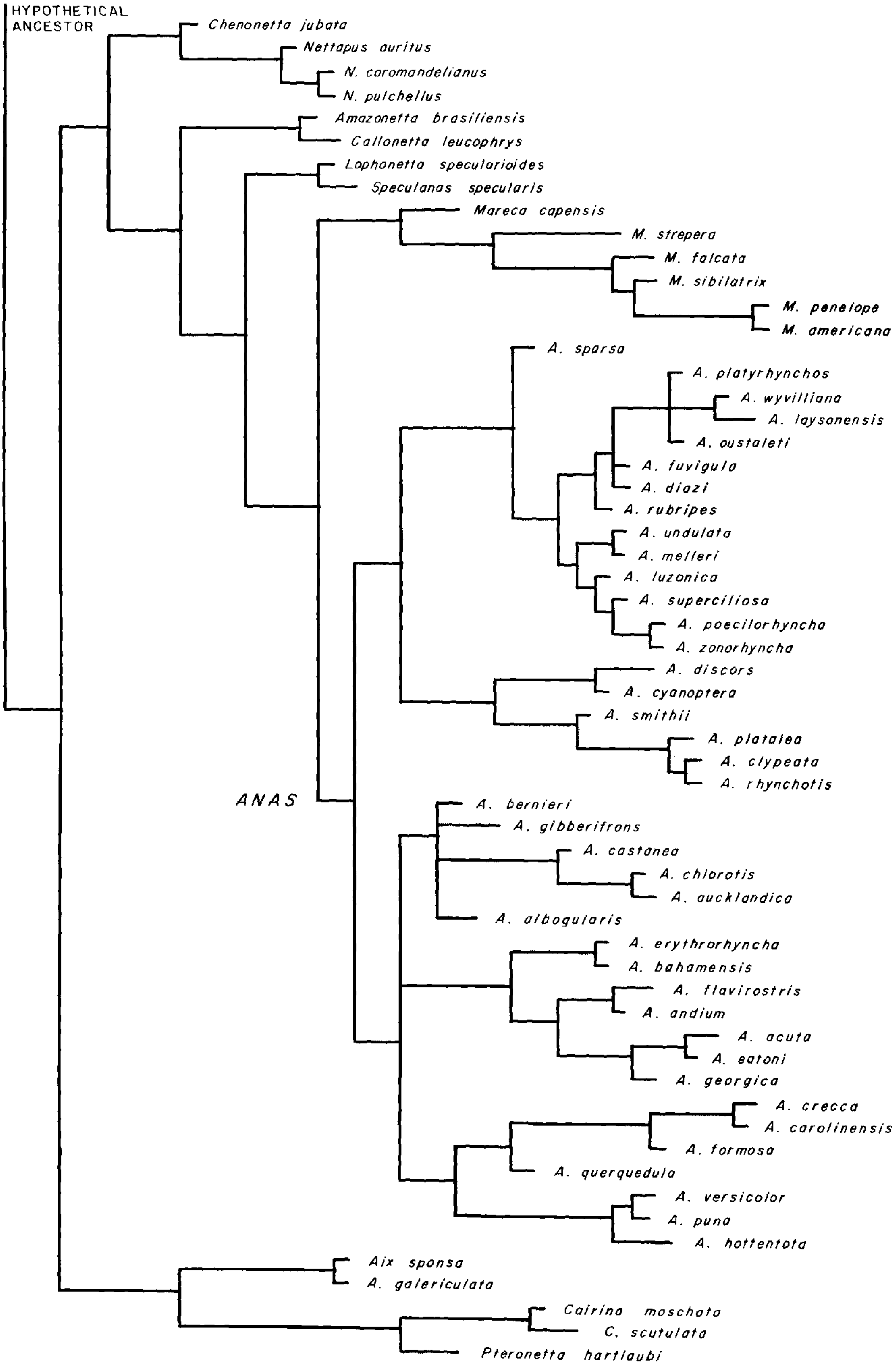
Tribal monophyly and "perching ducks."—Monophyly of the Anatini is only weakly supported by three character changes of which two were lost by reversal in subsequent groups. The "perching ducks" comprises two clades paraphyletic to the remainder of the Anatini, henceforth referred to as Anateae (Fig. 2). The first and more primitive of these was the clade composed of two species of *Cairina* and its monotypic sister-genus *Pteronetta*, and two species of *Aix*. The two species of *Aix* have been considered sister-species by most authorities in recent decades (e.g. Delacour and Mayr 1945, Delacour 1959, Johnsgard 1965, Numachi et al. 1983).

The second clade of "perching ducks," a group more closely related to the true dabbling ducks (Fig. 2), comprises two genera—*Chenonetta* (one species) and *Nettapus* (three species). The close relationship of these two genera, and the paraphyly of the smaller "perching ducks" differs from earlier reviews (e.g. Delacour and Mayr 1945; Delacour 1959; Johnsgard 1961a, 1965, 1978). Particularly divergent previous treatments include the placement of *Chenonetta* in the monotypic subfamily Chenonettinae (Salvadori 1895, Phillips 1922) or inclusion of *Chenonetta* within the true geese, subfamily Anserinae (Peters 1931). In contrast, *Chenonetta* and *Aix* were depicted as sister-genera by Johnsgard (1961a, 1978).

Basal Anateae.—Two monotypic genera of small, uniquely patterned waterfowl of South America—*Amazonetta* and *Callonetta*—were found to be sister-genera and together formed the sister-group to the rest of the subtribe Anateae (Fig. 2). Boetticher (1952) and Johnsgard (1960c, 1961a, 1965, 1978) included both genera among the "Cairinini," but Delacour (1964) retained them within the Anatini as formerly assigned (Delacour and Mayr 1945, Delacour 1959). Delacour (1964) also resisted the hypothesis of close relationship between *Amazonetta* and *Callonetta* supported by Derscheid (1938), Verheyen (1955), Johnsgard (1960b), and Woolfenden (1961).

I found another couplet of taxonomically controversial, relatively primitive, Neotropical dabbling ducks—*Lophonetta specularioides* and *"Anas" specularis*—to be sister-species, and these composed the sister-group to the true dabbling ducks (Fig. 2). With the exceptions of Delacour and Mayr (1945), Delacour (1954, 1964), Boetticher (1958), and Woolfenden (1961), who placed *Lophonetta* within the shelducks (Tadorninae), systematists have considered both forms to be somewhat aberrant members of the Anatini (e.g. Johnsgard 1961a, 1965; Brush 1976; Livezey 1986). The proposal of close relationship between *specularioides* and *specularis* has received less support by previous studies (e.g. Delacour and Mayr 1945). Although the two species were listed next to one another by Salvadori (1895), Phillips (1923), and Peters (1931), a sister-relationship was depicted by Johnsgard (1961a). Morphological evidence that indicates a close relationship was cited by Johnsgard (1965).

Wigeons and allies.—The remaining members of the tribe make up two major clades. Ranked as genera, they are the wigeons and close relatives (*Mareca*, 6 species) and the typical dabbling ducks (*Anas*, 40 species). The wigeons are typified by a combination of primitive syringeal bullae and uniquely derived natal and definitive plumages. In addition to the typical wigeons (*M. sibilatrix* and the sister-species *M. americana* and *M. penelope*), the unique Cape Teal (*M. capensis*) and two transitional forms (*M. strepera* and *M. falcata*) were included within this clade (Fig. 2). The Cape Teal (or Cape Wigeon, locally; Delacour 1956) formerly was in-


HYPOTHETICAL ANCESTOR
Chenonetta jubata
Nettapus auritus
N. coromandelianus
N. pulchellus
Amazonetta brasiliensis
Callonetta leucophrys
Lophonetta specularioides
Speculanas specularis
Mareca capensis
M. strepera
M. falcata
M. sibilatrix
M. penelope
M. americana
A. sparsa
A. platyrhynchos
A. wyvilliana
A. laysanensis
A. oustaleti
A. fuvigula
A. diazi
A. rubripes
A. undulata
A. melleri
A. luzonica
A. superciliosa
A. poecilorhyncha
A. zonorhyncha
A. discors
A. cyanoptera
A. smithii
A. platalea
A. clypeata
A. rhynchotis
ANAS
A. bernieri
A. gibberifrons
A. castanea
A. chlorotis
A. aucklandica
A. albogularis
A. erythrorhyncha
A. bahamensis
A. flavirostris
A. andium
A. acuta
A. eatoni
A. georgica
A. crecca
A. carolinensis
A. formosa
A. querquedula
A. versicolor
A. puna
A. hottentota
Aix sponsa
A. galericulata
Cairina moschata
C. scutulata
Pteronetta hartlaubi

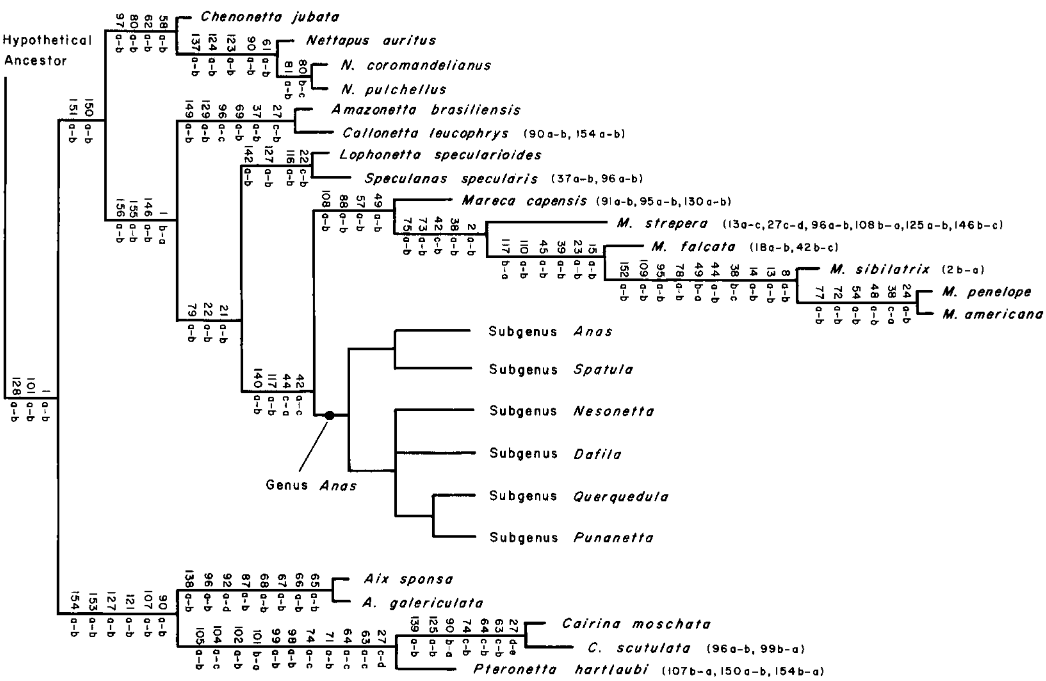


Fig. 2. Detailed topology of phylogeny of Anatini exclusive of genus *Anas*; taxonomy follows Appendix 2. Characters are explained in Appendix 1; autapomorphies are given in parentheses following corresponding taxa.

cluded with either the "spotted teal" (e.g. *A. versicolor*; Delacour 1956) or the "green-winged teal" (e.g. *A. crecca*; Johnsgard 1961a, 1965, 1979). *Mareca capensis* combines a natal plumage and several features of definitive plumages shared uniquely with typical wigeons with a moderately derived syringeal bulla and a diversity of autapomorphies of definitive plumage and soft parts.

The Gadwall (*M. strepera*), long known for a number of wigeon-like characters of behavior, plumage, and biochemistry (Delacour and Mayr 1945; Boetticher 1952; Delacour 1956; Johnsgard 1961a, 1965, 1978; Kessler and Avise 1984), proved to be a mosaic of a mallard-like natal plumage, several wigeon-like characters of definitive plumages, and a syrinx and soft parts that combine features of both groups with an assortment of unique autapomorphies. The close relationship of the Falcated Duck (*M. falcata*) to the typical wigeons was corroborated (four characters of adult plumage, two natal characters). Delacour and Mayr (1945) allied *falcata* most closely with the Baikal Teal (*A. formosa*), but most previous workers noted some "affinity" between *falcata* and the wigeons or *strepera* (e.g. Delacour and Mayr 1945, Delacour 1956, Boetticher 1958, Johnsgard 1978). Johnsgard (1961a) depicted a sister-relationship between *falcata* and the typical wigeons, a topology at variance with subsequent commentary (Johnsgard 1965). The terminal clade of typical wigeons—wherein the Chiloé Wigeon (*M. sibilatrix*) is the sister-species to the northern-hemisphere "superspecies" that comprises *M. penelope* and *M. americana* (Johnsgard 1979)—is especially well supported here (Fig. 2). A sister-relationship between these two species was intuited earlier by Johnsgard (1961a).

Typical dabbling ducks (Anas).—Approximately two thirds of the tribe Anatini are members of the large, comparatively derived clade of

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Fig. 1. Phylogeny of dabbling ducks (Anatini). Poorly resolved relationships within the lower clade of *Anas* and among austral teal shown as trichotomies; position of *A. bernieri* is tentative. Taxonomy follows Appendix 2.

"typical" dabbling ducks. The group includes several of the most widespread, numerous, and familiar species of waterfowl in the world. My analysis defines two weakly supported subclades within the group, which I informally refer to as "cohorts" (Fig. 3). The first cohort comprises two major subgroups, the mallards (subgenus *Anas;* 14 species) and the blue-winged ducks (subgenus *Spatula;* 6 species). The second cohort comprises three primary clades, which are shown as a trichotomy because of the poor resolution of this segment of the tree. It includes the Australasian Teal (subgenus *Nesonetta;* 6 species), the pintails (subgenus *Dafila;* 7 species), and a two-parted clade that comprises the Holarctic teal (subgenus *Querquedula;* 4 species) and the spotted teal (subgenus *Punanetta;* 3 species).

Mallards.—Monophyly of the mallard complex is supported by six characters of definitive and natal plumages, colors of soft parts, and syrinx (Fig. 3). The first dichotomy within the complex separated the African Black Duck (*Anas sparsa*), a species that combines primitive anatomical characters with atypical (evidently autapomorphic) behavioral attributes, from a speciose clade of more-typical mallards. Other investigators recognized the "distinctness" of *A. sparsa* (e.g. Delacour and Mayr 1945, Boetticher 1952, McKinney et al. 1978), and several even considered the species to be among the most primitive members of the Anatini (Delacour 1956; Johnsgard 1961a, 1965, 1978), although Johnsgard (1979) listed *A. sparsa* with the more typical mallards.

The sister-group of *A. sparsa* includes a subclade of the (largely) northern-hemisphere mallards and another, southern-hemisphere group that includes South Pacific mallards and two remaining African members (Fig. 3). Relationships among the northern mallards are incompletely resolved. The American Black Duck (*A. rubripes*) is the sister-group to a trichotomy that includes the Mottled Duck (*A. fulvigula*), Mexican Duck (*A. diazi*), and a reasonably well supported clade that includes the Mallard (*A. platyrhynchos*) and three closely related insular forms—the Marianas Duck (*A. oustaleti*) and the Hawaiian sister-species *A. wyvilliana* and *A. laysanensis.* The northern mallards have been considered closely related for decades, an hypothesis supported by biochemical comparisons (Kessler and Avise 1984, Patton and Avise 1985). Several authorities believe that most or all of the continental forms are conspecific and most also include the Pacific forms within an enlarged, polytypic *A. platyrhynchos* (e.g. Delacour and Mayr 1945; Boetticher 1952; Delacour 1956; Johnsgard 1960e, 1961a, 1961d, 1965, 1967, 1978, 1979). Others retained species rank for some members (e.g. Phillips 1923, Moulton and Weller 1984, Hepp et al. 1988).

The African mallards, Yellow-billed Duck (*A. undulata*) and Meller's Duck (*A. melleri*), consitute one of two clades included in the sister-group of the northern-hemisphere mallards (Fig. 3). Delacour and Mayr (1945: 21) stated that each *A. undulata* and *A. melleri* "stands alone" within the mallard complex but listed them next to one another within their "Group 9." There is a relatively long tradition of listing *A. undulata* next to *A. sparsa* (Salvadori 1895, Phillips 1923, Peters 1931, Johnsgard 1979). Johnsgard (1961a, 1965) concluded that *A. melleri* was very closely related to *A. platyrhynchos,* but later he (1978) concluded that available information did not permit a precise assessment of the relationships of *A. melleri.* Johnsgard (1978, 1979) listed *A. undulata* and *A. melleri* consecutively.

The sister-group of the two African forms comprises the four species of South Pacific mallards (Fig. 3). Within the Pacific complex, the Philippine Duck (*A. luzonica*) is the sister-group to a terminal clade in which the Pacific Gray Duck (*A. superciliosa*) is the sister-group to the spot-billed ducks, here considered to comprise two species (*A. poecilorhyncha* and *A. zonorhyncha*). With few exceptions (Boetticher 1952, Johnsgard 1961a), recent investigators inferred the close relationship among the South Pacific mallards. This led most taxonomists to merge *zonorhyncha* with *poecilorhyncha* (e.g. Johnsgard 1979), to combine both *zonorhyncha* and *superciliosa* within *poecilorhyncha* (Delacour 1956; Johnsgard 1961a, 1965, 1978), or (less frequently) to consider all four South Pacific forms (including the distinctive *luzonica*) as subspecies of a single species (Delacour and Mayr 1945; opposed by Ripley 1951).

Blue-winged ducks.—The first cohort also includes the clade that comprises the blue-winged teal and shovelers (Fig. 3). The two teal are sister-species, with *A. discors* significantly more autapomorphic (uniquely derived) than *A. cyanoptera.* The four species of shoveler constitute the sister group to the blue-winged teal. Within the

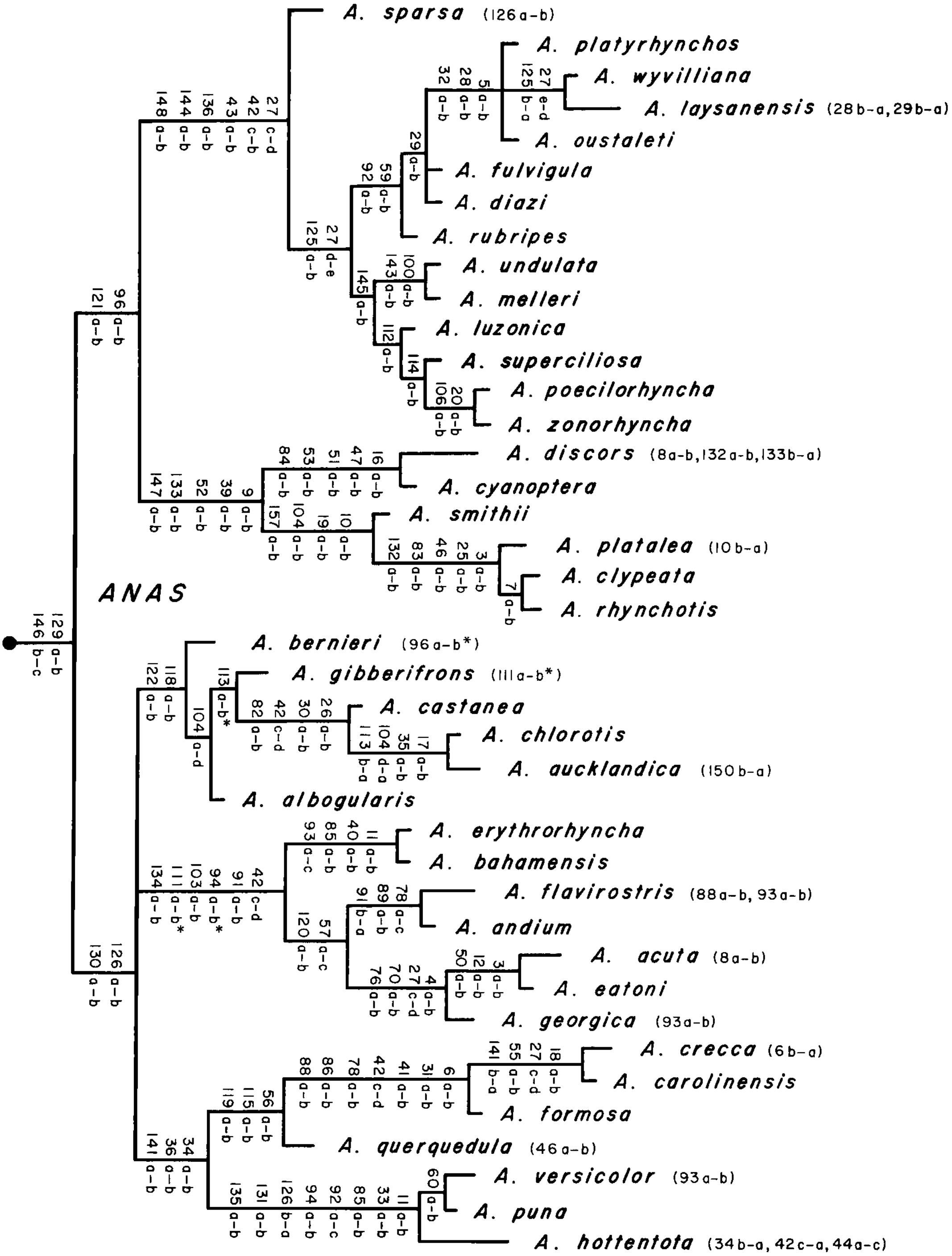

Fig. 3. Detailed topology of phylogeny of the genus *Anas*; position of *A. bernieri* tentative (see text). Characters are explained in Appendix 1; autapomorphies are given in parentheses following corresponding taxa. Character changes marked by asterisks are mutually contradictory, and alternative arrangements can support several distinct, equally parsimonious topologies within the trichotomy.

shovelers, *A. smithii* is the sister-group to a clade that comprises *A. platalea, A. rhynchotis*, and *A. clypeata*, within which the Australasian (*A. rhynchotis*) and Northern (*A. clypeata*) shovelers are sister-species (Fig. 3).

The blue-winged teal and shovelers have been considered to be closely related by most 20th-century taxonomists, an idea supported by recent biochemical comparisons (Kessler and Avise 1984, Patton and Avise 1985). However, the relationships inferred here differ in several ways. First, the Garganey (*A. querquedula*), traditionally grouped with the blue-winged teal, is shown (Fig. 3) to be more closely related to the green-winged teal (e.g. *A. formosa, A. crecca*) and (to a lesser degree) to the spotted teal (e.g. *A. versicolor*). Second, monophyly of the shovelers was confirmed, contrary to the suggestions of polyphyly by Delacour and Mayr (1945) and Delacour (1956). Specifically, the Red Shoveler (*A. platalea*) and Australasian Shoveler (*A. rhynchotis*) are less closely related to the superficially similar Cinnamon Teal (*A. cyanoptera*) and Blue-winged Teal (*A. discors*), respectively, than they are to each other and to the remaining shovelers (Fig. 3). The relationships proposed here also imply that the Cape Shoveler (*A. smithii*) is the "most primitive" member of the shovelers. Most extant taxonomic sequences (Delacour and Mayr 1945; Delacour 1956; Johnsgard 1965, 1978, 1979) and the tree depicted by Johnsgard (1961a) suggest instead that *A. platalea* "links" the shovelers with the blue-winged teal.

Australasian teal.—Five or six species of small, grayish or reddish-brown teal (if the poorly known *A. bernieri* is included) compose one of the three clades in the second "cohort" of *Anas* (Fig. 3). Three species—*A. bernieri, A. albogularis*, and *A. gibberifrons*—probably form a poorly resolved, basal grade paraphyletic to a well-supported clade of three, variably reddish-brown teal. The latter species—Chestnut Teal (*A. castanea*), Brown Teal (*A. chlorotis*), and Flightless Teal (*A. aucklandica*)—are limited in distribution to Australia, New Zealand, and the Auckland and Campbell islands, and show a pronounced trend toward smaller size, reduced sexual dichromatism, and flightlessness (Livezey 1990).

Members of this clade have been considered closely related by most taxonomists since Delacour and Mayr (1945). This concensus included a close relationship between the poorly known *A. bernieri* and other austral teal, especially *A. gibberifrons* and *A. albogularis* (e.g. Salvadori 1895; Phillips 1923; Peters 1931; Delacour and Mayr 1945; Verheyen 1955; Johnsgard 1961a, 1965, 1978, 1979), although most taxonomists also listed "*Anas*" *capensis* with or near this group. Several authorities discussed or recommended the conspecific or superspecies status of *A. bernieri* and *A. gibberifrons* (Boetticher 1952; Delacour 1956; Johnsgard 1965, 1979), and most authorities considered some or all of the Australasian "reddish" teal to be conspecific (e.g. Ripley 1942; Delacour and Mayr 1945; Boetticher 1952; Johnsgard 1978, 1979; Dumbell 1986).

Pintails.—The second major clade within the second "cohort" of *Anas* includes the pintails (Fig. 3). *Anas bahamensis* and *A. erythrorhyncha* form the first of three subgroups, species considered closely related by virtually all 20th-century taxonomists (e.g. Salvadori 1895; Phillips 1923; Peters 1931; Delacour and Mayr 1945; Johnsgard 1965, 1978, 1979). The second subclade of pintails includes two monophyletic groups (Fig. 3): two teal-sized species (*A. flavirostris* and *A. andium*), and three species of brown pintails (*A. georgica, A. acuta*, and *A. eatoni*). The inference of close relationship between the "pale-cheeked" and brown pintails has received widespread support, except for Delacour and Mayr (1945), who suggested that the "pale-cheeked" species are more closely related to the "spotted teal" (e.g. *A. versicolor*), Cape Teal ("*A.*" *capensis*, herein moved to *Mareca*), and Marbled Teal (*Marmaronetta angustirostris*, now placed in Aythyini; Livezey 1986). *Anas flavirostris* (including *A. andium*) was allied with *A. crecca* by Delacour and Mayr (1945), Lorenz (1951-1953), Boetticher (1952), Delacour (1956), and Johnsgard (1961, 1965, 1978, 1979). The Brown Pintail (*A. georgica*), here found to be the sister-group to *A. acuta* and *A. eatoni*, was placed "nearer to" the superficially similar *A. flavirostris* by several taxonomists (e.g. Salvadori 1895, Delacour and Mayr 1945), but Johnsgard (1965, 1978, 1979) indicated a close relationship between *A. acuta* (including *A. eatoni*) and *A. georgica*. *Anas flavirostris* and *A. andium* have been considered closely related for decades and, since Delacour and Mayr (1945), most authorities have treated them as a single species. The sister-species *A. acuta* and *A. eatoni* have been considered conspecific in recent decades (Delacour and Mayr 1945; Johnsgard 1965, 1978, 1979), but Stahl et al. (1984) supported species-status for both.

Holarctic and spotted teal.—Two well-supported clades of teal compose the third clade included within the second "cohort" of *Anas* (Fig.

3). The larger of these includes the Holarctic teal, a northern-hemispheric group composed of the Garganey (*A. querquedula*) and its sister-group the green-winged teal (*A. formosa* and the "superspecies" including *A. crecca* and *A. carolinensis*). The finding that *A. querquedula* is the sister-group to the green-winged teal, supported by three characters of definitive and natal plumages, opposes the traditional *A. querquedula* association with the blue-winged ducks (Salvadori 1895; Phillips 1923; Peters 1931; Delacour and Mayr 1945; Boetticher 1952; Verheyen 1955; Delacour 1956; Johnsgard 1961a, 1965, 1978, 1979). The classification of *A. querquedula* with the blue-winged ducks rested largely on the gray forewing of the species, a character that differs from the less extensive, *powder-blue* forewing of *Spatula* and that evidently was derived from the light gray wing-coverts of the green-winged and spotted teals. A close relationship between the Baikal Teal (*A. formosa*) and the green-winged teal "superspecies" has been hypothesized by all 20th-century taxonomists except Delacour and Mayr (1945), Boetticher (1952), and Delacour (1956), who considered *formosa* to be an "isolated" form of uncertain taxonomic position.

Spotted teal, the distinctive southern-hemisphere sister-group of the Holarctic teal, include the Hottentot Teal (*A. hottentota*), and the superspecies that comprises the Silver Teal (*A. versicolor*) and Puna Teal (*A. puna*) (Fig. 3). Although some writers failed to recognize that *A. hottentota* was a member of this well-defined group (Salvadori 1895, Phillips 1923, Peters 1931), this relationship was supported by Delacour and Mayr (1945) and subsequent taxonomists. The practice of listing *A. querquedula* between *A. versicolor* and the blue-winged ducks (Salvadori 1895; Heinroth 1911; Lorenz 1951–1953; Delacour 1956; Johnsgard 1961a, 1965, 1978, 1979) is not in accord with my results. This tradition apparently reflects the phenetic assessment of synapomorphies and symplesiomorphies between *A. querquedula* and the "spotted teal," and superficial (convergent) similarities between *A. querquedula* and the blue-winged ducks.

DISCUSSION

Poorly resolved relationships.—My results constitute a significant clarification of the generic relationships of Anatini presented earlier (Livezey 1986), but monophyly of the tribe remains only weakly demonstrated. Two of the three supportive characters had consistency indices of 0.50, one (character 1) characterized the basal grade Cairineae + Nettapodeae and the other (character 101) also supported (by reversal) the clade *Cairina* + *Pteronetta*. The single character supportive of the tribe (character 128, postorbital stripe in natal plumage) is not completely unambiguous. Although it is absent in most "allies" placed in other tribes (*Sarkidiornis, Merganetta, Malacorhynchus, Hymenolaimus,* and *Marmaronetta*), it is suggested in several others (*Plectropterus, Salvadorina,* and *Heteronetta*). In addition, a few other character states of these genera resembled those found within Anatini (particularly Anateae). These include variably metallic and bordered wing specula (*Merganetta, Salvadorina, Polysticta,* and *Heteronetta*) and a moderately derived condition of cranial foramina (*Heteronetta*). In all of these "allied" genera (except perhaps *Salvadorina*), there are other characters that indicate alliance with other tribes (Livezey 1986). Presumably the few characters shared with the Anatini are convergent. *Salvadorina* appears, on the basis of its (tadornine) carpal wing-spurs and peculiar, evidently derived wing specula, to be most closely related to *Merganetta,* which in turn is related to *Hymenolaimus* by osteological synapomorphies (Livezey 1986) and a dark, vertical supraorbital stripe in natal plumage (shared also with *Heteronetta*; pers. obs., Kear 1972). A close relationship among *Salvadorina, Merganetta,* and *Hymenolaimus* was inferred earlier by Kear (1975), but this hypothesis must remain tentative until skeletal comparisons are possible.

The two basal members of the genus *Mareca*—*M. capensis* and *M. strepera*—presented "conflicts" between definitive, natal, and syringeal characters, and require further investigation (Fig. 2). Also, the two "cohorts" of *Anas* are too poorly documented for formal recognition, but the determination of relationships among the included (and well supported) subgenera is important for biogeographic and ancillary evolutionary inferences (see below).

Relationships among the basal austral teal (*A. bernieri, A. albogularis,* and *A. gibberifrons*) are inadequately understood because of incomplete data for *A. bernieri* and apparent character conflicts between *A. albogularis* and *A. gibberifrons.* The most urgent anatomical needs for further study of Anatini concern three species endemic to the Indian Ocean: downy young and tracheae for *A. bernieri,* tracheae for *A. albogularis,* and tracheal specimens for *A. melleri.* Relationships among North American mallards have been studied intensively (Phillips 1912; Delacour 1956; Johnsgard 1960d, 1961d) but remain inadequately resolved. Of particular concern are the delimitation of species within the complex (Morgan et al. 1976, Ankney et al. 1986, Hepp et al. 1988, Avise et al. 1990) and the conservation of genetically "pure" populations of *A. rubripes* in the face of increased hybridization with *A. platyrhynchos* (Johnsgard 1967, Heusmann 1974, Johnsgard and Di Silvestro 1976, Brodsky and Weatherhead 1984, Ankney et al. 1987). *Anas oustaleti,* probably extinct, shows extraordinary plumage variability, wherein some specimens resemble the South Pacific *A. superciliosa* and others show characteristics of the Holarctic *A. platyrhynchos.* Most ornithologists consider *A. oustaleti* to be a subspecies of *A. platyrhynchos* or a hybrid swarm (Delacour and Mayr 1945, Yamashina 1948, Delacour 1956, Amadon 1966, Johnsgard 1978). The hybrid-swarm hypothesis is validated by the observation that characteristics of hybrid waterfowl frequently are not simple "intermediates" or mosaics of those of parental species (Scherer and Hilsberg 1982, Gillespie 1985). Detailed cladistic analysis of *A. oustaleti* should permit a test of its possibly hybrid origin and reticulate phylogeny (Humphries 1983, Wagner 1983).

Monophyly of terminal taxa was demonstrated unambiguously for all except *A. diazi, A. fulvigula, A. oustaleti, A. gibberifrons,* and *A. eatoni* (list available on request). Although the nominate subspecies of *A. gibberifrons* is characterized by a unique dorsal inflation of the frontal bones (Ripley 1942), the character evidently does not unite the entire species. Reduction of sexual dichromatism distinguishes *A. eatoni* from its continental sister-species *A. acuta.* Reduced dichromatism is evident in insular populations of many anatids (Weller 1980), including several Anatini (*A. wyvilliana, A. laysanensis, A. aucklandica,*) and the extinct, possibly specifically distinct *M.* (*strepera*) *couesi* (Ripley 1957a, b).

Hybridization, species concepts, and phylogenetic inference.—Frequency of interspecific hybridization (in the wild or in captivity) and the fertility of hybrid offspring have been weighed heavily by traditional systematists as criteria for the delimitation of species and for the assessment of relationships among species and higher taxa of waterfowl (e.g. Delacour and Mayr 1945; Lorenz 1951-1953; Delacour 1956, 1959; Sibley 1957; Johnsgard 1960b, 1961a, 1961d, 1965, 1968a, 1968b, 1978). In spite of an almost universal capacity for hybridization among Anseriformes (Scherer and Hilsberg 1982), such information has led to a diversity of inferences. Hybridization between captive *A. flavirostris* and wild *A. crecca* has "proved" a close interspecific relationship (Delacour 1964: 341). Infertility of hybrids between *"Anas" leucophrys* and *Amazonetta brasiliensis* was used in "excluding" a close relationship between the two (Delacour 1964: 343). The unique chromosomal number of *Aix galericulata* (Yamashina 1952) was interpreted by Delacour (1959: 99) as the explanation for the "strange" absence of interspecific hybrids in *Aix,* and a demonstration that karyotypic characters are not reliable taxonomic criteria.

Phylogenetic inferences based on hybridization and sterility are (at least implicitly) based on the concept of "isolating mechanisms," an idea central to the widely accepted "biological species" concept (*sensu* Mayr 1969), in which species are conceived of as groups of interbreeding, natural, reproductively isolated populations. The importance of "isolating mechanisms" in the formation and maintenance of species of waterfowl has been widely accepted (e.g. Sibley 1957; Johnsgard 1960d, 1963; but see McKinney 1970, 1975; McKinney et al. 1990), but it is supported only by circumstantial evidence and often contradictory reasoning. For example, Johnsgard (1963: 531) concluded that "This remarkable capacity for hybridization [among anatids] indicates that isolating mechanisms must be operating effectively if species are to retain their integrity under natural conditions. Since genetic isolation is practically absent in the Anatidae, other isolating mechanisms must, of course, have evolved to take their place. Of these, the most significant appear to be behavioral differences and various morphological (plumage and soft part) specializations. . . ." With respect to Anatini, however, Johnsgard (1963: 537) stated, "Thus, isolating mechanisms are least well developed in the group, in spite of the fact that courtship displays and male plumages tend to be elaborate and diversified." Johnsgard (1963: 539) reasoned that the frequency of hybrids among species of *Anas* ". . . appears to be the combined result of the great amount of natural sympatry [cited earlier (p. 538) as a distributional circumstance conducive to the evolution of isolating mechanisms], the relatively close relationships of all the species of *Anas*, and the very uniform precopulatory behavior of all the species in this genus [i.e., the failure of precopulatory isolating mechanisms to evolve]." Clearly, if isolating mechanisms have been selected in waterfowl, then this selection must have been of low intensity, or the genetic-behavioral capacity of anatids to evolve and respond to these mechanisms is singularly limited. The latter seems particularly improbable in light of the diversity of breeding plumages and capacity for recognition of mates characteristic of anatids (Butcher and Rohwer 1989).

An alternative model is to consider "isolating mechanisms" to be incidental *effects*, not the *causes*, of interspecific phenotypic divergence (West-Eberhard 1983, Paterson 1985) that results from sexual selection or divergent natural selection (McKinney 1970, Selander 1972). As such, it predictably would fail to preclude interspecific mating under a variety of circumstances. "Intraspecifically selected" (instead of isolation-oriented) phenotypic characters function in selection of mates and facilitate initiation of breeding (Selander 1972, West-Eberhard 1983, Andersson 1986). These characters would be subject to intense selection in anatids in which tertiary sex-ratios typically favor males (Bellrose et al. 1961, Breitwisch 1989), and they would be influenced by other life-history factors such as relative parental investment by males, territoriality, and predation (Trivers 1972, Endler 1978, Baker and Parker 1979, Butcher and Rohwer 1989).

A recently proposed alternative to the "biological species" concept is the "recognition concept" of species, in which species are defined (intrinsically) as populations of organisms that share a common, functionally adaptive system of fertilization (Paterson 1985, 1988; see also West-Eberhard 1983). The "recognition concept" was anticipated by students of waterfowl, at least with respect to proximate mechanisms, by an investigational emphasis placed on mechanisms of "species recognition" (Sibley 1957; Dilger and Johnsgard 1959; Hailman 1959; Klopfer 1959; Johnsgard 1960d, 1961d, 1963, 1968b; Schutz 1965; Williams 1983). Both concepts of species hinge—in fundamentally different ways—on the interfertility of populations. The first concept focuses on "isolation" or historico-adaptive partitioning of a common system of fertilization. The second emphasizes the internal mechanisms interpreted as adaptations for its maintenance through refinement of fertilization systems. Species concepts based on inferred or presumed patterns of gene flow and models of speciation are important for the development of evolutionary theory, but often they offer no practical (specimen-based) means for species delimitation.

For purposes of phylogenetic inference, interfertility is uninformative because it represents the retention of primitive "recognition systems" and capacity for interbreeding (i.e. it is a symplesiomorphous condition). A third alternative, the phylogenetic species concept, defines species as the smallest diagnosable (i.e. definable by *qualitative, apomorphic* characters) monophyletic group of organisms (reviewed by Cracraft 1983, 1988; McKitrick and Zink 1988) and permits the comparatively simple definition of terminal lineages in analyses (regardless of consideration of allopatry or fertilization systems) based on the observable *effects* of evolutionary divergence. Recognition of phylogenetic species permits the investigation of evolutionary problems that tend to be superficially considered with the merging of evolutionary entities into (phenetically defined) "biological" species (e.g. relationships within North American and Hawaiian mallards or among basal Australasian teal). Consequently, I adopted the phylogenetic species concept for data coding and the cladistic analyses, and for the classification proposed below.

A phylogenetic classification of Anatini.—Based on the phylogenetic relationships inferred herein (Fig. 1), I propose a Linnean classification of Recent dabbling ducks (Appendix 2). Recognition of subtribal and subgeneric taxa permitted the incorporation of additional phylogenetic information in the classification not possible within the traditional tribe-genus system. The limitations of simple binomial classification for *Anas* led Delacour (1956: 19) to conclude that ". . . Either 14 genera, or only one, must be recognized."

Although subspecies are not considered useful in the phylogenetic species concept (McKitrick and Zink 1988), recognized taxa are listed parenthetically (Appendix 2) following those species considered "polytypic" to clarify the content of species (e.g. populations included within *A. versicolor* and *A. puna*) and to indicate traditionally distinguished populations which may, with further study, be usefully elevated to species status. The second point is particularly important for widespread species characterized by comparatively great variation (e.g. *A. cyanoptera*), for poorly known, possibly diagnosable insular isolates (*M.* [*strepera*] *couesi*, *A.* [*aucklandica*] *nesiotis*), and for terminal taxa not shown to be monophyletic (e.g. *A. gibberifrons*).

Biogeographical patterns.—The distributional ranges of Anseriformes have been well-known for decades. Conversely, biogeographic inferences have been mostly scattered anecdotal speculations concerning "centers of origin," "relictual" distributions, and possible radiations of groups or "ancestral stock," and have been made in the absence of an explicit hypothesis of phylogeny (e.g. Ripley 1957b; Weller 1964; Johnsgard 1978; Murton and Kear 1975, 1978; Kear and Murton 1976). A tabular overlay of distributional information for my proposed classification permitted more explicit inferences concerning the historical biogeography of Anatini (Table 1). Four of six supergenera and eight of eleven genera are limited to the southern hemisphere. Within the genus *Anas*, only two subgenera (*Nesonetta* and *Punanetta*) are strictly limited to the southern hemisphere, although infragenera within two other subgenera are so distributed (Table 1). Like the genus *Mareca*, several subgroups of *Anas* include members from both hemispheres (subgenus *Anas*, infragenera *Pterocyanea*, *Spatula*, *Paecilonitta*, and *Dafila*). Only four groups of subgeneric or higher rank are limited to the northern hemisphere. These are the genus *Aix* of Cairineae, the grade that comprises the subgenera *Chaulelasmus* and *Eunetta* of *Mareca*, and the subgenus *Querquedula* of *Anas* (Table 1). The preponderance of southern-hemispheric clades, particularly among the early branches (Nettapodeae, and supergenera *Cairina*, *Amazonetta*, and *Lophonetta*), strongly suggest that the Anatini originated in the southern hemisphere, as inferred for the order Anseriformes (Livezey 1986).

Southern origins are indicated throughout the tribe (Fig. 1, Table 1). The tree originates with the Asian-African Cairineae (except for the more northern *Aix*), followed by the Australasian and African Nettapodeae and the strictly South American grade that comprises the supergenera *Amazonetta* and *Lophonetta*. Within the supergenus *Anas*, the genus *Mareca* forms an African branch (*M. capensis*) and a largely Holarctic sister-clade of wigeons and allies. The genus *Anas* has five major branches, of which one is Australasian (subgenus *Nesonetta*), three are characterized by African or South American, or both, basal members (subgenera *Anas*, *Spatula*, and *Dafila*), and one comprises groups of Afro-Neotropical (subgenus *Punanetta*) and Holarctic distributions (subgenus *Querquedula*). The typical mallards (subgenus *Anas* exclusive of *A. sparsa*) show pronounced geographical partitioning, with northern-hemisphere, African, and South Pacific clades (Fig. 3, Table 1). Departures from this general pattern are the Neotropical distribution of *M. sibilatrix* within the otherwise Holarctic clade *Chaulelasmus* + *Eunetta* + *Mareca*; the Australasian distribution of *A. rhynchotis*, the sister-species to the North American *A. clypeata*; and the insular isolation of *A. laysanensis* and *A. wyvilliana* (infragenus *Anas*) in the equatorial Pacific Ocean, and *A. eatoni* (infragenus *Dafila*) in the Indian Ocean. At least the last three were probably founded by wayward migrant flocks (Delacour 1956, Weller 1980).

Morphological correlates.—Several physical characteristics not used in inferring relationships within the Anatini showed strong phylogenetic patterns (Table 1). Body size, defined by three discrete intervals of mean body masses, varied little within genera of Cairineae and Nettapodeae, and (to a lesser degree) within *Mareca*. In the genus *Anas*, body-size diversity occurs within most subgenera. A majority of the size variation in the subgenus *Anas* is due to the dwarfism of the Pacific isolates (*A. wyvilliana*, *A. laysanensis*). In several other subgenera, the ranges in body mass reflect phylogenetically constrained variation among constituent clades (e.g. between *Pterocyanea* and *Spatula*, and between *Dafilonettion* and *Dafila*). Sexual size dimorphism, as measured by three intervals for ratios of mean body masses of males and females, was associated positively with mean body masses of species ($r = 0.54$, $n = 52$). That is, size dimorphism tended to be greater in large species than in small species (Table 1). Exceptions include the disproportionately small dimorphism of *Chenonetta* and some members of the infragenera *Polionettea* and *Paecilonitta*, and the disproportionately great dimorphism of *A. aucklandica* (subgenus *Nesonetta*).

Sexual dichromatism, either sexual differences in color or pattern, or both, in adults in definitive alternate (breeding) plumage, is less easily quantified. To permit broad comparisons with the tribe, I established three categories of sexual dichromatism: class I, *qualitative* (i.e. sex-

TABLE 1. Biogeographical, morphological, and reproductive correlates of phylogeny of Anatini. Classification follows that proposed in Appendix 2. Codings are explained in footnotes.

Taxonomic group	Biogeographic area[a]	Body mass[b]	Sexual size dimorphism[c]	Sexual dichromatism[d]	Egg mass[e]	Clutch size[f]
Subtribe Cairineae	AS, AF, NA	L–M	L–M	II	M–L	M–L
Supergenus *Cairina*	AF, AS	L–M	L–M	I–II	M–L	M–L
Genus *Cairina*	AF, AS	L	L	II	L	L
Genus *Pteronetta*	AF	M	M	II	M	M
Supergenus *Aix*	AS, NA	M	L	I	M	L
Genus *Aix*	AS, NA	M	L	I	M	L
Subtribe Nettapodeae	AU, AF	S–M	S	I–II	S–M	M–L
Supergenus *Chenonetta*	AU	S–M	S	I–II	S–M	M–L
Genus *Chenonetta*	AU	M	S	I	M	L
Genus *Nettapus*	AU, AF	S	S	II	S	M–L
Subgenus *Nettapus*	AF	S	S	II	S	M
Subgenus *Cheniscus*	AU	S	S	II	S	L
Subtribe Anateae	global	S–L	S–L	I–III	S–L	S–L
Supergenus *Amazonetta*	NE	S	S	I–II	S	M
Genus *Amazonetta*	NE	S	S	II	S	M
Genus *Callonetta*	NE	S	S	I	S	M
Supergenus *Lophonetta*	NE	M	M	II	M–L	S
Genus *Lophonetta*	NE	M	M	II	M	S
Genus *Speculanas*	NE	M	M	II	L	S
Supergenus *Anas*	global	S–L	S–L	I–III	S–L	S–L
Genus *Mareca*	HA, NE, AF	S–M	S–L	I–III	S–M	M
Subgenus *Notonetta*	AF	S	S	III	S	M
Subgenus *Chaulelasmus*	HA	M	M	I	M	M
Subgenus *Eunetta*	PA	M	L	I	M	M
Subgenus *Mareca*	HA, NE	M	M	I–II	M	M
Genus *Anas*	global	S–L	S–L	I–III	S–L	S–L
Subgenus *Anas*	HA, AF, SP, HI	S–L	S–L	I–III	S–L	S–M
Infragenus *Melananas*	AF	L	L	III	L	S
Infragenus *Anas*[g]	HA (HI)	M–L (S–M)	M–L (S–M)	I–III (II)	M–L (S–M)	S–M (S–M)
Infragenus *Polionetta*	SP	M–L	S–M	III	M	M
Infragenus *Afranas*[h]	AF	M	M	III	M	M
Subgenus *Spatula*	global	S–M	S–M	I–II	S–M	M–L
Infragenus *Pterocyanea*	NA, NE	S	S	I	S	L
Infragenus *Spatula*	global	M	S–M	I–II	M	M–L
Subgenus *Nesonetta*[i]	AU, AS	S–M	S–L	I–II	S–L	S–L
"Infragenus *Virago*"	AU, AS	S	S	II	S	M
Infragenus *Nesonetta*[j]	AU	M (S)	M (L)	I (II)	M–L (S)	S–L (S)
Subgenus *Dafila*	NE, HA, AF	S–M	S–M	I–III	S–M	S–M
Infragenus *Paecilonitta*	AF, NE	M	S	II	M	M
Infragenus *Dafilonettion*	NE	S	S	II	S	S
Infragenus *Dafila*	HA, NE	M	S–M	I, III	M	M
Subgenus *Querquedula*	HA	S	S	I	S	M
Infragenus *Querquedula*	PA	S	S	I	S	M
Infragenus *Nettion*	HA	S	S	I	S	M
Subgenus *Punanetta*	NE, AF	S–M	M	II	S	M
Infragenus *Punanetta*	NE	S–M	M	II	S	M
Infragenus *Micronetta*	AF	S	—	II	S	M

[a] *Region*: AF = Africa, AS = Asia, AU = Australia, HA = Holarctic, HI = Hawaiian, NA = Nearctic, NE = Neotropic, PA = Palearctic, SP = South Pacific.

[b] *Mean body mass*: S = small (<500 g), M = medium (500–1,000 g), L = large (>1,000 g); data taken primarily from Madge and Burn (1988).

[c] *Mass dimorphism ratio*, $\bar{x}$(males)/$\bar{x}$(females): S = small (1.00–1.10), M = medium (1.11–1.20), L = large (>1.21).

[d] *Chromatic differences*: I = qualitative, II = quantitative, III = absent.

[e] *Mean egg mass* (Rohwer 1988): S = small (25–40 g), M = medium (41–60 g), L = large (>61 g).

[f] *Mean clutch size* (Rohwer 1988): S = small (3–6), M = medium (7–9), L = large (>10).

[g] Parenthetical codes refer to "*Horizonetta*" (*Anas wyvilliana* and *A. laysanensis*).

[h] Reproductive data for *A. melleri* not available.

[i] Poorly known *A. bernieri* not included.

[j] Parenthetical codes refer to *A. aucklandica*.

es differ significantly in pattern as well as degree); class II, *quantitative* (i.e. sexes differ primarily in intensity or conspicuousness, but underlying pattern is essentially the same); and class III, obsolete or entirely absent. Despite problematic assignments of several species with "intermediate" levels (e.g. *Nettapus, Lophonetta, M. strepera, A. wyvilliana, A. flavirostris*), several patterns emerged (Table 1). First, 22 of 38 species (excluding *A. oustaleti*) are characterized by class-I dichromatism and 27 show class-II dichromatism. Together, 49 (84%) species of Anatini are sexual dichromatic. Second, sexually monochromatic species (class III) are limited to the supergenus *Anas* and include members of *Mareca* and the subgenus *Anas*. Third, class-I dichromatism characterizes *all* member species in only three named groups: the genus *Aix*, subgenus *Querquedula*, and infragenus *Pterocyanea*.

Sexual dichromatism within the subgenus *Anas* is exceptionally variable and ranges from the monochromatic condition of southern-hemisphere species and an insular isolate (*A. laysanensis*) to the conspicuous dichromatism of *A. platyrhynchos*. "Reduced" sexual dichromatism characterizes insular Anatini (especially *Anas*) and species of the southern hemisphere (Table 1). This pattern has been interpreted traditionally as the adaptive loss of "isolating mechanisms" in insular communities that lack phenotypically "confusable" congeners (Ripley 1957b, Sibley 1957, Johnsgard 1963, Lack 1970, Weller 1980). Alternatively, West-Eberhard (1983) suggested that the comparatively dull plumages of insular waterfowl reflect a reduced intensity of sexual selection related to the protracted pair-bonds and greater parental investment by males (Weller 1980). This hypothesis is supported by the strong association between biparental care of young and sexual monochromatism in Anatidae (Kear 1970). Another possibility is that the dull, juvenal-like plumages of insular anatids are nonadaptive characters developmentally linked to a selectively favored, paedomorphic reduction of the pectoral limb (Livezey 1989a, 1990).

Behavioral patterns.—Although homologies and polarities of behavioral characters were inadequately established for inclusion in the phylogenetic analysis, evolutionary trends in reproductive behavior of Anatini can be documented. Age of sexual maturity ranges from 2 yr in *Cairina* (characteristic of Tadorninae, *Plectropterus, Sarkidiornis* and evidently primitive) to 1 yr in all other Anatini (Johnsgard 1961a, 1965; Kear 1970). *Cairina* is also unique among Anatini in its promiscuous (polybrachygynous) mating system (Johnsgard 1961a) while monogamy is typical of dabbling ducks (McKinney 1985). Biparental attendance of broods characterizes most members of the outgroup (Kear 1970), *Pteronetta* (Kear 1970), Nettapodeae (Frith 1967), *Amazonetta* (Phillips 1923), *Callonetta* (Brewer 1989), *Lophonetta* (Buitron and Nuechterlein 1989), *Speculanas* (Kear 1970), some *Mareca* (Weller 1968, Siegfried 1974), and to varying degrees the members of most subgenera of *Anas* (Weller 1968, Siegfried 1974, McKinney 1985, Norman and McKinney 1987, McKinney and Brewer 1989). *Cairina* and (to a lesser extent) *Aix* are exceptional among basal Anatini in the virtual lack of brood attendance by males (Kear 1970). This pattern strongly suggests that biparental brood-rearing is a primitive character among Anatini (*contra* Kear 1970), and this polarity explains, at least in part, the preponderance of southern-hemispheric dabbling ducks having protracted pair-bonds (Weller 1968, Kear 1970, McKinney 1985). This trait presumably coevolved with a number of characters including migratory habit, seasonal plumage dichromatism, predictability of food resources, and tertiary sex-ratios (Weller 1968, McKinney 1985).

Most Anatini (especially Anateae) are characterized by monosyllabic distress calls of downy young (Lorenz 1951–1953) and preflight "intention" movements (McKinney 1965). A number of presumably derived courtship behaviors further characterize most or all members of the supergenera *Lophonetta* and *Anas*. These include marked "inciting displays," variably long "decrescendo calls," and postcopulatory bathing by females; ritualized head-turning and wing-preening displays by males; and precopulatory "head-pumping" displays by both sexes (Lorenz 1951–1953; Johnsgard 1961a, 1965). Other behavioral characters, including most "comfort movements" (McKinney 1965), photoperiodic rhythms of reproduction (Murton and Kear 1975, 1978; Kear and Murton 1976), and other details of courtship displays (Johnsgard 1961a, 1962, 1965, 1978), are less readily interpreted phylogenetically, primarily because of inadequate information for a number of species.

Reproductive parameters.—Selected quantitative parameters of reproduction also show moderately pronounced phylogenetic patterns (Table 1). Hierarchical relationships preclude simple statistical comparisons among members (Felsenstein 1985), but correlations provide useful indices to patterns within the tribe. Rohwer (1988) found that the mean egg masses of 53 species of Anatini was positively correlated with mean body masses ($r = 0.85$). The egg masses have phylogenetic patterns similar to those described for body mass (Table 1). As noted by Rohwer (1988), insular isolates represent significant, statistically influential deviations from the overall relationship between egg mass and body mass. Notable examples among Anatini are *A. eatoni*, *A. chlorotis*, and (especially) *A. aucklandica* (Table 1). The evolutionary implications of egg size in *A. aucklandica* are considered elsewhere (Livezey 1990).

Clutch size (data from Rohwer 1988) is not correlated with body mass among 53 species of Anatini ($r = 0.12$, log-transformed data). Extreme examples include the small clutch-sizes of the comparatively massive *S. specularis* and *A. sparsa*, and the large clutch-sizes of tiny *Nettapus* (Table 1). This finding, and a modest negative correlation (Rohwer 1988) between clutch size and egg mass in 53 Anatini ($r = -0.62$) or 43 noninsular Anatini ($r = -0.39$), suggests that clutch mass (product of egg mass and clutch size) is phylogenetically constrained (see Cody 1966), and that, of the two interrelated parameters, egg mass has the greater phylogenetic component. The primary determinant of clutch sizes of waterfowl is thought to be energy resources available to the female (Lack 1968, Klomp 1970), confounded as well by proximate variations in availability of food (Johnsgard 1973). Other egg characteristics, such as relative thickness of shells and membranes, and proportions of soluble and insoluble nitrogen in the shell (Tyler 1964), showed no clear phylogenetic patterns among Anatini. These correlative assessments within tribes, like the studies by Laurila (1988) and Rohwer (1988), are only partly successful in discriminating between phylogenetic constraint and adaptive changes of life-history parameters. Comprehensive assessments of phylogenetic constraint must incorporate more completely resolved phylogenies and multivariate techniques that use hierarchically nested designs (Grafen 1989, Funk and Brooks 1990).

Evolutionary consistencies and rates of character evolution.—The consistency index of the proposed phylogenetic hypothesis is moderately high, compared with other cladistic analyses of avian groups, including an earlier, genus-level analysis of Anseriformes (Livezey 1986). This consistency was achieved despite the comparatively large number of taxa analyzed and the exclusion of unique autapomorphies. Generally, character consistencies tend to decrease as the number of taxa analyzed increases (Sanderson and Donoghue 1989). In addition, the four major groups of characters had comparable consistency indices (Table 2). It is commonly assumed that character suites differ in phylogenetic "reliability" or informativeness (e.g. Delacour and Mayr 1945), and these judgments may influence the weights characters are given in phylogenetic inference (Bryant 1989).

TABLE 2. Summary statistics for consistency indices of p characters by anatomical-developmental group.

Character group	p	Mean	Range
Definitive plumage & soft parts			
Analyzed set	107	0.850	0.250–1.000
Additional[a]	165	0.903	0.250–1.000
Natal plumage	22	0.777	0.250–1.000
Trachea	21	0.865	0.500–1.000
Skeleton			
Analyzed set	7	0.809	0.333–1.000
Additional[a]	10	0.866	0.333–1.000

[a] Includes autapomorphies not in formal analysis; list available.

A related issue concerns the rates at which characters evolve, which may in turn determine the phylogenetic and taxonomic level at which the characters are informative in a particular group. Although some inequality of effort expanded on character-groups was unavoidable, I believe that the distributions of characters analyzed are representative of their relative availabilities. Tallies of character changes, grouped by both morphological groups and five major taxonomic levels of the resultant phylogeny (Figs. 2, 3), indicate that character types were unevenly distributed among levels within the tree (Table 3). In particular, characters of definitive plumages and soft parts were useful throughout the tree but were especially useful at the lowest levels. Relationships at the level of subtribes, supergenera, genera, and subgenera were supported disproportionately by state changes in characters of natal plumage and tracheal anatomy. Nontracheal skeletal characters, of paramount importance for the establishment

TABLE 3. Numbers of character changes, by anatomical-developmental group, that support topological divergences at five taxonomic levels.

Taxonomic level	Character group			
	Definitive external	Natal	Tracheal	Skeletal
Tribe and subtribe	7	5	1	5[a]
Supergenus and genus	41	5	9	3
Cohort and subgenus	21	8	10	0
Infragenus and species-group	76	9	6	1
Species	72+	1	2	4
Analyzed set	14	1	2	1
Additional[b]	58+	0	0	3

[a] Includes four skeletal synapomorphies of Anatinae (Livezey 1986).

[b] Characters not included in formal analysis but compiled to confirm monophyly of species; list available on request.

of genus-level relationships in Anseriformes (Livezey 1986), were primarily useful in this analysis for resolutions at the tribal and subtribal levels (Table 3). This heterogeneity of character change strongly suggests that characters evolve at significantly different rates. They are of greatest phylogenetic utility for segments of the tree where rates of evolutionary change are moderately high. Consequently systematists should select those character suites that evolutionarily "target" the phylogenetic relationships of concern.

Osteological studies of Anatini indicate a paucity of phylogenetically informative characters of the skeleton (Woolfenden 1961, Livezey 1986, present study), which underscores the need for extreme caution in the classification of fossil dabbling ducks. Although avian paleontologists generally are cognizant of the difficulties of classifying fragmentary specimens (e.g. Howard 1964, Olson 1985), the phenetic assignment of fossils and widespread preoccupation with discovery of possibly ancestral lineages have seriously compromised the contributions of traditional paleontology to an understanding of avian phylogeny (Cracraft 1980). Based on an osteologically based analysis of Recent genera of Anseriformes (Livezey 1986), many fossil anseriforms, including a number of purported anatines and most pre-Pliocene forms assigned to "*Anas*," were incorrectly classified (Livezey and Martin 1988, Livezey 1989b). Ten post-Miocene fossils assigned to *Anas* (or generic synonyms) appear, on the basis of the compendia of Brodkorb (1964) and Howard (1964), to have been classified based on assessments of size and phenetic comparisons of unreliable skeletal features. Size is not phylogenetically deterministic within the Anatini, and most skeletal variation has not proved reliable for classification. Although analysis of fossils can contribute much to phylogenetic systematics (Schoch 1986), I agree with Howard (1964: 237) that evolutionary insights to be gained from fossil waterfowl must await an improved knowledge of phylogenetic relationships among Recent representatives of the Anseriformes.

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APPENDIX 1. Characters used in the phylogenetic analysis of Anatini. The sequence corresponds to that used in the figures and text. Presumed primitive character states are defined as "a"; derived states are designated alphabetically thereafter (with the exception of character 27). Characters with two or more derived states, with the exception of rectrix number (character 27), were analyzed as unordered. Characters are grouped by general anatomical or developmental class, but groupings of some bill characters that involved the integument and underlying bones were necessarily arbitrary. To avoid biased comparisons of character groups, two particularly difficult cases involving bill shape (characters 97 and 157) were assigned to "soft-parts" and "skeleton," respectively. Potentially confusable characters are cross-referenced parenthetically. Unless indicated otherwise, characters of definitive plumages pertain to both alternate and basic plumages and to both sexes. Characters of syringeal bulla pertain to males. Consistency indices (CI) for each character correspond to the topology given in Figures 2 and 3.

ADULT (DEFINITIVE) PLUMAGES

1. Tail: (a) moderately short; (b) long, broad, rounded, generally black (extends well beyond feet in normally prepared skins); CI = 0.50.

2. Rump of definitive males: (a) not as follows; (b) with contrasting black lateral margins; CI = 0.50.

3. Lateral vanes of outer rectrices: (a) colored as medial vanes; (b) whitish, contrasting with medial vanes, producing fine pale borders of tail; CI = 0.50.

4. Central pair of rectrices: (a) of approximately equal length to other rectrices; (b) distinctly elongate relative to other rectrices; CI = 1.00.

5. Central pair of rectrices: (a) straight; (b) dorsally curled; CI = 1.00.

6. White vertical shoulder mark: (a) absent; (b) present in males; CI = 0.50.

7. Narrow white antorbital facial crescent: (a) absent; (b) present in males (only in basic of *A. clypeata;* occurs also in hybrids involving *A. clypeata,* see Scherer and Hilsberg 1982); CI = 1.00.

8. Pale flank patches, formed by laterodorsal extensions of pale venter to sides of rump: (a) absent; (b) present in males, alternate plumage (compare with character 18); CI = 0.33.

9. Secondary coverts pale *blue,* forming contrasting blue forewing patch: (a) absent; (b) present (excludes more extensive, *gray* forewing of *A. querquedula* and Infragenus *Punanetta*); CI = 1.00.

10. Distinct, whitish "horseshoe"-shaped marks on breast feathers, all definitive plumages (exclusive of alternate plumage of male *A. clypeata*): (a) absent; (b) present (variable, weak in *A. smithii;* compare with character 38); CI = 0.50.

11. Dark, contrasting cap, extending to below orbit and including nape: (a) absent; (b) present; CI = 0.50.

12. Contrasting, white vertical neck stripe: (a) absent; (b) present (reduced in *A. eatoni;* Stahl et al. 1984); CI = 1.00.

13. Secondary coverts white, forming contrastingly pale forewing patch: (a) absent; (b) present; CI = 1.00.

14. Contrasting, pale buff or white forecrown: (a) absent; (b) present; CI = 1.00.

15. Greenish postorbital patch, washed with purplish-bronze iridescence, lacking contrasting border: (a) absent; (b) present (compare with characters 28, 31); CI = 1.00.

16. Smudgy black crown, from bill base to occiput: (a) absent; (b) present in definitive alternate plumages of males; CI = 1.00.

17. Sharply defined, narrow white eye-ring: (a) absent; (b) present, both sexes; CI = 1.00.

18. Black-bordered buff flank patches: (a) absent; (b) present in males, alternate plumage; CI = 0.50.

19. Rump: (a) not as follows; (b) dark *brown* with greenish iridescence, in males; CI = 1.00.

20. Broad white stripes on lateral vanes of tertials: (a) absent; (b) present in both sexes; CI = 1.00.

21. "True" speculum, a contrastingly colored, *metallic* patch *limited to secondaries:* (a) absent (includes the nonmetallic white "speculum" or generalized alar iridescence of Cairineae and Chenonetteae); (b) present; CI = 1.00.

22. Color of (true) speculum (where present; not codable for autapomorphic *M. strepera*): (a) metallic purplish-bronze; (b) metallic green and blue, variably washed with purplish or black (obsolete in *A. bernieri*); CI = 1.00.

23. Rufous or pinkish-red sides: (a) absent; (b) present, both sexes; CI = 1.00.

24. Pinkish-brown wash on breast: (a) absent; (b) present, both sexes; CI = 1.00.

25. Cinnamon wash on sides and belly: (a) absent; (b) present in males, alternate plumage; CI = 1.00.

26. Chestnut wash on sides, belly and breast: (a) absent; (b) present; CI = 1.00.

27. Number of pairs of rectrices (state "b" considered primitive; modal condition in nonmolting adults): (a) 6; (b) 7; (c) 8; (d) 9; CI = 0.33.

28. Entire head and neck (including chin and throat) of male in alternate plumage a bright, metallic green: (a) not so (includes green iridescence on sides of head in male *A. clypeata*); (b) as described (vestigial in *A. oustaleti* and *A. wyvilliana*); CI = 0.50.

29. Brick-red coloring of breast, as distinct from sides, belly: (a) absent; (b) present in males, especially in alternate plumage (vestigial in *A. fulvigula, A. oustaleti,* and *A. wyvilliana*); CI = 0.50.

30. Generalized, poorly differentiated greenish postorbital iridescence: (a) absent; (b) present; CI = 1.00.

31. Intense, metallic-green postorbital patch with black and/or buff border: (a) absent; (b) present; CI = 1.00.

32. Entire rump contrastingly black with green iridescence: (a) not so (includes the purplish-brown rump of *A. poecilorhyncha* and greenish-brown rump of male *A. clypeata*); (b) as described (vestigial in *A. oustaleti, A. wyvilliana, A. laysanensis*); CI = 1.00.

33. Sharp, black-and-white vermiculations on undertail coverts: (a) absent; (b) present; CI = 1.00.

34. Sharp, black-and-white barring on flanks: (a) absent; (b) present; CI = 0.50.

35. Fine blackish vermiculations on flanks: (a) absent; (b) present; CI = 1.00.

36. Fine blackish vermiculations on whitish or pale buff belly feathers of males: (a) absent; (b) present; CI = 0.50.

37. Constrasting black wing linings: (a) absent; (b) present; CI = 0.50.

38. Alternating brown and white, U-shaped marks on breast feathers: (a) absent; (b) present, males in alternate plumage (Fig. 4a; compare with character 10); CI = 0.67.

39. Contrastingly pale caudal border on speculum (where present): (a) present, white or buffy; (b) obsolete; CI = 0.50.

40. Pale caudal border of speculum (where present): (a) narrow, (cranio-caudal) width significantly less than that of metallic speculum; (b) broad, width approximating or exceeding that of speculum; CI = 1.00.

41. Breast feathers of males in alternate plumage: (a) not as follows; (b) with dark central subterminal spot subtended proximally by transverse row of four lighter spots (Fig. 4b); CI = 1.00.

42. Cranial border of speculum, formed by tips of caudal-most row of greater secondary coverts: (a) not contrastingly colored; (b) black; (c) white; (d) buff or rufous; CI = 0.38.

43. Tips of greater secondary coverts (character 42) subtended with contrasting white or light brown subterminal band: (a) not so; (b) as described; CI = 1.00.

44. Basal half of greater secondary coverts: (a) brown; (b) white; (c) black; CI = 0.67.

45. Lateral vane of tertials of males in alternate plumage: (a) not as follows; (b) with sharply defined, narrow white edge, bordered medially by black (excludes white edge subtended by brown in *M. capensis, A. querquedula*); CI = 1.00.

46. Scapulars of males in alternate plumage: (a) not as follows; (b) with distally widened, sharply defined, typically asymmetrical, white central stripe (Fig. 5d); CI = 0.50.

47. Scapulars of males in alternate plumage: (a) not as follows; (b)

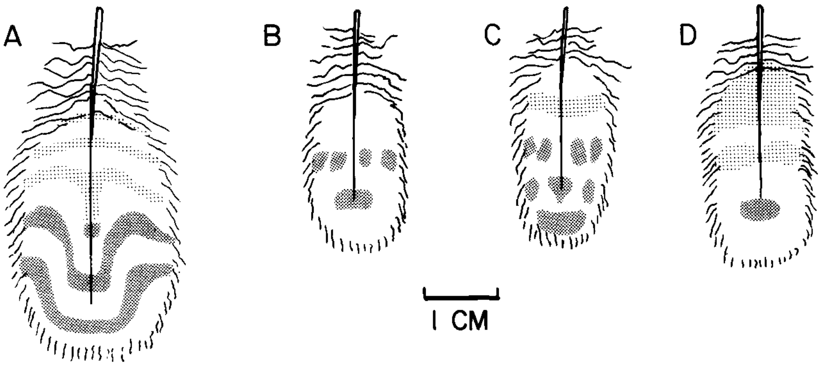

Fig. 4. Breast feathers of four species of Anateae (definitive alternate plumages of males, ventral views): (A) *Mareca falcata* (AMNH 732,314), (B) *Anas crecca* (AMNH 424,195), (C) *A. discors* (AMNH 749,780), and (D) *A. erythrorhyncha* (AMNH 262,156).

with distal portion of lateral vane blue, and medial vane blackish with distally widening buff stripe along rachis (Fig. 5c); CI = 1.00.

48. Back feathers of both sexes in alternate plumage: (a) brownish with margins variously lighter; (b) finely vermiculated with buff; CI = 1.00.

49. Back feathers of males in alternate plumage: (a) not as follows; (b) crossed by 3–4 straight bars of white; CI = 0.50.

50. Back feathers of females: (a) not as follows; (b) marked in midvane by wide, whitish, U-shaped bar; CI = 1.00.

51. Back feathers: (a) not as follows: (b) dichromatic—with buffy-cinnamon crescent distally and similarly colored, irregular line proximally in males, and a single central buffy crescent in females; CI = 1.00.

52. Shape of scapulars of males in alternate plumage: (a) typically pinnate; (b) tapering abruptly to long narrow point (Fig. 5c, d); CI = 1.00.

53. Buff mottling on basal half of lateral vanes of scapulars of males in alternate plumage: (a) absent; (b) present; CI = 1.00.

54. Uppertail coverts of both sexes: (a) not as follows; (b) largely black with distal edges of medial vanes buff; CI = 1.00.

55. Scapulars of males in alternate plumage: (a) not as follows; (b) finely vermiculated with gray and white, especially medial vane; CI = 1.00.

56. Sharply defined black chin patch: (a) absent; (b) present in males in alternate plumage; CI = 1.00.

57. Fine, black, circular speckling of head: (a) absent; (b) present on whitish background in basic plumage of males and all definitive plumages of females; (c) present on brownish background (all definitive plumages except alternate of male *A. acuta*); CI = 1.00.

58. Short mane of feathers on nape, relatively well developed in lower (nuchal) portion: (a) absent; (b) present (compare with characters 87, 88); CI = 1.00.

59. Dorsal contour feathers characterized by an irregular buff marginal and one irregular central buff mark: (a) not so; (b) as described; CI = 1.00.

60. One or two V-shaped white marks on dorsal contour feathers: (a) absent; (b) present; CI = 1.00.

61. Entire back and crown iridescent green: (a) not so; (b) as described; CI = 1.00.

62. Faces of females with three adjacent cheek stripes, alternating white, black, and white: (a) not so; (b) as described; CI = 1.00.

63. Entire underwing, excluding remiges: (a) variably mottled or black; (b) immaculate white; (c) dark chestnut; CI = 1.00.

64. Coloration of body, including dorsum, tail, sides, venter, head, and neck: (a) various, but not as follows; (b) black; (c) dark brown; CI = 1.00.

65. Primary remiges: (a) uniformly dark; (b) dark with fine, whitish lateral margins; CI = 1.00.

66. Alternating black and white crescents on sides of breast: (a) absent; (b) present in males in alternate plumage; CI = 1.00.

67. Black-and-white scalloping on sides: (a) absent; (b) present in males in alternate plumage; CI = 1.00.

68. White, drop-shaped postocular streaks: (a) absent; (b) present in females; CI = 1.00.

69. Crown and nape darkened by a contrastingly dark, dull-brown "hood": (a) not so; (b) present in males in alternate plumage; CI = 1.00.

70. Speculum (where present and "true"): (a) not as follows; (b) strongly washed with iridescent bronze and distinctly dichromatic, those of females having little or obsolete iridescence; CI = 1.00.

71. Wings rounded, primary remex 10 distinctly shorter than primary remiges 8 and 9: (a) not so (includes uniquely rounded condition in *A. aucklandica*, in which both remex 9 and 10 are shorter than remex 8); (b) characteristic of both sexes; CI = 1.00.

72. Rectrices progressively shortened laterally, producing wedge-shaped tail: (a) not so; (b) as described; CI = 1.00.

73. Scapulars of males in alternate plumage: (a) not as follows; (b) patterned with fine, white, obliquely oriented vermiculations (Figs. 5a vs. 5b); CI = 1.00.

74. Entire upper forewing, including all secondary coverts and lesser primary coverts (alular region): (a) not contrastingly patterned; (b) immaculate white; (c) pale blue; CI = 1.00.

75. Color of lower breast and belly: (a) variously colored, often mottled, but if pale not distinctly demarcated from color of sides, flanks, and breast; (b) white, sharply contrasting with darker sides, flanks, and breast; CI = 1.00.

76. Scapulars of adults, especially males: (a) not as follows; (b) with contrasting black stripe along rachis; CI = 1.00.

77. Uppertail coverts distinctly pointed with pale lateral edges: (a) not so; (b) as described; CI = 1.00.

78. Axillars of adults (both sexes): (a) not as follows; (b) white with minute grayish spotting distally; (c) with minute brown spotting distally; CI = 0.67.

79. Diffuse greenish iridescence of dorsum of wing, if present: (a) variable in intensity, typically including secondary converts, secondary remiges, tertials, and (in some) primary remiges; (b) limited to specular region of secondary remiges; CI = 1.00.

80. Upperwing: (a) not as follows; (b) generally iridescent green (particularly intense on secondary remiges) with laterally widening, white band formed by tips of greater secondary coverts (reduced proximally in *N. auritus*); (c) generally iridescent green with white band on secondary coverts obsolete; CI = 1.00.

81. Rump paler than rectrices, finely scalloped with dark gray: (a) not so; (b) as described; CI = 1.00.

82. Flanks of males in alternate plumage: (a) not as follows; (b) marked by subrectangular whitish patch surrounded by dark areas; CI = 1.00.

83. Flanks of males in alternate plumage: (a) not as follows; (b) marked by subcircular whitish patch surrounded by dark areas; CI = 1.00.

84. Breast feathers of males in alternate plumage: (a) not as follows;

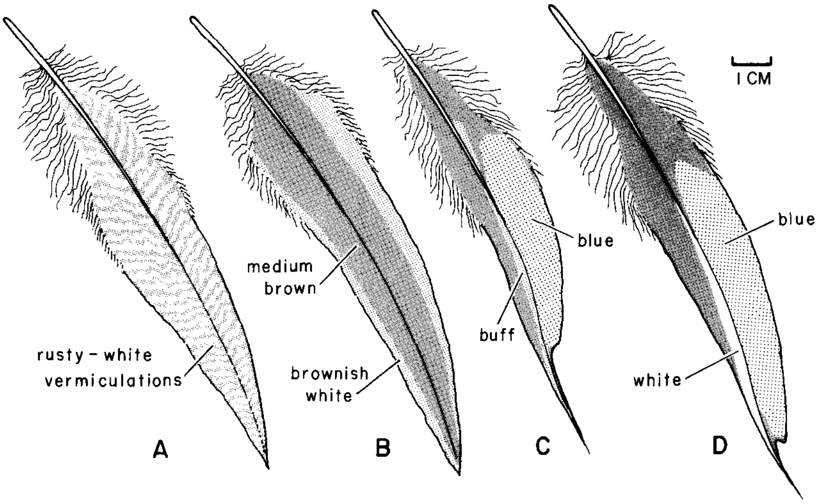

Fig. 5. Scapulars of four species of Anateae (definitive alternate plumages of males, dorsal views, right pterylae): (A) *Mareca americana* (AMNH 350,657), (B) *M. sibilatrix* (AMNH 443, 631), (C) *Anas cyanoptera* (AMNH 731,952), and (D) *A. rhynchotis* (AMNH 732,785).

(b) with one dark, central terminal spot, subtended by a staggered row of three dark spots, followed by a more-proximal row of four paler spots (Fig. 4c); CI = 1.00.

85. Breast feathers of males in alternate plumage: (a) not as follows; (b) with one dark, central terminal spot, subtended by two variably distinct dark spots, followed by a blurred basal line (Fig. 4d); CI = 0.50.

86. Edge of lateral vane of tertials of males in alternate plumage: (a) not as follows; (b) with sharp defined, narrow black border, subtended medially by buffy brown (interrupted proximally by white in *A. crecca*); CI = 1.00.

87. Long crest, emerging from crown to nape, the longest plumes originating anteriorly: (a) absent; (b) present in *both* sexes; CI = 1.00.

88. Nuchal crest of moderate, relatively uniform length: (a) absent; (b) present, longer in males (comparatively long in *M. falcata*; cf. characters 58, 87); CI = 0.33.

89. Heads of adults of both sexes: (a) poorly demarcated from breast, or differs *qualitatively* from breast in color; (b) sharply demarcated *quantitatively* from breast in the darkness of brownish-gray color; CI = 1.00.

90. Ground color of axillars (both sexes): (a) white; (b) dark brown to black; CI = 0.25.

91. Axillars: (a) without conspicuous dark transverse barring or spotting; (b) so marked, especially pronounced in females (excludes dull brownish mottling of *A. laysanensis* and *A. aucklandica*; includes reduced, subspecifically variable markings of *A. bahamensis* and almost completely darkened *A. georgica*; CI = 0.33.

SOFT PARTS

92. Background color of bill: (a) dark gray; (b) greenish yellow to orange (less bright in *A. wyvilliana*, *A. laysanensis*; excludes lemon-yellow of *N. auritus*); (c) bright bluish gray; (d) scarlet, in males (excludes unique red-colored bills of *M. capensis*, *Amazonetta*); CI = 1.00.

93. Lateronasal regions of bill: (a) of same color as rest of bill; (b) marked by contrasting yellow patches; (c) marked by contrasting red patches; CI = 0.50.

94. Sharply defined, dark stripes along culmen, especially conspicuous in males: (a) absent; (b) present (Fig. 6c; brownish in *A. erythrorhyncha*, obscured by background color in *A. bahamensis*); CI = 0.50.

95. Dark stripe along tomium and forming variably broad, dark line of base of bill: (a) absent; (b) present; CI = 0.50.

96. Color of feet: (a) dark gray; (b) yellow to reddish orange; (c) bright pink or coral red; CI = 0.29.

97. Bill (lateral view): (a) with concave dorsal ridge, nostrils basal to midpoint of culmen; (b) short, stout, with convex dorsal ridge, nostrils located approximately at midpoint of culmen (Fig. 6b); CI = 1.00.

98. Base of bill swelling in breeding males: (a) not so; (b) as described (Fig. 6a); CI = 1.00.

99. Variable, flesh-colored subterminal patch on dorsum of bill: (a) absent; (b) present (Fig. 6a); CI = 0.50.

100. Contrasting, dark nasal patches on dorsum of bill (obscured in most older skin specimens): (a) absent; (b) present in both sexes (see photograph in Hosking and Kear [1985: 98]; excludes the perinasal patches of *S. specularis* and the sexually dichromatic, irregularly shaped, comparatively blurred markings in some members of subgenus *Anas*); CI = 1.00.

101. Base of bill: (a) with marked angular dorsal prominences (Fig. 6a); (b) sloping, without angular prominence (Fig. 6: b–c); CI = 0.50.

102. Claws of pedal phalanges: (a) straight or moderately curved; (b) strongly curved, very robust; CI = 1.00.

103. Contrastingly dark tomial stripe (without basal extension): (a) absent; (b) present (Fig. 6c); CI = 1.00.

104. Iris color: (a) brown, both sexes; (b) yellow in males, brown in females; (c) reddish-yellow, both sexes; (d) red, both sexes, males brighter (excludes sexually dichromatic, scarlet irides of *Aix sponsa*, and variable iris color of *M. capensis*, *L. specularioides*); CI = 0.75.

105. Cartilaginous carpal knobs (without elongation of underlying process of metacarpal I as in Tadorninae): (a) absent; (b) present, often naked of feathers in adult males (excludes suggestions of knobs present in males of some Anateae, e.g. *L. specularioides*, *S. specularis*, and *A. sparsa*); CI = 1.00.

106. Bright yellow patch on upper bill tip, immediately caudad to nail: (a) absent; (b) present (both sexes); CI = 1.00.

NATAL PLUMAGES

(The most variable and problematical characters used in this analysis are natal characters. Evaluations of states requires reference to series of specimens of *very young* ducklings. Caution is required to avoid badly "foxed" or faded skins or specimens of uncertain species identification, including hybrid birds from avicultural holdings; detection of facial and dorsal markings can be difficult in the convergently darkened, variable natal plumages of some insular forms, e.g. *A. albogularis* and *A. laysanensis*.)

107. Sharp, dark postorbital stripe *without* any trace of preorbital stripe: (a) absent; (b) present; CI = 0.50.

108. Diffuse, darkish, suborbital cheek patch extending from base of bill: (a) absent; (b) present (Fig. 7b); CI = 0.50.

109. Buffy supraorbital spot: (a) absent; (b) present; CI = 1.00.

110. Background color of face: (a) white or yellowish; (b) washed with tannish-rust; CI = 1.00.

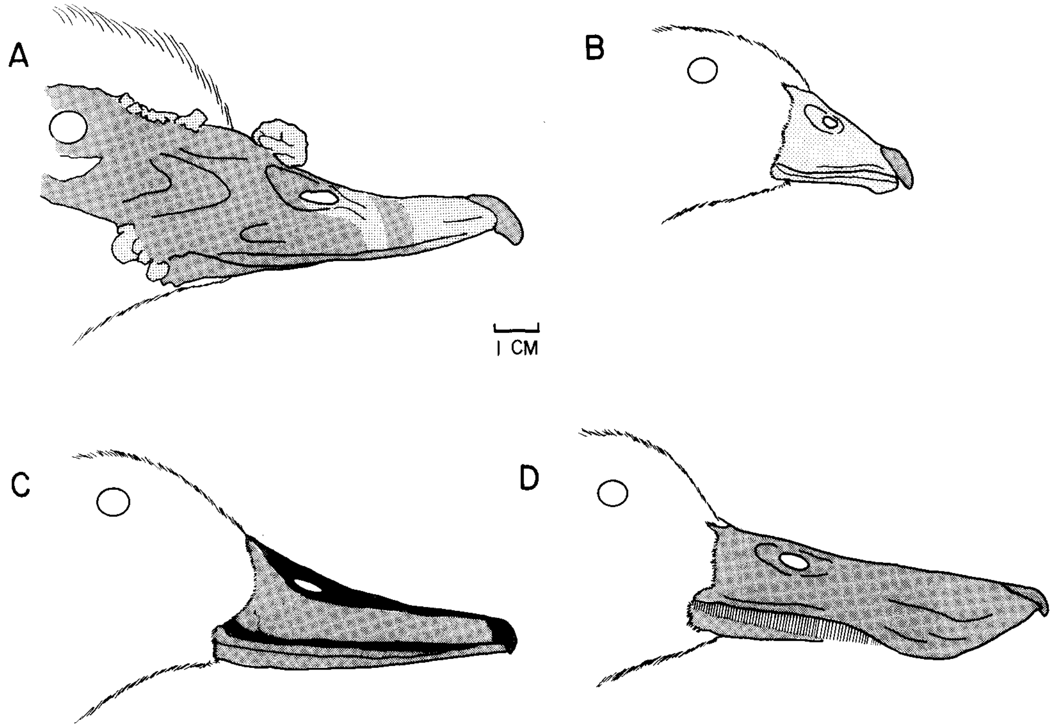

Fig. 6. Bills of four species of Anatini (adult males in breeding season, lateral views): (A) *Cairina moschata* (KUMNH 28,524), (B) *Nettapus auritus* (KUMNH 36,230), (C) *Anas acuta* (KUMNH 9,593), and (D) *A. clypeata* (KUMNH 64,924).

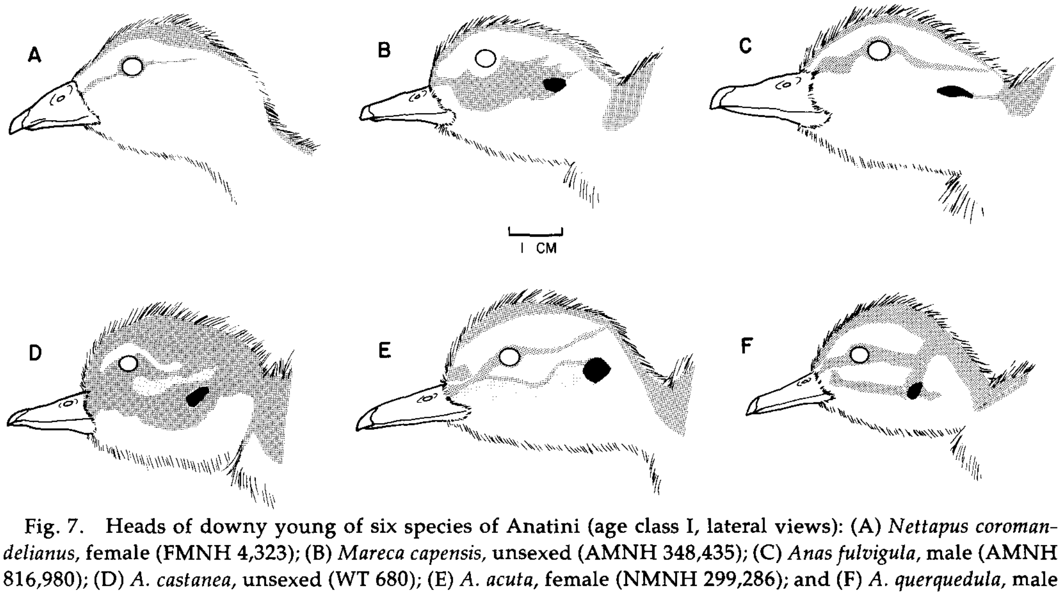

Fig. 7. Heads of downy young of six species of Anatini (age class I, lateral views): (A) *Nettapus coromandelianus*, female (FMNH 4,323); (B) *Mareca capensis*, unsexed (AMNH 348,435); (C) *Anas fulvigula*, male (AMNH 816,980); (D) *A. castanea*, unsexed (WT 680); (E) *A. acuta*, female (NMNH 299,286); and (F) *A. querquedula*, male (WT 622).

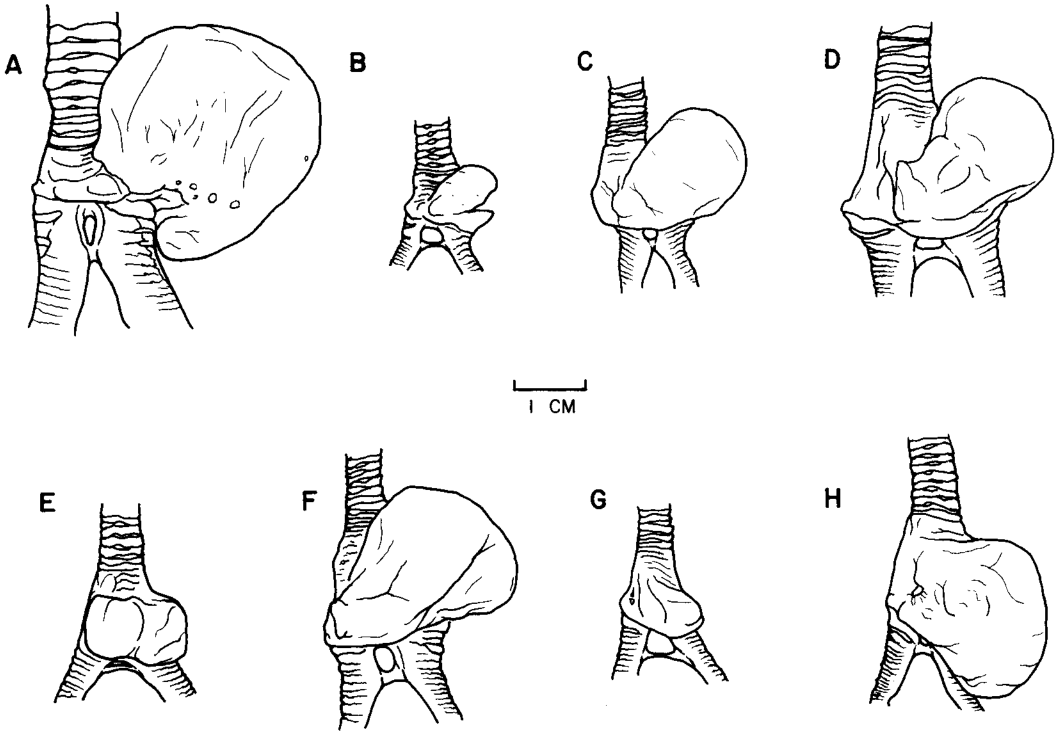

Fig. 8. Syringeal bullae of eight species of Anatini (adult males, ventral views): (A) *Cairina moschata* (WT 1,252), (B) *Callonetta leucophrys* (WT 1,652), (C) *Mareca penelope* (WT 1,043), (D) *Anas rubripes* (WT 2,164), (E) *A. platalea* (WT 922), (F) *A. erythrorhyncha* (WT 938), (G) *A. formosa* (WT 130), and (H) *A. puna* (WT 1,442).

111. Pale scapular and rump spots: (a) rounded, well separated; (b) elongated, the lateral pairs sometimes joining to form pale dorsal stripes; CI = 0.50.

112. Sides, flanks, and belly: (a) colored like breast and throat; (b) distinctly mottled with irregular blotches of dark gray; CI = 1.00.

113. Fine, dark, sharply contrasting breast band: (a) absent; (b) present (Fig. 7d); CI = 0.50.

114. Dark malar spot: (a) absent; (b) present; CI = 1.00.

115. Black-bordered, contrasting orange-buff gape spot: (a) absent; (b) present; CI = 1.00.

116. Darkish orbital stripe passing from bill to nape, sharply defined along dorsal edge but blending with color of cheeks ventrally: (a) absent; (b) present; CI = 1.00.

117. Dark auricular spot: (a) absent (Fig. 7a); (b) present (Fig. 7: b–f); CI = 0.50.

118. Cheek stripe (if present) wide, incorporating dark auricular patch, forming the ventral border to a very narrow, pale suborbital stripe, and typically converging broadly with dark orbital stripe anterior to orbit: (a) not so (includes unique two-toned, "false" cheek stripe of *Chenonetta*); (b) as described (Fig. 7d); CI = 1.00.

119. Cheek stripe (if present) narrow, well separated from orbital stripe by wide white band (rarely occluded anteriorly): (a) not so (includes unique two-toned cheek stripe of *Chenonetta*); (b) as described (Fig. 7f); CI = 1.00.

120. Cheek stripe (if present) broad, bordered dorsally by relatively wide white suborbital band, variably convergent with orbital stripe anteriorly, and widening posteriorly: (a) not so (includes unique two-toned, "false" cheek stripe of *Chenonetta*); (b) as described (Fig. 7c); CI = 1.00.

121. *Bright* yellow wash on throat and upper breast: (a) absent; (b) present (especially variable in some species); CI = 0.50.

122. Pale stripe between dark orbital and cheek stripes *buffy*, contrasting with whitish of throat: (a) absent; (b) present (Fig. 7d); CI = 1.00.

123. Pale supraorbital stripes: (a) terminate at nape (Fig. 7: b–f); (b) continue caudally to meet across nape (Fig. 7a); CI = 1.00.

124. Rectrices: (a) short, not stiffened; (b) disproportionately long, stiff; CI = 1.00.

125. Wing linings: (a) variably mottled with dark; (b) immaculate white or yellow; CI = 0.25.

126. Dark cheek stripe: (a) absent (Fig. 7: a–c); (b) present (Fig. 7: d–f); CI = 0.33.

127. Uneven, variable dark streak passing obliquely from orbit through auricular region to nape: (a) absent; (b) present; CI = 0.50.

128. Dark, variably extensive postorbital stripe (often retained in juvenal and definitive basic plumages of both sexes, as well as definitive basic of males): (a) absent; (b) present (Fig. 7); CI = 1.00.

TRACHEA AND SYRINX (ADULT MALES)

129. Medial margin of syringeal bulla: (a) subcircular in outline (Fig. 8: b–c; includes intermediate conditions of *M. strepera* and *M. americana*); (b) flattened or concave, bulla often tending toward subtriangular shape (Fig. 8: d–h); CI = 0.50.

130. Medial extremity of syringeal bulla: (a) variably rounded; (b) distinctly pointed (Fig. 8f; not codable for uniquely conformed bullae of the subgenera *Spatula* and *Punanetta*, or for *A. querquedula* and *A. formosa*); CI = 0.50.

131. Trachea: (a) without distinct swellings craniad to syrinx; (b) with one (*versicolor* and *puna*) or two (*hottentota*) swellings; CI = 1.00.

132. Syrigneal bulla (uniquely derived bulla of *A. formosa* not comparable): (a) large, lateromedial width more than twice that of trachea; (b) small, lateromedial width less than twice that of trachea (Fig. 8e, see also Fig. 8g); CI = 0.50.

133. Syringeal bulla: (a) distinctly asymmetrical, medial extremity

uninflated (Fig. 8: a–d, f–h); (b) almost symmetrical, medial extremity inflated, producing a distinct medial lobe aligned with trachea (Fig. 8e); CI = 0.50.

134. Laterocaudal margin of syringeal bulla: (a) smoothly inflated or slightly depressed (Fig. 8: b–d); (b) with distinct depression in ventral surface (Fig. 8f; not codable for the uniquely conformed bullae of *A. querquedula*, *A. formosa*, and the subgenus *Punanetta*); CI = 1.00.

135. Syringeal bulla uniformly inflated so as to obscure lobing and produce a subcubic ventral appearance: (a) not so (Fig. 8: a–g); (b) as described (Fig. 8h); CI = 1.00.

136. Medial lobe of syringeal bulla enlarged (at least one-half as large as lateral lobe); ventrally knobbed, and demarcated from lateral lobe by distinct constriction: (a) not so; (b) as described (Fig. 8d); CI = 1.00.

137. Syringeal bulla: (a) absent, conspicuous; (b) obsolete; CI = 1.00.

138. Syringeal bulla: (a) comparatively densely walled, opaque; (b) thinly walled, uniformly translucent; CI = 1.00.

139. Syringeal bulla: (a) rounded ventrally; (b) distinctly dorsoventrally compressed (Fig. 8a); CI = 1.00.

140. Syringeal bulla: (a) tracheal involvement in syrinx comparatively small, typically four rings fused into syrinx, and pessulus thin, weakly supported dorsally (Fig. 8: a–b); (b) tracheal chamber large, typically incorporating at least six rings, and pessulus dense, folded, and stoutly supported dorsally (Fig. 8: c–h); CI = 1.00.

141. Distinct ventro-caudal bulge in bulla in vicinity of divergence of bronchii: (a) absent (Fig. 8: a–f); (b) present (Fig. 8: g–h); CI = 0.50.

142. Paired, laterally and medially directed flanges on caudal margin of pessulus (visible within syringeal bulla in caudal view): (a) absent; (b) present; CI = 1.00.

143. Laterocranial elongation of lateral lobe of syringeal bulla: (a) absent; (b) apparent; CI = 1.00.

144. A distinct cranial displacement of lateral lobe of syringeal bulla, producing an indentation lateral to caudal tracheal aperture: (a) absent; (b) present (Fig. 8d); CI = 1.00.

145. Craniocaudal compression of lateral lobe of syringeal bulla, producing lateral lobe of approximately uniform width: (a) absent; (b) present; CI = 1.00.

146. Medial rim of trachea, within syringeal bulla: (a) remains distinct ventrally; (b) reduced, merging with wall of bulla ventrally; CI = 0.67.

147. Prominent, square, lateral flange of pessullus: (a) absent; (b) present; CI = 1.00.

148. Caudodorsal extremity of caudal tracheal aperture of syringeal bulla: (a) rounded; (b) pointed, angular; CI = 1.00.

149. Lateral lobe of syringeal bulla: (a) uniformly walled; (b) typically with unossified gap caudally (Fig. 8b); CI = 1.00.

Skeleton (Exclusive of Trachea)

150. Ventral manubrium of sternum: (a) without conspicuous prominence; (b) with prominent, peg-like, medial spine (includes *L. specularioides*, state incorrectly given in Livezey 1986: fig. 4); CI = 0.33.

151. Dorsal manubrium of sternum: (a) marked medially by rounded notch; (b) marked medially by a rounded notch enclosing a small, central prominence (variable); CI = 1.00.

152. Distal elongation of entepicondylar process, relative to ectepicondylar process of humerus: (a) lacking; (b) evident; CI = 1.00.

153. Supraorbital processes of skull: (a) lacking or elongate, essentially coplanar with dorsal surface of interorbital surface; (b) substantial, flat, medially appressed to dorsal margin of orbit; (c) moderately elongated, with comparatively great dorsolateral prominence; CI = 1.00.

154. Brachial tuberosity of coracoid: (a) nonpneumatic; (b) with pneumatic depression under caudal edge (variable, especially in *A. galericulata*); CI = 0.33.

155. Ventral surface of basioccipital shield of skull: (a) rounded; (b) with medial ridge; CI = 1.00.

156. Posterior surface of orbit, anterolateral view of skull: (a) foramen nervus maxillomandibularis distinctly smaller than foramen opticum; (b) foramen nervus maxillomandibularis approaching size of foramen opticum; CI = 1.00.

157. Bill shape: (a) typically anatine; (b) spatulate, with anterior third laterally expanded and (externally) lamellae lengthened so as to protrude ventrally from tomium (Fig. 6d); CI = 1.00.

Appendix 2. A Linnean classification of modern dabbling ducks, Tribe Anatini; subtribal names were formed in the manner of the sections given by Boetticher (1942) based on the included genus first elevated to suprageneric rank. *Sedis mutabilis* indicates that included taxa of next-lower rank are of undetermined sequence. Asterisks mark extinct forms. Currently recognized subspecific taxa included within "polytypic" species are listed parenthetically (nominate subspecific taxa abbreviated as "nom.").

- Order Anseriformes (Wagler, 1831)
  - Suborder Anseres Wagler, 1831
    - Family Anatidae Vigors, 1825
      - Subfamily Anatinae Swainson, 1837

- Tribe Anatini Delacour and Mayr, 1945; Surface-feeding Ducks[a]
  - Subtribe Cairineae Boetticher, 1942; Long-billed Wood Ducks
    - Supergenus *Cairina* Fleming, 1822; Greater Wood Ducks
      - Genus *Cairina* Fleming, 1822; Muscovy Ducks
        - *C. moschata* (Linnaeus, 1758); Muscovy Duck
        - *C. scutulata* (Müller, 1842); White-winged Duck
      - Genus *Pteronetta* Salvadori, 1895
        - *P. hartlaubi* (Cassin, 1859); Hartlaub's Duck
    - Supergenus *Aix* Boie, 1828
      - Genus *Aix* Boie, 1828; Northern Wood Ducks
        - *A. sponsa* (Linnaeus, 1758); American Wood Duck
        - *A. galericulata* (Linnaeus, 1758); Mandarin Duck
  - Subtribe Nettapodeae, new taxon; Stout-billed Wood Ducks
    - Supergenus *Chenonetta* Brandt, 1836
      - Genus *Chenonetta* Brandt, 1836
        - *C. jubata* (Latham, 1801); Maned Duck
      - Genus *Nettapus* Brandt, 1836; Pygmy-geese
        - Subgenus *Nettapus* Brandt, 1836
          - *N. auritus* (Boddaert, 1783); African Pygmy-goose
        - Subgenus *Cheniscus* Eyton, 1838; Pale-rumped Pygmy-geese
          - *N. coromandelianus* (Gmelin, 1789); Cotton Pygmy-goose (nom., *albipennis*)
          - *N. pulchellus* (Gould, 1842); Green Pygmy-goose
  - Subtribe Anateae Boetticher, 1942; Dabbling Ducks
    - Supergenus *Amazonetta* Boetticher, 1929; Micro-teal
      - Genus *Amazonetta* Boetticher, 1929
        - *A. brasiliensis* (Gmelin, 1789); Brazilian Teal (nom., *ipecutiri*)
      - Genus *Callonetta* Delacour, 1936
        - *C. leucophrys* (Vieillot, 1816); Ringed Teal
    - Supergenus *Lophonetta* Riley, 1914; Proto-dabbling Ducks
      - Genus *Lophonetta* Riley, 1914
        - *L. specularioides* (King, 1828); Crested Duck (nom., *alticola*)
      - Genus *Speculanas* Boetticher, 1929
        - *S. specularis* (King, 1828); Bronze-winged Duck
    - Supergenus *Anas* Linnaeus, 1758; True Dabbling Ducks
      - Genus *Mareca* Stephens, 1824; Wigeons
        - Subgenus *Notonetta* Roberts, 1922
          - *M. capensis* (Gmelin, 1789); Cape Teal
        - Subgenus *Chaulelasmus* Bonaparte, 1838
          - *M. strepera* (Linnaeus, 1758); Gadwall (nom., *couesi**)

APPENDIX 2. Continued.

- Subgenus *Eunetta* Bonaparte, 1856
  - *M. falcata* (Georgi, 1775); Falcated Duck
- Subgenus *Mareca* Stephens, 1824; True Wigeons
  - *M. sibilatrix* (Poeppig, 1829); Chiloé Wigeon
  - *M. penelope* (Linnaeus, 1758); Eurasian Wigeon
  - *M. ameriana* (Gmelin, 1789); American Wigeon
- Genus *Anas* Linnaeus, 1758; Typical Dabbling Ducks, *sedis mutablis*
  - Subgenus *Anas* Linnaeus, 1758; Mallards
    - Infragenus *Melananas* Roberts, 1922
      - *A. sparsa* Eyton, 1838; African Black Duck (nom., *leucostigma*)
    - Infragenus *Anas* Linnaeus, 1758; Northern Mallards, *sedis mutabilis*
      - *A. rubripes* Brewster, 1902; American Black Duck
      - *A. fulvigula* Ridgway, 1874; Mottled Duck (nom., *maculosa*)
      - *A. diazi* Ridgeway, 1886; Mexican Duck
      - *A. platyrhynchos* Linnaeus, 1758; Mallard (nom., *conboschas*)
      - *A. wyvilliana*[b] Sclater, 1878; Hawaiian Duck
      - *A. laysanensis*[b] Rothschild, 1892; Laysan Duck
      - [*A. oustaleti*[c] Salvadori, 1894; Marianas Duck]
    - Infragenus *Polionetta* Oates, 1899; South Pacific Mallards
      - *A. luzonica* Fraser, 1839; Philippine Duck
      - *A. superciliosa* Gmelin, 1789; Pacific Gray Duck (nom., *pelewensis, rogersi*)
      - *A. poecilorhyncha* Forster, 1781; Indonesian Spot-billed Duck (nom., *haringtoni*)
      - *A. zonorhyncha* Swinhoe, 1845; Chinese Spot-billed Duck
    - Infragenus *Afranas* Roberts, 1922; African Mallards
      - *A. undulata* Dubois, 1839; Yellow-billed Duck (nom., *ruppelli*)
      - *A. melleri* Sclater, 1865; Meller's Duck
  - Subgenus *Spatula* Boie, 1822; Blue-winged Ducks
    - Infragenus *Pterocyanea* Bonaparte, 1841; Blue-winged Teal
      - *A. discors* Linnaeus, 1766; Blue-winged Teal
      - *A. cyanoptera* Vieillot, 1816; Cinnamon Teal (nom., *orinomus, borreroi, tropica, septentrionalium*)
    - Infragenus *Spatula* Boie, 1822; Shovelers
      - *A. smithii* Hartert, 1891; Cape Shoveler
      - *A. platalea* Vieillot, 1816; Red Shoveler
      - *A. rhynchotis* Latham, 1801; Australasian Shoveler (nom., *variegata*)
      - *A. clypeata* Linnaeus, 1758; Northern Shoveler
  - Subgenus *Nesonetta* Gray, 1844; Australasian Teal
    - Infragenus *incertae sedis*
      - *A. bernieri*[d] Hartlaub, 1860; Madagascan Teal
    - [Infragenus *Virago* Newton, 1871; Gray Teal][e]
      - *A. albogularis* Hume, 1873; Andaman Teal
      - *A. gibberifrons* Muller, 1842; Gray Teal (nom., *gracilis, remissa**)
    - Infragenus *Nesonetta* Gray, 1844; Reddish Teal
      - *A. castanea* Eyton, 1838; Chestnut Teal
      - *A. chlorotis* (Gray, 1845); Brown Teal
      - *A. aucklandica* (Gray, 1844); Flightless Teal (nom., *nesiotis*)
  - Subgenus *Dafila* Stephens, 1824; Pintails
    - Infragenus *Paecilonitta*[f] Eyton, 1838; Pale-cheeked Pintails
      - *A. bahamensis* Linnaeus, 1758; White-cheeked Pintail (nom., *rubrirostris, galapagensis*)
      - *A. erythrorhyncha* Gemlin, 1789; Red-billed Pintail
    - Infragenus *Dafilonettion* Boetticher, 1937; Speckled Teal
      - *A. flavirostris* Vieillot, 1816; Yellow-billed Teal (nom., *oxyptera*)
      - *A. andium* (Sclater and Salvin, 1873); Andean Teal (nom., *altipetans*)
    - Infragenus *Dafila* Stephens, 1824; Brown Pintails
      - *A. georgica* Gmelin, 1789; Brown Pintail (nom., *spinicauda, niceforoi**)
      - *A. acuta* Linnaeus, 1758; Northern Pintail
      - *A. eatoni* Sharpe, 1875; Eaton's Pintail (nom., *drygalskii*)
  - Subgenus *Querquedula* Stephens, 1824; Holarctic Teal
    - Infragenus *Querquedula* Stephens, 1824
      - *A. querquedula* Linnaeus, 1758; Garganey Teal
    - Infragenus *Nettion* Kaup, 1829; Green-winged Teal
      - *A. formosa* Georgi, 1775; Baikal Teal
      - *A. crecca* Linnaeus, 1758; Common Green-winged Teal (nom., *nimia*)
      - *A. carolinensis* Gmelin, 1789; American Green-winged Teal
  - Subgenus *Punanetta* Bonaparte, 1856; Spotted Teal
    - Infragenus *Punanetta* Bonaparte, 1856; Pale-cheeked Teal
      - *A. versicolor* (Vieillot, 1816); Silver Teal (nom., *fretensis*)
      - *A. puna* (Tschudi, 1844); Puna Teal
    - Infragenus *Micronetta* Roberts, 1922
      - *A. hottentota* (Eyton, 1838); Hottentot Teal

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[a] Nine monotypic genera of waterfowl, included by some authors in the Anatini (or Cairinini), are here included in other tribes or subfamilies (Livezey 1986): *Stictonetta naevosa* to Stictonettinae; *Plectropterus gambensis* to Plectropterinae; *Sarkidiornis melanotos, Malacorhynchus membranaceus, Hymenolaimus malacorhynchos, Merganetta armata,* and *Salvadorina waigiuensis* to Tadorninae; and *Marmaronetta angustirostris* and *Rhodonessa caryophyllacea* to Aythyini.

[b] Assignable to lesser subgeneric taxon *Horizonetta* Oberholser, 1917, the North Pacific Mallards.

[c] Status tentative, possibly of hybrid origin (*A. platyrhynchos* × *A. superciliosa*; cf. Yamashina 1948); probably extinct.

[d] Position tentative.

[e] Possibly paraphyletic.

[f] Frequently used variants—*Poecilonitta* Gray 1840, *Poecilonetta* Reichenbach 1845, and *Paecilonetta* Bonaparte 1856—are junior synonyms.

APPENDIX 3. Data matrix for phylogenetic analysis of dabbling ducks (Tribe Anatini). Missing data are indicated by one of the following symbols: "?" if unknown because of a lack of specimens and not hypothesized in any analysis; "X" if state was not coded because of noncomparability; or state is given in lower case if unknown but hypothesized for some provisional analyses (see text).

Taxon	Character																															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1 Ancestor	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	
2 *moschata*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	E	A	A	A	A	
3 *scutulata*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	E	A	A	A	A	
4 *hartlaubi*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A
5 *sponsa*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
6 *galericulata*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
7 *jubata*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
8 *auritus*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
9 *coromandelianus*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
10 *pulchellus*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A
11 *brasiliensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
12 *leucophrys*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
13 *specularioides*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	C	A	A	A	A	A
14 *specularis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	C	A	A	A	A	A
15 *capensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
16 *strepera*	A	B	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	B	X	A	A	A	A	D	A	A	A	A	A
17 *falcata*	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A	B	C	B	A	A	A	C	A	A	A	A	A
18 *sibilatrix*	A	A	A	A	A	A	A	B	A	A	A	A	B	B	B	A	A	A	A	A	B	C	B	A	A	A	C	A	A	A	A	A
19 *penelope*	A	B	A	A	A	A	A	B	A	A	A	A	B	B	B	A	A	A	A	A	B	C	B	B	A	A	C	A	A	A	A	A
20 *americana*	A	B	A	A	A	A	A	B	A	A	A	A	B	B	B	A	A	A	A	A	B	C	B	B	A	A	C	A	A	A	A	A
21 *sparsa*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	A	A	A	A	A
22 *platyrhynchos*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	B	B	A	A	B
23 *fulvigula*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	B	A	A	A
24 *diazi*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	B	A	A	A
25 *rubripes*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	A	A	A	A
26 *wyvilliana*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	B	B	A	A	B
27 *laysanensis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	A	A	A	A	B
28 *oustaleti*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	B	B	A	A	B
29 *undulata*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	A	A	A	A
30 *melleri*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	A	A	A	A
31 *luzonica*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	A	A	A	A
32 *superciliosa*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	E	A	A	A	A	A
33 *poecilorhyncha*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	C	A	A	A	A	E	A	A	A	A	A
34 *zonorhyncha*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	C	A	A	A	A	E	A	A	A	A	A
35 *discors*	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	B	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
36 *cyanoptera*	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	B	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
37 *smithii*	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	B	A	B	C	A	A	A	A	C	A	A	A	A	A
38 *platalea*	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	A	B	C	A	A	B	A	C	A	A	A	A	A
39 *clypeata*	A	A	B	A	A	A	B	A	B	B	A	A	A	A	A	A	A	A	B	A	B	C	A	A	B	A	C	A	A	A	A	A
40 *rhynchotis*	A	A	B	A	A	A	B	A	B	B	A	A	A	A	A	A	A	A	B	A	B	C	A	A	B	A	C	A	A	A	A	A
41 *bernieri*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A

APPENDIX 3. Continued.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
42 *gibberifrons*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
43 *albogularis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
44 *castanea*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	B	C	A	A	B	A	A
45 *chlorotis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	C	A	A	A	B	C	A	A	B	A	A
46 *aucklandica*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	C	A	A	A	B	C	A	A	B	A	A
47 *erythrorhyncha*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
48 *bahamensis*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
49 *flavirostris*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
50 *andium*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
51 *acuta*	A	A	B	B	A	A	A	B	A	A	A	B	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	A	A	A	A	A
52 *eatoni*	A	A	B	B	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	A	A	A	A	A
53 *georgica*	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	D	A	A	A	A	A
54 *crecca*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	C	A	A	A	A	D	A	A	A	B	A
55 *carolinensis*	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	C	A	A	A	A	D	A	A	A	B	A
56 *formosa*	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	B	A
57 *querquedula*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
58 *versicolor*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
59 *puna*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A
60 *hottentota*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	C	A	A	A	A	C	A	A	A	A	A

Taxon	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
1 Ancestor	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
2 *moschata*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B
3 *scutulata*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B
4 *hartlaubi*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	C
5 *sponsa*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
6 *galericulata*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
7 *jubata*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A
8 *auritus*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	B	A	A
9 *coromandelianus*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	B	A	A
10 *pulchellus*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	B	A	A
11 *brasiliensis*	A	A	A	A	B	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
12 *leucophrys*	A	A	A	A	B	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
13 *specularioides*	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
14 *specularis*	A	A	A	A	B	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
15 *capensis*	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A
16 *strepera*	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A
17 *falcata*	A	A	A	A	A	B	B	A	A	C	A	A	B	A	A	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A
18 *sibilatrix*	A	A	A	A	A	C	B	A	A	B	A	B	B	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A
19 *penelope*	A	A	A	A	A	A	B	A	A	B	A	B	B	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A
20 *americana*	A	A	A	A	A	A	B	A	A	B	A	B	B	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A
21 *sparsa*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

APPENDIX 3. Continued.

	Character																														
Taxon	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
22 *platyrhynchos*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
23 *fulvigula*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
24 *diazi*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
25 *rubripes*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
26 *wyvilliana*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
27 *laysanensis*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A
28 *oustaleti*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	?	A	A	A	A	A
29 *undulata*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
30 *melleri*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
31 *luzonica*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
32 *superciliosa*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
33 *poecilorhyncha*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
34 *zonorhyncha*	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
35 *discors*	A	A	A	A	A	A	B	A	A	C	A	A	A	A	B	A	A	A	B	B	B	A	A	A	A	A	A	A	A	A	A	A
36 *cyanoptera*	A	A	A	A	A	A	B	A	A	C	A	A	A	A	B	A	A	A	B	B	B	A	A	A	A	A	A	A	A	A	A	A
37 *smithii*	A	A	A	A	A	A	B	A	A	C	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A
38 *platalea*	A	A	A	A	A	A	B	A	A	C	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A
39 *clypeata*	A	A	A	A	A	A	B	A	A	C	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A
40 *rhynchotis*	A	A	A	A	A	A	B	A	A	C	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A
41 *bernieri*	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
42 *gibberifrons*	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
43 *albogularis*	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
44 *castanea*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
45 *chlorotis*	A	A	B	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
46 *aucklandica*	A	A	B	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
47 *erythrorhyncha*	A	A	A	A	A	A	A	B	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
48 *bahamensis*	A	A	A	A	A	A	A	B	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
49 *flavirostris*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A
50 *andium*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A
51 *acuta*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	B	A	A	A	A	A	A	C	A	A	A	A	A	A	A
52 *eatoni*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	B	A	A	A	A	A	A	C	A	A	A	A	A	A	A
53 *georgica*	A	A	A	A	A	A	A	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A
54 *crecca*	A	B	A	B	A	A	A	A	B	D	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A
55 *carolinensis*	A	B	A	B	A	A	A	A	B	D	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	A	A
56 *formosa*	A	B	A	B	A	A	A	A	B	D	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A
57 *querquedula*	A	B	A	B	A	A	A	A	A	C	A	A	A	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A
58 *versicolor*	B	B	A	B	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A
59 *puna*	B	B	A	B	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A
60 *hottentota*	B	A	A	B	A	A	A	A	A	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A

APPENDIX 3. Continued.

Taxon	Character																															
	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
1 Ancestor	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
2 *moschata*	A	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
3 *scutulata*	A	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
4 *hartlaubi*	A	A	A	A	A	A	B	A	A	C	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A
5 *sponsa*	B	B	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	D	A	A	A	B
6 *galericulata*	B	B	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	D	A	A	A	B
7 *jubata*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
8 *auritus*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A
9 *coromandelianus*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A
10 *pulchellus*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A
11 *brasiliensis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	C
12 *leucophrys*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C
13 *specularioides*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
14 *specularis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
15 *capensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	B	A	A	B	A	A	A	B	A
16 *strepera*	A	A	A	A	A	A	A	A	B	A	B	A	A	A	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	B
17 *falcata*	A	A	A	A	A	A	A	A	B	A	B	A	A	A	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A
18 *sibilatrix*	A	A	A	A	A	A	A	A	B	A	B	A	A	B	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	B	A
19 *penelope*	A	A	A	A	A	A	A	B	B	A	B	A	B	B	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	B	A
20 *americana*	A	A	A	A	A	A	A	B	B	A	B	A	B	B	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	B	A
21 *sparsa*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
22 *platyrhynchos*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
23 *fulvigula*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
24 *diazi*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
25 *rubripes*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
26 *wyvilliana*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
27 *laysanensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
28 *oustaleti*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B
29 *undulata*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
30 *melleri*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
31 *luzonica*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
32 *superciliosa*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
33 *poecilorhyncha*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
34 *zonorhyncha*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
35 *discors*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B
36 *cyanoptera*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B
37 *smithii*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
38 *platalea*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B
39 *clypeata*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B
40 *rhynchotis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B
41 *bernieri*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
42 *gibberifrons*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
43 *albogularis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
44 *castanea*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A

APPENDIX 3. Continued.

	Character																															
Taxon	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96
45 *chlorotis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A
46 *aucklandica*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A
47 *erythrorhyncha*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	B	A	C	B	A	A
48 *bahamensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	B	A	C	B	A	A
49 *flavirostris*	A	A	A	A	A	A	A	A	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	B	B	A	A	A	B	B	A	A
50 *andium*	A	A	A	A	A	A	A	A	A	A	A	A	A	C	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A
51 *acuta*	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A
52 *eatoni*	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A
53 *georgica*	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	B	A	B	B	A	A
54 *crecca*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	B	A	B	A	A	A	A	A	A	A	A
55 *carolinensis*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	B	A	B	A	A	A	A	A	A	A	A
56 *formosa*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A	B	A	B	A	A	A	A	A	A	A	A
57 *querquedula*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
58 *versicolor*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	C	B	B	A	A
59 *puna*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	C	A	B	A	A
60 *hottentota*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	C	A	B	A	A

	Character																															
Taxon	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
1 Ancestor	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
2 *moschata*	A	B	B	A	A	B	A	C	B	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	B	B
3 *scutulata*	A	B	A	A	A	B	A	C	B	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	B	B
4 *hartlaubi*	A	B	B	A	A	B	A	C	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	B
5 *sponsa*	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	B
6 *galericulata*	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	B
7 *jubata*	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
8 *auritus*	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	B
9 *coromandelianus*	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	B
10 *pulchellus*	B	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	B
11 *brasiliensis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
12 *leucophrys*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
13 *specularioides*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B	B
14 *specularis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B	B
15 *capensis*	A	A	A	A	B	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B
16 *strepera*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	B	A	A	B
17 *falcata*	A	A	A	A	B	A	A	A	A	A	A	B	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
18 *sibilatrix*	A	A	A	A	B	A	A	A	A	A	A	B	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
19 *penelope*	A	A	A	A	B	A	A	A	A	A	A	B	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
20 *americana*	A	A	A	A	B	A	A	A	A	A	A	B	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B
21 *sparsa*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	B	A	B
22 *platyrhynchos*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
23 *fulvigula*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B

APPENDIX 3. Continued.

Taxon	Character																														
	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120	121	122	123	124	125	126	127	128
24 *diazi*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
25 *rubripes*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
26 *wyvilliana*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
27 *laysanensis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
28 *oustaleti*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	?	?	A	B	A	A	A	B	?	A	A	?	A	A	B
29 *undulata*	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
30 *melleri*	A	A	A	B	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
31 *luzonica*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	B	A	A	A	B	A	A	A	B	A	A	B
32 *superciliosa*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B	A	B	A	A	B	A	A	A	B	A	A	A	B	A	A	B
33 *poecilorhyncha*	A	A	A	A	B	A	A	A	A	B	A	A	A	A	A	B	A	B	A	A	B	A	A	A	B	A	A	A	B	A	A	B
34 *zonorhyncha*	A	A	A	A	B	A	A	A	A	B	A	A	A	A	A	B	A	B	A	A	B	A	A	A	B	A	A	A	B	A	A	B
35 *discors*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
36 *cyanoptera*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
37 *smithii*	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
38 *platalea*	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
39 *clypeata*	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
40 *rhynchotis*	A	A	A	A	B	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	A	A	A	B
41 *bernieri*	A	A	A	A	B	A	A	A	A	A	a	a	a	a	a	a	?	a	a	a	b	b	a	a	a	b	a	a	a	b	a	b
42 *gibberifrons*	A	A	A	A	B	A	A	D	A	A	A	A	A	A	B	A	B	A	A	A	B	B	A	A	A	B	A	A	A	B	A	B
43 *albogularis*	A	A	A	A	B	A	A	D	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	B	A	A	A	B	A	B
44 *castanea*	A	A	A	A	B	A	A	D	A	A	A	A	A	A	A	A	B	A	A	A	B	B	A	A	A	B	A	A	A	B	A	B
45 *chlorotis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	?	A	A	A	B	A	B
46 *aucklandica*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	?	A	A	?	B	A	B
47 *erythrorhyncha*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	B	A	B
48 *bahamensis*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	A	A	A	B	A	B
49 *flavirostris*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	B	A	B
50 *andium*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	B	A	B
51 *acuta*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	B	A	B
52 *eatoni*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	B	A	B
53 *georgica*	A	A	A	A	B	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	B	A	A	A	A	A	B	A	B
54 *crecca*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	B	A	B	A	A	A	A	A	A	B	A	B
55 *carolinensis*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	B	A	B	A	A	A	A	A	A	B	A	B
56 *formosa*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	B	A	B	A	A	A	A	A	A	B	A	B
57 *querquedula*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	B	A	B	A	A	A	A	A	A	B	A	B
58 *versicolor*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B
59 *puna*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B
60 *hottentota*	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	B

APPENDIX 3. Continued.

	Character																												
Taxon	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157
1 Ancestor	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
2 *moschata*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A
3 *scutulata*	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A
4 *hartlaubi*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	A	A	A	A
5 *sponsa*	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A
6 *galericulata*	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A
7 *jubata*	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	B	A	A	A	A	A	A
8 *auritus*	X	X	A	X	X	X	X	X	B	X	X	X	X	X	X	X	X	X	X	X	X	B	B	A	A	A	A	A	A
9 *coromandelianus*	X	X	A	X	X	X	X	X	B	X	X	X	X	X	X	X	X	X	X	X	X	B	B	A	A	A	A	A	A
10 *pulchellus*	X	X	A	X	X	X	X	X	B	X	X	X	X	X	X	X	X	X	X	X	X	B	B	A	A	A	A	A	A
11 *brasiliensis*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	B	B	A	A	A	B	B	A
12 *leucophrys*	B	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	B	B	B	A	A	B	B	B	A
13 *specularioides*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	A	A	A	B	B	A
14 *specularis*	A	A	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	A	A	A	B	B	A
15 *capensis*	A	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	B	B	A	A	A	B	B	A
16 *strepera*	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
17 *falcata*	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	B	B	A	A	A	B	B	A
18 *sibilatrix*	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	B	B	B	A	A	B	B	A
19 *penelope*	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	B	B	B	A	A	B	B	A
20 *americana*	A	A	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	B	A	A	A	B	B	B	A	A	B	B	A
21 *sparsa*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
22 *platyrhynchos*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
23 *fulvigula*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
24 *diazi*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
25 *rubripes*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
26 *wyvilliana*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
27 *laysanensis*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
28 *oustaleti*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	A	C	A	B	A	B	B	A	A	A	B	B	A
29 *undulata*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	B	B	B	C	A	B	A	B	B	A	A	A	B	B	A
30 *melleri*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	B	B	A	A	A	B	B	A
31 *luzonica*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	C	A	B	A	B	B	A	A	A	B	B	A
32 *superciliosa*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	C	A	B	A	B	B	A	A	A	B	B	A
33 *poecilorhyncha*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	C	A	B	A	B	B	A	A	A	B	B	A
34 *zonorhyncha*	B	A	A	A	A	A	A	B	A	A	A	B	A	A	A	B	B	C	A	B	A	B	B	A	A	A	B	B	A
35 *discors*	B	X	A	B	A	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	A
36 *cyanoptera*	B	X	A	A	B	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	A
37 *smithii*	B	X	A	A	B	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	B
38 *platalea*	B	X	A	B	B	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	B
39 *clypeata*	B	X	A	B	B	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	B
40 *rhynchotis*	B	X	A	B	B	A	A	A	A	A	A	B	A	A	A	A	A	C	B	A	A	B	B	A	A	A	B	B	B
41 *bernieri*	b	b	a	a	a	a	a	a	a	a	a	b	a	a	a	a	a	c	a	a	a	?	?	?	?	?	?	?	A
42 *gibberifrons*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
43 *albogularis*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	A

APPENDIX 3. Continued.

Taxon	Character																												
	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148	149	150	151	152	153	154	155	156	157
44 *castanea*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
45 *chlorotis*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
46 *aucklandica*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	A	B	A	A	A	B	B	A
47 *erythrorhyncha*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
48 *bahamensis*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
49 *flavirostris*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
50 *andium*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
51 *acuta*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
52 *eatoni*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
53 *georgica*	B	B	A	A	A	B	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
54 *crecca*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
55 *carolinensis*	B	B	A	A	A	A	A	A	A	A	A	B	A	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
56 *formosa*	B	X	A	A	A	X	A	A	A	A	A	B	B	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
57 *querquedula*	B	X	A	A	A	X	A	A	A	A	A	B	B	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
58 *versicolor*	B	X	B	A	A	X	B	A	A	A	A	B	B	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
59 *puna*	B	X	B	A	A	X	B	A	A	A	A	B	B	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A
60 *hottentota*	B	X	B	A	A	X	B	A	A	A	A	B	B	A	A	A	A	C	A	A	A	B	B	A	A	A	B	B	A