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A PHYLOGENETIC ANALYSIS OF MODERN POCHARDS (ANATIDAE: AYTHYINI)

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ABSTRACT.—A phylogenetic analysis of modern pochards (Aythyini) was performed using 99 characters of the skeleton, trachea, natal plumage, and definitive integument. Three shortest trees were found (length = 148; consistency index for informative characters = 0.68) which: (1) placed *Marmaronetta* as the sister group to other members; (2) defined a basal clade comprising as sister groups *Rhodonessa caryophyllacea* + *Netta rufina* and *N. peposaca* + *N. erythrophthalma*; and (3) defined as the sister group to the preceding clade all other pochards, in which the three redheads (*Aythya valisineria*, and the sister species *A. ferina* and *A. americana*) are the sister group to the mutually monophyletic white-eyes (*A. australis*, *A. innotata*, and the sister species *A. nyroca* and *A. baeri*) and scaup (in order of increasingly close relationship, *A. novaeseelandiae*, *A. collaris*, *A. fuligula*, *A. marila*, and *A. affinis*). The three shortest trees differed only in the topology among the white-eyes. These nodes, and that supporting the sister relationship between *N. peposaca* and *N. erythrophthalma*, were the only nodes not conserved in a majority of bootstrapped replicates; Bremer (decay) indices provided similar assessments of empirical support. Evolutionary trends in body mass, clutch size, preferred nest site, diel activity pattern, and biogeographic patterns are evaluated in the context of this phylogenetic hypothesis. Quantitative comparisons with previously proposed phylogenetic hypotheses, particularly that of Johnsgard, are made using constrained searches based on these data, and a revised classification of the Aythyini is proposed. *Received 16 June 1995, accepted 6 September 1995.*

POCHARDS OR BAY DUCKS (Aythyini), one of four tribes of the subfamily Anatinae, comprise 17 modern species of waterfowl (Delacour and Mayr 1945, Delacour 1959, Wolters 1976, Livezey 1986). The Aythyini range in size from the Marbled Duck (*Marmaronetta angustirostris*; mean body mass <500 g) to the Canvasback (*Aythya valisineria*; 1,200 g). Most species regularly employ diving during foraging and are characterized by moderately heavy wing loadings and significant specialization for subaquatic locomotion (Müllenhoff 1885, Townsend 1930, Poole 1938, Woolfenden 1961, Raikow 1970, 1973, Hoerschelmann 1971, Livezey 1986, Tome and Wrubleski 1988, Faith 1989). Members of the tribe are distributed in both the Northern and Southern hemispheres, with the greatest diversity of members occurring in temperate Eurasia (Weller 1964a). A modest fossil record of the tribe has been described (Brodkorb 1964, Howard 1964), but limited material and inadequate diagnoses of the described taxa render questionable most of the earliest records assigned to the tribe (Livezey and Martin 1988). Most species of Aythyini are migratory and breed primarily near permanent bodies of fresh water (Delacour 1959, Weller 1964a, b). One species of Aythyini, the Pink-headed Duck (*Rhodonessa caryophyllacea*), was extirpated in the early twentieth century (Bucknill 1924, Wright 1925). In addition, the Madagascan White-eye (*Aythya innotata*) is considered endangered and may have become extinct within the last decade (Young and Smith 1989, Wilmé 1993, 1994, S. M. Goodman pers. comm.), and serious declines have been reported in the Marbled Duck (Green 1993), as well as the Ferruginous (*A. nyroca*) and Siberian (*A. baeri*) white-eyes (Collar et al. 1994, Tucker and Heath 1994).

With the exception of the tribal assignment of the Marbled Duck (Johnsgard 1961a, b, c) and the comparatively late inclusion of the Pink-headed Duck within the Aythyini (Johnsgard 1961a, c, Woolfenden 1961, Humphrey and Ripley 1962), the notion that the Aythyini formed a natural group has received virtually unanimous support by systematists for almost a century (Salvadori 1895, Phillips 1925, Peters 1931, Delacour and Mayr 1945, Boetticher 1952, Verheyen 1953, Delacour 1959, Johnsgard 1961a, 1978, 1979, Livezey 1986). Johnsgard (1961a: 80) described the Aythyini as "a remarkably homogeneous group of species, behaviourally as well as anatomically." Although arrangements of taxa within the tribe have been comparatively stable in recent decades (Delacour and Mayr 1945, Delacour 1959, Johnsgard 1961a, 1978, 1979), explicit investigations of relationships among Aythyini have been limited to: intuitive phenetic comparisons of behavioral characteristics (Delacour and Mayr 1945, Johnsgard 1961a, 1965) and of syringeal bullae (Johnsgard 1961c); phenetic comparisons of allozymes (Brush 1976, Numachi et al. 1983, Patton and Avise 1985) or uropygial secretions (Jacob and Hoerschelmann 1993); phenetically rooted, cladistic analyses of mitochondrial DNA (Kessler and Avise 1984, 1985; also see Omland 1994); and a cladistic analysis of the four included genera using morphological characters (Livezey 1986). Using DNA-DNA hybridization, Madsen et al. (1988) included only one member of the tribe, and Sibley and Ahlquist (1990) included no Aythyini in their studies; the companion classification by Sibley and Monroe (1990), which did not include tribal groupings within the Anatinae, apparently was taken from existing works. Only Johnsgard (1961a), based on a nonquantitative assessment of behavioral and (to a lesser extent) morphological similarity, proposed an explicit, species-level hypothesis for the phylogeny of the Aythyini.

In this paper, I describe a phylogenetic analysis of the 17 Recent species of Aythyini based on characters of the skeleton, trachea, and natal and definitive integument. The resulting hypothesis is used as the basis for analysis of historical biogeography, selected comparisons of life-historical characteristics, and a classification of modern pochards.

METHODS

Taxonomy.—Composition of the Aythyini follows Livezey (1986) and specific taxa recognized conform with currently accepted classifications (Delacour 1959, Johnsgard 1965, 1978, 1979, AOU 1983). Only three species of Aythyini are considered polytypic: Southern Pochard (*Netta erythropthalma*), partitioned into Neotropical (nominate) and African races (*brunnea*); the Australian White-eye (*Aythya australis*), with continental (nominate) and Banks Islands (*extima*) races recognized; and the Greater Scaup (*A. marila*), with Palearctic (nominate) and Pacific Basin (*mariloides*) forms distinguished taxonomically. With the possible exception of the Southern Pochard (which shows weak differentiation in plumage and merits further study), these subspecies did not differ in the characters analyzed; therefore, all were merged for purposes of character description and phylogenetic inference. Common names of the Aythyini employed in the text, a few of which differ from those listed by Johnsgard (1979), conform with the phylogenetic relationships inferred here and the resulting classification.

Specimens.—Skeletons and skin specimens of adults of the 17 species of Aythyini (and outgroups, discussed below) were studied directly for character analysis. Tracheae of adult males were studied as part of skeletal specimens for most species; separately mounted tracheae of a number of species also were studied, mostly at the Wildfowl and Wetlands Trust (WWT). The mounted trachea of a male Pink-headed Duck illustrated by Garrod (1875) was examined at the British Museum (Natural History). The trachea of a male Madagascan White-eye was studied in a fluid-preserved specimen at the British Museum (Natural History); a complete skeleton of this species, not listed by Wood and Schnell (1986), was borrowed from the Field Museum of Natural History (FMNH). Specimens of downy young of all species but the extinct Pink-headed Duck (undescribed) were compared; natal specimens of the Madagascan White-eye were available only as fluid-preserved birds. Homologies, states, and basal polarities of characters were confirmed using published descriptions and illustrations of plumages and tracheae (Latham 1798, Eyton 1838, Garrod 1875, Phillips 1922, 1925, Schiøler 1926, Broman 1942, Delacour and Mayr 1945, 1946, Kagelmann 1951, Delacour 1956, 1959, 1964, Weller 1957, Dzubin 1959, Johnsgard 1961b, c, 1962, 1965, 1979, Woolfenden 1961, Humphrey and Ripley 1962, Humphrey and Clark 1964, Gillham et al. 1966, Beer 1968, Warner 1971, Palmer 1976, Amat 1986, Madge and Burn 1988, Wilson and Ankney 1988, King 1989, 1993, McLelland 1989, Marchant and Higgins 1990, del Hoyo et al. 1992, Nelson 1993).

Definition of characters.—I identified 99 morphological characters that defined or varied within the Aythyini: 14 skeletal characters (after Livezey 1986), 7 tracheal characters, 9 characters of natal plumage, and 69 characters of the plumage and soft parts of adults (Appendix 1). Osteological and syringeal nomenclature follows the recommendations of the International Committee on Avian Anatomical Nomenclature (Baumel and Witmer 1993, King 1993). Each character comprised a primitive (plesiomorphic) state and one or more derived (apomorphic) states. Each character was coded for all species except natal characters of the Pink-headed Duck, which were assigned missing-datum codes. The resulting 17 × 99 data matrix (with an additional vector for the hypothetical ancestor, discussed below) is presented in Appendix 2. Characters having more than one derived state were analyzed as unordered. An effort was made to reduce multistate characters (characters having more than one derived state) to two or more binary characters to simplify analyses. Characters for which the derived state(s) was possessed by single species (autapomorphies) were included in the analysis to confirm the monophyly of terminal taxa (in the same way that synapomorphies unite more inclusive groups) and permit estimates of evolutionary divergence.

Outgroups, derivation of trees, and classification.—As for the working assumption of monophyly of the ingroup, outgroups were selected on the basis of intergeneric relationships inferred by Livezey (1986, 1991); these included several species of Anatini (sensu Livezey 1991; primary exemplars were *Cairina moschata, Mareca americana, Anas platyrhynchos*), as well as basal Oxyurini (*Heteronetta atricapilla*) and Mergini (*Polysticta stelleri*). The hypothetical ancestor, a vector of primitive character states based on outgroup comparisons, was used to root the phylogenetic tree(s). This method provides a single root for the ingroup (see Livezey 1986, 1989, 1995a, b, c, Livezey and Martin, 1988), while avoiding analytical digressions concerning relationships among outgroups (considered elsewhere; Livezey 1996). Empirical support for monophyly of the ingroup is comensurate with the number of unambiguous synapomorphies for the ingroup taxa relative to the hypothetical ancestor.

Trees were constructed cladistically under the principle of global parsimony (Wiley 1981), using the phylogenetic software PAUP 3.1 (Swofford 1993); supplementary topological analyses and printing of trees were performed on MacClade 3.01 (Maddison and Maddison 1992). I used the branch-and-bound algorithm to find the shortest tree(s). The skewness statistic (g_1) for the distribution of tree lengths, a crude indicator of phylogenetic signal (Hillis 1991, Källersjö et al. 1992), was calculated based on 1,000 trees randomly generated from the matrix. A branch-and-bound bootstrapping procedure was employed to generate 100 topological replications. Support for branches within the final tree was summarized by a 50% majority-rule consensus tree of these 100 replicate trees. This application of bootstrapping was used as an index to the empirical support for branches in the shortest tree(s) but, because of the likely interdependence of characters, was not used for strict probabilistic inferences (Felsenstein 1985, Sanderson 1989). The Bremer or "decay" index (Bremer 1988), which equals the number of additional steps required to disrupt a given node, was calculated for each node using converse topological constraints and random addition of taxa to avoid local optima (Swofford 1993); the index for the most-basal node was approximated by including two duplicate ancestral taxa in the constrained analysis. Topological constraints also were used to assess the additional steps required to accomodate previously proposed phylogenetic hypotheses using the present data set.

Phylogenetic classification.—The resulting phylogenetic tree(s) formed the basis for a Linnean classification using the methods described by Wiley (1981). Unconventional taxonomic ranks—subtribes, supergenera, and subgenera—were based on senior taxa of appropriate rank, in part based on the classifications of Boetticher (1942, 1952) and the synonomies of Phillips (1922, 1925), Brodkorb (1964), and Wolters (1976).

Mapping of attributes.—Selected general ecological and functional attributes of evolutionary interest varied among the Aythyini. These attributes—including body mass, clutch size, nest-site selection, diel activity pattern, and dietary preferences—were compiled for the Aythyini based on the information taken from specimens and the literature (Wright 1925, Townsend 1930, Cottam 1939, Delacour 1959, Ali 1960, Schönwetter 1961, Weller 1964b, c, d, Kear 1970, Raikow 1973, Prestwich 1974, Bellrose 1976, Palmer 1976, Cramp and Simmons 1977, Johnsgard 1978, Brown et al. 1982, Eadie et al. 1988, Madge and Burn 1988, Rohwer 1988, Tome and Wrubleski 1988, Rohwer and Freeman 1989, Scott and Clutton-Brock 1989, Marchant and Higgins 1990, Amat 1991, del Hoyo et al. 1992, McNeil et al. 1992, Dunning 1993). Mean body masses of species were estimated by the unweighted mean of the mean masses for adults of the two sexes separately. Sexual size dimorphism was evaluated using the ratio of the mean body mass of males divided by the mean body mass of females. Relative clutch mass was defined as the product of mean clutch size and mean egg mass divided by the mean body mass of an adult female. Data for many attributes of the Pink-headed Duck and Madagascan White-eye were not available, and reliable estimates of some parameters were not attainable for several others (e.g. *"Netta" peposaca, Aythya baeri*). I employed *a posteriori* mappings of selected ecomorphological attributes on trees using MacClade 3.01 (Maddison and Maddison 1992).

RESULTS

Most-parsimonious topologies.—Three most-parsimonious trees of length 148 were discovered; unambiguous character changes, those supporting the branches common to all three trees, are detailed in Figure 1. Summary statistics for these most-parsimonious trees were: consistency index, 0.750; consistency index excluding uninformative characters, 0.684; retention index, 0.818; rescaled consistency index, 0.613. Topological differences among these three trees were limited to the relationships within one clade involving three species or species groups—*Aythya innotata, A. australis,* and the couplet *A. nyroca* + *A. baeri*—depicted as a trichotomy in the detailed tree (Fig. 1). The skewness statistic (g_1) for 1,000 trees randomly generated for the matrix was −0.829. A majority-rule consensus tree of 100 bootstrapped replicates revealed that the sister-group relationship

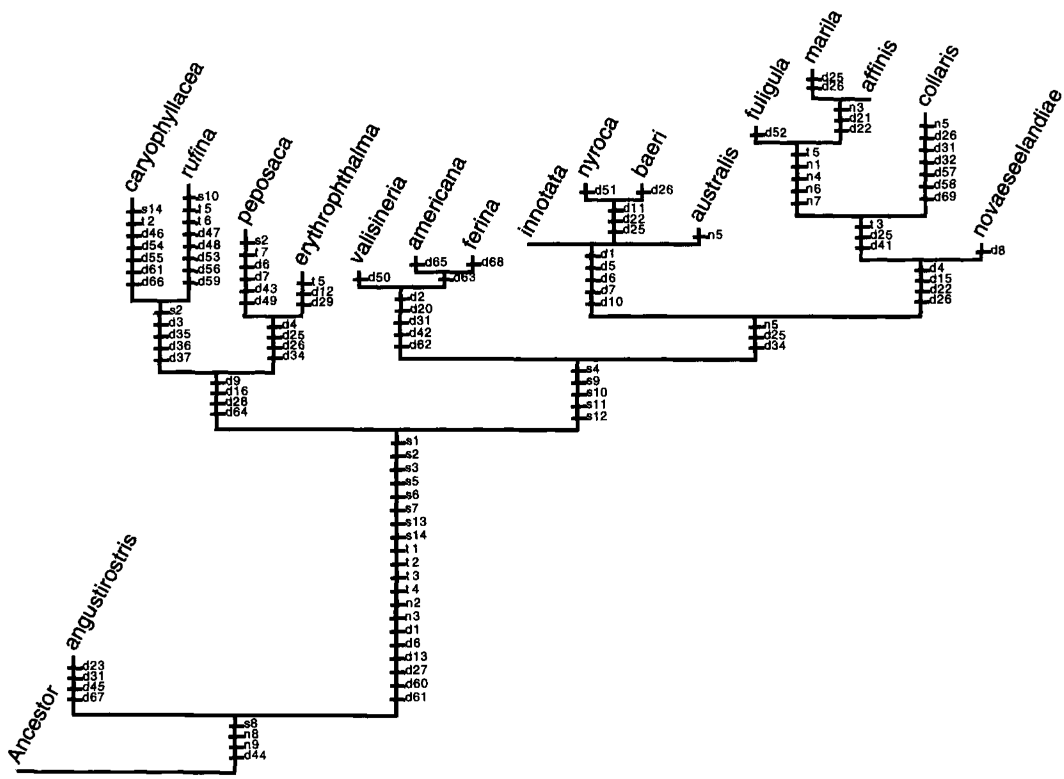


Fig. 1. Detailed topology showing unambiguous character changes supporting branches common to three most-parsimonious phylogenetic trees for Aythyini based on 99 morphological characters. Labels identify skeletal (s), tracheal (t), natal (n), and definitive (d) characters; see Appendices 1 and 2 for definitions and distributions of states.

between the Rosy-billed Pochard (*Netta peposaca*) and Southern Pochard (*N. erythrophthalma*) had only modest support (Fig. 2). Similar patterns of empirical support were indicated by the Bremer indices for nodes common to the shortest trees (Fig. 3).

Phylogenetic inferences.—Monophyly of the tribe was supported by four unambiguous synapomorphies—one skeletal, two of the natal plumage, and one of the definitive plumage (Fig. 1). Members of the tribe exclusive of the Marbled Duck were determined to be monophyletic on the basis of 20 unambiguous synapomorphies—eight skeletal, four tracheal, two natal, and six of the definitive integument (Fig. 1). This large clade comprised two monophyletic subgroups, one including the four species of "stem" pochards and the other including all other Aythyini. The four "stem" pochards comprise two couplets of sister species: the Pink-headed Duck and the Red-crested Pochard (*N. rufina*); and the Rosy-billed and Southern pochards (Fig. 1).

The remaining Aythyini comprised three clades: the "redheads" (three species, five supporting synapomorphies), the "white-eyes" (four species, five unambiguous synapomorphies), and the "scaup" (five species, four unambiguous synapomorphies). Within the redheads, the sister group of the other two clades, the Canvasback (*A. valisineria*) was hypothesized on the basis of a single unambiguous synapomorphy to be the sister group of a clade comprising the Redhead (*A. americana*) and Eurasian Pochard (*A. ferina*). Relationships within the white-eyes remain unresolved, but a sister relationship between the Ferruginous White-eye (*A. nyroca*) and the Siberian White-eye (*A. baeri*) was inferred in all three of the most-parsimonious trees (Fig. 1) and proved robust with respect to bootstrapping (Fig. 2). The three equally parsimonious topologies for the white-

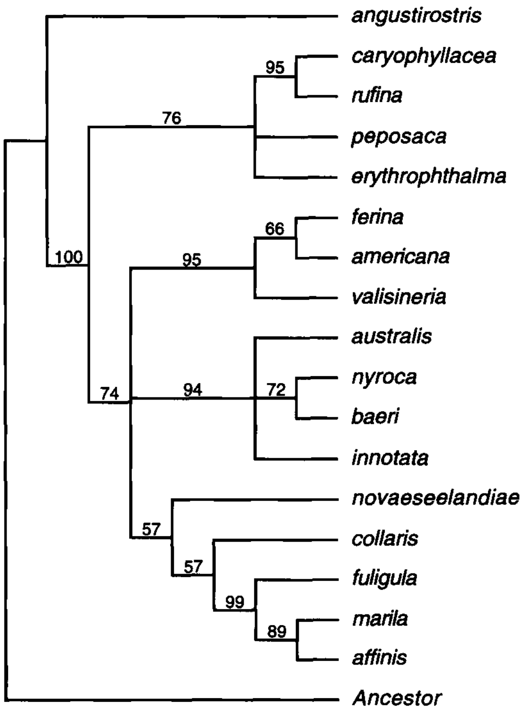


Fig. 2. Majority-rule consensus tree of 100 bootstrapped replicates for Aythyini. Percentages of replicates in which each node was conserved are given.

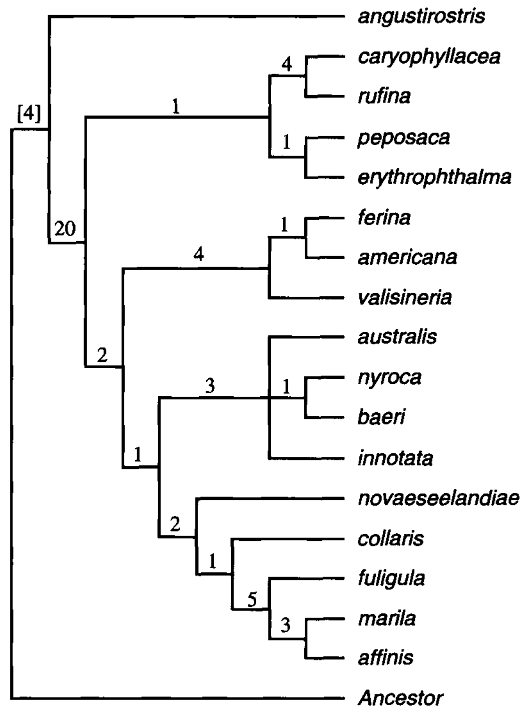


Fig. 3. Strict-consensus tree for three shortest phylogenetic trees for Aythyini showing Bremer (decay) indices for each node.

eyes were: (1) *A. innotata* and *A. australis* as sister species, together composing the sister group of the clade *A. nyroca* + *A. baeri*; (2) *A. innotata* as the sister group of *A. australis* and the clade *A. nyroca* + *A. baeri*; and (3) *A. australis* as the sister group of *A. innotata* and the clade *A. nyroca* + *A. baeri*. Within the scaup (Fig. 1), the New Zealand Scaup (*A. novaeseelandiae*) was inferred to be the sister-group of the remaining species; within the latter, the Ring-necked Duck (*A. collaris*) was placed as the sister species of the Tufted Duck (*A. fuligula*) and the clade comprising the Greater Scaup (*A. marila*) and Lesser Scaup (*A. affinis*). The latter three-species group was defined by five unambiguous synapomorphies (Fig. 1). At least one unambiguous autapomorphy defined all species except the Madagascan White-eye (Fig. 1). Several species were highly autapomorphic, notably the Pink-headed Duck (7 autapomorphies), Red-crested Pochard (8), Rosy-billed Pochard (6), and Ring-necked Duck (7).

Ecomorphological trends.—A mapping of selected attributes on one of the shortest trees for the Aythyini (arbitrarily selected) revealed several different evolutionary patterns having varying degrees of phylogenetic conservatism within the tribe (Fig. 4). Mean body mass varied significantly among member species, which tended to fall into three major size groups used for mapping. A primitive small body size is retained by *Marmaronetta*, but the distribution of medium and large body masses within the three major clades in the remaining Aythyini prevents the determination of ancestral states for much of the tribe; notable, however, are the substantial, independent reductions in body mass undergone by the Eurasian Pochard and New Zealand Scaup (Fig. 4A).

Mean clutch size in the tribe evidently underwent several independent decreases: (1) in the Pink-headed Duck, although data are few for this species; (2) in the Canvasback and Eurasian Pochard, perhaps homologously with an autapomorphic reversal in the highly nest-parasitic Redhead; and (3) in the New Zealand Scaup, coincident with a decrease in body mass (Fig. 4B). Preferred nest sites showed at least two comparatively marked transitions within the tribe (Fig. 4C): (1) a shift from ground sites to those in emergent vegetation in the ancestor of the tribe exclusive of *Marmaronetta;* and (2) and a subsequent reversal to ground sites in the Greater and Lesser scaups, with the three other, more basal members of this clade showing intermediate preferences. Diel activity pattern evidently underwent two changes of like direction within the tribe; a shift from plesiomorphic diurnal activity to crepuscular habit is hypothesized for the ancestor of the tribe, followed by a shift to largely nocturnal feeding in the ancestor of the clade comprising the redheads, white-eyes, and scaups (Fig. 4D).

In accordance with the homogeneity of pochards cited by Johnsgard (1961a), however, many ecomorphological attributes that vary within other tribes of Anseriformes showed negligible variation in the Aythyini. For example, egg mass averages 50 to 65 g for the Aythyini, exceptions being the *Marmaronetta* (31 g) and the sister species *Aythya nyroca* and *A. baeri* (43 g). Relative clutch mass showed remarkable uniformity in the group, with species retaining the primitive average of 50 to 70% of mean body mass of females. Sexual size dimorphism also varied little within the tribe, with members retaining the evidently primitive mean ratio of 1.05 to 1.15. Sexual dichromatism, the presence of which is probably primitive for the Aythyini, is absent (probably autapomorphically lost) only in basal *Marmaronetta.* Moderate occurence of intraspecific and interspecific nest parasitism characterizes the Aythyini and most other Anseriformes (Andersson 1984, Eadie et al. 1988, Rohwer and Freeman 1989, Amat 1991); only the exceptionally high frequency for the Redhead is noteworthy (Weller 1959).

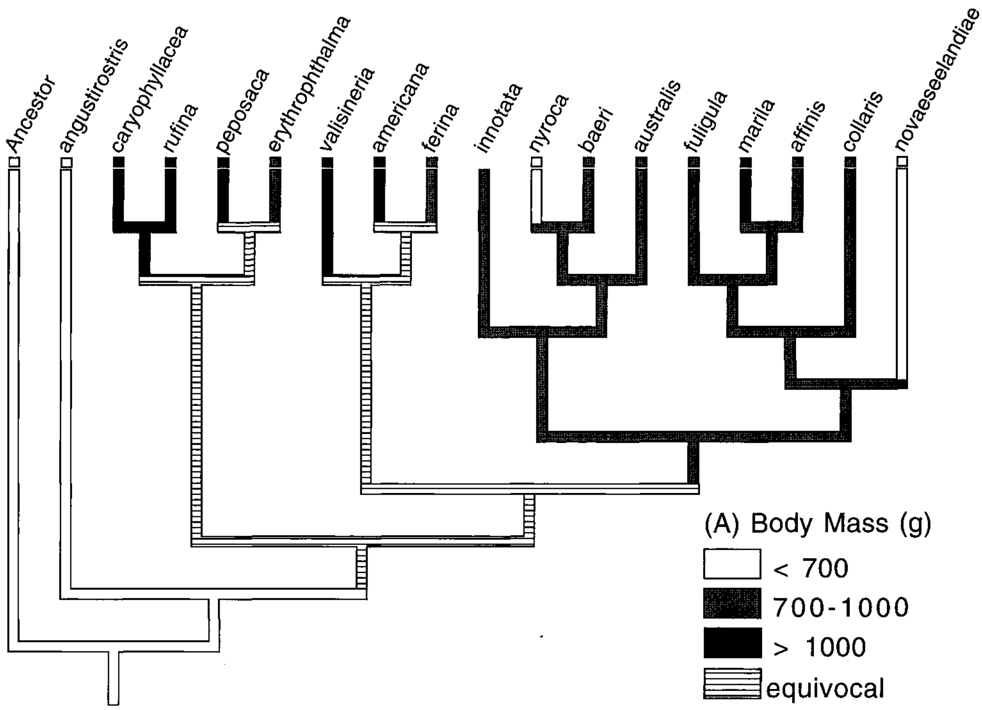
Diving habit shows a simple, weakly defined trend within the tribe, in which the presumably primitive reliance on surface feeding is retained by *Marmaronetta,* a co-reliance on surface feeding and diving characterizes the four species of stem pochards, and a primary reliance on diving unites the remaining members of the tribe. A similarly weak but topologically distinct pattern in dietary preference is evident, in which the primitive general preference for vegetable material (with secondary use of invertebrate prey) is retained by all members of the Aythyini except the three most-derived species of scaups (*Aythya fuligula, A. marila,* and *A. affinis*), which tend to favor invertebrate prey over vegetable items. This subtle difference in food preference is reflected only in part by interspecific differences in feeding anatomy (Kehoe and Ankney 1985, Kehoe and Thomas 1987, Lagerquist and Ankney 1989), however, and the dietary importance of invertebrates increases during the breeding season in most Aythyini (Bartonek and Hickey 1969).

Discussion

Problematic characters and groups.—Several inferences in the present analysis differ from traditional placements (Peters 1931, Delacour and Mayr 1945, Delacour 1959, Johnsgard 1961a, 1965, 1978, 1979) and, in one instance, with the generic relationships proposed in my earlier work (Livezey 1986). The inclusion of the Marbled Duck as the sister group of other pochards, the intertribal "linking" position of which was first suggested by Johnsgard (1961b), is strongly supported by this analysis (Fig. 1). The monophyly of the "stem" pochards inferred herein agrees with the grouping of these species (excluding the Pink-headed Duck, considered an aberrant dabbling duck) as "narrow-billed pochards" by Delacour (1959). Placement of the Pink-headed Duck within a clade of "stem" species and as the sister species of the Red-crested Pochard (Fig. 1), instead of as the sister group to the Aythyini exclusive of *Marmaronetta* (Johnsgard 1961a, Livezey 1986), also was unexpected. The unique autapomorphies of the Pink-headed Duck, in particular the bright pink coloration of the head, undoubtedly led to its assignment to a monotypic genus. The monophyly of the "typical" pochards confirmed here (Fig. 1) conforms with the grouping of these species as "broad-billed pochards" by Delacour (1959).

The traditional view of a sister-group relationship between the Canvasback and Eurasian Pochard, either implied by taxonomic sequences (Delacour and Mayr 1945, Delacour 1959, Sibley and Monroe 1990) or explicitly indicated (e.g. Johnsgard 1961a, 1965, 1978, 1979), differs from the marginally supported arrangement inferred here (Fig. 1). The monophyly of the four species of white-eye confirmed herein was recognized explicitly by Delacour and Mayr (1945), but the poor resolution within this clade (Figs. 1 and 2) represents an only marginal improvement over the vague and contradictory arrangements of species suggested by other investigators (e.g. Delacour 1959, Johnsgard 1961a, 1978).

The composition and interspecific relation-



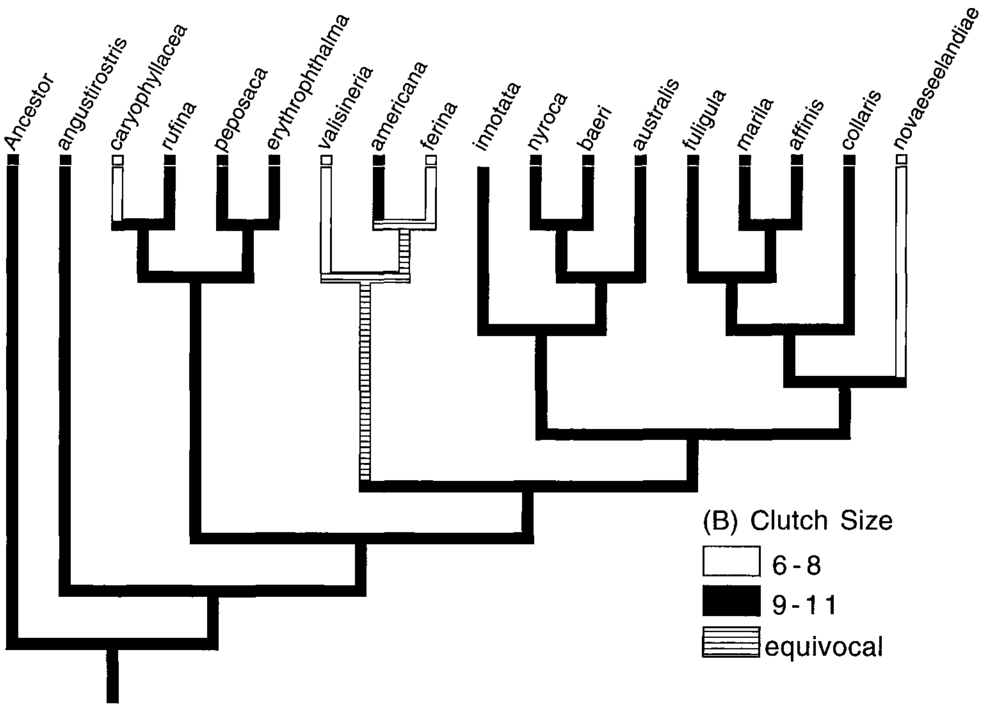
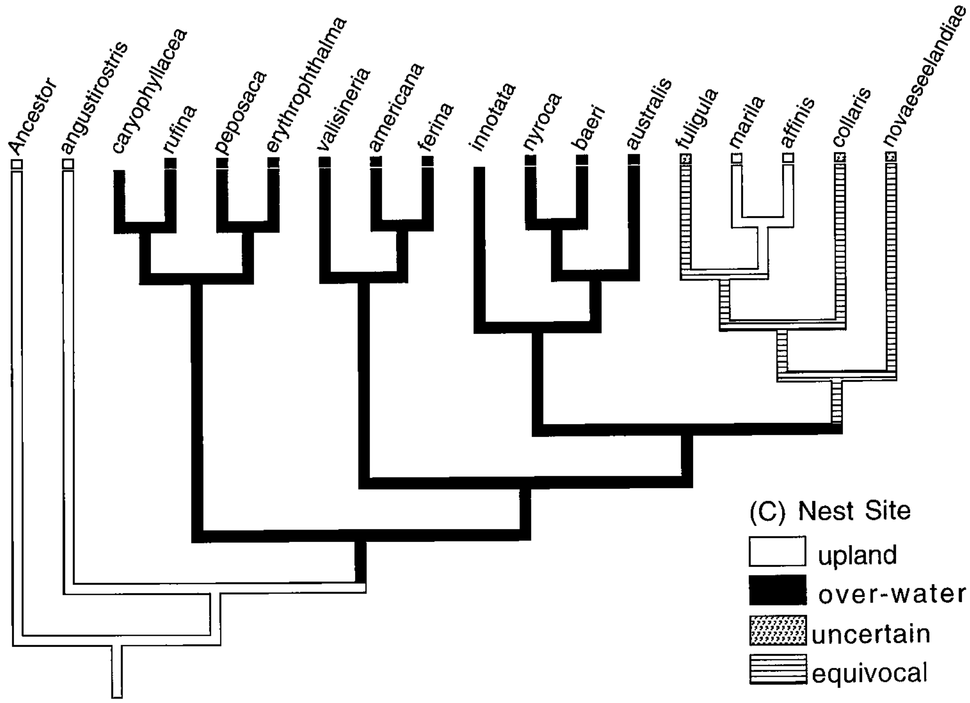


Fig. 4. Traces of four selected ecomorphological attributes on one of three most-parsimonious phylogenetic trees for Aythyini: (A) mean body mass, (B) mean clutch size, (C) preferred nest site, and (D) diel activity period. See Appendices 1 and 2 for definitions and distributions of states.



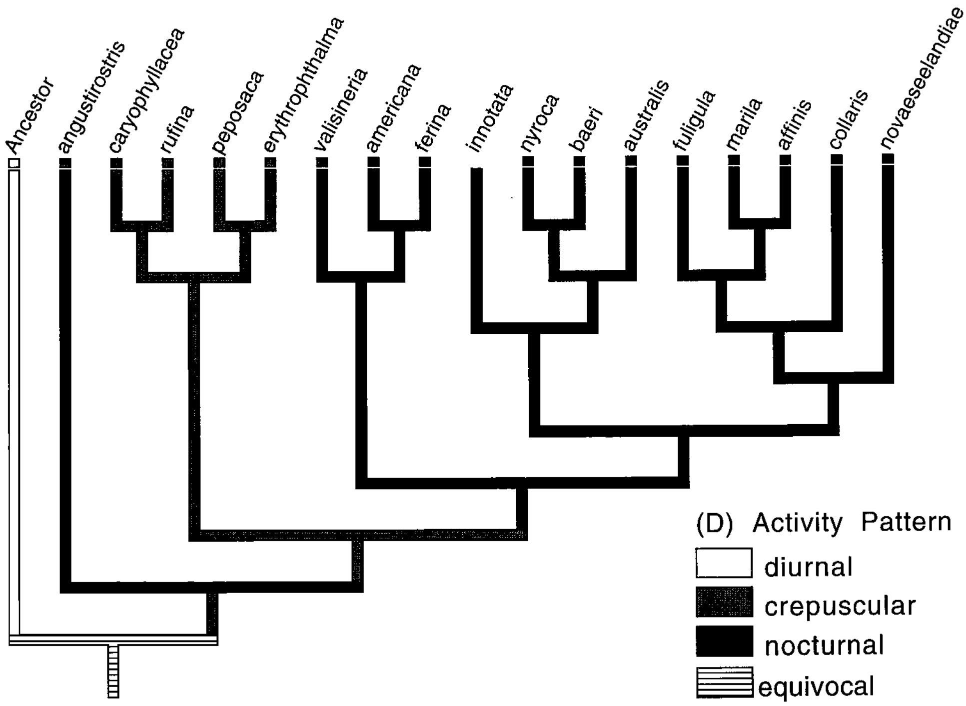


Fig. 4. Continued.

ships of the five species of "scaups" in the present analysis differs in several comparatively contentious ways from current arrangements. The relationships inferred here, in which *Aythya collaris* is interposed between *A. novaeseelandiae* and *A. fuligula* in a grade subtending the sister species *A. affinis* and *A. marila* (Fig. 1), agrees with the sequence of species given by Delacour and Mayr (1945); these authors, however, implied the monophyly of the first three species by bracketing them as a "superspecies." The placements of *A. collaris* among the "scaups" or as especially closely related to *A. fuligula* were among the earliest taxonomic arrangements of this group (e.g. Salvadori 1895, Hollister 1919, Peters 1931, Boetticher 1942, 1952, Delacour 1959), and the similarities of appearance between the two species led several early naturalists to confuse the species (Mendall 1958). Johnsgard (1961a, 1965, 1978, 1979), however, concluded that *A. collaris* is more closely related to the "redheads" (*A. valisineria*, *A. americana*, and *A. ferina*), citing similarities of natal plumages, trachea, and courtship behavior.

Quantitative comparison with a tree figured by Johnsgard (1961a) revealed that adoption of his phylogeny using the present data set required an additional 33 steps, a 22% increase in total length of the tree. This comparison assumes that the tree depicted by Johnsgard (1961a: fig. 6) can be interpreted as a formal phylogenetic tree, an assumption that is problematic for two reasons: (a) inclusion of *Marmaronetta* with the pochards is not shown in his tree, but is suggested in text, whereas the genus was depicted as the sister group of the dabbling ducks by Johnsgard (1968: fig. 1), but was shown later as the sister group of other pochards by Johnsgard (1978: xviii); and (b) the genus *Netta* delimited by Johnsgard (1961a) is explicitly polyphyletic, two of three of the member species (*peposaca* and *erythrophthalma*) being depicted as basal members of two different, graphically overlapping groups. Four additional steps alone are required for the placement of *Rhodonessa* as the sister group of the tribe exclusive of *Marmaronetta*. Imposition of monophyly of the three species traditionally included in *Netta* required five additional steps in the tree. The placement of *A. collaris* as the sister group of the three species of "redhead" by Johnsgard (1961a) entailed an increase in total tree length of three steps, and his placement of *A. fuligula* as less closely related to *A. marila* and *A. affinis* than is *A. novaeseelandiae* required six extra steps. *Aythya collaris* remains, however, somewhat enigmatic in its combination of character states; the species is unique by reversal or homoplasy within its five-species clade in three characters of the natal and definitive plumages (Fig. 1), as well as combining significant intraspecific variation in several other characters with a substantial number of autapomorphies (Appendices 1 and 2).

Congruence with behavioral characters.—Loss (most species) or great reduction in frequency (possibly in some stem pochards) of the "decrescendo call" by females, typical of dabbling ducks, unites the Aythyini (Johnsgard 1960a, 1961a, b, 1962, 1965, McKinney 1978). Similarly, "head-pumping" precopulatory displays are absent or rudimentary in the Aythyini (including *Marmaronetta*), a distinction from the dabbling ducks (Johnsgard 1965). Other courtship displays of pochards, most either shared with dabbling ducks (and presumably plesiomorphic) or for which clearly homologous displays are known in other tribes (Johnsgard 1960b, 1965), are homogeneous within the tribe and include displays by males ("kinked-neck call," "coughing," "turning the back-of-the-head," "head-throw," "sneaking," and "neck-stretching"), by females ("inciting calls"), and by both sexes ("preening behind the wing").

Interspecific hybridization.—Possibly related at least in part to the homogeneity of courtship displays within the Aythyini, interspecific hybridization is comparatively high among members of the tribe (Johnsgard 1960c, Scherer and Hilsberg 1982). The frequency of hybridization among pochards and the confusing phenotypes of hybrid progeny have prompted repeated commentary (Salvadori 1895, Johnsgard 1960c, Milstein 1979, Scherer and Hilsberg 1982, Smallshire 1986), and anatomical comparisons of hybrids include plumage patterns (Gillham et al. 1966, Madge and Burn 1988) and tracheae (Beer 1968). Interspecific hybridization traditionally has been interpreted as the breakdown of evolutionarily "adaptive" isolating mechanisms (Johnsgard 1963). An alternative view, in which such "mechanisms" reflect the hierarchical accumulation of morphological and behavioral characters of undetermined selective value within lineages, has been suggested for other tribes of waterfowl (Livezey 1991, 1995a, b, c). The frequency of hybridization and the viability of hybrid progeny also have been con-

TABLE 1. Phylogenetic classification of modern Aythyini.

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

Tribe Aythyini Delacour & Mayr, 1945.—Pochards
  Subtribe Marmaronetteae, new taxon
    Genus *Marmaronetta* Riechenbach, 1853
      Marmaronetta angustirostris (Ménétries, 1832).—Marbled Duck
  Subtribe Rhodonesseae Boetticher, 1952.—Stem (narrow-billed) pochards
    Genus *Rhodonessa* Reichenbach, 1853 (>*Netta* Kaup, 1859)
      Rhodonessa caryophyllacea (Latham, 1790).—Pink-headed Pochard
      Rhodonessa rufina (Pallas, 1773).—Red-crested Pochard
    Genus *Metopiana* Bonaparte, 1856 (>*Phaeoaythia* Delacour, 1937)
      Metopiana peposaca (Vieillot, 1816).—Rosy-billed Pochard
      Metopiana erythrophthalma (Wied, 1832).—Southern Pochard
  Subtribe Aythyeae Boetticher, 1952.—True (broad-billed) pochards
    Genus *Aythya* Boie, 1822.—Typical pochards
      Subgenus *Aristonetta* Baird, 1858.—Redheads
        Aythya valisineria (Wilson, 1814).—Canvasback (Canvas-backed Pochard)
        Aythya ferina (Linnaeus, 1758).—Eurasian Pochard
        Aythya americana (Eyton, 1838).—Redhead (Red-headed Pochard)
      Subgenus *Nyroca* Fleming, 1822.—White-eyes
        Aythya australis (Eyton, 1838).—Australian White-eye
        Aythya innotata (Salvadori, 1894).—Madagascan White-eye
        Aythya nyroca (Güldenstädt, 1769).—Ferruginous White-eye
        Aythya baeri (Radde, 1863).—Siberian White-eye
      Subgenus *Aythya* Boie, 1822.—Scaup
        Aythya novaeseelandiae (Gmelin, 1789).—New Zealand Scaup
        Aythya collaris (Donovan, 1809).—Ring-necked Scaup
        Aythya fuligula (Linnaeus, 1758).—Tufted Scaup
        Aythya marila (Linnaeus, 1761).—Greater Scaup
        Aythya affinis (Eyton, 1838).—Lesser Scaup

sidered directly indicative of closeness of phylogenetic relationship (Sibley 1957, Johnsgard 1960c). For example, Johnsgard (1960c: 30) stated: "The high percentage of the potential hybrids among species of diving ducks that are actually realized . . . forces one to conclude that the Aythyini represent a very closely related group of species, with two being the maximum number of genera that can be reasonably allowed." However, interspecific hybridization reflects a primitive intercompatibility of lineages and, therefore, does not reflect phylogenetic relationship (Livezey 1991), and the number of genera to be recognized within a tribe hinges primarily on investing the greatest amount of phylogenetic information in the chosen taxonomy (Wiley 1981). Moreover, in contrast with the diversity of intergeneric hybrids known for the Aythyini generally, hybrids between the sister species *A. marila* and *A. affinis* in the wild have not been reported, although difficulties in identification of the latter may account for the absence of reports (Madge and Burn 1988).

Biogeographical patterns.—The collective distributional limits of the members of the Aythyini encompass: (1) a broad band of temperate habitats throughout the Northern Hemisphere, reaching a maximal diversity in the central Palearctic; and (2) a more fragmented, Southern Hemisphere range including much of South America, southernmost Africa (including Madagascar), and the Australasian region (Weller 1964a). Within the context of the present phylogenetic hypothesis (Figs. 1 and 2), a few biogeographical inferences beyond this broad outline can be attempted. Several of the most-basal members of the tribe—Marbled Duck, Pink-headed Duck, and Red-crested Pochard—share Palearctic distributions; species in the sister group of the latter two species have Neotropical or Neotropical-African distributional limits. Of the 12 remaining species in the tribe, all but three are limited to the Northern Hemisphere; the austral members are the Madagascan White-eye, Australian White-eye, and New Zealand Scaup. One phylogenetic interpretation of this pattern of distributions is that the group was originally limited to the Northern Hemisphere (perhaps the Palearctic), with three or four subsequent transequatorial radiations: (1) by the ancestor of the Rosy-billed and Southern pochards; (2) by the common ancestor of the Madagascan and Australian white-eyes (if these are sister species, but currently unresolved) or by each independently; and (3) by the New Zealand Scaup.

Revised classification of the Aythyini.—A phylogenetic classification for the Aythyini is presented in Table 1, the goal of which was to incorporate maximal phylogenetic information while minimizing violence to existing taxonomic traditions. Inclusion of the tribe within the Anatinae is justified on the basis of synapomorphies presented by Livezey (1986). Diagnostic characters for included taxa are shown on corresponding branches of Figure 1, described in Appendix 1, and compiled in matrix form in Appendix 2. The fundamental structure of the tribe is defined by a sequence of three subtribes; the subtribe for *Marmaronetta* is new and defines the sister group of the other two subtribes. Both of the two-species clades of "stem" or narrow-billed pochards were given generic rank, based on the phylogenetic relationships inferred here and seniority of corresponding taxa. The well supported monophyly of the "true" or broad-billed pochards, and the resolved relationships of the three included subgroups (redheads, white-eyes, and scaups; the latter including *Aythya collaris*), permit a largely dichotomous definition of genera and subgenera traditionally included in *Aythya*. This revision subdivides three nested subgenera within *Aythya* for the redheads, white-eyes, and scaups. An alternative, strictly dichotomous classification would entail the elevation of *Aristonetta* to generic rank for the redheads, reserving the genus *Aythya* for the white-eyes and scaups; this somewhat more informative scheme is not advocated for reasons of taxonomic stability. These three groups and species included within each are listed in order of increasing relationship, except as limited by incomplete resolution within the white-eyes. Where indicated, common names of species were altered to describe more accurately tribal, generic, and subgeneric membership.

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APPENDIX 1.—Character descriptions. Primitive states correspond to state "a" unless another state is highlighted in boldface. *CI* = consistency index.

Skeleton.—Index numbers of osteological characters derived from those given by Livezey (1986) are given in parentheses after character name; most were recorded to restrict the states to those found in the Aythyini, those described as "revised" indicate new character definitions, and those in which corrections in codings based on the wider, species-level comparisons made here are so indicated. *CI* was 1.00 for all but characters 10 and 14, which were 0.50.

1. Columna vertebralis, vertebrae cervicales, modal number (character 21): (a) 16; (b) 17. **2.** Sternum, rostrum sterni, spina externa (character 79, revised): (a) long, peglike; (b) obsolete; (c) short, squarish; (d) medially separated, sharp, pair of points. **3.** Sternum, rostrum sterni, labrum interna (character 82): (a) a rounded notch; (b) rounded notch with small medial point. **4.** Humerus, extremitas proximalis humeri, fossa pneumotricipitalis, foramen pneumaticum (character 28): (a) present; (b) absent. **5.** Humerus, extremitas distalis, relative caudal prominence of epicondyla dorsalis and ventralis (character 33, revised): (a) epicondyla essentially equal; (b) epicondylus dorsalis cranial to epicondylus ventralis. **6.** Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum dorsalis, rounded prominence on distal terminus (character 37; corrected with respect to labrum involved): (a) present; (b) absent. **7.** Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, impressio m. extensor metacarpi ulnaris, position relative to synostosis metacarpalis proximalis (character 43): (a) completely proximal; (b) opposite, at least in part. **8.** Carpometacarpus, extremitas proximalis carpometacarpi, trochlea carpalis, labrum ventralis, orientation relative to corpus carpometacarpi, facies ventralis (character 48): (a) coplanar; (b) laterally rotated. **9.** Femur, corpus femoris, craniocaudal curvature in lateral perspective (character 55, revised): absent; (b) present. **10.** Femur, extremitas distalis, fossa poplitea (character 56, revised): (a) shallow; (b) deep. **11.** Tibiotarsus, extremitas distalis tibiotarsi, condyla medialis et lateralis, relative cranial prominence (character 64): (a) condylus medialis distinctly greater than condylus lateralis; (b) condyla equally prominent. **12.** Tibiotarsus, extremitas proximalis tibiotarsi, crista cnemialis cranialis, distinct ridge continuing distally along corpus tibiotarsi, facies cranialis, margo cranialis (character 65): (a) absent; (b) present. **13.** Tarsometatarsus, extremitas distalis tarsometatarsi, canalis interosseus tendineus, osseus lamina covering dorsal (of two) canaliculi (character 69): (a) present; (b) largely or completely lacking. **14.** Tarsometatarsus, corpus tarsometatarsi, relative dorsal prominence of facies subcutanea medialis and facies subcutanea lateralis (character 75): (a) equal, no torsion of corpus evident; (b) medialis less prominent than lateralis, related to significant torsion of corpus about long axis.

Trachea.—Pertain to males (see Fig. 5). *CI* was 1.0 for all but character 2, which was 0.50.

1. Syrinx, bulla syringealis (primary chamber): (a) solid; (b) with fenestrae. **2.** Syrinx, bulla syringealis (primary chamber): (a) rounded; (b) flattened "whorl". **3.** Bulbus trachealis, single, gradually dialated: (a) absent (includes modal reversals in *fuligula, collaris, affinis,* and *marila*); (b) variably evident (includes *angustirostris;* unique shapes in *peposaca, rufina* coded separately, below). **4.** Syrinx, bulla syringealis, solid, bulbous, basal chamber: (a) absent; (b) present. **5.** Syrinx, tympanum: (a) not enlarged; (b) enlarged, subequal to bulla syringealis in volume (includes intermediate state in *fuligula*). **6.** Bulbus trachealis (if present), constriction in middle, forming two bulbiculi tracheales: (a) absent; (b) present. **7.** Bulbus trachealis (if present), shape abrupt, cylindrical: (a) absent; (b) present.

Natal integument.—Pertain to fresh, class-Ia downy young (see Fig. 6). CI was 1.0 for all but characters 3 (*CI* = 0.50) and 5 (*CI* = 0.33).

1. Pale scapular and rump spots: (a) present; (b) obsolete. **2.** Dark postorbital stripe (variable): (a) present; (b) reduced or obsolete. **3.** Ground color of plumage: (a) whitish; (b) yellowish. **4.** Pale alar stripe: (a) present; (b) obsolete. **5.** Crural region: (a) pale, like adjacent regions of venter; (b) contrastingly, extensively dusky (*novaeseelandiae* variable). **6.** Distinct dusky breast band: (a) absent; (b) present. **7.** Cheeks: (a) pale; (b) variably darkened, typically by irregular stripe(s). **8.** Dark preorbital stripe (problematic): (a) present (outgroups); (b) obsolete or absent (includes *fuligula, marila,* and *affinis,* in which face darkened). **9.** Dark, contrasting auricular spot: (a) present; (b) absent.

Definitive integument.—Pertain to definitive alternate plumages of males unless indicated otherwise.

1. Breast: (a) not distinguished; (b) black with iridescence, comparatively sharp (including *caryophyllacea* with dark brown, no break); (c) brown with iridescence, comparatively sharp. *CI* = 1.00. **2.** Head, contrasting chestnut coloration: (a) absent; (b) present. *CI* = 1.00. **3.** Head, contrasting pinkish-red coloration: (a) absent; (b) present (comparatively pink in *caryophyllacea*). *CI* = 1.00. **4.** Head, contrasting iridescent *black* coloration: (a) absent; (b) present. *CI* = 0.50. **5.** Head, contrasting dull (chocolate) *brown* with iridescence: (a) absent; (b) present. *CI* = 1.00. **6.** Undertail coverts, contrasting black color: (a) absent; (b) present, but center region white; (c) present, including entire venter. *CI* = 0.67. **7.** Undertail coverts, sharp white color with black border: (a) absent; (b) present.

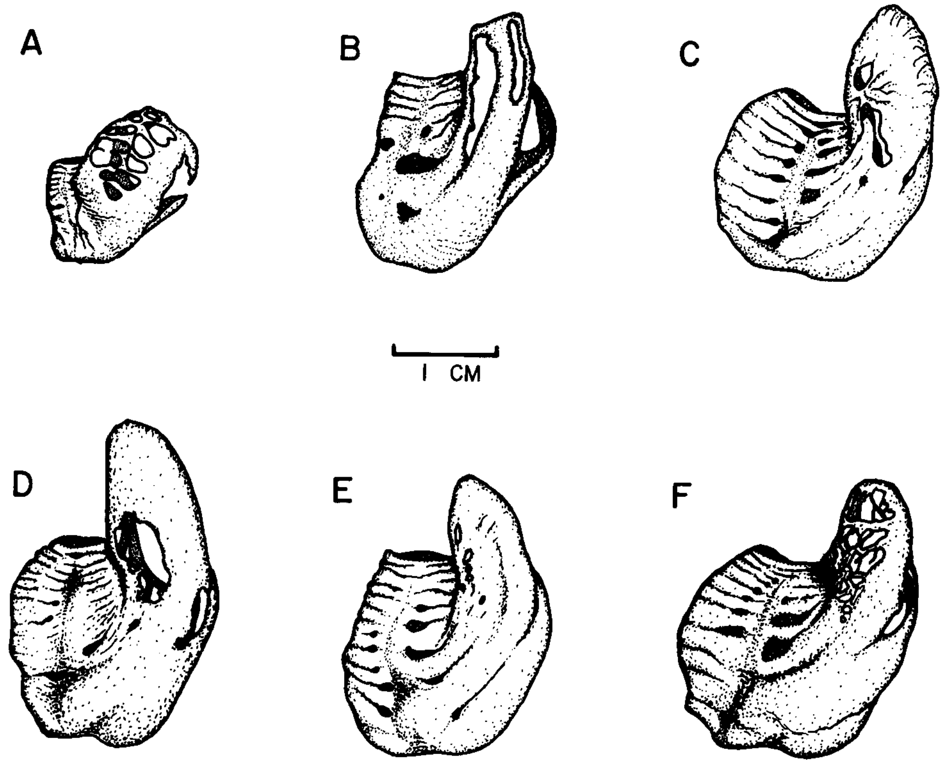

Fig. 5. Bullae ossea syringeales of selected Aythyini, males, ventral views: (A) *M. angustirostris* (LACM 101686); (B) *R. rufina* (USNM 490521); (C) *M. peposaca* (KUMNH 81984); (D) *A. americana* (KUMNH 21244); (E) *A. australis* (KUMNH 85354); and (F) *A. affinis* (KUMNH 15238).

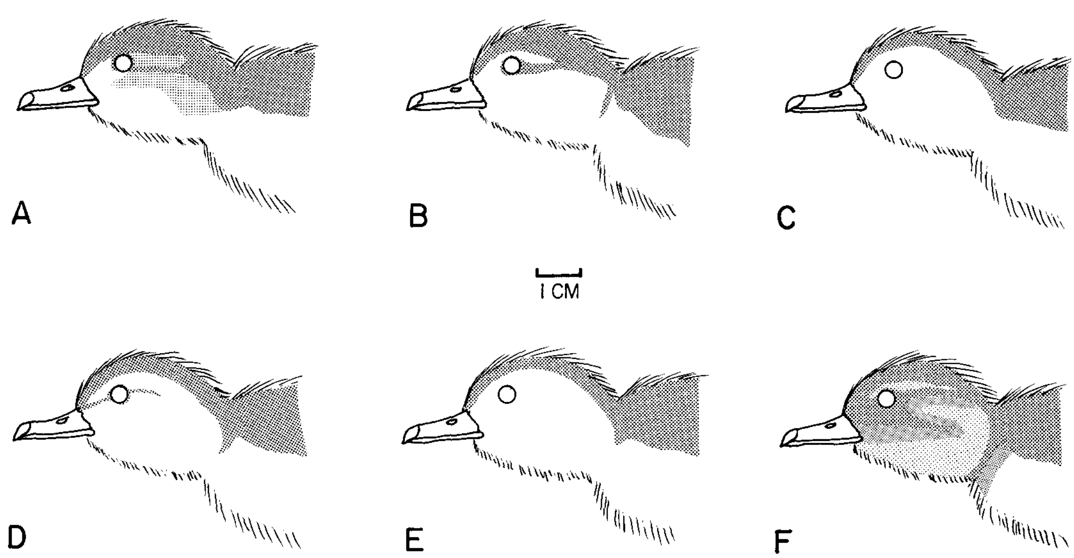

Fig. 6. Diagrams of natal patterns of selected Aythyini (age class I), lateral views: (A) *M. angustirostris* (WWT 712); (B) *R. rufina* (FMNH 351541); (C) *M. peposaca* (USNM 307515); (D) *A. valisineria* (AMNH 351049); (E) *A. baeri* (FMNH 12891); and (F) *A. marila* (AMNH 76833).

CI = 0.50. **8.** Venter, essentially dark color throughout, produced by unevenly distributed dark brown feathers: (a) absent; (b) present. *CI* = 1.00. Also, see next character. **9.** Upper belly, ground color: (a) white; (b) brown (includes unique, problematical, black-and-white vermiculations of *peposaca*). *CI* = 1.00. **10.** Lower belly, distinct and contrasting brownish suffusion (especially on crural region): (a) absent; (b) present. *CI* = 1.00. **11.** Dorsum, yoke of iridescent blackish from nape to upper back along midline: (a) absent; (b) present (variable in *baeri*). *CI* = 1.00. **12.** Axillaries (adults of both sexes): (a) white; (b) brown. *CI* = 1.00. **13.** Hallux, cutaneous lobation: (a) absent; (b) present (small in *caryophyllacea*). *CI* = 1.00. **14.** Chin and throat (female): (a) pale color conspicuous, extending well down throat; (b) pale color inconspicuous, only moderately extensive; (c) pale color (if any), distinct but confined posteriorly to chin area by dark region. *CI* = 1.00. **15.** Feathers at base of bill, contrastingly white, lateral patches, confined to small region dorsal to gape (female): (a) absent (includes more conspicuous, complex patterns of some *Netta*); (b) present (includes comparatively crescent-shaped state of *collaris*; variable in *novaeseelandiae*). *CI* = 1.00. **16.** Facial pattern, strongly demarcated by caudoventrally sloping white areas at bill base broadly confluent with white throat and somewhat ventrally curved, typically whitish postorbital stripe (definitive female): (a) absent; (b) present (comparatively less distinct in *caryophyllacea*). *CI* = 1.00. **17.** Bill, ephemeral, variably conspicuous, pale subterminal band (especially males): (a) absent (includes suggestion in *angustirostris*); (b) present (most marked in *americana*, *australis*, and *collaris*). *CI* = 0.50. **18.** Bill, ground color: (a) dark; (b) bright red (comparatively pink in *caryophyllacea*). *CI* = 0.50. **19.** Foot, color (adults, both sexes): (a) greenish or yellowish; (b) orange or reddish; (c) gray. *CI* = 0.67. **20.** Mantle, scapulars, and typically tertials, white ground color with fine, wavy, transverse black bars: (a) absent; (b) present. *CI* = 1.00. **21.** Mantle, scapulars, and typically tertials, black ground color with fine, wavy, transverse white bars: (a) absent; (b) present. *CI* = 1.00. **22.** Mantle, scapulars, and typically tertials, black ground color with greenish iridescence and fine white speckling: (a) absent; (b) present. *CI* = 0.33. **23.** Mantle, scapulars, and typically tertials, brown ground color with pale buff scalloping produced by rhomboid, terminal, white spots on feathers: (a) absent; (b) present. *CI* = 1.00. **24.** Iris, color: (a) dark brown; (b) red (brighter in adults, males); (c) orange; (d) yellow. *CI* = 1.00. **25.** Iridescence of crown: (a) absent; (b) present, green; (c) present, purple. *CI* = 0.40. **26.** Iridescence of auricular region: (a) absent; (b) present, green; (c) present, purple. *CI* = 0.40. **27.** Rump, and usually also undertail coverts, contrasting blackish color: (a) absent; (b) present (vestigial to obsolete in *australis*). *CI* = 1.00. **28.** Modal number of pairs of rectrices: (a) seven; (b) eight. *CI* = 1.00. **29.** Wing linings, ground color: (a) essentially white (with pinkish wash in *caryophyllacea*); (b) black. *CI* = 1.00. **30.** Wing linings, cranial margin: (a) white; (b) dark brown or black; (c) faintly mottled with pale gray. *CI* = 0.67. **31.** Dorsal surface of remiges, contrastingly pale silvery gray wash basally: (a) absent; (b) present. *CI* = 0.33. **32.** Dorsal surface of remiges, contrastingly white color basally: (a) absent; (b) present (varying to salmon color in *caryophyllacea*). *CI* = 0.33. **33.** Dorsal surface of forewing (coverts), white border along leading (cranial) edge: (a) absent; (b) present. *CI* = 0.50. **34.** Dorsal surface of forewing (coverts), ground color: (a) pale grayish brown; (b) green-iridescent black (vestigial iridescence and paler in insular *australis* [subspecies *extima*]). *CI* = 0.50. **35.** Rectrices: (a) approximately the color of other contour feathers; (b) contrastingly pale, whitish. *CI* = 1.00. **36.** Dertrum: (a) dark, if rest of maxilla pale, sharply contrasting; (b) pale, like rest of maxilla. *CI* = 1.00. **37.** Face, color largely pale brown, with only dark confined to crown stripe (female): (a) absent; (b) present (uniquely toned in *caryophyllacea*). *CI* = 1.00. **38.** Dusky dorsal neck stripe (female): (a) absent; (b) present. *CI* = 0.50. **39.** Sides and flanks, uniform dark, ventrally extensive, typically continuous with dark venter: (a) absent; (b) present (comparatively restricted with jagged ventral margin in *rufina*). *CI* = 0.50. **40.** Sides and flanks, uniformly dark brown, ventrally restricted band of uniform width: (a) absent; (b) present, brown; (c) present, chestnut. *CI* = 0.50. **41.** Sides and flanks, uniformly white: (a) absent; (b) present. *CI* = 1.00. **42.** Sides and flanks, white with grayish vermiculations: (a) absent; (b) present. *CI* = 1.00. **43.** Sides and flanks, white with fine black barring: (a) absent; (b) present. *CI* = 1.00. **44.** Metallic-colored speculum: (a) present; (b) absent. *CI* = 1.00. **45.** Blackish eye patches: (a) absent; (b) present. *CI* = 1.00. **46.** Bright pink head coloration: (a) absent; (b) present. *CI* = 1.00. **47.** Rounded, bushy crest: (a) absent; (b) present. *CI* = 1.00. **48.** Ventrally extensive white flank patches: (a) absent; (b) present. *CI* = 1.00. **49.** Maxilla, bright red basal swelling: (a) absent; (b) present. *CI* = 1.00. **50.** Dark blackish crown, nape, mentum: (a) absent; (b) present. *CI* = 1.00. **51.** Chestnut breast: (a) absent; (b) present. *CI* = 1.00. **52.** Long, slender crown tuft: (a) absent; (b) present. *CI* = 1.00. **53.** Black breast (if present) continued caudally by ventromedial band to undertail coverts: (a) absent; (b) present. *CI* = 1.00. **54.** Uniformly black body plumage: (a) absent; (b) present. *CI* = 1.00. **55.** Short, restricted, rounded occipital crest: (a) absent; (b) present. *CI* = 1.00. **56.** Upper wing coverts, cranial margin at bend of wing, narrow white patch: (a) absent; (b) present. *CI* = 1.00. **57.** White, vertical pectoral stripe, caudal to black breast: (a) absent; (b) present. *CI* = 1.00. **58.** Fine, white, ventrally curved postorbital stripe (females): (a) absent; (b) present. *CI* = 1.00. **59.** Narrow, dark dorsal stripe from base of neck to nape: (a) absent; (b) present. *CI* = 1.00. **60.** Proximal secondary remiges, fine black external margin: (a) absent; (b) present. *CI* = 1.00. **61.** Secondary remiges, dark (sub)terminal band: (a) absent; (b) present. $CI = 0.50$. **62.** Dorsum and sides, fine white speckling (females): (a) absent; (b) present. $CI = 1.00$. **63.** Venter, lower belly, dusky wash contrasting with white cranially: (a) absent; (b) present. $CI = 1.00$. **64.** Proximal secondary remiges, narrow, white terminal bars: (a) present; (b) absent. $CI = 0.33$. **65.** Maxilla, narrow black line at base: (a) absent; (b) present. $CI = 1.00$. **66.** Neck, ventral surface, dark brown stripe from mentum to breast: (a) absent; (b) present. $CI = 1.00$. **67.** Crown, speckling with brown and white: (a) absent; (b) present. $CI = 1.00$. **68.** Proximal secondary remiges, black-and-white vermiculations: (a) absent; (b) present. $CI = 1.00$. **69.** Chestnut collar contrasting with metallic black of head and neck: (a) absent; (b) present. $CI = 1.00$.

Ecomorphological attributes.—Where logical ordination of states within multistate character was evident, attribute was treated as ordered.

A. Mean body mass (g; ordered): (a) < 700; (b) 700-1,000; (c) > 1,000. **B.** Mean clutch size: (a) 6-8; (b) 9-11. **C.** Nest site: (a) upland; (b) emergent aquatic vegetation; (a/b) variable. **D.** Activity pattern (ordered): (a) diurnal; (b) crepuscular; (c) nocturnal.

APPENDIX 2. Matrix of 99 morphological characters used in phylogenetic analysis of Aythyini and hypothetical ancestor, followed by four attributes mapped *a posteriori* (lettered A–D). Skeletal characters labelled "s1" to "s14," tracheal characters "t1" to "t7," natal characters "n1" to "n9," and those of definitive integument "d1" to "d69." States coded as lowercase letters, and question marks signify undetermined states.

	Character																						
Taxon	1 s1	2 s2	3 s3	4 s4	5 s5	6 s6	7 s7	8 s8	9 s9	10 s10	11 s11	12 s12	13 s13	14 s14	15 t1	16 t2	17 t3	18 t4	19 t5	20 t6	21 t7	22 n1	23 n2
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
2 *angustirostris*	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3 *caryophyllacea*	b	b	b	a	b	b	b	b	a	a	a	a	b	a	b	a	b	b	a	a	a	?	?
4 *rufina*	b	b	b	a	b	b	b	b	a	b	a	a	b	b	b	b	b	b	b	b	a	a	b
5 *peposaca*	b	c	b	a	b	b	b	b	a	a	a	a	b	b	b	b	b	b	a	a	b	a	b
6 *erythrophthalma*	b	d	b	a	b	b	b	b	a	a	a	a	b	b	b	b	b	b	b	a	a	a	b
7 *ferina*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
8 *americana*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
9 *valisineria*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
10 *australis*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
11 *nyroca*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
12 *innotata*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
13 *baeri*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
14 *novaeseelandiae*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	b
15 *collaris*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b	a	a	a	a	b
16 *fuligula*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b	b	a	a	b	b
17 *marila*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b	b	a	a	b	b
18 *affinis*	b	d	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	b	b	a	a	b	b

	Character																					
Taxon	24 n3	25 n4	26 n5	27 n6	28 n7	29 n8	30 n9	31 d1	32 d2	33 d3	34 d4	35 d5	36 d6	37 d7	38 d8	39 d9	40 d10	41 d11	42 d12	43 d13	44 d14	45 d15
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *angustirostris*	a	a	a	a	a	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3 *caryophyllacea*	?	?	?	?	?	?	?	b	a	b	a	a	c	a	a	b	a	a	a	b	a	a
4 *rufina*	b	a	a	a	a	b	b	b	a	b	a	a	c	a	a	b	a	a	a	b	a	a
5 *peposaca*	b	a	a	a	a	b	b	b	a	a	b	a	b	b	a	b	a	a	a	b	a	a
6 *erythrophthalma*	b	a	a	a	a	b	b	b	a	a	b	a	c	a	a	b	a	a	b	b	a	a
7 *ferina*	b	a	a	a	a	b	b	b	b	a	a	a	c	a	a	a	a	a	a	b	b	a
8 *americana*	b	a	a	a	a	b	b	b	b	a	a	a	c	a	a	a	a	a	a	b	b	a
9 *valisineria*	b	a	a	a	a	b	b	b	b	a	a	a	c	a	a	a	a	a	a	b	b	a
10 *australis*	b	a	a	a	a	b	b	c	a	a	a	b	a	b	a	a	b	a	a	b	c	a
11 *nyroca*	b	a	b	a	a	b	b	c	a	a	a	b	a	b	a	a	b	b	a	b	c	a
12 *innotata*	b	a	b	a	a	b	b	c	a	a	a	b	a	b	a	a	b	a	a	b	c	a
13 *baeri*	b	a	b	a	a	b	b	c	a	a	a	b	a	b	a	a	b	b	a	b	c	a
14 *novaeseelandiae*	b	a	b	a	a	b	b	b	a	a	b	a	c	a	b	a	a	a	a	b	c	b
15 *collaris*	b	a	a	a	a	b	b	b	a	a	b	a	c	a	a	a	a	a	a	b	c	b
16 *fuligula*	b	b	b	b	b	b	b	b	a	a	b	a	c	a	a	a	a	a	a	b	c	b
17 *marila*	a	b	b	b	b	b	b	b	a	a	b	a	c	a	a	a	a	a	a	b	c	b
18 *affinis*	a	b	b	b	b	b	b	b	a	a	b	a	c	a	a	a	a	a	a	b	c	b

APPENDIX 2. Continued.

Taxon	Character 46 d16	47 d17	48 d18	49 d19	50 d20	51 d21	52 d22	53 d23	54 d24	55 d25	56 d26	57 d27	58 d28	59 d29	60 d30	61 d31	62 d32	63 d33	64 d34	65 d35
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *angustirostris*	a	a	a	a	a	a	a	b	a	a	a	a	a	a	a	b	a	a	a	a
3 *caryophyllacea*	b	a	b	b	a	a	a	a	b	a	a	b	b	a	a	a	b	b	a	b
4 *rufina*	b	a	b	b	a	a	a	a	b	a	a	b	b	a	a	a	b	b	a	b
5 *peposaca*	b	a	b	b	a	a	a	a	b	b	c	b	b	a	b	a	b	b	b	a
6 *erythrophthalma*	b	a	a	c	a	a	a	a	b	b	c	b	b	b	b	a	b	a	b	a
7 *ferina*	a	b	a	c	b	a	a	a	c	a	a	b	a	a	c	b	a	a	a	a
8 *americana*	a	b	a	c	b	a	a	a	c	a	a	b	a	a	c	b	a	a	a	a
9 *valisineria*	a	a	a	c	b	a	a	a	c	a	a	b	a	a	c	b	a	a	a	a
10 *australis*	a	b	a	c	a	a	a	a	d	b	a	b	a	a	b	a	b	a	b	a
11 *nyroca*	a	b	a	c	a	a	b	a	d	a	a	b	a	a	b	a	b	a	b	a
12 *innotata*	a	b	a	c	a	a	a	a	d	b	a	b	a	a	b	a	b	a	b	a
13 *baeri*	a	b	a	c	a	a	b	a	d	a	b	b	a	a	b	a	b	a	b	a
14 *novaeseelandiae*	a	b	a	c	a	a	b	a	d	b	c	b	a	a	b	a	b	a	b	a
15 *collaris*	a	b	a	c	a	a	b	a	d	c	b	b	a	a	b	b	a	a	b	a
16 *fuligula*	a	b	a	c	a	a	b	a	d	c	c	b	a	a	b	a	b	a	b	a
17 *marila*	a	b	a	c	a	b	a	a	d	b	b	b	a	a	b	a	b	a	b	a
18 *affinis*	a	b	a	c	a	b	a	a	d	c	c	b	a	a	b	a	b	a	b	a

Taxon	Character 66 d36	67 d37	68 d38	69 d39	70 d40	71 d41	72 d42	73 d43	74 d44	75 d45	76 d46	77 d47	78 d48	79 d49	80 d50	81 d51	82 d52	83 d53	84 d54	85 d55
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
2 *angustirostris*	a	a	a	a	a	a	a	a	b	b	a	a	a	a	a	a	a	a	a	a
3 *caryophyllacea*	b	b	b	b	a	a	a	a	b	a	b	a	a	a	a	a	a	a	b	b
4 *rufina*	b	b	b	b	a	a	a	a	b	a	a	b	b	a	a	a	a	b	a	a
5 *peposaca*	a	a	a	a	a	a	a	b	b	a	a	a	a	b	a	a	a	a	a	a
6 *erythrophthalma*	a	a	b	b	a	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
7 *ferina*	a	a	a	a	a	a	b	a	b	a	a	a	a	a	a	a	a	a	a	a
8 *americana*	a	a	a	a	a	a	b	a	b	a	a	a	a	a	a	a	a	a	a	a
9 *valisineria*	a	a	a	a	a	a	b	a	b	a	a	a	a	a	b	a	a	a	a	a
10 *australis*	a	a	a	a	c	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
11 *nyroca*	a	a	a	a	c	a	a	a	b	a	a	a	a	a	a	b	a	a	a	a
12 *innotata*	a	a	a	a	b	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
13 *baeri*	a	a	a	a	b	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
14 *novaeseelandiae*	a	a	a	a	b	a	a	a	b	a	a	a	a	a	a	a	a	a	a	a
15 *collaris*	a	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a	a	a	a	a
16 *fuligula*	a	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a	b	a	a	a
17 *marila*	a	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a	a	a	a	a
18 *affinis*	a	a	a	a	a	b	a	a	b	a	a	a	a	a	a	a	a	a	a	a

Taxon	Character 86 d56	87 d57	88 d58	89 d59	90 d60	91 d61	92 d62	93 d63	94 d64	95 d65	96 d66	97 d67	98 d68	99 d69	100 A	101 B	102 C	103 D
1 Ancestor	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a
2 *angustirostris*	a	a	a	a	a	a	a	a	a	a	a	b	a	a	a	b	a	b
3 *caryophyllacea*	a	a	a	a	b	a	a	a	b	a	b	a	a	a	c	a	?	b
4 *rufina*	b	a	a	b	b	b	a	a	b	a	a	a	a	a	c	b	b	b
5 *peposaca*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	c	b	b	b
6 *erythrophthalma*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	b	b	b	b
7 *ferina*	a	a	a	a	b	b	b	b	a	a	a	a	b	a	b	a	b	c
8 *americana*	a	a	a	a	b	b	b	b	a	b	a	a	a	a	c	b	b	c
9 *valisineria*	a	a	a	a	b	b	b	a	a	a	a	a	a	a	c	a	b	c
10 *australis*	a	a	a	a	b	b	a	a	a	a	a	a	a	a	b	b	b	c
11 *nyroca*	a	a	a	a	b	b	a	a	a	a	a	a	a	a	a	b	b	c
12 *innotata*	a	a	a	a	b	b	a	a	a	a	a	a	a	a	?	?	?	?
13 *baeri*	a	a	a	a	b	b	a	a	a	a	a	a	a	a	b	b	b	c

APPENDIX 2. Continued.

Taxon	86 d56	87 d57	88 d58	89 d59	90 d60	91 d61	92 d62	93 d63	94 d64	95 d65	96 d66	97 d67	98 d68	99 d69	100 A	101 B	102 C	103 D
14 *novaeseelandiae*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	a	a	a/b	c
15 *collaris*	a	b	b	a	b	b	a	a	a	a	a	a	a	b	b	b	a/b	c
16 *fuligula*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	b	b	a/b	c
17 *marila*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	c	b	a	c
18 *affinis*	a	a	a	a	b	b	a	a	b	a	a	a	a	a	b	b	a	c