A PHYLOGENETIC ANALYSIS OF GEESE AND SWANS (ANSERIFORMES: ANSERINAE), INCLUDING SELECTED FOSSIL SPECIES

BRADLEY C. LIVEZEY

Abstract.—A phylogenetic analysis of modern and selected fossil geese and swans was performed using 165 characters of the skeleton, trachea, and natal and definitive integument. Five shortest trees were found (length = 318; consistency index for informative characters = 0.634), which differed only in details of relationships among three species of Branta. The trees supported (1) Cnemiornis as sister group to other taxa analyzed; (2) a sister group relationship between the moa-nalos of Hawaii and other geese and swans; (3) Cereopsis as sister group of Anser, Branta, Coscoroba, and Cygnus (contra Livezey, 1986, Auk 103:737–754); (4) monophyly of Anser, Branta, and Geochen and confirmation of generic monophyly of each; and (5) Coscoroba as sister group to Cygnus. Selective exclusion of fossil taxa from the analysis variably affected inferred relationships and had substantial impacts on computational efficiency. Some nodes were not robust to bootstrapping: (1) nodes relating species groups within Anser, Cygnus, and Thambetochen and (2) the node uniting Anser, Branta, Coscoroba, and Cygnus relative to Cereopsis. Bremer (decay) indices indicated similar differences in relative support for nodes. Skeletal characters were comparatively important in establishing higher order relationships, whereas integumentary characters were critical for lower order inferences. Constrained analyses revealed that other proposed phylogenetic hypotheses entailed variable penalties in parsimony. The shortest tree(s) was considered with respect to selected ecomorphological attributes (e.g., body mass, sexual size dimorphism, clutch size) and biogeography, and a revised phylogenetic classification of the geese and swans is proposed. [Anseriformes; Anserinae; cladistics; comparative analysis; fossils; geese; morphology; swans; waterfowl.]

The geese and swans (Anatidae: Anserinae; sensu Livezey, 1986) are among the most conspicuous and familiar of waterfowl, in part because of a long and economically important history of domestication (Delacour, 1954, 1964b; Schudnagis, 1975) and widespread exploitation for sport and subsistence hunting (Weller, 1964e; Dawnay, 1972). The group is largely limited to the Northern Hemisphere (Weller, 1964b, 1964d) and has, at least by avian standards, a substantial fossil record (Lambrecht, 1933; Brodkorb, 1964; Howard, 1964; Olson and James, 1991). Geese feed primarily by terrestrial grazing, and swans feed by submergence of the head and neck to reach aquatic plants; species in neither group routinely dive for food (Delacour, 1954; Weller, 1964a, 1964c; Johnsgard, 1978). The subfamily includes the most massive members of the Anseriformes (Scott, 1972), and most flighted species breed at high latitudes, are migratory (Ogilvie, 1972), and have elongate skeletal wing elements and moderate wing loadings relative to body mass (Poole, 1938; Meunier, 1959; Hoerschelmann, 1971). Members of the group retain the primitive anseriform characters of sexual monochromatism and the absence of metallic plumage coloration (Delacour, 1954; Boyd, 1972; Johnsgard, 1978).

Early classifications recognized the relationship between the geese and swans and other waterfowl, although there was considerable disagreement concerning taxonomic ranks and details of composition (Willughby and Ray, 1676; Linnaeus, 1758; Brisson, 1760; Eyton, 1838; Gray, 1871; Sclater, 1880; Salvadori, 1895; Peters, 1931). With few exceptions (e.g., Verheyen, 1953), modern classifications differ principally in the taxonomic ranks given to the geese and swans or the inclusion of the Cape Barren Goose (Cereopsis novaehollandiae) among the “true” geese (Boetticher, 1942, 1952; Delacour and Mayr, 1945; Delacour, 1954,
Classificatory schemes for the geese and swans based on explicit attempts to reconstruct phylogeny generally have confirmed this early consensus, whether based primarily on behavioral (Johnsgard, 1961a, 1974; Kear and Murton, 1973), morphological (Tyler, 1964; Livezey, 1986, 1989), or molecular (Jacob and Glaser, 1975; Brush, 1976; Morgan et al., 1977; Jacob, 1982; Bottjer, 1983; Numachi et al., 1983; Patton and Avise, 1985; Scherer and Sonntag, 1986; Shields and Wilson, 1987a; Jacob and Hoerschelmann, 1993) comparisons. However, most of these studies, as well as the well-publicized studies based on DNA hybridization (Sibley et al., 1988; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990), are phenetic and include comparatively few anseriform taxa; the DNA hybridization work has been the subject of diverse criticism (Cracraft, 1987, 1992; Sarich et al., 1989; Lanyon, 1992; Mindell, 1992). Despite broad areas of agreement among phylogenetic studies of waterfowl based on diverse methods (Bledsoe and Raikow, 1990; Omland, 1994), debate persists regarding the membership of Cereopsis and the position of Coscoroba within the Anserinae (e.g., Johnsgard, 1961a, 1965; Kear and Murton, 1973; Livezey, 1986; Zimmer et al., 1994), and only very limited study has been undertaken to establish interspecific relationships among geese.

In this paper, I present a phylogenetic analysis of geese and swans, one of a series of species-level analyses of groups of waterfowl based on diverse methods (Bledsoe and Raikow, 1990; Omland, 1994), debate persists regarding the membership of Cereopsis and the position of Coscoroba within the Anserinae (e.g., Johnsgard, 1961a, 1965; Kear and Murton, 1973; Livezey, 1986; Zimmer et al., 1994), and only very limited study has been undertaken to establish interspecific relationships among geese. In this paper, I present a phylogenetic analysis of geese and swans, one of a series of species-level analyses of groups of waterfowl (Livezey, 1991, 1995a, 1995b, 1995c, 1996a, 1996b, 1997) prompted by an earlier phylogenetic analysis of genera of Anseriformes (Livezey, 1986). The role of fossils in phylogenetic inference has received increasing attention in recent years (Patterson, 1981; Novacek and Norell, 1982; Gauthier et al., 1988; Donoghue et al., 1989; Huelsenbeck, 1991b; Smith, 1994; Springer, 1995); accordingly, several adequately represented fossil taxa were included in the analyses. This paper includes a phylogenetic analysis of 31 taxa using 165 morphological characters, an assessment of support and the analytical impacts of fossil species, maps of selected ecomorphological attributes on the resultant trees, and a classification of modern and included fossil species of geese and swans.

**METHODS**

**Delimitation of Taxa**

Conceptual frameworks and criteria used in the delimitation of species are a perennial source of debate (Cracraft, 1988b; McKitrick and Zink, 1988; Frost and Hillis, 1990; Frost and Kluge, 1994). In this analysis, all taxa diagnosably distinct using the qualitative characters included in the analysis were treated as species, thus delimiting species in rough accordance with the "phylogenetic" species concept. Of the modern geese and swans (Cereopsis, Branta, Anser, Coscoroba, and Cygnus sensu lato), 12 species are considered monotypic under currently accepted classifications (e.g., Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1978, 1979): Cereopsis novaehollandiae, Anser cygnoides, A. rossii, A. indicus, A. canagicus, Branta sandvicensis, B. leucopsis, B. ruficollis, Coscoroba coscoroba, Cygnus melanocoryphus, C. atratus, and C. olor.

The Bean Goose (Anser fabalis) comprises five variable continental subspecies (Alpheraky, 1905; Delacour, 1951, 1954; Burgers et al., 1991) grading from orange-billed, taiga-breeding forms (fabalis, johannseni, middendorffii) to largely black-billed, tundra-breeding forms (serrirostris, rossicus); the continental forms were treated as a single taxon for analysis. The Pink-footed Goose (A. brachyrhynchus) of Greenland and Iceland, although considered conspecific with the Bean Goose by some taxonomists (Delacour, 1951, 1954; Delacour and Mayr, 1945; Delacour, 1951, 1954; Burgers et al., 1991) grading from orange-billed, taiga-breeding forms (fabalis, johannseni, middendorffi) to largely black-billed, tundra-breeding forms (serrirostris, rossicus); the continental forms were treated as a single taxon for analysis. The Pink-footed Goose (A. brachyrhynchus) of Greenland and Iceland, although considered conspecific with the Bean Goose by some taxonomists (Delacour, 1954; Johnsgard, 1978), is diagnosably distinct and was analyzed separately here (Owen, 1980; Madge and Burn, 1988). The two recognized forms of Greylag Goose (A. [a.] anser, A. [a.] rubirostris) differ in at least one of the characters analyzed and were treated separately. The Greater White-fronted Goose (A. albirostris) and Lesser White-fronted Goose (A. erythropus) were ana-
lyzed separately. The four subspecies of *A. albifrons*, comprising weakly differentiated continental (*albifrons*, *frontalis*, *gambeli*) and Greenland (*flavirostris*) forms, were combined into a single taxon coded as polymorphic for bill color because of substantial variation in this character (Fox and Stroud, 1981; Kaufman, 1994). The two color morphs of the Snow Goose (*A. caerulescens*) were treated as a single polymorphic species showing dynamic, geographically variable frequencies of the two morphs and substantial intergradation (Cooch, 1961, 1963; Cooke et al., 1975, 1988; Rockwell and Cooke, 1977; Quinn, 1992).

Species limits within the *Branta bernicla* complex remain problematic (Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1965, 1978, 1979); in this analysis the Atlantic pale-bellied form (*hrota*) and the three Pacific black-bellied forms (*bernida*, *orientalis*, *nigricans*) were treated as two separate species. Most current classifications list 12 subspecies of the Canada Goose (*B. canadensis*), each variably distinct and having largely allopatric breeding ranges, among which there are indications of localized reproductive isolation (Sutton, 1932), genetic differentiation (Baker and Hanson, 1966; Van Wagner and Baker, 1986, 1990; Shields and Wilson, 1987b), and graded differences in voice, body mass (1.5–5.2 kg), darkness of plumage, shape of bill, and presence of a narrow white collar (Brooks, 1926; Aldrich, 1946; Hanson and Smith, 1950; Todd, 1951; De- lacour, 1954; Hatch and Hatch, 1983). Widespread intergradation and an absence of critically identified skeletons, tracheae, and downy young of many populations made separate coding of these taxa impractical; therefore *B. canadensis* was treated as a single taxon showing limited polymorphism.

The northern swans, *Olor* sensu Livezey (1986), have been subjected to diverse classifications (Delacour and Mayr, 1945; Delacour, 1954; Johnsgard, 1965, 1974, 1979; Mayr and Short, 1970; American Ornithologists’ Union, 1983). However, the diagnosibility of the Whooper Swan (*Cygnus cygnus*) as compared with the Trumpeter Swan (*C. buccinator*) and qualitative differences between the Whistling (*C. columbianus*) and Bewick’s (*C. bewickii, including jankowskii*) swans necessitated treating the four taxa separately.

Included genera known only from fossil or subfossil remains (henceforth preceded by daggers) were †Cnemiornis, a large flightless “goose” of New Zealand comprising two allospecies (larger southern †*C. calcitrans*, smaller northern †*C. gracilis*) and analyzed as a single taxon (Howard, 1964; Livezey, 1989); subfossil *Branta hylobadistes* of Maui, Hawaiian Islands (Olson and James, 1982, 1991); †Geochen rhuais, a large goose from the island of Hawaii (Wetmore, 1943), largely characterized using newly collected, tentatively referred material of the “very large Hawaii goose” (Olson and James, 1991:48); and four species of flightless “moa-nalos” (†Thambetochen chauliodous, †*T. xanion*, †*Paiochen pae*, †*Chelychelynechen quassus*) from the Hawaiian islands of Kauai, Oahu, Molokai, and Maui, respectively (Olson and Wetmore, 1976; Olson and James, 1982, 1991). The possible, unique loss of the furcula in the Molokai population of †Thambetochen chauliodous is indicated as a polymorphism for this species.

Specimens Examined

Plumage patterns of adults of modern species were compared using series of study skins, most importantly those in the National Museum of Natural History (NMNH) and American Museum of Natural History (AMNH). Colors of the irides, bill, tarsi, and feet of adults were confirmed using published descriptions (Delacour, 1954; Johnsgard, 1974, 1978; Todd, 1979; Kear and Berger, 1980; Brazil, 1981; Scott, 1981; Madge and Burn, 1988; Marchant and Higgins, 1990; del Hoyo et al., 1992) and photographs. Natal patterns were characterized using study skins and published descriptions (Delacour and Mayr, 1945; Delacour, 1954; Nelson, 1976, 1993). Skeletal specimens of adults of modern species, generally five or more specimens of each species, were included in osteological comparisons. Tracheal char-
acters of modern species were confirmed using ossified elements in skeletal specimens and intact tracheae removed from fluid-preserved specimens (some previously mounted and dried). Fossil taxa were represented by most major skeletal elements, and for *Thambetochen*, *Ptaiochen*, and *Geochen* at least one bulla syringealis or tympanum was examined. Osteological and tracheal characters were confirmed using the anatomical literature (Shufeldt, 1888, 1913; Miller, 1937; Wetmore, 1951; Humphrey, 1958; Johnsgard, 1961b, 1962; Woolfenden, 1961; Humphrey and Clark, 1964; Möller, 1969a, 1969b; McLelland, 1989). Descriptive nomenclature follows King (1989, 1993), Baumel and Witmer (1993), and Clark (1993).

**Definition of Characters**

A total of 165 morphological characters that defined or varied among the Anserinae and other included taxa were included in the analysis: 76 skeletal characters (most after Livezey, 1986), 8 tracheal characters, 10 characters of the natal plumage, and 71 characters of the definitive plumage and soft parts (Appendix 1). Each character comprised a primitive (plesiomorphic) state and one or more derived (apomorphic) states. Where available specimens did not permit the determination of states, missing-datum codes (?) were entered into the matrix; these accounted for all characters of the integument (567 entries), 129 osteological character states, and 36 tracheal character states for fossil species. Missing-datum codes also were entered 46 times for noncomparable states, i.e., where the determination of states was impossible because of the absence or profound modification of the structure in question (e.g., general diminution of a wing element in a flightless species or the obfuscation of certain characters of plumage pattern in the "all-white" swans).

States for several characters differed within one or more of the subfamilial and generic taxa; where resolution of phylogenetic relationships (Livezey, 1991, 1995a, 1995b, 1995c, 1996a, 1996b, 1997) or the distribution of character states precluded the confident coding of basal states for these groups, these were coded either as polymorphic (where states included a subset of the states present within the Anserinae; 17 instances) or missing (where states not present within the Anserinae were represented or where states encompassed all those present within the Anserinae; 12 instances). In addition, five entries for geese or swans were coded as polymorphic. Characters resolving the relationship between *Dendrocygna* and *Thalassornis* were taken from Livezey (1995a); for purposes of this analysis, only one (character 94) of two natal characters (Livezey, 1995a: characters 19 and 23) amenable to mutually exclusive synapomorphic interpretations in these two genera was included, and character changes unique to either of these two genera were not included (see Livezey, 1995a). Characters that establish monophyly of the Tadorninae or Anatinae are considered elsewhere (Livezey, 1996b). The resultant 39 × 165 data matrix (including a hypothetical ancestor, discussed below) is presented in Appendix 2.

Of the 35 characters having more than one derived state, 13 represented naturally ordinal series (e.g., numbers of cervical vertebrae or rectrices) or gradations in degree (e.g., relative sizes of contrasting loral patches) and were analyzed as ordered; the analytical impact of ordering was assessed through analyses in which all characters were treated as unordered. Characters in which a derived state(s) was possessed by a single species (autapomorphy) were included in the analysis to confirm monophyly of terminal taxa of geese and swans and to permit estimates of total evolutionary divergence.

**Phylogenetic Analysis and Classification**

**Topological searches.**—Trees were derived under the principle of global parsimony (Wiley, 1981) using PAUP 3.1 (Swofford, 1993) and MacClade 3.01 (Maddison and Maddison, 1992) on a Macintosh Quadra 800. Topological searches were undertaken using heuristic techniques retaining 10 trees at each step of the search; this algorithm was implemented using options for
both simple and random order of entry of taxa and retention of multiple equally parsimonious trees throughout the search. Also, three branch-swapping methods (nearest-neighbor interchanges, tree-bisection–reconnection, subtree-pruning–regrafting) were used to avoid local optima or "islands" of suboptimal topologies (Maddison, 1991; Page, 1993). Summary statistics used to describe the inferred trees were total tree length; consistency index, both including (CI) and excluding (CI*) uninformative characters; homoplasy index, both including (HI) and excluding (HI*) uninformative characters; retention index (RI); and rescaled consistency index (RC).

Where multiple equally parsimonious trees were discovered using the same set of analytical options, strict consensus trees (showing only those nodes shared by all equally parsimonious trees) and majority-rule consensus trees were employed to summarize the supported regions in the trees. Consensus trees are seldom interpretable in the same ways as the actual trees from which they are compiled (Miyamoto, 1985; Swofford, 1991; Wiley et al., 1991); therefore, consensus methods were used simply to summarize areas of congruence among equally parsimonious trees.

Hypothetical ancestor.—Trees were rooted using a set primitive states inferred through reference to the sister genera of the analyzed taxa (Livezey, 1986), i.e., the Magpie Goose (Anseranatidae: Anseranas semipalmata) and the screamers (Anhimidae: Anhima and Chauna). As in previous phylogenetic analyses of the order (Livezey, 1986, 1989, 1995a, 1995b, 1995c; Livezey and Martin, 1988), this method facilitated rootings of trees without digressions into relationships among outgroups. Basal polarities of one natal character and one character of the definitive integument were not determinable; a missing-datum code was entered for these two states in the hypothetical ancestor.

Assessments of support.—One measure of the phylogenetic signal is the skewness statistic (g1) for the distribution of tree lengths (Hillis, 1991; Huelsenbeck, 1991a; Hillis and Huelsenbeck, 1992; Källersjö et al., 1992); skewness statistics were estimated using a random sample of 10^6 trees (excluding the hypothetical ancestor). Stability of nodes in minimal-length trees was assessed using bootstrapping with 100 replicates; this method remains controversial (Hillis and Bull, 1993). The characters analyzed violate the assumption of statistical independence required for formal statistical inferences (Felsenstein, 1985; Sanderson, 1989) and resultant percentages may be biased (Li and Zharkikh, 1995); therefore, the procedure was employed simply as an index to empirical support. The support (decay) index of Bremer (1988), the minimal increase in tree length at which topologies not supporting a given node are discovered, was estimated using inverse topological constraints, random taxon addition (10 replicates), and several search algorithms to avoid local optima (Swofford, 1993).

Quantitative comparisons with other hypotheses.—Searches constrained to preserve specific phylogenetic relationships were used to quantify the sacrifices in parsimony required by previously proposed topologies or classifications using the present data set. Comparisons with the phylogenetic hypothesis proposed by Sibley and Ahlquist (1990) and Sibley and Monroe (1990) necessitated the partitioning of the Anatinae into the stiff-tailed ducks (Oxyurini) and the Anatinae exclusive of the Oxyurini (designated as Anatinae*); using the characters defined here, the Oxyurini differed from other Anatinae in the absence of a bulla syringealis (character 81) and the restriction of two characters polymorphic in other Anatinae to single states (characters 86 and 110).

Phylogenetic classification.—The resultant phylogenetic tree(s) formed the basis for a classification using the methods described by Wiley (1981). Unconventional taxonomic ranks, e.g., subtribes, superfamilies, and subgenera, were based on senior taxa of appropriate rank, in part based on the classifications of Boetticher (1942, 1952)
and the synonymies of Brodkorb (1964) and Wolters (1976).

Ecomorphological Attributes and Biogeography

Nine general ecological and functional attributes of evolutionary interest were coded for comparative analysis (Brooks and McLennan, 1991; Harvey and Pagel, 1991). A number of attributes showing variation in other waterfowl were essentially invariant in the Anserinae: perching habit (not developed), diving habit (absent), activity period (variably diurnal), migratory habit (characteristic except in insular endemics), and participation by male in nest construction (absent, except in Cereopsis) and incubation (absent). Several other attributes were too poorly documented for many species of Anserinae for analysis: frequency of intraspecific and interspecific nest parasitism (Rohwer and Freeman, 1989), formation of créches (Eadie et al., 1988), or parental carrying of young (Johnsgard and Kear, 1968). Codings were based on the literature (Johnsgard, 1960a, 1962, 1965, 1978; Schonwetter, 1961; Frith, 1967; Wilmore, 1974; Bellrose, 1976; Cramp and Simmons, 1977; Kear and Berger, 1980; Brown et al., 1982; Rohwer, 1988; Marchant and Higgins, 1990; del Hoyo et al., 1992; McNeil et al., 1992; Dunning, 1993). Mean body masses of species were estimated by averaging the mean masses of the two sexes. Sexual size dimorphism was expressed as the ratio of the mean body mass of males divided by that 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 the adult female. Maps of attributes were made using MacClade 3.01 (Maddison and Maddison, 1992).

Area cladograms were constructed by coding distributional information for terminal taxa and ancestral nodes by hierarchical summation using the inferred phylogenetic tree (Wiley et al., 1991); area cladograms were derived using the branch-and-bound algorithm. Although primarily used to reveal geographical congruences across distantly related taxonomic groups (Cracraft, 1988a; Kluge, 1988; Wiley, 1988), the approach was employed here to summarize patterns across genera in the Anserinae. The presence of a fossil swan (†Cygnus sumnerensis) in New Zealand, inferred to be a member of the grade of swans between Coscoroba and the monophyletic “Olor” group (Livezey, 1989), was incorporated in the codings for areas.

RESULTS

Higher Order Relationships

For the 38-taxon matrix that included fossil species, five shortest trees were found, each having length = 318, CI = 0.733 (CI* = 0.634), HI = 0.336 (HI* = 0.396), RI = 0.866, and RC = 0.634. The CI* for the trees exceeds the expected values for phylogenetic analyses of comparable scale (Sanderson and Donoghue, 1989; Klassen et al., 1991). The skewness statistic (g1) for 106 randomly generated trees for this matrix (including ordered characters) was −0.674 (P < 0.01; Hillis, 1991). The five trees differed only in the topology inferred for Branta canadensis, B. sandvicensis, and B. hylobadistes, resulting in a polytomy in Branta in a strict consensus tree (Fig. 1).

Numbers of unambiguous synapomorphies supporting each node (Fig. 2) varied from 10 for the entire group exclusive of the hypothetical ancestor, for the swans (Coscoroba and Cygnus), and for the genus Cygnus, to 1 for a number of clades supported by single unambiguous character changes (two subgroups of Anser, one subgroup of Branta, two subgroups of Cygnus, two subgroups within the moa-nalos). The trees supported (1) a basal position of †Cnemiornis, (2) the monophyly of the Dendrocygninae (Dendrocygna and Thalassornis), contra Livezey (1986) but in agreement with Livezey (1995a), (3) the sister group relationship between Stictonetta and the clade comprising the Tadorninae and Anatinae (Livezey, 1996b), (4) a sister group relationship between the moa-nalos and the true geese and swans, (5) the monophyly of the moa-nalos, within which †Chelychelynechen is the sister group of †Ptaiochen and †Thambetochen, (6) a sister group relationship between Cereopsis...
and other geese (Anser and Branta) and the swans, contra Livezey (1986), (7) a sister group relationship between the monophyletic genera Anser and Branta, with the fossil +Geochen placed as the sister group of Branta on the basis of a single synapomorphy, and (8) a sister group relationship between Coscoroba and other swans.

**Subgeneric Relationships**

In the typical swans (Cygnus), C. melanocoryphus + C. atratus is inferred to be the sister group of other swans (Figs. 1, 2); within the other swans, C. olor is the sister group of the four species segregated as Olor by Livezey (1986). Within Anser, there is a primary dichotomy between a basal four-species clade, which includes A. indicus, and a clade containing the other seven species (Figs. 1, 2). Within Branta, B. bernicla and B. hrota compose the sister group of B. ruficollis and B. leucopsis (Figs. 1, 2). Among the anserine taxa, aberrant Cereopsis novaehollandiae showed the greatest number of autapomorphies, with several others (Branta ruficollis, Coscoroba coscoroba,

**Fig. 1.** Strict consensus tree of five shortest trees for modern and fossil Anserinae and related taxa. A. = Anser; B. = Branta; Ce. = Cereopsis; Ch. = +Chelychelynechen; Co. = Coscoroba; Cy. = Cygnus; G. = +Geochen; P. = +Ptaiochen; T. = +Thambetochen.
FIGURE 2. Detailed depiction of one of five shortest trees for modern and fossil Anserinae and related taxa. Boxes enclose number of unambiguous synapomorphies supporting associated nodes. A. = Anser; B. = Branta; Ce. = Cereopsis; Ch. = †Chelychelynechen; Co. = Coscoroba; Cy. = Cygnus; G. = †Geochen; P. = †Ptaiochen; T. = †Thambetochen.
Anser canagicus, †Chelychelynechen) showing significant numbers as well (Figs. 2, 3). The following modern taxa lacked an unambiguous apomorphic and therefore the monophyly of each was not explicitly confirmed: three swans (Cygnus columbianus, C. bewickii, C. cygnus), Anser rubrirostris, A. albifrons, and A. caerulescens (Fig. 2).

Reanalysis of this matrix treating all characters as unordered resulted in 1,890 trees of length 315 (CI* = 0.635, RI = 0.860, RC = 0.636); g1 for 106 random trees was −0.611 (P < 0.01). A majority-rule consensus tree differed from that for trees including ordered characters in several ways: (1) Cereopsis, the typical goose (Anser, †Geochen, Branta), and the swans (Coscoroba, Cygnus) form a trichotomy; (2) the swans Cygnus melanocoryphus and C. atratus form a trichotomy with other members of the genus; (3) †Geochen is included in a trichotomy with Anser and Branta; and (4) Anser comprised a grade in which subgroups (in order of increasingly close relationship) were A. cygnoides, A. fabalis + A. brachyrhynchos, A. anser + A. rubrirostris, A. albifrons + A. erythropus, A. indicus, A. canagicus, and A. caerulescens + A. rossii.

Exclusion of Fossil Taxa

The impact of fossil taxa on phylogenetic inferences was assessed by selective exclusion of taxa and reanalysis of the remaining taxa. Deletion of †Geochen rhuax and †Branta hylobadistes, fossil taxa placed in comparatively terminal positions and including the single species responsible for multiple shortest trees (†B. hylobadistes) in the all-taxon analysis, resulted in a single most-parsimonious tree: length = 314, CI = 0.732 (CI* = 0.636), HI = 0.338 (HI* = 0.394), RI = 0.866, RC = 0.635, g1 (106 random trees) = −0.671 (P < 0.01). The topology among remaining taxa in this tree was identical to that of the consensus tree for the all-taxon analysis, with an additional resolution within †Branta (Fig. 3) permitted through the exclusion of †B. hylobadistes and additional topologies stemming from missing data.

Deletion of †Cnemiornis from the analysis, inferred to be the sister group of all other taxa analyzed here (Figs. 1, 2), resulted in two trees that were topologically identical for the remaining taxa with the exception that one placed Dendrocygna and Thalassornis as paraplythic with respect to the other taxa (cf. Livezey, 1986). This outcome occurred whether †Cnemiornis was excluded alone or in combination with other fossil taxa.

Deletion of all four species of moa-nalos (†Thambetochen spp., †Ptaiochen, †Chelychelynechen), alone or in combination with the deletion of †Cnemiornis, placed the Dendrocygninae (Dendrocygna and Thalassornis as sister genera) as the sister group of Stictonetta, Tadorninae, and Anatinae (the last two being sister groups); this departure from the other trees (Figs. 1–3) was one of three topological alternatives described by Livezey (1989). Deletion of only the most well-known member of the moa-nalos (†Thambetochen chauliodous) had the same effect on the shortest trees, except that the remaining moa-nalos were placed as more closely related to the Anatinae and Tadorninae than to Stictonetta. Conversely, deletion of the moa-nalos exclusive of †T. chauliodous resulted in a single tree that was otherwise topologically identical to those found in the all-taxon analysis (Figs. 1, 2).

Assessments of Support

Fossil taxa, regardless of their topological effects on inferred phylogenetic trees, pose substantial computational problems because of the significant numbers of missing data that necessarily characterize fossils in analyses including nonosteological characters. For example, otherwise identical heuristic searches of all taxa required approximately six times the computing time of those in which only †Geochen rhuax and †Branta hylobadistes were deleted. For example, an attempt to bootstrap the all-taxon matrix was terminated at replicate 10 after more than 24 hr, whereas exclusion of these two species permitted the compila-tion of 100 bootstrapped replicates in 40 hr; an analysis in which two modern taxa were excluded at random (but the fossils were retained) required more than 28 hr to reach replicate 10. Fortunately, the minimal
FIGURE 3. Shortest phylogenetic tree for modern Anserinae and related taxa, but excluding †Geochen rhuax and †Branta hylobadistes. Boxes enclose number of unambiguous synapomorphies supporting associated nodes. A. = Anser; B. = Branta; Ce. = Cereopsis; Ch. = †Chelychelynechen; Co. = Coscoroba; Cy. = Cygnus; P. = †Platochen; T. = †Thambetochen.
A majority-rule consensus tree for 100 bootstrapped replicates of the matrix excluding Geochen rhuax and Branta hylobadistes (Fig. 4) indicated that most nodes in the shortest tree (Fig. 3) were well supported. Nodes not conserved in a majority of the 100 replicates were (contrasting Figs. 3, 4) the three nodes uniting species groups within the seven-taxon subclade of Anser, the node uniting Anser indicus with its congeners in its four-taxon subclade, the node defining Cereopsis as the sister group of the swans (Coscoroba and Cygnus) and the typical geese (Anser and Branta), the nodes defining the nested relationships among the geese and swans, moa-nalos, and nonanserine clades exclusive of Cnemiornis, and the node uniting the two species of Thambetochen within the moa-nalos. Within the genus Anser, the branches
not robust to bootstrapping closely resembled those not conserved in a majority of trees based on unordered data.

Of the nodes not robust to bootstrapping, seven had Bremer indices of 1 and the other had an index of 2 (Fig. 5). However, six nodes robust to bootstrapping also had Bremer indices of 1. Greatest support for internal nodes, as indicated by Bremer indices (Fig. 5), was found for the nodes uniting Coscoroba with Cygnus, species within Cygnus, Anser, and Branta, the genera of moa-nalos, the sister species Anser caerulescens and A. rossii, and the "Olor" subgroup of swans.

Patterns of Character Evolution

The four groups of characters used in this analysis (skeletal, tracheal, natal integumentary, definitive integumentary) had virtually identical mean consistency indices. Based on the all-taxon trees, consistency indices ($\bar{x} \pm SD, n$) were computed for each character group: skeletal (0.83 ± 0.24, 76), tracheal (0.84 ± 0.23, 8), natal integumentary (0.85 ± 0.24, 10), and definitive
integumentary (0.86 ± 0.23, 71). The distribution of changes in these character groups throughout the all-taxon trees (not including changes defining subfossil groups, which were necessarily restricted to skeletal characters) differed substantially, however, indicating different mean rates of evolution in the groups. Nodes defining families and subfamilies were supported by 38 (72%) skeletal, 2 (4%) tracheal, 5 (9%) natal integumentary, and 8 (15%) definitive integumentary character changes. Nodes delimiting tribes within the Anserinae incorporated 23 (52%) skeletal, 3 (7%) tracheal, 2 (5%) natal integumentary, and 16 (36%) definitive integumentary character changes. Character changes supporting genera within the Anserini and Anatinae comprised 11 (30%) skeletal, 2 (5%) tracheal, 5 (14%) natal integumentary, and 19 (51%) definitive integumentary apomorphies. Character changes within Anser, Branta, and Cygnus comprised 9 (8%) skeletal, 5 (5%) tracheal, 7 (6%) natal integumentary, and 88 (81%) definitive integumentary apomorphies. The opposite trends in frequencies of skeletal and integumentary apomorphies when moving from higher to lower taxonomic levels strongly indicate that skeletal changes are more conservative evolutionarily than are characters of the integument in Anseriformes (Livezey, 1991, 1995c, 1996a).

Comparisons with Other Phylogenetic Hypotheses

†Cnemiornis, here inferred to be the sister group to all other included taxa, has been considered by others to occupy several other phylogenetic positions (Livezey, 1989). Increases in tree length entailed by these alternatives are (1) †Cnemiornis as sister group to the Tadorninae, 13 steps longer (4% increase in total tree length); (2) †Cnemiornis as sister group to Cereopsis, 8 steps longer (3%); and (3) †Cnemiornis as sister group of the true geese (Cereopsis, Anser, Branta), 10 steps longer (3%).

Olson and Wetmore (1976) and Olson and James (1982) considered †Thambetochen chauliodous to be a true goose, but Olson and James (1991) subsequently concluded that this genus and the subsequently described moa-nalos are instead derivatives of the shelducks (Tadorninae) or dabbling ducks (Anatinae), primarily on the basis of the presence of asymmetrically enlarged bullae syringeales attributed to †Thambetochen and †Ptaiochen. As in the foregoing analyses, the somewhat dissimilar bullae of the moa-nalos were coded as homologous to those of most Tadorninae and Anatinae (Appendices 1, 2). Under this assumption and bearing in mind the substantial numbers of missing data for these species, the minimal penalty (two additional steps) for requiring the monophyly of the moa-nalos, Tadorninae, and Anatinae is not unexpected. Furthermore, one of these additional steps for including the moa-nalos with the Tadorninae and Anatinae is negated if the questionable state for number of cervical vertebrae (character 16) of †T. chauliodous is treated as missing (Appendices 1, 2).

Other explicit hypotheses of relationship concern only modern taxa, and therefore comparisons of these were made using constrained analyses excluding all fossil taxa \((g_i = -0.706\) for 10\(^6\) random trees, including ordered characters; \(P < 0.01\)). Also, to accommodate the hypothesis proposed by Sibley and Ahlquist (1990), comparisons were made with a matrix in which the stiff-tailed ducks (Oxyurini) were segregated from other Anatinae. The shortest unconstrained tree for this modified matrix had a length of 271 steps, 1 step shorter than the tree constrained to conform to the relationships among modern taxa inferred in the all-taxon analysis (Figs. 1, 2), associated with the placement of Dendrocygna and Thalassornis as the sister group of taxa exclusive of the geese and swans. Alternative hypotheses were compared with the shortest tree (length = 272) for this suite of taxa that conformed to the global solution (Fig. 2).

Johnsgard (1961a: fig. 2) depicted a species-level diagram of "evolutionary relationships" for the geese and swans based primarily on comparative behavior; this tree, the slightly revised relationships he proposed (Johnsgard, 1978:xviii), and the
accompanying narrative provided the basis for the Johnsgard constraint tree (Fig. 6a). This summary tree was constructed under the assumption that the trees depicted by Johnsgard (1961a, 1978) are interpretable phylogenetically and that where Johnsgard (1961a) merged two taxa into a single species he considered them to
be sister groups. This global constraint tree was 30 steps (11%) longer than the shortest tree conforming with the global hypotheses in the present analysis (Figs. 1, 2). Much of the increase in length for the Johnsgard (1961a, 1978) tree derived from the relationships for taxa other than geese and swans, only vaguely indicated by Johnsgard (1961a, 1978), and from the position of Cereopsis. Differences within Cygnus accounted for only six additional steps, and relationships within the "Olor" subgroup of Cygnus required only one additional step.

The Sibley constraint tree was based on that of Sibley and Ahlquist (1990: fig. 357), with supplementary details inferred from the associated classification (Sibley and Monroe, 1990). This constraint tree includes several polytomies (Fig. 6b), which correspond to ambiguities of relationships among the geese, Tadorninae, and Anatinae implied by Sibley and Monroe (1990) and the few taxa sampled by Sibley and Ahlquist (1990). Despite these allowances, the Sibley constraint tree required an increase of 21 steps (8%) in total length.

Zimmer et al. (1994) proposed, on the basis of DNA sequence data, that Coscoroba might be the sister group of the geese and swans, as opposed to being the sister group of the swans alone (cf. Johnsgard, 1978; Livezey, 1986). This single change required an increase of nine steps (3%) in total tree length, regardless of the position assumed in the constraint tree for Cereopsis (not analyzed by Zimmer et al. [1994]).

Phylogenetic Classification

The inferred phylogenetic trees (Figs. 1-3) and associated assessments of support (Figs. 4, 5), combined with a secondary goal of conserving existing taxonomy where possible, formed the basis for a revised classification of the Anserinae (Appendix 3). Important aspects of the proposed classification include (1) placement of Cereopsis in a monotypic tribe, contra Livezey (1986), (2) erection of a separate tribe for the moa-nalos, a group only provisionally included within the Anserinae, (3) placement of Coscoroba as the sister group of other swans, (4) retention of the monotypic genus Geochen, for which available evidence prompts the conservation of generic rank within the Anserini, and (5) revision of the subgeneric classification of Cygnus (contra Livezey, 1986) to avoid delimitation of a paraphyletic taxon Cygnus at generic or subgeneric levels.

Ecomorphological Maps

Based on the inferred phylogenetic tree (Fig. 3), mean body mass underwent several evolutionary changes among modern Anserinae, including (Fig. 7a) (1) an initial increase in the ancestor of the Anserinae (not shown), (2) a decrease in the common ancestor of Anser and Branta followed by one or more increases in A. cygnoides and A. anser + A. rubrirostris, and (3) two or more increases in the swans, attaining maxima in Cygnus olor and C. buccinator. Sexual size dimorphism of Anserinae, which in most members approximates that shown by many Anseriformes (Livezey and Humphrey, 1984), paralleled in part trends in body mass (Fig. 7b): (1) a substantial increase in Cereopsis, (2) a decrease in Anser and Branta followed by a reversal in B. ruficollis, and (3) an increase in the swans, with independent further increases in Cygnus melanocoryphus and C. cygnus.

Evolutionary changes in clutch size (Fig. 7c) closely followed changes in body mass within the Anserinae, showing (1) one or two increases in A. cygnoides, A. anser, and A. rubrirostris and (2) an increase in the swans followed by independent further increases in Coscoroba and Cygnus olor and independent decreases in Cygnus melanocoryphus and C. columbianus. Combined changes in body mass (Fig. 7a), egg mass (not shown), and clutch size (Fig. 7c) produced a divergent evolutionary pattern in relative clutch mass (Fig. 7d), including (1) a basal increase in the ancestor of Anser, Branta, Coscoroba, and Cygnus, (2) further increases independently in B. ruficollis, B. sandvicensis, and some populations of polymorphic B. canadensis, and (3) an increase in Coscoroba and a decrease in Cygnus olor and basal Olor followed by a reversal in Cygnus bewickii and C. cygnus.
FIGURE 7. Mappings of evolutionary patterns in selected ordered ecomorphological attributes of modern Anserinae. A. = Anser; B. = Branta; Ce. = Cereopsis; Co. = Coscoroba; Cy. = Cygnus. (a) Body mass. State a (confined to other taxa) and polymorphism of B. canadensis are not shown. • = b; • = c; • = d; • = e; • = equivocal. (b) Sexual size dimorphism. State a is confined to other groups and is not shown. □ = b; □ = c; □ = d; □ = equivocal. (c) Clutch size. □ = a; □ = b; □ = c; □ = d; □ = equivocal. (d) Relative clutch mass. Polymorphism of B. canadensis is not shown. □ = a; □ = b; □ = c; □ = equivocal.
FIGURE 7. Continued.
Preferred nest site, in which the primitive state of ground nesting was retained by the three genera of geese, was replaced by overwater sites in the swans (including Coscoroba); this shift was coincident with an increase from 2 to \( \geq 3 \) years for age at sexual maturity and a change from terrestrial grazing to aquatic feeding habit (Appendices 1, 2). Semicolonical nesting habits appear to have evolved in three groups of geese independently: (1) the ancestor of Anser fabalis and A. brachyrhynchus, (2) the ancestor of A. caerulescens and A. rossii, and (3) the ancestor of Branta bernicla, B. hrota, B. leucopsis, and B. ruficollis. Typical habitat during nesting appears to have undergone two independent shifts from inland to coastal localities, one in Cereopsis and one in the ancestor of the species pair Branta bernicla and B. hrota.

Biogeographic Patterns

Although most basal anseriform taxa include Southern Hemisphere members, of the Anserinae only Cereopsis (Australia), Coscoroba (South America), and three basal Cygnus (C. atratus of Australia, C. melanocoryphus of South America, C. sumnerensis of New Zealand) have Southern Hemisphere distributions. This southern grade appears to have given rise to two major radiations throughout the Northern Hemisphere (Figs. 1–3): (1) Anser and Branta and (2) Cygnus olor and the subgenus Olor. These generalities were summarized by four equally parsimonious area cladograms for continental regions (CI = 0.75, RI = 0.85, RC = 0.63). A strict consensus tree (Fig. 8) reveals that (1) regions of the Southern Hemisphere compose a basal “grade” of areas, two of which (Africa, India) are included only in the distributions of nonanserine taxa; (2) this grade of southern areas gives rise to a closely related group of Holarctic areas; (3) the seven subregions of the Holarctic realm compose two major continental subregions, equivalent to the Nearctic and Palearctic (the latter including Greenland and Iceland); and (4) within the Nearctic and the Palearctic, subregions are increasingly closely related progressing from west to east.

**DISCUSSION**

**Problematic Groups**

Although the present analysis succeeded in producing a completely dichotomous phylogenetic tree for modern taxa (Fig. 3), several of the included nodes have only moderate support (Figs. 4, 5). Constrained analyses of several competing phylogenetic hypotheses for modern members, especially those involving Cereopsis and Coscoroba (Fig. 6), revealed that these alternative proposals require modest to severe penalties in parsimony relative to the shortest trees discovered for these data (Fig. 3). Congruence among independent analyses is a crucial adjunct to statistical assessments of support (Bledsoe and Rai-kow, 1990; Hillis, 1995), but few phylogenetic studies of Anseriformes are available. Where trees based on molecular data have been presented, regardless of methodology, congruence with the present hypothesis for modern Anserinae is substantial, at least to the extent that differing taxonomic
representations among studies permit comparisons (Brush, 1976; Patton and Avise, 1985; Scherer and Sontag, 1986; Shields and Wilson, 1987a; Madsen et al., 1988; Quinn et al., 1991).

The subfamilial relationships of the moa-nalos (†Chelychelynechen, †Ptaiochen, and †Thambetochen), here tentatively included as a separate tribe of the Anserinae, remains the greatest analytical challenge among the taxa analyzed here. The lack of compelling evidence for this assignment largely results from the strictly osteological material available for all three genera, and several available elements are so derived (principally related to giantism and flightlessness) as to render a number of osteological characters problematic (Olson and James, 1991). Possible sources for additional data include extraction and amplification of adequate segments of DNA or the recovery of mummified remains in which critical portions of the integument are intact (e.g., the acrotarsium).

Analytical Influences and Challenges of Fossils

Many fossil anserines are known from comparatively few, fragmentary elements (Lambrecht, 1931; Tate and Martin, 1968; Northcote, 1988, 1992). These limitations can reduce the reliability of classification; e.g., Wetmore (1943) inferred that the fragmentary type material of †Geochen suggested a closer relationship to the Australian Cereopsis than to either Anser or Branta (see Figs. 1, 2). The traditional referral of fossil anseriforms to the most similar modern genus (Livezey and Martin, 1988) and a preoccupation with identifying ancestral lineages has led to important misinterpretations of the avian fossil record (Cracraft, 1979, 1980b). However, inclusion of fossils in phylogenetic analyses can provide important evolutionary insights and impose critical constraints on the phylogenetic hypotheses generated, especially for adequately known fossil taxa representing otherwise poorly documented regions of trees (Novacek and Norell, 1982; Donoghue et al., 1989; Huelsenbeck, 1991b; Smith, 1994).

The fossils included in this analysis spanned the range of inferential and analytical significance described by Novacek (1992) for fossil eutherian mammals. The logistic penalty for including fossils in phylogenetic analyses is related to the impact of missing data on computational times and the numbers of equally parsimonious trees (Wiens and Reeder, 1995; Wilkinson, 1995). In this study, the availability of skeletal material and the early divergence of †Cnemiornis resulted in an important contribution to an understanding of basal relationships in the order, with minimal increase in computational time and no increase in the number of minimum-length trees (Figs. 1–3). Analytical inclusion of the moa-nalos did not affect relationships within the geese and swans and had only a modest impact on the other groups; however, inferences were profoundly influenced by the taxa included in analyses (Figs. 1, 2, 4, 5). Inclusion of the comparatively well known †Geochen rhuaux and †Branta hylobadistes significantly increased computational times in this analysis without providing important insights into relationships among extant taxa, and missing data permitted five equally parsimonious topologies among congeners (Fig. 1). Inclusion of any of the many poorly represented fossil Anserinae, even limiting the selections to those for which association of elements is not a major concern (e.g., Short, 1969; Martin and Mengel, 1980; Northcote, 1988, 1992), would almost certainly render some analytical algorithms impractical (e.g., bootstrapping).

Evolutionary Ecology and Biogeography

Prominent morphological trends in the Anserinae, including those for sexual size dimorphism, egg mass, and clutch size, are correlated to a substantial degree with patterns in body mass (Fig. 7). Several other evolutionary transitions characterize the swans, including a preference for overwater nest sites, a shift to aquatic “tipping up” for foraging, and an increase in age at sexual maturity. The phylogenetic position of Coscoroba inferred here, as sister group to Cygnus, suggests a simpler evolutionary
scenario for the unique ecological attributes shared by the Cygnini than that proposed by Zimmer et al. (1994).

Behavioral patterns, with adequate information on homologies and polarities, can be reliable indicators of phylogenetic relationship (de Queiroz and Wimberger, 1993). However, with the exception of the possession of a ritualized “triumph ceremony,” performed by mated pairs after territorial encounters, there are no evidently derived behaviors that unite the Anserinae (Johnsgard, 1961a, 1962, 1965, 1968, 1978). The well-developed capacity for vocalization in the Anserinae, especially geese, may represent an additional corroboration of subfamilial monophyly (Johnsgard, 1965, 1971). Vocalizations are involved in mate selection in the Anserinae (Johnsgard, 1963), but the frequency of intrageneric and intergeneric hybridization in the group (Johnsgard, 1960b; Scherer and Hilsberg, 1982) argues against a highly evolved system of selectively refined isolating mechanisms (Sibley, 1957; Johnsgard, 1963). Many behaviors shared by the geese and swans, e.g., protracted monogamous pair bonds and paternal attendance of broods, like sexual monochromatism of plumage, are primitive in the Anseriformes (Johnsgard, 1965; Kear, 1970; Sigurjónsdóttir, 1981; Scott and Clutton-Brock, 1989). Other specific displays, such as threat postures, precopulatory “head dipping,” sexually uniform postcopulatory displays, and preflight movements (Johnsgard, 1965, 1978), remain inadequately understood for formal phylogenetic analysis.

The traditional view of a northern origin for the Anseriformes evidently derives from the probably artifactual higher diversity of Holarctic fossils (Brodkorb, 1964; Howard, 1964) and the greater number of modern Holarctic species (Howard, 1950; Weller, 1964d). However, phylogenetic analyses strongly indicate a Southern Hemisphere origin for the order (Cracraft, 1980a; Livezey, 1986, 1989); the present analysis indicates a southern origin for the Anserinae as well, one somewhat obscured by comparatively recent northern radiations in Anser, Branta, and Cygnus (Figs. 1–3, 8). The west-to-east biogeographic patterns within the Holarctic and Nearctic regions evident for the Anserinae (Fig. 8), however, are difficult to explain. Coincident patterns of glaciation seem the most plausible vicariant events (Rand, 1948; Ploeger, 1968), but such interpretations of present distributions may be overly simplistic (Avise et al., 1992). The biogeographic origins of the endemic waterfowl of the Hawaiian Islands, not amenable to analysis through area cladograms, must await the construction of phylogenetic hypotheses for other avian groups showing endemism, e.g., ibises (Plataleidae), rails (Rallidae), crows (Corvidae), and finches (Fringillidae), with ancillary analyses of the most probable geographic sources for ancestral colonists (James and Olson, 1991; Olson and James, 1991).

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APPENDIX 1

CHARACTER DESCRIPTIONS

Characters employed by Livezey (1986), often considerably revised or restricted, are so indicated. All multistate characters were analyzed as unordered, except where indicated as ordered. Basal polarities are coded as state a unless another state is given in bold; characters for which polarity was undetermined are marked by an asterisk. Consistency index (CI) for each character was based on the ordered analysis including fossil species.

Skeleton

**Skull**

1. Facies, arcus suborbitalis: (a) absent; (b) typical. CI = 1.00.
2. Facies, pila supranasalis, dorsal convexity: (a) absent; (b) present, but not pronounced; (c) present, pronounced (Livezey, 1986: character 19, revised). CI = 0.67. See character 99; some *Anser* show slight, variable convexity.
3. Facies, apertura nasalis: (a) large, distinctly craniocaudally elongate; (b) reduced, weakly dorsoventrally elongate. CI = 1.00.
4. Mandibula, ventral curvature: (a) essentially lacking; (b) pronounced. CI = 0.50.
5. Mandibula, regio coronoidae: (a) not markedly deep (others); (b) markedly deep. CI = 1.00.
6. Os prefrontale, synostosis with os frontale: (a) lacking; (b) present (Livezey, 1986: character 10, part). CI = 1.00.
7. Os prefrontale, processus supraorbitalis: (a) small, variably laterally oriented; (b) large, flat, mediually appressed to dorsolateral margin of orbit (Livezey, 1986: character 11, part). CI = 1.00.
8. Ossa nasale et frontale, immediately caudal to zona elastica craniofacialis; rounded, pneumatic, dorsal swelling(s): (a) absent (includes uniquely ornamented Anhimidae and *Anseranas*); (b) present, variably prominent, especially mediially (*Ceropsis*, *Anser cygnoides*, and *Cygnus olor* extreme; *Branta* less pronounced) (Livezey, 1986: character 16, corrected, much revised). CI = 1.00. See Möller (1969a, 1969b); intraspecifically variable, sometimes manifested only by bilateral swellings with shallow medial sulcus; particularly developed in adult males, can be extreme in domestic varieties of *Anser*.
9. Os frontale, facies dorsalis, sulcus glandulae nasalis: (a) absent; (b) present, typically lateral, not enclosed dorsally by osseus lamina (*Branta sandvicensis* and *B. hylobadistes* vestigial); (c) present, enclosed dorsally by osseus lamina. CI = 0.33.
10. Os premaxillare, anterior terminus, pronounced ventral curvature: (a) present; (b) absent (Livezey, 1986: character 12, part). CI = 1.00.
11. Os premaxillare, crista tomialis, and os dentale, margo dorsalis; blunt, bony projections ("pseudodontes"); (a) absent; (b) present. CI = 1.00.
12. Os premaxillare, crista tomialis, and os dentale, margo dorsalis: (a) comparatively sharp; (b) flattened, chelonian. CI = 1.00.
13. Maxilla (ossa premaxillare et maxillare): (a) not extraordinarily deep, broad; (b) extraordinarily deep, broad. CI = 1.00.
14. Ossa maxillare et palatinum, elongate sulcus medialis: (a) indistinct or moderately deep; (b) extremely deep, broad. CI = 1.00.
15. Ossa maxillare et palatinum, paired, elongate sulci laterales: (a) lacking; (b) indistinct; (c) deep. CI = 1.00.

**Columna vertebralis**

16. Vertebrae cervicales, modal number (ordered, primitive in bold): (a) 16 (Anatinae); (b) 17; (c) 19 or 20; (d) 21; (e) 22–25 (Livezey, 1986: character 21, revised). CI = 1.00. Intraspecifically variable; state for *T. thambetochen* estimated based on holotype in which the series evidently was incomplete.
17. Vertebrae thoracae (et caudales), modal number synostotic in synsacrum (ordered): (a) 15 or 16; (b) 17–19; (c) 20–22. CI = 0.67.
18. Vertebrae caudales, modal number of elements (not synostotic with synsacrum), including modally conformed pygostyle as single unit (ordered): (a) 7; (b) 8; (c) 9 or 10, less frequently 8. CI = 0.50.

**Sternum**

19. Corpus sterni, trabecula mediana; caudal, irregularly shaped, roughly circular extension of thin bone: (a) absent; (b) present (Livezey, 1986: character 85). CI = 1.00.
20. Corpus sterni, processus caudolateralis: (a) extend significantly caudal to margo caudalis; (b) caudal extent subequal to margo caudalis (Livezey, 1986: character 81). CI = 0.50.
21. Corpus sterni, incisura medialis: (a) present; (b) obsolete. CI = 1.00.
22. Corpus sterni, facies muscularis sterni, linea intermuscularis: (a) extends caudally to margo caudalis; (b) angling mediially to carina well cranial margo caudalis (Livezey, 1986: character 88, revised). CI = 0.33.
23. Corpus sterni, pars cardiaca, pori pneumatici: (a) widely scattered throughout; (b) essentially absent; (c) limited to caudal margin of pila coracoideus (Livezey, 1986: character 89, revised). CI = 1.00.
24. Corpus sterni, foramen pneumaticum: (a) present, largely occluded by medial lamina; (b) present, open; (c) absent (Livezey, 1986: character 78, revised). *Cheniothecis* noncomparable. CI = 0.50.
25. Corpus sterni, margo costalis, processus costales, modal number per side (ordered, primitive in bold): (a) 4; (b) 6; (c) 7; (d) 8. CI = 0.60.
26. Corpus sterni, margo caudalis: (a) entire; (b) unossified medially. CI = 1.00.
27. Corpus sterni, margo cranialis, sulcus articularis coracoideus, medial foramen pneumaticum: (a) absent; (b) present (Livezey, 1986: character 90). CI = 1.00.
28. Rostrum sterni, spina interna: (a) essentially a rounded notch with variably prominent lateral eminences; (b) rectanguloid flange (Livezey, 1986: character 82, revised). CI = 1.00.
29. Rostrum sterni, spina externa: (a) present, a thick wedgelike prominence (*Anseranas* tending to b); (b) lacking; (c) present, a peglike or spatulate flange (Livezey, 1986: character 79). CI = 1.00. *Stictonetta*, Tadorninae, Anatinae variable or represented state not found among ingroup taxa, coded as missing.
30. Carina sterni, margo cranialis, fenestra (ordered): (a) absent; (b) present, but not accommodating ansae tracheales; (c) present, accommodating ansae tracheales (Livezey, 1986: character 87). CI = 1.00.
31. Carina sterni, ventral prominence: (a) comparatively great, lateral profile conspicuously convex (e.g., *Branta sandvicensis*) or essentially straight (e.g., *Branta hylabadiestis*); (b) greatly reduced, vestigial restricted to cranial portion of facies muscularis sterni (cf. Livezey, 1986: character 80). CI = 0.50.

**Furcula**

32. Claviculae: (a) well developed, not widely divergent dorsally; (b) relatively weakly developed, widely divergent dorsally, craniocaudally compressed; (c) lacking. CI = 0.67.
33. Extremitas sternalis claviculae, apophysis furculae (hypocleideum): (a) present; (b) obsolete (cf. Livezey, 1986: character 102). CI = 0.50.
34. Extremitas sternalis claviculae: (a) forming a continuous curve with scapus; (b) markedly bowed caudodorsally, accomodating derivations of carina sterni and enclosed ansae tracheales (Livezey, 1986: character 106). CI = 1.00.
35. Scapus claviculae, facies lateralis: (a) lacking foramina pneumatica; (b) perforated by several small foramina pneumatica in shallow depressions; (c) perforated by large foramina pneumatica within a prominent depression (Livezey, 1986: character 105). CI = 0.33.
36. Extremitas omalis claviculae, processus acrocoracoideus: (a) indistinct; (b) distinct (Livezey, 1986: character 101, revised). CI = 0.50.

**Scapula**

37. Extremitas cranialis scapulae, caput, foramen pneumaticum: (a) present but variably conflormed; (b) absent (Livezey, 1986: character 111, revised). CI = 0.50.
38. Extremitas cranialis scapulae, acromion: (a) approximating tuberculum coracoideum in cranial extent; (b) extending significantly cranial to tuberculum coracoideum (Livezey, 1986: character 109). CI = 0.50.
39. Collum scapulae, facies lateralis: (a) marked by one prominent tuberculum muscularis; (b) marked by two prominent tuberculi musculares, cranially by tuberculum retinaclai and caudally by tuberculum scapulare (Livezey, 1986: character 112). CI = 1.00.
40. Scapus scapulae, relative width: (a) essentially uniform throughout; (b) margo dorsalis et margo ventralis divergent in middle, width maximal cranial to extremitas caudalis scapulae (Livezey, 1986: character 108). CI = 1.00.

**Coracoideum**

41. Extremitas omalis coracoidei, processus acrocoracoideus: (a) present; (b) obsolete. CI = 1.00.
42. Extremitas omalis coracoidei, processus acrocoracoideus, facies articularis clavicularis, foramina pneumatica under caudomedial margin: (a) lacking; (b) present but comparatively few; (c) present, interspersed within larger fossae pneumatica (Livezey, 1986: character 95). CI = 0.67.
43. Extremitas omalis coracoidei, processus prococoroideus, foramen pneumaticum (typically within dorsoventral fenestra in processus; somewhat variable): (a) present; (b) absent (Livezey, 1986: character 92). CI = 1.00. Ligamentum ossificans occurs uncommonly in *Cereopsis* (Livezey, 1989).
44. Corpus coracoidei, facies dorsalis, impressio m. supracoracoideus: (a) indistinct; (b) deep, distinct (*Stictonetta* extreme) (Livezey, 1986: character 96). CI = 0.50.
45. Corpus coracoidei, facies ventralis, impressio m. supracoracoideus: (a) indistinct; (b) deep, distinct (*Stictonetta* extreme) (Livezey, 1986: character 96). CI = 0.50.
46. Extremitas sternalis coracoidei, processus lateralis: (a) broad, rounded flange extending well laterad to facies articularis sternalis; (b) variably shaped, approximating facies articularis sternalis in lateral extent (Livezey, 1986: character 99). CI = 0.50.
47. Angulus scapulo-coracoidei: (a) acute; (b) obtuse. CI = 0.50.
48. Synostosis with scapula and/or sternum: (a) absent; (b) frequent, if not typical. CI = 1.00.

**Ossa alae**

49. Pneumaticity, especially of distal elements: (a) present; (b) absent (cf. Livezey, 1986: character 50, revised). CI = 1.00.
50. Humerus, extremitas proximalis humeri, tuberculum ventrale: (a) distal to caput humeri; (b) proximal to caput humeri. CI = 1.00.
51. Humerus, margo caudalis, "eminencia caudalis" ("capital shaft ridge"): (a) prominent, directed toward caput; (b) prominent, directed toward tuberculum dorsale; (c) obsolete (Livezey, 1986: character 22, revised). CI = 1.00.
52. Ulna et radius, extremitas distalis, exostosis associated with elongation of carpometacarpus, processus extensorius into prominent spur: (a) absent; (b) present (VLG). CI = 1.00.
53. Ulna, extremitas proximalis, depressio m. bra-
chialis: (a) distinct but not deeply undercutting cotylae proximales; (b) very prominent, deeply undercutting cotylae proximales. \( CI = 1.00 \).

54. Ulno-radial and/or carpometacarpo-digital s ynostosis: (a) absent; (b) infrequent. \( CI = 1.00 \).

55. Carpometacarpus, extremitas proximalis carpometacarpi, trochea carpalis, facies articularis ulnacarpalis, margo dorsalis: (a) essentially continuous, entire; (b) prominently notched (Livezey, 1986: character 38). \( CI = 1.00 \).

56. Carpometacarpus, extremitates proximalis carpometacarpi, os metacarpale alulare, processus extensorius, enlargement into blunt "spur" (calcar alae) having length greater than craniocaudal width of rest of element (especially conspicuous in adult males): (a) absent; (b) present (Livezey, 1986: character 42, revised). \( CI = 0.33 \).

57. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, impressio m. extensor metacarpi ulnaris ("flexor" of Woolfenden, 1961): (a) completely proximal to synostosis metacarpalis proximalis; (b) opposite, at least partly, synostosis metacarpalis proximalis (Livezey, 1986: character 43, revised). \( CI = 0.50 \). Cnemiornis, moa-nalos considered noncomparable and coded as missing.

58. Carpometacarpus, corpus carpometacarpi, os metacarpale majus, facies dorsalis, proximal segment: (a) flattened or angular; (b) rounded (Livezey, 1986: character 39). \( CI = 1.00 \). Moa-nalos considered noncomparable and coded as missing.

59. Carpometacarpus, corpus carpometacarpi, os metacarpale minus, facies ventrocaudalis, proximal segment: (a) rounded; (b) concave, with elongate sulcus (Livezey, 1986: character 44). \( CI = 0.50 \). Cnemiornis and moa-nalos considered noncomparable and coded as missing.

60. Carpometacarpus, corpus carpometacarpi, spatium intermetacarpale: (a) present; (b) occluded through synostosis of osa metacarpale majus et minus. \( CI = 1.00 \).

61. Carpometacarpus, extremitates distalis carpometacarpi, faciei articulares digitorum, relative distal extent: (a) faciei articulares digitum minor distad to facies articularis digitus major; (b) faciei articulares digitum of approximately equal distal extent (Livezey, 1986: character 45). \( CI = 0.50 \).

Ossa cinguli membri pelvici

62. Os coxae, foramen ilioschiadicum: (a) entire; (b) frequently (if not modally) open caudally. \( CI = 1.00 \).

63. Os coxae, fossa renalis, recessus iliacus: (a) present; (b) absent (Livezey, 1986: character 120). \( CI = 1.00 \).

64. Ilium, ala postacetabularis ili, margo lateralis, crista iliaca dorsolateralis: (a) distinct to margo caudalis; (b) obsolete cranial to margo caudalis (Livezey, 1986: character 118). \( CI = 1.00 \).

65. Ischium, ala ischii, margo caudalis, caudal extent relative to ala ilii, margo caudalis: (a) well caudal; (b) subequal, margo caudalis pelvici oblique-

ly sloping (Livezey, 1986: character 114). \( CI = 0.50 \).

66. Pubis, corpus pubis, margo dorsalis (lateral view): (a) concave; (b) convex (Livezey, 1986: character 115). \( CI = 1.00 \).

67. Pubis, apex pubis, shape: (a) of uniform width with corpus or monotonically widened caudally; (b) widened into semicircular flange, especially extensive craniocaudally (Livezey, 1986: character 117). \( CI = 1.00 \).

Ossa membri pelvici

68. Femur, extremitas proximalis femoris, caput, proximal extent relative to trochanter: (a) approximately equal; (b) proximal. \( CI = 1.00 \).

69. Femur, extremitas proximalis femoris, caput, orientation relative to corpus femoris, facies lateralis: (a) significantly caudal; (b) essentially perpendicular (Livezey, 1986: character 51). \( CI = 1.00 \). Moa-nalos somewhat intermediate.

70. Tibiotarsus, extremitas proximalis tibiotarsi, crista cnemiornis cranialis, lateral deflection: (a) lacking; (b) present (Livezey, 1986: character 63). \( CI = 1.00 \).

71. Tarsometatarsus, hypotarsus: (a) laterally situated on corpus, fossa parahypotarsalis medialis distinct (deep in Anseranus), only two prominent crista hypotarsi present; (b) centered on corpus, lacking distinct fossa parahypotarsalis medialis, three or four prominent crista hypotarsi present (Livezey, 1986: character 72). \( CI = 1.00 \). Position of hypotarsus intermediate in T. thambetochen.

72. Tarsometatarsus, corpus tarsometatarsi, fossa metatarsi I: (a) deep; (b) obsolete (Livezey, 1986: character 71). \( CI = 1.00 \).

73. Tarsometatarsus, extremitas distalis tarsometatarsi, trochlea metatarsi IV, margo dorsalis, margo proximalis, deep sulcus: (a) absent; (b) present. \( CI = 1.00 \).

74. Tarsometatarsus, extremitas distalis tarsometatarsi, foramen vasculare distale, orientation and depth relative to corpus tarsometatarsi, facies plantaris: (a) perpendicular to corpus, coplanar with facies plantaris; (b) dislocated to corpus, distinctly recessed in sulcus between trochlea metatarsi III et IV (Livezey, 1986: character 77). \( CI = 1.00 \).

75. Tarsometatarsus, extremitas distalis tarsometatarsi, trochlea metatarsi II, distal extent relative to trochlea metatarsi IV: (a) approximately equal; (b) significantly proximal (Livezey, 1986: character 68). \( CI = 1.00 \).

76. Tarsometatarsus, extremitas distalis tarsometatarsi, trochlea metatarsi II, sulcus intertoticlaris: (a) obsolete; (b) distinct (Livezey, 1986: character 74). \( CI = 0.50 \).

Trachea and Syrinx

77. Trachea, ansae tracheales, intrasternal (ordered): (a) absent; (b) rudimentary, a single short ventral, furcular bend; (c) present, well developed (C. buccinator uniquely extensive). \( CI = 1.00 \). Ho-
Figure A1. Tympani syringeales of selected Anserinae, caudal views (dorsal surfaces above). (a) Cereopsis novaehollandiae (USNM 430244). (b) Anser cygnoides (USNM 19374). (c) Branta hrota (USNM 553108). (d) Cygnus buccinator (USNM 430204). Caudal portion of first right cartilaginis bronchiosyringealis of *C. buccinator* is not shown.

81. Trachea, fenestra et membrana tracheosyringealis dorsalis (females): (a) absent; (b) present. CI = 1.00.

79. Trachea, bulbus tracheosyringealis (most marked in males): (a) absent, trachea cranial to syrinx of essentially uniform diameter; (b) present, variably marked by constriction cranial to tympanum. CI = 0.50.

80. Syrinx, tympanum, lateromedial compression: (a) present; (b) absent, tympanum essentially cylindrical. CI = 0.50. See Figure A1.

81. Syrinx, bulla syringealis (asymmetrical synostosis of relatively few, caudal-most ossa tracheales, with weakly developed pessulus and interchamber septum): (a) absent; (b) present (presumably only in males), single chamber; (c) present, large and small chambers, blind chamber (cf. Livezey, 1986: character 6, much revised). CI = 0.75. See Figure A2; homology of state b in moa-nalos is questionable. This character was coded as poly-

Figure A2. Bullae syringeales of moa-nalos, presumptive males, ventral (a, c) and caudal (b, d) views. (a, b) †Thambetochen chauliodous (USNM uncataloged), cranial aspect of which was shown by Olson and James (1991: fig. 8), missing portions shown in diagonal overlay. (c, d) †Pitaochen pau (BPBM 158937).
morphic for Anatinae, in which only Oxyurini lacks bulla.

82. Syrinx, pessulus osseus (ordered): (a) complete, firmly synostotic with midline of tympanum; (b) incomplete, reduced to dorsal and ventral tubercula; (c) absent. CI = 1.00. Small hiatus in some worn specimens of moa-nalos coded as state a.

83. Syrinx, membrana tympaniformis lateralis: (a) absent or inconspicuous; (b) bilaterally enlarged, associated with deeply concave, often craniolaterally recessed margo caudolateralis of tympanum. CI = 1.00.

84. Syrinx, bulbus bronchiosyringealis, cartilagines bronchiales syringes, latticelike synostosis among elements cranially: (a) absent; (b) present. CI = 1.00. See Figure A3.

85. Bill color: (a) gray; (b) flesh. CI = 1.00.

86. Foot color: (a) gray; (b) orange or yellow; (c) pink. CI = 1.00.

87. Dorsum (crown, back, rump, wings): (a) darker than venter (slight in A. rossii, C. atratus); (b) does not contrast with pale venter (“all white”). CI = 1.00.

88. Dusky periorbital patch: (a) present but variably extensive (vestigial in A. caerulescens, A. rossii); (b) absent. CI = 1.00.

89. Darkish cap (separate from cheek patch by pale supraorbital stripe, if present): (a) present; (b) absent. CI = 1.00.

90. Dark corona sharply contrasting with comparatively wide, pale frons: (a) absent; (b) present (B. sandvicensis comparatively faint). CI = 0.50.
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FIGURE A4. Diagrams of natal patterns of selected Anserinae, lateral views. (a) Cereopsis novaehollandiae (AMNH 744127). (b) Anser erythropus (FMNH 14032). (c) Branta canadensis leucopareia (USNM 530208). (d) Coscoroba coscoroba (PMNH 16703). (e) Cygnus atratus (USNM 385928). (f) Cygnus buccinator (AMNH 744385).

91. Ground color of down*: (a) white; (b) yellow. CI = 0.50.
92. Distinct, pale scapular and rump spots: (a) present; (b) absent. CI = 0.50.
93. Pale scapular and rump spots (if present): (a) separate; (b) confluent, forming bilateral dorsal stripes. CI = 1.00.
94. Pale suborbital stripe (ordered): (a) terminating at nape; (b) separated dorsally by narrow, dark nuchal stripe; (c) meeting across nape. CI = 1.00.

Definitive Integument

95. Rhamphotheca, ground color: (a) gray to black; (b) flesh-colored or pink; (c) orange; (d) red. CI = 0.63. Variably orange tones of rhamphotheca of Anser albifrons flavirostris of questionable reliability in comparison with Nearctic forms (Palmer, 1976; Kaufman, 1994) and not detectable using study skins, necessitated coding A. albifrons as polymorphic (b/c).
96. Maxilla, basal "knob": (a) absent; (b) present, orange; (c) present, black. CI = 1.00.
97. Maxilla, rhamphotheca, small, grayish, basal caruncles: (a) absent; (b) present. CI = 1.00.
98. Cere, bright green color: (a) absent; (b) present. CI = 1.00.
99. Maxilla, tomium, contrasting blackish color: (a) absent; (b) present (least conspicuous in A. canagicus, most conspicuous in A. caerulescens). CI = 1.00.
100. Maxilla, tomium, narrow reddish basal stripe: (a) absent; (b) present. CI = 1.00.
101. Maxilla (ordered): (a) of typical proportion; (b) intermediate in profile; (c) short, high-based, subconical. CI = 1.00. Branta canadensis variable, apparently size related, and coded as polymorphic (b/c).
102. Maxilla, tomium, marked ventral decurvature, tending to expose lamellae laterally and associated with ventral prominence of maxillary integument near gape, most conspicuous in males (ordered): (a) absent; (b) present but moderate; (c) present, marked. CI = 1.00. Evidently convergent, variably developed in some Tadorninae (Alopochen, Chloephaga).
103. Maxilla, rhamphotheca, dertrum, color: (a) black; (b) pale. CI = 0.33.
104. Mandibula, rhamphotheca of rami: (a) colored like rest of bill; (b) contrastingly blackish. CI = 1.00.
105. Maxilla, rhamphotheca, dorsal surface: (a) not marked with black; (b) variably marked with black, contrasting with paler ground color. CI = 1.00.
106. Maxilla, rhamphotheca, contrasting, bright yellow lateral patches (ordered): (a) absent; (b) present, restricted to loral strip; (c) present, comparatively extensive. CI = 1.00. Intraspecifically variable.
107. Maxilla, rhamphotheca, caudal margin: (a) terminates well anterior to orbit; (b) extends posteriorly to orbit as narrow strip (covered with down in very young cygnets). CI = 1.00. Not considered homologous with bare cere and orbital region in Anhimidae and Anserinae.
108. Maxilla, rhamphotheca, tomium, laterally prominent subterminal flaps with enlarged lamellae, presenting subspatulate aspect: (a) absent; (b) present. CI = 1.00.
109. Mandibula, interramal region: (a) lacks feathers anteriorly; (b) completely feathered. CI = 0.50.
110. Foot color*: (a) orange; (b) pink; (c) black. CI = 0.43. Problematic coding for Tadorninae, Anatinae.
111. Interspecific webbing of feet (exclusive of hallux): (a) truly semipalmate; (b) palmate (includes variably incised webbing in Cereopsis, Branta sandvicensis) (LIVEZEY, 1986: character 4, revised). CI = 0.50.

112. Tarsal integument, facies dorsalis: (a) reticulate; (b) scutellate. CI = 1.00.

113. Molt of remiges: (a) sequential; (b) simultaneous (LIVEZEY, 1986: character 1). CI = 1.00.

114. Ground color of primary remiges, proximal portions of vanes: (a) medium brown; (b) silvery gray (not evident in white morphs of Anser); (c) blackish brown; (d) white. CI = 0.60.

115. Contrastingly black tips of distal primary remiges: (a) absent; (b) present. CI = 1.00.

116. Primary remiges, rachises, color of proximal segment: (a) white; (b) brownish. CI = 1.00.

117. Secondary remiges, ground color: (a) essentially gray; (b) pale brownish gray; (c) bluish silver. CI = 1.00.

118. Ground color of primary remiges, proximal portions of vanes: (a) plain grayish brown; (b) pale brownish gray; (c) bluish silvery gray (not evident in white morphs of Anser); (d) white. CI = 1.00.

119. Lesser (cranial-most) dorsal primary and secondary coverts: (a) not pale silvery gray; (b) contrastingly pale silvery gray. CI = 1.00.

120. Tips of greater secondary coverts: (a) without contrastingly pale margins; (b) with narrow, contrastingly pale margins, forming a weak bar; (c) with comparatively broad, contrasting white margins. CI = 0.40. Cygnini considered noncomparable.

121. Tertials: (a) dark with pale margins, margins generally broader on lateral vanes; (b) elongate, three-toned, dark (blackish) medially, brownish in middle of vanes, pale laterally (not evident in white phases); (c) immaculately black, lacking pale margins. CI = 1.00. Cygnini considered noncomparable.

122. Wing linings: (a) dark, like remiges; (b) white; (c) pale gray. CI = 1.00. Cygnini considered noncomparable.

123. Axillaries: (a) generally dark, comparable to color of adjacent feathers of side; (b) pale, silvery gray; (c) white (essentially immaculate), contrasting with sides (not evident in white morph of Anser). CI = 0.50. Cygnini considered noncomparable.

124. Rectrices, modal number of pairs in birds not in molt (ordered): (a) 6; (b) 7; (c) 8; (d) 9; (e) 10–12. CI = 0.71. Subspecies of Branta canadensis polymorphic, coded b/c in in most species.

125. Rectrices, color: (a) essentially black; (b) grayish black medially with pale lateral and terminal edges (not evident in white morphs of Anser); (c) white. CI = 0.67.

126. White (caudal) upper tail coverts producing white band at base of rectrices: (a) present; (b) absent. CI = 0.50.

127. Contrastingly black "basal" upper tail coverts producing black rump: (a) absent, rump similar in color to back; (b) present. CI = 1.00.

128. Upper tail coverts, contrastingly pale gray color: (a) absent; (b) present. CI = 1.00.

129. Plumage of head, neck, and (in some) entire body exclusive of remiges uniform charcoal black (ordered): (a) absent; (b) present, limited to head and neck; (c) present, entire body exclusive of remiges. CI = 1.00.

130. Dark (blue) and pale (white) color phases: (a) absent; (b) present but geographically variable frequencies (very rare in Anser caerulescens atlanticus, rare in A. rossii). CI = 1.00.

131. Mantle, ground color*: (a) medium brown; (b) gray; (c) blackish; (d) white. CI = 0.50. States of Tadorninae and Anatinae were problematic and coded as missing.

132. Mantle, shape of feathers: (a) comparatively narrow to moderately broad, terminus rounded; (b) distinctly broad with truncate tips. CI = 0.33.

133. Mantle and upper wing coverts, distinct whitish terminal bars producing scalloped appearance: (a) absent; (b) present. CI = 0.25.

134. Boldly barred dorsum, formed by sharply defined black subterminal bands and narrow white terminal bands on otherwise gray dorsum: (a) absent; (b) present (Branta leucopsis intermediate, B. ruficollis comparatively dark and obscure). CI = 0.50.

135. Large black central spots on dorsal contour feathers: (a) absent; (b) present. CI = 1.00.

136. Rump, prominent barring of black and white on gray: (a) absent; (b) present. CI = 1.00.

137. Rump, contrastingly white color: (a) absent; (b) present. CI = 1.00.

138. Contrastingly black undertail coverts: (a) absent; (b) present. CI = 1.00.

139. Sharply demarcated dark breast: (a) absent; (b) present, black; (c) present, chestnut. CI = 1.00.

140. Fine white breast stripe, contrasting with black ventrally: (a) absent; (b) present. CI = 1.00.

141. Coarse black spotting on lower breast, belly (ordered): (a) absent; (b) present (more conspicuous in Anser albirostris [especially A. flavirostris] and A. erythropus than in A. anser). CI = 0.50.

142. Coarse gray and black barring on belly and ventrum: (a) absent; (b) present. CI = 1.00.

143. Dark gray or black continuing ventrally from black breast (if present): (a) absent; (b) present. CI = 0.50.

144. Fine, caudally jagged, white side stripes, contrasting with black breast, belly: (a) absent; (b) present. CI = 1.00.

145. Flank: (a) not marked as follows (including superfluffly similar pattern of Branta ruficollis produced by unique white feathers with black edges); (b) barred with whitish on dusky-black background (produced by dark feathers with pale edges; includes taxa in which white phases necessarily lack the pattern), darkening caudally, most pronounced craniolateral to crural region. CI = 1.00.
### Character-State Matrix

Matrix of 165 morphological characters (Appendix 1) used in the phylogenetic analysis of 38 anserine and related taxa and a hypothetical ancestor, followed by 10 mapped attributes (A–J). States are coded as lowercase letters, and combinations of states in polymorphisms are shown as follows: g = a/b; i = a/b/c. ? = missing data. 

#### Ecomorphological Attributes

<table>
<thead>
<tr>
<th>Character</th>
<th>States</th>
<th>CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Mean body mass (ordered)*:</td>
<td>(a) &lt;1,000 g; (b) 1,000–3,000 g; (c) 3,000–5,000 g; (d) 5,000–10,000 g; (e) &gt;10,000 g.</td>
<td></td>
</tr>
<tr>
<td>B. Sexual size dimorphism (ratio, mean mass for males divided by mean mass for females; ordered)*:</td>
<td>(a) &lt;1.01; (b) 1.01–1.20; (c) 1.21–1.30; (d) &gt;1.30.</td>
<td></td>
</tr>
<tr>
<td>C. Mean clutch size (ordered)*:</td>
<td>(a) 4 or 5; (b) 5 or 6; (c) 6 or 7; (d) 7 or 8; (e) 8 or 9; (f) &gt;9.</td>
<td></td>
</tr>
<tr>
<td>D. Mean egg mass (ordered)*:</td>
<td>(a) &lt;100 g; (b) 100 or 140 g; (c) 140 or 200 g; (d) &gt;200 g.</td>
<td></td>
</tr>
<tr>
<td>E. Relative clutch mass (percentage of mean female body mass; ordered)*:</td>
<td>(a) &lt;20%; (b) 20% or 30%; (c) 30% or 40%; (d) &gt;40%.</td>
<td></td>
</tr>
<tr>
<td>F. Preferred nest site (ordered):</td>
<td>(a) over water; (b) terrestrial (includes Dendrocygna, which uses both terrestrial sites and cavities).</td>
<td></td>
</tr>
<tr>
<td>G. Age at sexual maturity (ordered):</td>
<td>(a) 1 yr; (b) 2 yr; (c) ≥3 yr.</td>
<td></td>
</tr>
<tr>
<td>H. Semicoloniality:</td>
<td>(a) not characteristic; (b) characteristic.</td>
<td></td>
</tr>
<tr>
<td>I. Feeding habitat, diet:</td>
<td>(a) surface aquatic; (b) diving; (c) terrestrial grazing.</td>
<td></td>
</tr>
<tr>
<td>J. Typical aquatic habitat during nesting:</td>
<td>(a) fresh-water; (b) salt water.</td>
<td></td>
</tr>
</tbody>
</table>

#### Character-State Matrix

<table>
<thead>
<tr>
<th>State</th>
<th>Character</th>
<th>Description</th>
<th>CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. anser</td>
<td>Head:</td>
<td>(a) not entirely black; (b) entirely black.</td>
<td>1.00.</td>
</tr>
<tr>
<td>B. bernida</td>
<td>Crown, sides of head, neck:</td>
<td>(a) not as follows; (b) white, in contrast with dark of mantle.</td>
<td>1.00.</td>
</tr>
<tr>
<td>C. canadensis</td>
<td>Black crown, anterior region of face (down-tilted cap):</td>
<td>(a) absent; (b) present.</td>
<td>1.00.</td>
</tr>
<tr>
<td>D. cygnoides</td>
<td>Complete brown dorsal nuchal stripe connecting crown with mantle:</td>
<td>(a) absent; (b) present.</td>
<td>1.00.</td>
</tr>
<tr>
<td>E. cygnus</td>
<td>Black neck “stocking,” circumcomplete, at least in pars intermedia:</td>
<td>(a) absent; (b) present (cranially obscured by enlarged cheek patches in B. sandvicensis, problematical in B. ruficollis).</td>
<td>1.00.</td>
</tr>
<tr>
<td>F. fabalis</td>
<td>Black neck stocking, pars caudalis, forming circumcomplete collar at base of neck and sharply contrasting with adjacent breast:</td>
<td>(a) absent; (b) present (narrow in B. sandvicensis).</td>
<td>1.00.</td>
</tr>
<tr>
<td>G. fabalis</td>
<td>Broad, gray stripes on throat and nape separated laterally by narrower white stripes:</td>
<td>(a) absent; (b) present.</td>
<td>1.00.</td>
</tr>
<tr>
<td>H. fabalis</td>
<td>Black chin and upper throat grading to grayish barring ventrally:</td>
<td>(a) absent; (b) present.</td>
<td>1.00.</td>
</tr>
<tr>
<td>I. fabalis</td>
<td>Semicircular white loral patches:</td>
<td>(a) absent; (b) present.</td>
<td>1.00.</td>
</tr>
</tbody>
</table>
APPENDIX 3. Phylogenetic classification of the Anserinae and closely related outgroups. Only anserine taxa are classified at subgenetic levels. Within higher taxa, three or more included taxa of equal rank are listed in order of increasingly close relationship (i.e., terminal pair inferred to be sister species). Fossil taxa are preceded by daggers. Sedis mutabilis indicates groups including three or more taxa of undetermined relationship and provisionally accorded equal rank.

Order Anseriformes (Wagler, 1831)
Suborder Anseres Wagler, 1831
Family Anseranatidae Sclator, 1880
†Family Cnemiornithidae Stejneger, 1885
Family Anatidae Leach, 1820—true geese, swans, and ducks
Subfamily Dendrocygninae Reichenbach, “1850”—whistling-ducks and allies
Genus Dendrocygna Swainson, 1837—whistling-ducks
Genus Thalassornis Eyton, 1838—White-backed Duck
Subfamily Anserinae Vigors, 1825—geese and swans
Tribe Cereopsini (Vigors, 1825)
Genus Cereopsis Latham, 1801
Cereopsis novaehollandiae Latham, 1801—Cape Barren Goose
Tribe Anserini (Vigors, 1825)—true geese; sedis mutabilis
Genus Anser Brisson, 1760—pale-breasted geese
Subgenus Anser Brisson, 1760
Anser cygnoides (Linnaeus, 1758)—Swan Goose
Anser fabalis (Latham, 1787)—Bean Goose
Anser brachyrhynchus Baillon, 1833—Pink-footed Goose
Anser anser (Linnaeus, 1758)—greylag geese
Anser (a.) anser (Linnaeus, 1758)—Western Greylag Goose
Anser (a.) rubrirostris Swinhoe, 1871—Eastern Greylag Goose
Anser altrifrons (Scopoli, 1789)—Greater White-fronted Goose
Anser erythropus (Linnaeus, 1758)—Lesser White-fronted Goose
Subgenus Chen Boie, 1822
Anser indicus (Latham, 1790)—Bar-headed Goose
Anser canagicus (Sevastianov, 1802)—Emperor Goose
Anser caerulescens (Linnaeus, 1758)—Snow Goose
Anser rossii (Cassin, 1861)—Ross's Goose
†Genus Geochen Wetmore, 1943
Geochen rhuax Wetmore, 1943—Large Hawaiian Goose
Genus Branta Scopoli, 1769—Brent (dark-breasted) geese
Subgenus Leucopleuron Baird, 1858; sedis mutabilis
†Branta hylobadistes Olson and James, 1991—Greater Nene
Branta sandvicensis (Vigors, 1833)—Lesser Nene
Subgenus Branta Scopoli, 1769
Branta (b.) bernicla (Linnaeus, 1758)—Dark-bellied Brent
Branta (b.) hrota (Müller, 1776)—Pale-bellied Brent
Subgenus Leucopareia Reichenbach, 1853
Branta leucopsis (Bechstein, 1803)—Barnacle Goose
Branta ruficollis (Pallas, 1769)—Red-breasted Goose
Tribe Cygnini (Vigors, 1825)—swans
Subtribe Coscorobina (Boetticher, 1936–1938), new rank
Genus Coscoroba Reichenbach, 1853
Coscoroba coscoroba (Molina, 1782)—Coscoroba Swan
Subtribe Cygniina (Vigors, 1825)
Genus Cygnus Bechstein, 1803
Subgenus Chenopis Wagler, 1823
Cygnus atratus (Latham, 1790)—Black Swan
Cygnus melanocoryphus (Molina, 1782)—Black-necked Swan
Subgenus Cygnus Bechstein, 1803
Cygnus olor (Gmelin, 1789)—Mute Swan
Subgenus Olor Wagler, 1832—tundra swans
Olor buccinator (Richardson, 1831)—Trumpeter Swan
Olor columbianus (Ord, 1815)—Whistling Swan
Olor bewickii (Yarrell, 1830)—Bewick’s Swan
Olor cygnus (Linnaeus, 1758)—Whooper Swan

†Tribe Thambetochenini, new taxon—moa-nalos
Genus Chelychelynechen Olson and James, 1991
Chelychelynechen quassus Olson and James, 1991—Turtle-billed Moa-nalo
Genus Ptaiochen Olson and James, 1991
Ptaiochen pau Olson and James, 1991—Short-billed Moa-nalo
Genus Thambetochen Olson and Wetmore, 1976
Thambetochen chauliodous Olson and Wetmore, 1976—Greater Moa-nalo
Thambetochen xanion Olson and James, 1991—Oahu Moa-nalo

Subfamily Stictonettinae (Boetticher, 1950)
Genus Stictonetta Reichenbach, 1853—Freckled Duck
Subfamily Tadorninae Reichenbach, “1850”—shelducks and allies
Subfamily Anatinae (Leach, 1820)—surface-feeding ducks and allies (including Oxyurini, stiff-tailed ducks)

*a Recognition of subgenus based on weak support for sister group relationship between C. atratus and C. melanocoryphus.

b Subfamilial assignment of moa-nalos provisional; only slightly less parsimonious to consider them more closely related to the Tadorninae and Anatinae.