PHYLOGENY AND COMPARATIVE ECOLOGY OF STIFF-TAILED DUCKS (ANATIDAE: OXYURINI)

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ABSTRACT.—A cladistic analysis of the stiff-tailed ducks (Anatidae: Oxyurini) was conducted using 92 morphological characters. The analysis produced one minimum-length, completely dichotomous phylogenetic tree of high consistency (consistency index for informative characters, 0.74). Monophyly of the tribe was supported by 17 unambiguous synapomorphies. Within the tribe, *Heteronetta* (1 species) is the sister-group of other members; within the latter clade (supported by 21 unambiguous synapomorphies), *Nomonyx* (1 species) is the sister-group of *Oxyura* (6 species) + *Biziura* (1 species). The latter clade is supported by 10 unambiguous synapomorphies. Monophyly of *Oxyura* proper is supported by three unambiguous synapomorphies. All branches in the shortest tree except that uniting *Oxyura*, exclusive of *jamaicensis*, were conserved in a majority-rule consensus tree of 1000 bootstrapped replicates. *Biziura* and (to a lesser extent) *Heteronetta* were highly autapomorphic. Modest evolutionary patterns in body mass, reproductive parameters, and sexual dimorphism are evident, with the most marked, correlated changes occurring in *Heteronetta* and (especially) *Biziura*. The implications of these evolutionary trends for reproductive ecology and biogeographic patterns are discussed, and a phylogenetic classification of the tribe is presented. *Received 27 April 1994, accepted 10 Nov. 1994.*

The stiff-tailed ducks (Anatidae: Oxyurini) include some of the most distinctive species of waterfowl; among its members are the only obligate nest-parasite (Black-headed Duck; *Heteronetta atricapilla*) and the species showing the greatest sexual size dimorphism (Musk Duck; *Biziura lobata*) in the order Anseriformes (Delacour 1959; Johnsgard 1962, 1978; Weller 1968; Livezey 1986). Members of the Oxyurini are foot-propelled diving birds (Townsend 1909, Brooks 1945, Tome and Wrubleski 1988) and range in diving ability from the largely surface-feeding Black-headed Duck to the highly specialized Musk Duck (Raikow 1970, 1973; Livezey 1986). Stiff-tailed ducks generally inhabit freshwater lakes and marshes, typically construct over-water nests, and occur in most major land areas worldwide (Delacour 1959; Weller 1964a–d; Johnsgard 1978).

Since the reclassification of the White-backed Duck (Dendrocygninae: *Thalassornis leuconotus*) on behavioral and morphological grounds (Johnsgard 1967; Raikow 1971; Livezey 1986, 1995), systematic controversies concerning the stiff-tailed ducks have focused on the tribal position of the Black-headed Duck, currently considered to be a comparatively primitive member of the Oxyurini (e.g., Salvadori 1895; Phillips 1925, 1926; Peters 1931; Boetticher 1942, 1952; Delacour and Mayr 1945; Ver-

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heyen 1953; Delacour 1959; Johnsgard 1961a, 1965a, 1978; Rees and Hilgarth 1984; Livezey 1986; Sibley and Monroe 1993). Intergeneric relationships within the tribe were considered explicitly by Johnsgard (1961a; figs. 8, 9), who depicted *Heteronetta* as the sister-group of *Oxyura* and *Biziura*.

Species of *Oxyura* have been grouped, either by implication through the taxonomic sequences (Salvadori 1895; Phillips 1926; Peters 1931; ·Boetticher 1942, 1952; Delacour 1959; Wolters 1976) or by explicit argument or diagram (Delacour and Mayr 1945; Johnsgard 1961a, 1965a, 1967, 1968), as follows: (1) the unusual Masked Duck ("*O.*" *dominica*) of the neotropics, segregated in the monotypic genus *Nomonyx* by some (Salvadori 1895, Phillips 1926, Peters 1931, Woolfenden 1961, Livezey 1986); (2) the Northern Ruddy Duck (*O. jamaicensis*; sometimes including the Peruvian Ruddy Duck, *O. ferruginea*) and White-headed Duck (*O. leucocephala*) of the northern hemisphere; and (3) the variously partitioned and ranked southern-hemisphere forms (Argentine Ruddy Duck, *O. vittata*; Maccoa Duck, *O. maccoa*; Blue-billed Duck, *O. australis*; and Peruvian Ruddy Duck, *O. [jamaicensis] ferruginea*). Johnsgard (1966) described particular behavioral similarities between the Blue-billed Duck of Australia and the Argentine Ruddy Duck of southern South America. In two later works, Johnsgard (1978, 1979) proposed that the White-headed Duck was more closely related to the Maccoa Duck than to the Northern Ruddy Duck. The status and relationships of the Peruvian Ruddy Duck and the Colombian Ruddy Duck remain controversial (Delacour and Mayr 1945; Delacour 1959; Johnsgard 1961a, 1965a, 1967, 1968, 1978, 1979; Siegfried 1976; Adams and Slavid 1984).

An understanding of the marked evolutionary patterns in this unique group of waterfowl is contingent on a proposal of a robust, explicit phylogenetic hypothesis. This paper presents a species-level phylogenetic (cladistic) analysis of the stiff-tailed ducks, using morphological characters. This analysis is followed by an examination of evolutionary trends in selected life-history traits in the context of the phylogeny presented. Biogeographic issues also are considered and a phylogenetic classification of modern Oxyurini is proposed.

MATERIALS AND METHODS

Taxonomy.—As in my previous genus-level analysis of the Anseriformes (Livezey 1986), I recognize four genera in the tribe Oxyurini, of which three are monotypic: *Heteronetta, Nomonyx, Oxyura,* and *Biziura.* Opinions have varied regarding the number and composition of species to be recognized within *Oxyura* (exclusive of *dominica*); e.g., three species were recognized by Delacour and Mayr (1945), whereas Johnsgard (1961a, 1978, 1979) listed five. I adopted a conservative scheme, treating as a species any lineage diagnosable by the qualitative characters used in the phylogenetic analysis, an approach that admits a maximal

number of possible phylogenetic inferences and that is compatible with the phylogenetic species concept (Cracraft 1983, 1988). The following six species of *Oxyura* were recognized: *jamaicensis* (including *rubida*), *ferruginea, vittata, australis, leucocephala,* and *maccoa.* In addition, the *andina* population of northern South America (typically included in *O. jamaicensis*) was analyzed separately in some analyses in an attempt to assess the likelihood of its purportedly hybrid origin; the only defining character detected for *andina* is its variably black-marked, white cheeks, a character interpretable as evidence of introgression (Adams and Slavid 1984).

Definition of characters.—Characters were defined on the basis of direct examination of study skins, skeletons, and tracheae of stiff-tailed ducks and other Anatinae, as well as a review of the relevant literature (Pycraft 1906; Phillips 1925, 1926; Delacour and Mayr 1945; Delacour 1959, 1964; Johnsgard 1961b, 1962, 1965b, 1967, 1978; Humphrey and Clark 1964; Lowe 1966; Weller 1968; Siegfried 1970; Palmer 1976; Madge 1984; Torres 1984; Torres and Ayala 1986; Madge and Burn 1988; King 1989; McLelland 1989; Marchant and Higgins 1990; del Hoyo et al. 1992; Nelson 1993). The natal pattern of *O. (j.) andina* was examined using photographs of three specimens. A unique set of tracheal, esophageal, and gular diverticula in the Oxyurini, which produce the inflation of the neck during courtship in males, are confusingly described in the literature and remain incompletely known (e.g., Johnsgard 1961b, 1965a, 1967; Clark 1964; Siegfried 1976); states for these characters were based on direct examination of *Heteronetta atricapilla, Nomonyx dominicus, Oxyura jamaicensis, O. maccoa, O. australis,* and *Biziura lobata* and the few adequately detailed anatomical descriptions (Forbes 1882; Wetmore 1917, 1918, 1926, 1965; McLelland 1989).

Each character is a trait, judged to be homologous across taxa, that comprised a primitive (plesiomorphic) state and one or more derived (apomorphic) states. A total of 92 morphological characters were defined—39 skeletal characters (most after Livezey 1986), three characters of the trachea or esophagus, 10 characters of natal plumage, and 40 characters of the plumage and soft parts of adults (available from the author on request). Species for which a character state could not be ascertained were assigned a missing-datum code for that character. These character-states, together with a "hypothetical ancestor" vector (see below) compose a data matrix of dimension 10 × 92 (available from the author on request). Characters having more than one derived state were considered unordered unless a logical, consistent ordination by count, degree, or relative extent was evident (e.g., number of pairs of rectrices was analyzed as ordinal). Characters in which the derived state(s) were possessed by single species (autapomorphies) were included in the analysis because of the pervasive influence such differences have had on traditional classification and because this permits estimates of evolutionary divergence and phenetic differences among species.

Outgroups and polarities.—Representatives of the three other tribes of the Anatinae—Anatini, Mergini; Aythyini (*sensu* Livezey 1986, 1991)—were chosen as outgroups, in accordance with the preponderance of anatomical and behavioral evidence (e.g., Woolfenden 1961; Johnsgard 1961a, 1965a, 1978) and a phylogenetic analysis of the order (Livezey 1986). Although the inclusion of Mergini and Oxyurini in the Anatinae is reasonably well supported (Livezey 1986), the relationships among the tribes of Anatinae remain poorly resolved (Livezey, unpubl. data). Polarities (directionalities of character change) were established by ascertaining the distributions of states of each character in the other tribes of Anatinae; these states were hypothesized to be the primitive conditions (plesiomorphous states) for the characters with respect to the ingroup (Oxyurini). These individual plesiomorphous states were combined into a single vector or "hypothetical ancestor" which in turn was used to root the tree(s).

An early divergence of the Oxyurini from most other Anseriformes was proposed by

Madsen et al. (1988) and Sibley and Ahlquist (1990) and adopted by Sibley and Monroe (1990). This view (Sibley and Ahlquist 1990: fig. 357) implies that any member of the Anseriformes exclusive of the Anhimidae, *Anseranas*, and *Dendrocygna* is equally closely related to the Oxyurini, a diverse set of outgroups indeed. This proposal, however, is not considered credible in light of numerous substantive criticisms of DNA hybridization as a tool for phylogenetic inference (Cracraft 1987, Houde 1987, Sarich et al. 1989), additional irregularities in the application of the technique by Sibley and colleagues (Lewin 1988a, b; Krajewski 1991; Mindell 1992), the subjective placement of the Oxyurini within the Anseriformes and unfavorable metric properties associated with sparse data matrices (Lanyon 1992), inconsistent classificatory methodology (Siegel-Causey 1993), and the inadequate representation of the tribe in the analysis (the sole representative being one species of *Oxyura*). Other molecular studies including at least one representative of the Oxyurini, all of which also were phenetic, included too few genera or failed to resolve intergeneric relationships adequately for meaningful comparisons (Brush 1976, Patton and Avise 1985, Scherer and Sontag 1986).

P. J. Fullagar (in Marchant and Higgins 1990) suggested that the unique and primitive Freckled Duck (*Stictonetta naevosa*) is closely related to the stiff-tailed ducks, primarily on the basis of the phenetic findings of Madsen et al. (1988) and Sibley and Monroe (1990), similarities in selected behavioral and anatomical characters, and a misinterpretation of a study by Faith (1989). Although polarities of most skeletal characters used herein were unchanged, use of *Stictonetta* as the outgroup necessitated equivocal, mutually contradictory changes in polarities in seven osteological characters (*Stictonetta* exclusively sharing three with *Heteronetta*, three others with *Biziura*, and one with Oxyurini exclusive of *Heteronetta*). Also, postulation of *Stictonetta* as the sister-group of the Oxyurini required six additional changes in osteological characters shared by the Tadorninae and Anatinae (Livezey 1986), while saving only one step in the inferred polarity of the bulla syringealis. Natal characters of Oxyurini proved all but non-comparable with the unique natal pattern of *Stictonetta*. Characters of the definitive integument of Oxyurini also were difficult to compare with *Stictonetta* and require additional homoplasies in the wing speculum and tarsal scutellation in a global analysis. Pending documentation and phylogenetic analysis of the alleged similarities between *Stictonetta* and the Oxyurini mentioned by Fullagar (including the questionably homologous coloration of the maxillary rhamphotheca and undescribed details of the hemipenes) or other corroborating evidence, use of the Anatinae as the outgroup for the Oxyurini seems justified, and (for the characters analyzed here) probably of negligible topological effect within the tribe.

Derivation of trees.—Trees were derived according to the principles of phylogenetic analysis under the criterion of global parsimony (Wiley 1981). Trees were constructed using the phylogenetic software PAUP 3.1 (Swofford 1993); supplementary topological analyses, *a posteriori* character mappings, and printing of trees were performed on MacClade 3.01 (Maddison and Maddison 1992). Both programs were implemented on a Macintosh Quadra 800. I used the deterministic "branch-and-bound" algorithm to find the shortest tree(s). The character-state optimization used was accelerated transformation (ACCTRAN); employment of delayed transformation (DELTRAN) did not affect the solution set. A bootstrapping procedure using the branch-and-bound algorithm, intended as an index to empirical support for branches and not rigorous statistical inference (Felsenstein 1985, Sanderson 1989), was employed to generate 1000 topological replications. Stability of branches within the final tree was summarized by a 50% majority-rule consensus tree of these replicate trees.

Ecomorphological trends.—Selected functionally important but presumptively nonhomologous characteristics were compiled for assessment of evolutionary patterns; these attributes were mapped *a posteriori* onto the independently inferred phylogenetic tree, thereby

permitting phylogenetically based comparative analyses (Smith and Patterson 1988, Brooks and McLennan 1991, Harvey and Pagel 1991). States of these attributes–including body mass, clutch size, egg size, nesting habits, diet, and diving behavior—were taken from the literature (Delacour 1959, Schönwetter 1961, Frith 1967, Raikow 1973, Palmer 1976, Cramp and Simmons 1977, Todd 1979, Brown et al. 1982, Livezey 1986, Madge and Burn 1988, Rohwer 1988, Marchant and Higgins 1990, del Hoyo 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 measured by the ratio of the mean body mass of males divided by the mean body mass of females. "Relative clutch mass" was defined by the product of mean clutch size and mean egg mass divided by the mean body mass of an adult female.

Phylogenetic classification.—The resultant phylogenetic tree(s) formed the basis for a Linnean classification that maximally reflects the relationships inferred for the ingroup. 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 synonymies of Phillips (1925, 1926), Brodkorb (1964), and Wolters (1976).

RESULTS

Shortest tree.—A single, completely dichotomous, shortest tree was found for the Oxyurini, having a total length of 127, a consistency index (excluding autapomorphies) of 0.81, a retention index of 0.81, and a rescaled consistency index of 0.71. Monophyly of the tribe is supported by 17 unambiguous synapomorphies (Fig. 1). Within the tree, *Heteronetta* is the sister-group of all other Oxyurini; the latter group (supported by 20 unambiguous synapomorphies) comprises two major subgroups—(1) *Nomonyx* and (2) *Oxyura* + *Biziura* (Fig. 1). Monophyly of the clade comprising *Oxyura* and *Biziura* is supported by 10 unambiguous synapomorphies; three unambiguous synapomorphies support the monophyly of *Oxyura*. Within *Oxyura, O. jamaicensis* is resolved to be the sister-group of its congeners. The latter clade (supported by a single synapomorphy) comprises two basic subgroups, both polyspecific (Fig. 1): (1) *O. ferruginea* and its sister-group *O. vittata* + *O. australis* (each branch supported by one synapomorphy) and (2) the sister-species *O. maccoa* and *O. leucocephala* (supported by four synapomorphies).

An analysis in which the Colombian Ruddy-Duck (*O. "andina"*) was included as a separate operational unit placed the taxon in two equally parsimonious positions within *Oxyura* exclusive of *O. jamaicensis*: (1) as the sister-group of the clade comprising the remaining *Oxyura* or (2) as a monotypic branch in a trichotomy including two other clades, *ferruginea* + *vittata* + *australis* and *maccoa* + *leucocephala*.

Apomorphic divergence.—The three monotypic genera each had several autapomorphies: *Heteronetta* (8), *Nomonyx* (5), and *Biziura* (28). The genus *Biziura* exceeds all other Anseriformes in autapomorphic divergence, both in this analysis (Fig. 1) and an earlier genus-level study (Liv-
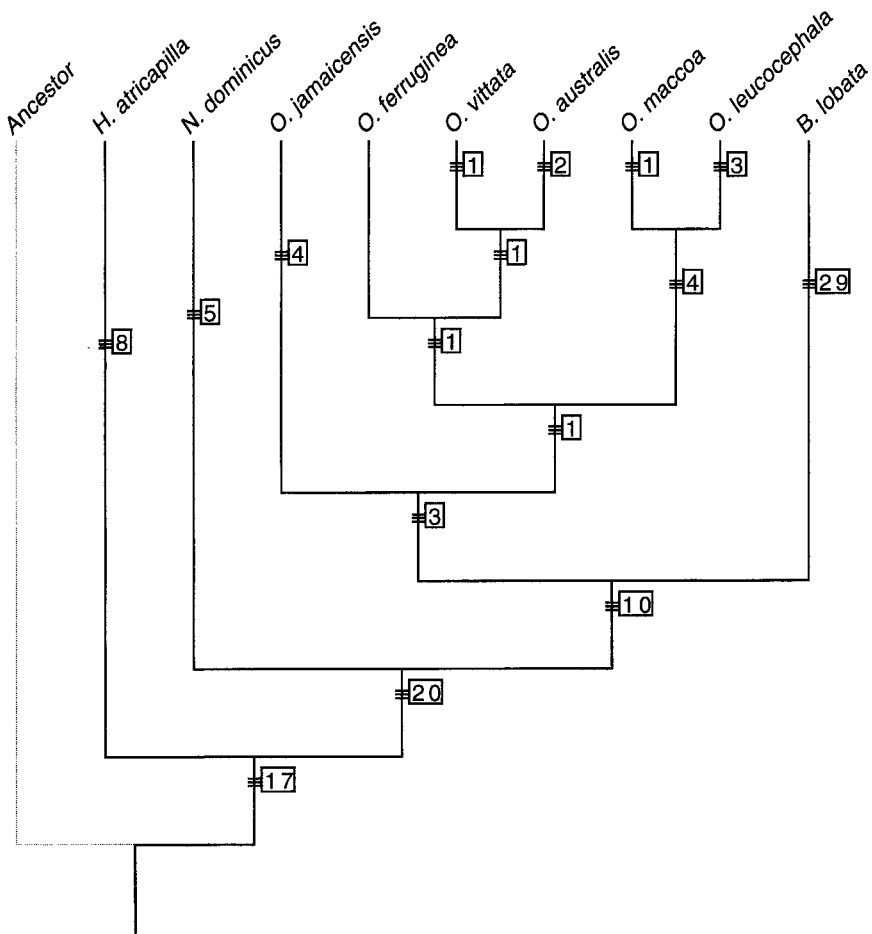
FIG. 1. Most-parsimonious phylogenetic tree for the Oxyurini based on 92 morphological characters. Numbers of unambiguous character changes supporting each branch are indicated.

ezey 1986). Within the genus *Oxyura* (excluding *Oxyura* "*andina*"), only *O. ferruginea* lacked a defining autapomorphy (Fig. 1); numbers of autapomorphies in the other five species ranged from four in *O. jamaicensis* to one each in *O. vittata* and *O. maccoa* (Fig. 1).

Robustness of tree.—Bootstrapping revealed that all branches in the shortest tree (Fig. 1), with the exception of that uniting *Oxyura* exclusive of *jamaicensis*, were conserved in a majority of replications with varying frequency (Fig. 2). The branches defining the entire tribe and uniting
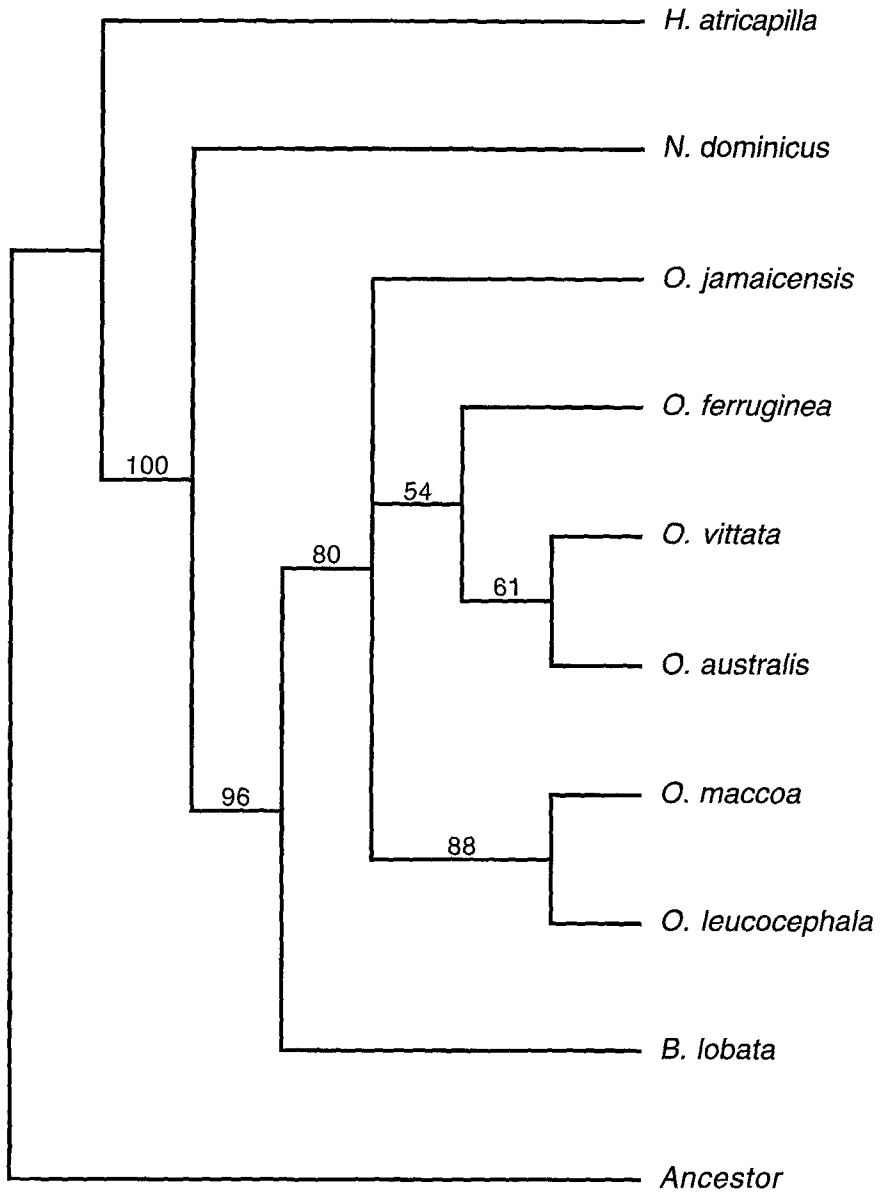
FIG. 2.　Fifty-percent majority-rule consensus tree of 1000 bootstrapped replications of the shortest phylogenetic tree of the Oxyurini (Fig. 1). Percentages of replications in which each branch was conserved are indicated.

the Oxyurini exclusive of *Heteronetta* were retained in 100% of the bootstrapped replicates (Fig. 2). The branch supporting the clade comprising *Oxyura* and *Biziura* was conserved in 96% of the bootstrapped replicates. Nodes within *Oxyura* were conserved in 54–88% of the replicates (Fig. 2).

Ecomorphological patterns.—Body mass showed only moderate phylogenetic conservatism in the Oxyurini (CI = 0.60), evidently having undergone one autapomorphic decrease in *Nomonyx* and independent increases in *O. ferruginea, O. australis,* and (especially) *Biziura* (Fig. 3). Clutch size was comparable to body mass in consistency (CI = 0.67); this parameter appears to have increased in *O. jamaicensis* and to have decreased in *Biziura* and is undetermined in the strictly nest-parasitic *Heteronetta* (Fig. 4). Egg mass (CI = 0.67) evidently increased homologously in *Oxyura* exclusive of *O. jamaicensis* and independently to a greater degree in *Biziura* (Fig. 5). Taken together, these patterns in egg mass and clutch size (relative to female body mass) indicate modest, independent increases in relative clutch mass in *Nomonyx* and in two lineages of *Oxyura* (*O. jamaicensis* and in *O. maccoa* + *O. leucocephala*), and a decrease in this parameter in *Biziura* (CI = 0.60).

Sexual size dimorphism showed a moderately complex evolutionary pattern in the Oxyurini, evidently having (Fig. 6; CI = 0.60) (1) shifted to female-larger dimorphism in *Heteronetta,* (2) increased paraphyletically in *Nomonyx, O. jamaicensis,* and (especially) *Biziura,* and (3) undergone a reversal in other *Oxyura* (especially *O. australis*). Sexual dichromatism of plumage, however, showed a very different pattern, with a reduction of sexual differences in *Heteronetta* and an independent reversal to monochromatism in *Biziura* (CI = 0.60).

DISCUSSION

Phylogenetic inferences and classification.—The trees presented by Johnsgard (1961a: figs. 8, 9) are the only species-level hypotheses of the phylogeny of the Oxyurini available for comparison. The relationships depicted by Johnsgard (1961a) differ from those proposed here in three major ways: (1) the positions of "*N.*" *dominicus* and *B. lobata* were reversed, (2) *Oxyura* was partitioned into two major groups—*leucocephala* + *jamaicensis* and *vittata* + *maccoa* + *australis,* and (3) *O. ferruginea* was merged with *O. jamaicensis.* Based on the data matrix complied here, the topology proposed by Johnsgard (1961a) is 13 steps (10%) longer (less parsimonious) than the shortest tree inferred here (Fig. 1). Six of these additional steps are attributable to the inclusion by Johnsgard (1961a) of *Nomonyx* as the sister-group of *Oxyura* (instead of *Biziura*), a topology implied also by all classifications in which *dominicus* is listed
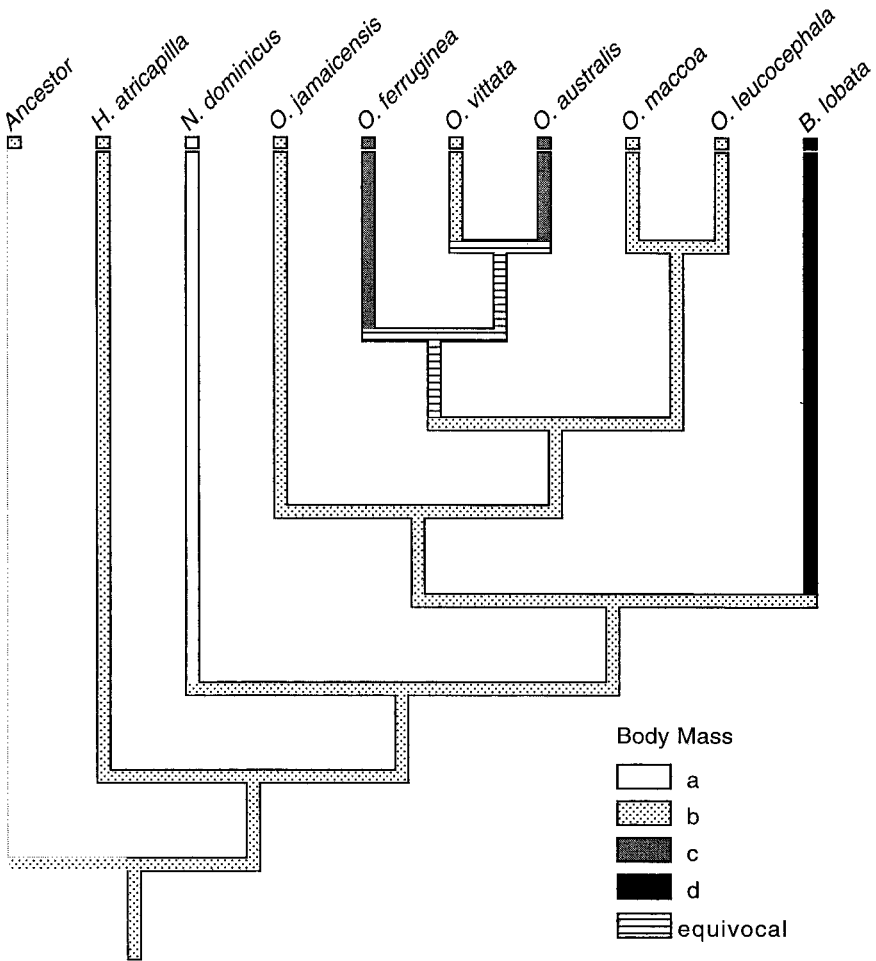
FIG. 3. Map of mean body mass (g) on phylogeny of the Oxyurini (primitive state for tribe in boldface): a—<500, **b—500–750**, c—751–1000, d—>1000. Character descriptions and data matrix available from author on request.

first within *Oxyura* (e.g., Delacour and Mayr 1945; Delacour 1959; Johns-gard 1978, 1979). If *Biziura* is to be generically distinguished from *Oxyura* (its sister group), the present analysis requires (at least) that *Nomonyx dominicus* also be generically separated. Another classificatory recommendation deriving from the present analysis is that *O. ferruginea* not be merged with *O. jamaicensis* but instead be grouped separately with two other southern-hemisphere species (see classification in Appendix I).
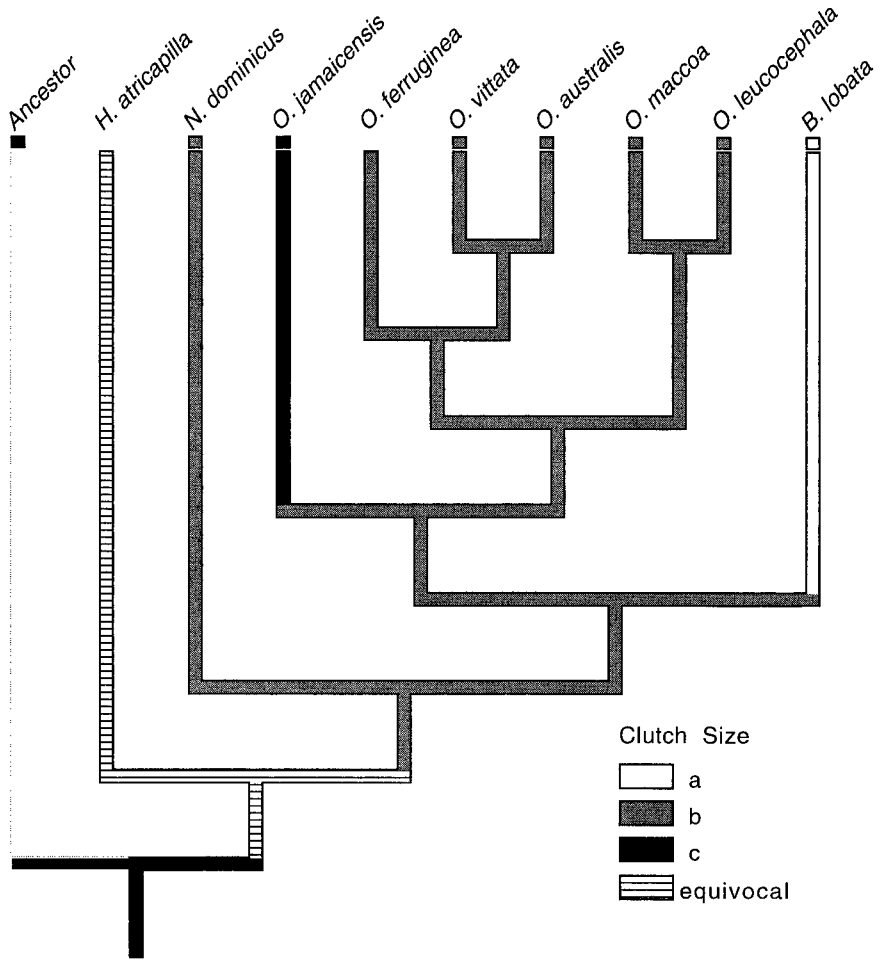
FIG. 4. Map of mean clutch size on phylogeny of the Oxyurini (primitive state for tribe in boldface): a—<3, b—3–6, c—>6. Character descriptions and data matrix available from author on request.

The taxonomic status of the variable *O. (j.) andina* remains unresolved, and its purported hybrid status deserves intensive study; it is merged provisionally with *O. jamaicensis*. Moreover, if *O. (j.) andina* were to be confirmed to be a hybrid swarm between *O. jamaicensis* and *O. ferruginea*, no reliable inferences concerning the phylogenetic relationship between the two "parent" forms could be made. Although propensity for interspecific hybridization traditionally has been considered to be pre-
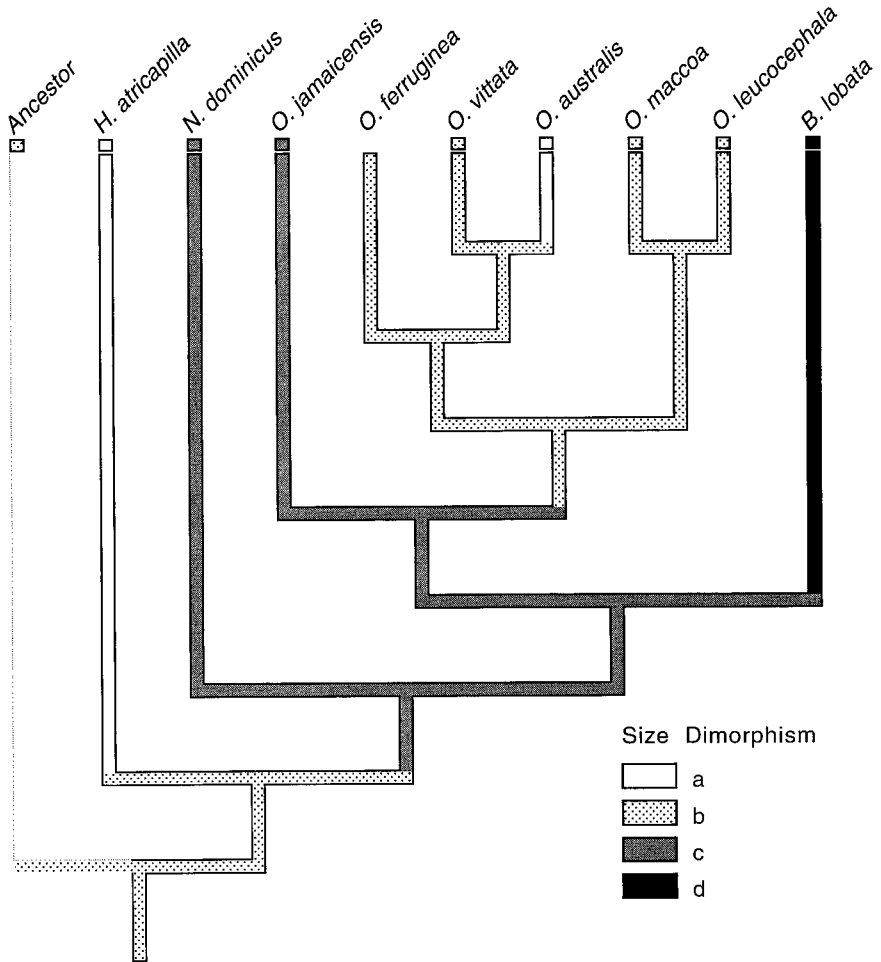
FIG. 5. Map of mean egg mass (g) on phylogeny of the Oxyurini (primitive state for tribe in boldface): **a—50–75**, b—76–100, c—>100. Character descriptions and data matrix available from author on request.

vented by adaptive "isolating mechanisms" and to indicate closeness of phylogenetic relationship (Sibley 1957; Johnsgard 1960b, 1963), inter-specific hybridization instead reflects the retention of primitive interfer-tility subsequent to speciation, and therefore this symplesiomorphy pro-vides no direct evidence of relatedness (Livezey 1991). Furthermore, the great diversity of recorded interspecific, intergeneric, and intertribal hy-brids among Anseriformes further undermines any evolutionary insights

FIG. 6. Map of sexual size dimorphism (ratio of means [g] for sexes) on phylogeny of the Oxyurini (primitive states for tribe in boldface): a—<1.00, **b—1–1.15**, c—1.16–1.30, d—>1.30. Character descriptions and data matrix available from author on request..

to be gained from patterns of hybridization (Johnsgard 1960b, Scherer and Hilsberg 1982).

Evolutionary trends.—Of the several quantitative parameters mapped onto the phylogenetic tree for the Oxyurini, probably the most distinct patterns emerged for egg mass (Fig. 5). The general increase in absolute egg mass evident in the tribe (Fig. 5), coincident with a general decrease in clutch size (Fig. 4), conforms with a weak, inverse relationship between

sizes of eggs and clutches in Anseriformes (Lack 1967, Rohwer 1988). Egg masses predicted by the equation of Rahn et al. (1975) relating egg mass to female body mass for the Anseriformes confirm that the egg masses of Oxyurini are large relative to the corresponding mean body masses of females (Lack 1967, Briggs 1988). The combination of small clutch size and large (absolute) egg size in the Oxyurini resembles that of many insular species of dabbling ducks (Anatini; Livezey 1990, 1993), but clearly the selection regimes of the latter differ significantly from those shared by the Oxyurini (Weller 1964a–c). Moreover, two comparatively massive species of Oxyurini—*Oxyura australis* and *Biziura lobata*—have relative egg masses typical of most Anatini, whereas egg size in most insular endemics is especially high relative to body mass (Livezey 1993). Unfortunately, the proportion of egg mass composed of yolk, a relationship with important implications for growth rates, is not known for the Oxyurini (Lack 1968).

In addition to the complex changes in body mass, general decreases in clutch size, and changes in egg mass evident in the Oxyurini (Fig. 5), evolutionary patterns in several other aspects of the life-history of the stiff-tailed ducks can be inferred in the context of the phylogenetic hypothesis proposed here (Fig. 1). Sexual dichromatism underwent reduction or loss in two very different lineages but manifests little correlation with sexual size dimorphism (Fig. 6). Comparatively inconspicuous sexual differences color of plumage and soft parts characterize *Heteronetta,* an obligate nest parasite showing modest female-larger size dimorphism (Weller 1967, 1968; Maynard Smith 1977), and the virtually monochromatic *Biziura,* a polygynous species showing extreme male-larger size dimorphism (Frith 1967, Livezey and Humphrey 1984). Infrequent nest parasitism evidently characterizes all other Oxyurini and is probably plesiomorphous in the Anatinae (Attiwill et al. 1981, Eadie et al. 1988, Rohwer and Freeman 1989). The Oxyurini exclusive of *Heteronetta* also share a moderate tendency toward (at least infrequent) crepuscular or nocturnal feeding, a habit perhaps most developed in *Nomonyx* (Weller 1968, McNeil et al. 1992).

The courtship displays of the Oxyurini include several distinctive behaviors, although the behaviors of several species remain inadequately known (Delacour 1959; Johnsgard 1960a, 1961a, 1962, 1965a, 1978). Males of at least *Nomonyx* and *Oxyura* perform unique displays involving the rapid thumping of the bill on the inflated throat sac(s); other displays that unite males of most Oxyurini include "tail cocking," "bill dipping," various surface rushes, and "sousing" (Johnsgard 1961a, 1962, 1965a, b, 1966, 1967, 1968, 1978; Fullagar and Carbonell 1986). Male Musk Ducks perform bizarre courtship displays, which typically involve a number of

acoustically and visually conspicuous components, including "paddling kicks," "whistle kicks," "plonk kicks," and exhibition of the fleshy gular lobe or palear (Johnsgard 1965a, 1966, 1967; Frith 1967; Fullagar and Carbonell 1986). Females of the Oxyurini, including *Heteronetta,* lack the "decrescendo" and "inciting" vocalizations that characterize female Anatini.

Biogeographic patterns.—Modern members of the Oxyurini are limited in distribution to the Neotropics, southern Nearctic, southern Africa, the Mediterranean, central Palearctic, and southern Australia (Weller 1964d). Fossils of the tribe are limited to a few weakly differentiated forms from these same regions that were assignable to modern genera (Brodkorb 1964, Howard 1964). Subfossil remains merely extend the former ranges of the two Australian members—*O. australis* and *B. lobata*—to New Zealand (Brodkorb 1964, Horn 1983).

The phylogenetic hypothesis proposed here strongly indicates a southern-hemispheric origin for the tribe, in that the two deepest branches (*Heteronetta* and *Nomonyx*) are Neotropical in distribution, and the next earliest branch (*Biziura*) is Australian (Fig. 1). Within *Oxyura,* the first branch corresponds to a northern-hemisphere species (*jamaicensis*), with the remaining members grouped into Palearctic-African (*maccoa* and *leucocephala*) and Neotropical-Australian clades (*ferruginea, vittata,* and *australis*). A strict vicariance model for the Oxyurini, in which a nested subdivision of regions corresponds with phylogenetic patterns, is not possible for extant species (Fig. 1). The complete absence of insular populations of Oxyurini suggests that members of the tribe, although most are migratory, are among the poorest dispersers in the Anseriformes (Weller 1964a). Field observations substantiate the poor flying abilities of most Oxyurini (Johnsgard 1978). Musk Ducks have especially high wing-loadings (Frith 1967), and large males not in wing molt may be at least temporarily flightless (Goodwin 1974, Marchant and Higgins 1990). The lack of insular isolates in the Oxyurini, however, may be related as much to the freshwater habitats of the member species (Weller 1964b, c), a preference that would deter trans-oceanic migration and insular colonization.

Evolutionary anomalies of the Musk Duck.—The Musk Duck, in addition to its unusual courtship displays, is unique among Oxyurini in its comparatively huge body size, highly autapomorphic skeletal anatomy, predominantly animal diet, frequency of maternal feeding of young, delayed sexual maturation (two years of age), lack of pair-bonds and associated "promiscuous" or polybrachygynous mating system, absence of sexual dichromatism of plumage, extreme sexual size dimorphism, dark natal plumage (Fig. 7), and small clutch size (Frith 1967; Johnsgard
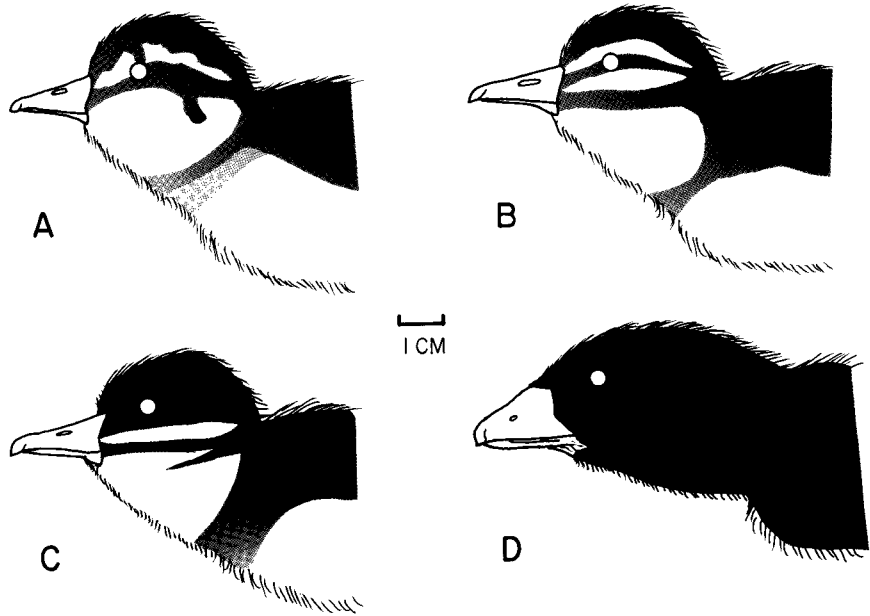
FIG. 7. Plumage patterns of natal Oxyurini, lateral views: A—*Heteronetta atricapilla* (USNM 337995); B—*Nomonyx dominicus* (AMNH 2240); C—*Oxyura jamaicensis* (USNM 259366); and D—*Biziura lobata* (AMNH 734131).

1965a, b, 1966, 1978; Kear 1970; Livezey 1986). The association of exaggerated sexual size dimorphism with low parental investment by males in *Biziura* conforms with broad patterns documented for birds (Selander 1972, Trivers 1972, Payne 1984; but see Höglund 1989), but this association is comparatively weak among waterfowl generally (Sigurjónsdóttir 1981). Similarly, the coincidence of the loss of sexual dichromatism with polygyny in *Biziura* opposes general avian patterns (Butcher and Rohwer 1989) but conforms with the comparatively poor correspondence between plumage dimorphism and paternal investment in Anseriformes (Sigurjónsdóttir 1981, Scott and Clutton-Brock 1989). The unique gular lobe or palear in male *Biziura,* and its use in courtship, performs some of the advertising functions of bright plumage (Frith 1967; Johnsgard 1965a, b, 1966). The possible role of the seasonally pungent uropygial secretions of male *Biziura,* if any, remains obscure (Frith 1967).

Magnitude of sexual size dimorphism is weakly associated with body size in some avian groups (Reiss 1986), but the sexual size differences of *Biziura* exceeds that attributable to the comparatively large body size of the species. The importance of body size to thermodynamics, metab-

olism, energy requirements, survivorship, and reproductive investment is profound, therefore, the evolutionary trade-offs implicit in the increased body size of male Musk Ducks (and other ecological peculiarities) deserve detailed study, especially within a phylogenetic context (Fig. 1) and with special attention to comparisons involving the partly sympatric *O. australis.*

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APPENDIX I

CLASSIFICATION OF OXYURINI

Tribe Oxyurini Delacour & Mayr, 1945.—Stiff-tailed ducks.
  Subtribe Heteronetteae Boetticher, 1952.
    Genus *Heteronetta* Salvadori, 1865.
      Heteronetta atricapilla (Merrem, 1841).—Black-headed Duck.
  Subtribe Oxyureae Boetticher, 1942.—True stiff-tailed ducks.
    Supergenus *Nomonyx* Ridgway, 1880.
    Genus *Nomonyx* Ridgway, 1880.
      Nomonyx dominicus (Linnaeus, 1766).—Masked Duck.
    Supergenus *Oxyura* Bonaparte, 1828.—Typical stiff-tailed ducks.
    Genus *Oxyura* Bonaparte, 1828.
      Subgenus *Oxyura* Bonaparte, 1828 (>*Erismatura* Bonaparte, 1832).
        Oxyura jamaicensis (Gmelin, 1789).—Northern Ruddy Duck.
      Subgenus *Cerconectes* Wagler, 1832.
        Species-group "A."
          Oxyura ferruginea (Eyton, 1838).—Peruvian Ruddy Duck.
          Oxyura vittata (Philippi, 1860).—Argentine Ruddy Duck.
          Oxyura australis (Gould, 1836).—Blue-billed Duck.
        Species-group "B."
          Oxyura maccoa (Eyton, 1836).—Maccoa Duck.
          Oxyura leucocephala (Scopoli, 1796).—White-headed Duck.
    Genus *Biziura* Stephens, 1824.
      Biziura lobata (Shaw, 1796).—Musk Duck.