PHYLOGENETIC RELATIONSHIPS AND INCIPIENT FLIGHTLESSNESS OF THE EXTINCT AUCKLAND ISLANDS MERGANSER

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Abstract.—Phylogenetic relationships and evidence for pectoral reduction in the extinct Auckland Islands Merganser (*Mergus australis*) were investigated using a plumage-based phylogenetic analysis of the six Recent species of merganser and morphometric comparisons of study skins and skeletal specimens. The hypothesized phylogeny indicates that *M. australis* diverged from the other *Mergus* immediately after the Hooded Merganser (*Lophodytes cucullatus*) and is a member of a basal grade of comparatively small, southern hemisphere mergansers; the Brazilian Merganser (*M. octosetaceus*) branched next and is the sister-group to the larger, more derived, northern hemisphere species of *Mergus*. *M. australis* was unique in its natal and adult plumage characters, including the sexually monochromatic plumage of adults. Morphometric analyses revealed that *M. australis* was the smallest member of its genus but possessed the longest bills and relatively short wings and tails. Based on regression estimates of body mass and wing area for *M. australis,* the species had estimated wing-loadings which exceed those for other Mergini and approach the threshold of flightlessness hypothesized by Meunier (1951). Skeletal comparisons confirmed that *M. australis* had exceptionally long bills, and this also revealed that the species possessed relatively short wing elements and scapulae, as well as sterna characterized by shallow carinae and small caudal widths. These morphological characteristics, hypothesized phylogenetic relationships, and ecological information for *M. australis* are compared to the typical correlates of insularity in waterfowl listed by Weller (1980), and the evolutionary implications of these characteristics are considered. *Received 26 May 1988, accepted 1 Nov. 1988.*

The mergansers (*Lophodytes cucullatus* and five species of *Mergus*) are highly derived members of the sea ducks (Mergini), most closely related to the Smew (*Mergellus albellus*) and goldeneyes (*Bucephala* spp.) (Livezey 1986). Mergansers are capable divers and are largely piscivorous, but unlike several other genera of the Mergini (e.g., *Somateria, Melanitta,* and *Clangula*), are strictly foot-propelled divers, i.e., strokes of the feet provide the sole propulsion at submergence and for underwater loco-motion (Townsend 1909; Kelso 1922; Brooks 1945; Humphrey 1957, 1958). Most mergansers, like other Mergini, are limited in distribution to the northern hemisphere, show striking sexual dichromatism, and are migratory (Delacour 1959; Johnsgard 1965, 1978).

The Auckland Islands Merganser (*Mergus australis*) was one of two Recent species of merganser with southern-hemisphere distributions (the

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other being the Brazilian Merganser [*M. octosetaceus*]), being limited, at least in historical times, to the Auckland Islands (50°S, 165°E), a small group of islands located 330 km south of the South Island of New Zealand (Phillips 1925, Delacour 1959, Williams 1964, Greenway 1967, Kear and Scarlett 1970, Weller 1980). Subfossil specimens of *Mergus,* mensurally comparable to *M. australis,* have been found as well on the main islands of New Zealand (Kear and Scarlett 1970). Extirpated during the first decade of the twentieth century, this insular species is represented in museum collections by some 26 skins (including downy young), three virtually complete skeletons, some additional skeletal parts, and one carcass preserved in alcohol (Kear and Scarlett 1970). In addition to its southern-hemisphere insular distribution, the Auckland Islands Merganser has been noted for its small size, lack of sexual dichromatism, relatively long bill, and unusual plumage pattern of its downy young (Mathews and Iredale 1913, Humphrey 1955, Kear and Scarlett 1970, Weller 1980).

The Auckland Islands Merganser was not, as claimed by Luther (1967), flightless; individuals were observed in flight by Hutton and Ranfurly (*fide* Kear and Scarlett 1970). The notion that *M. australis* was flightless may have originated with the mistaken inclusion of *M. australis* as a synonym of the Auckland Islands Flightless Teal (*Anas aucklandica*) by Gray (1844). Based on a study of skeletal measurements, however, Humphrey (1955) concluded that the humerus of *M. australis* showed evidence of reduction in length. Humphrey further inferred from proportions of wing elements that the species also showed reduction of the ulna and manus.

The unusual distribution and morphology of *M. australis,* particularly the evidence of wing reduction, prompted its inclusion in an ongoing study of flightlessness in diving birds. In this paper I propose a phylogenetic hypothesis for the six Recent species of mergansers using published descriptions of natal and adult plumages. This analysis is followed by morphometric comparisons of external and skeletal measurements to determine interspecific patterns of size, shape, and sexual dimorphism within the group and to examine in greater detail the evidence for reduction of the pectoral limb in *M. australis* and the possibility that the species was evolving toward flightlessness.

MATERIAL AND METHODS

Phylogenetic characters. — Characters of natal and adult plumages, as well as colors of soft parts, were taken from illustrations and text in Partridge (1956), Delacour (1959), Kear and Scarlett (1970), and Bartmann (1988). Kear and Scarlett (1970) pointed out several errors in the illustration of a downy *M. australis* in Delacour (1959). Characters used in the phylogenetic analysis were those that varied within the in-group (*Lophodytes* and *Mergus*) and for which polarities (primitive states) could be determined by comparison with its sister

genera, *Bucephala* and *Mergellus* (Livezey 1986). I endeavored to reduce all character complexes to binary characters (i.e., having but a primitive and a single derived state); those for which this was not possible were analyzed as unordered. Autapomorphies (derived character states unique to a single terminal taxon) were included in the analysis because such differences have been considered of taxonomic value in traditional, phenetic classifications (e.g., Humphrey 1955, Delacour 1959, Johnsgard 1961a, Kear and Scarlett 1970). The tree was constructed using the criterion of parsimony (Wiley 1981). It was hoped that phylogenetic relationships inferred from plumage characters would be effectively independent of the morphometric patterns that were investigated. In addition to the plumage characters, I attempted to include courtship behaviors (Johnsgard 1960, 1961a, b, 1965) and syringeal morphology (Humphrey 1955) in the analyses, but was unsuccessful because of uncertain homologies, polarities, continuous variation (in syringeal bullae), and missing data for crucial species (e.g., *M. australis* and *M. octosetaceus*).

Specimens and morphometric data.—Mensural data from 15 skins of (fully grown) *M. australis* were collected by me or provided by colleagues. Where possible, I also made counts of the primary remiges in *M. australis*. I measured 10 skins of adults of each sex of the Hooded Merganser (*Lophodytes cucullatus*), Red-breasted Merganser (*M. serrator*), and Common Merganser (*M. merganser*); smaller samples of skins of the Brazilian Merganser (N = 5 males, 5 females) and the Chinese Merganser (*M. squamatus*; N = 8, 6) were available for measurement. Measurements taken on skins were as follows: total body length; length of exposed culmen on midline; nail width; length of the chord of the unstraightened wing; length of the tail, measured medially; length of the tarsus on anterior surface; and length of the middle toe, excluding nail. Total lengths were measured only on properly prepared study skins (i.e., realistically extended, unmounted skins), had coefficients of variation ($s/\bar{x}$) comparable to those for other external variables, and their *means* were used, in part, for estimates of body size of *M. australis*, *M. octosetaceus*, and *M. squamatus*—for which published records of body mass were not available. Specifically, body masses were estimated using external "body lengths" (mean total lengths minus the mean lengths of culmen and tail), which were independent of interspecific variation in relative lengths of bills and appendages. Together with estimates of wing area based on wing length, these estimated body masses were used to infer the approximate wing-loadings of the three species of *Mergus* lacking these data. Wing areas, where available, were measured as described by Raikow (1973), and wing-loadings for species (g of mean body mass divided by cm² of mean total wing area) were calculated as recommended by Clark (1971). Additional data on body masses and wing areas of mergansers and other Mergini were taken from Müllenhoff (1885), Magnan (1912, 1922), Poole (1938), Meunier (1959), Dement'ev and Gladkov (1967), Raikow (1973), Madge and Burn (1988), and P. S. Humphrey (unpubl. data).

Three virtually complete skeletons and a few disassociated skeletal elements of *M. australis* were available for study. I sought to measure 15 skeletons of each sex of the other mergansers, although only one complete skeleton of *M. squamatus* and a partial skeleton of *M. octosetaceus* were available. Thirty-three skeletal variables were used in the comparisons, most of which were described in Livezey and Humphrey (1984, 1986) and Livezey (1988, 1989). Several nontraditional measurements require definition, however: LWM's of limb elements refer to "least widths at the midpoints" of shafts; LMW of the tarsometatarsus is the "lateromedial width" of the shaft (at midpoint); and length of digit-III (middle toe) is the sum of lengths of the three proximal phalanges of the digit. All skeletal measurements were made with dial calipers to within 0.1 mm.

Statistical analyses.—Simple measurements of skins and skeletons were compared using two-way analysis of variance (ANOVA); missing data resulted in slight variations in sample sizes in univariate analyses. Wing-loadings were log-transformed for tests with ANOVA.

Significances of differences (and associated *P*-values) based on correlated data were judged using the Bonferroni method of simultaneous inference (Milliken and Johnson 1984). Intra-alar proportions of skeletal wing elements were calculated as lengths of the single elements divided by skeletal wing length (sum of the lengths of the humerus, ulna, carpometacarpus, and the two phalanges of the major digit); arcsines of square roots of proportions were used in ANOVA (Sokal and Rohlf 1981).

Allometry of wing areas with body mass, in which both variables include error (model II; Sokal and Rohlf 1981), was investigated through "geometric mean" regressions or central trend lines (Ricker 1984) of log-transformed species means. The slopes of regressions using log-transformed means are estimates of the "allometric coefficients" (*b*) and reflect inter-specific scaling between the variables (Gould 1966); in this application the slope reflects scaling of wing area (and wing-loading) with body size.

Stepwise multivariate analysis of variance (MANOVA; see appendix 23 in Dixon 1985) was used to test for interspecific, intersexual, and species-sex interactive differences in mean vectors of external and skeletal measurements; summary statistics (Wilks' lambda and *F*-statistics) were based on backstep-selected subsets ($P < 0.05$) of the variables submitted (Jennrich and Sampson 1985). Canonical analysis (CA), a technique which defines mutually orthogonal multivariate axes that maximally separate predefined groups (relative to their pooled within-group covariances), was used to explore multivariate differences among species and sexes (Pimentel 1979). CAs also were used to isolate the multivariate differences between *M. australis* and the other species (referred to as "canonical contrasts"). Importance of interspecific and intersexual differences on the canonical variates (CVs) was tested through two-way ANOVAs of scores on these CVs (referred to as "ANOVAs of scores"). For MAN-OVA and CA *only,* external and skeletal data sets were subjected to a missing-data program (Frane 1985) in which measurements missing for reasons of deformity or bilateral breakage (for specimens lacking a small minority of data) were estimated using separate stepwise regressions on specimens grouped by species; these estimates permitted the inclusion of 99 skins and 91 skeletons in MANOVAs and CAs and comprised only 1.0% and 2.0% of the sets, respectively. Both data sets were log-transformed for CA and MANOVA (Jolicoeur 1963).

Statistical programs employed are part of the 1987 version of the Biomedical Computer Programs (BMDP; Dixon 1985), performed on an IBM computer at the University of Kansas.

PHYLOGENETIC ANALYSIS

Based on published descriptions and illustrations, I defined 11 characters of natal plumages and 11 of adult plumages of mergansers (Table 1). Four of the latter included two derived states (characters 16, 17, 18, 20), of which the first three involved the unique plumage aspect of *M. australis*. The problematic black-and-orange bill of *M. australis* was coded as a unique character state (15c); the tree depicted remains most parsimonious if bill color of *M. australis* is treated instead as a (partial) reversal from an orange bill (15b). Both *M. australis* and *M. octosetaceus* lack significant sexual dichromatism (character 16), but these conditions are not homologous (illustrated in Delacour 1959, Scott 1972). In *M. australis,* plumages of both sexes closely resemble females and juveniles of *Mergus* generally, and monochromatism of this species evidently is the result of the loss of the distinctive alternate plumage of males. This plumage condition rendered several characters (17–19) not comparable in this species (Appendix I). In contrast, the plumage pattern shared by the sexes of *M. octosetaceus* differs significantly from the rest of the genus and, although not as striking as those for adult males of most other mergansers, is not juvenal-like and is evidently uniquely derived.

Although complicated by these few instances of multiple and/or noncomparable states

(Appendix I), the 22 plumage characters formed the basis for a phylogenetic tree for the Recent mergansers (Fig. 1) of high consistency (consistency index = 1.0). The sister-group relationship of *Lophodytes* with *Mergus*, supported by osteological comparisons in Livezey (1986), was corroborated by three plumage characters of downy young (Table 1, Fig. 1). *M. australis* emerged as the second branch in the basal grade of mergansers and was characterized by four autapomorphies. Based on characters of its natal plumages, *M. octosetaceus* was the next branch to diverge in *Mergus*, and this neotropical species possessed four autapomorphies of the adult plumage (Fig. 1). The presence of a pale suborbital stripe in the natal plumage (character 4b) is shown as a synapomorphy uniting *M. octosetaceus* with the three remaining species (Fig. 1); this stripe was shown as conspicuous in *M. octosetaceus* by Partridge (1956) and Delacour (1959), but it was not indicated in photographs included by Bartmann (1988). If the latter state is taken as representative, then the change in character 4 supports the monophyly of only *M. serrator, M. squamatus,* and *M. merganser,* but the topology shown (Fig. 1) is unchanged. The sister clade of *M. octosetaceus* comprised the more "typical" mergansers of the northern hemisphere; of these three species, *M. serrator* and *M. squamatus* appear to be closest relatives (Fig. 1), although this relationship is supported by only one synapomorphy, and the topology for these three species conservatively might be considered a trichotomy. Based on this preliminary analysis, *M. australis* represents an early but uniquely derived branch in the merganser clade and, although comparable in grade to *M. octosetaceus,* the two southern-hemisphere species are not closest relatives.

MORPHOMETRIC COMPARISONS

Univariate comparisons of external measurements. — A substantial range of body size and a diversity of shape was indicated by comparisons of skin characters of mergansers. Total length of the body, probably the best directly measurable "size" measure which is independent of wing size and available for all species, differed significantly among species ($F = 35.75$; df $= 5, 84$; $P < 0.0001$) and ranked *L. cucullatus* as the smallest, followed (in order of increasing size) by *M. australis, M. octosetaceus, M. serrator, M. squamatus,* and *M. merganser* (Table 2); males were larger than females within species ($F = 10.43$; df $= 1, 84$; $P < 0.005$). Available mean body masses — 617 g (N $= 97$) for *L. cucullatus,* 984 g (79) for *M. serrator,* and 1382 g (197) for *M. merganser* — confirmed these size rankings. "Body lengths" (total lengths minus lengths of culmen and tail) mirrored these interspecific ($F = 27.35$; df $= 5, 83$; $P < 0.0001$) and intersexual differences ($F = 5.68$; df $= 1, 83$; $P < 0.05$). Regressions of mean body masses on mean "body length" (log-transformed data, N $= 3$, $r = 0.988$) provided rough estimates of body mass for the remaining three species: *M. australis,* 898 g; *M. octosetaceus,* 983 g; and *M. squamatus,* 1234 g. Comparison of actual and estimated body masses with the phylogenetic tree (Fig. 1) indicates that the merganser clade is characterized by a strong evolutionary trend toward increased body size.

Tarsus length differed significantly among species ($F = 195.40$; df $= 5, 87$; $P < 0.0001$) and between the sexes ($F = 157.61$; df $= 1, 87$; $P < 0.0001$), and conformed closely with body length in interspecific rankings

TABLE 1
CHARACTERS AND CHARACTER STATES USED IN PHYLOGENETIC TREE DEPICTED IN FIG. 1

Group	Character	States[a]
Natal plumage	(1) Breast band	a = present; b = absent
	(2) Flank spots	a = confined by dark; b = open ventrally
	(3) Head color	a = gray; b = reddish brown
	(4) Subocular stripe	a = absent; b = present
	(5) Distal forewing	a = dark; b = white
	(6) Cheek patch	a = large, above gape; b = small, ventral to gape
	(7) White back spots	a = present; b = absent
	(8) White preorbital spots	a = absent; b = present
	(9) Breast color	a = gray or white; b = tawny washed
	(10) Dorsal spotting	a = distinct; b = vestigial
	(11) Chestnut subocular spot	a = none; b = present
Adult plumage	(12) Chin	a = dark; b = whitish
(definitive	(13) Breast (males)	a = white; b = dark red
alternate)	(14) Dark nape stripe (males)	a = absent; b = present
	(15) Bill color[b]	a = grayish; b = orange; c = orange with culmen and nail black
	(16) Sexual dichromatism[b]	a = present; b = absent, males like females; c = absent, unique plumage
	(17) Background color of sides, flanks (males)[b]	a = white; b = red; c = gray
	(18) Barring of sides (males)[b]	a = black; b = white; c = none
	(19) Barring of sides	a = linear vermiculations; b = scalloping
	(20) Crest[b]	a = 1-parted, from crown; b = emerges continuously from crown to occiput; c = 2-parted
	(21) Crest	a = present in both sexes; b = absent in males
	(22) Ventral barring	a = absent; b = present

[a] Primitive state = a, derived states b–c.
[b] Analyzed as unordered.

(Table 2); middle-toe lengths (not tabulated) mirrored tarsus lengths in interspecific and intersexual differences. Culmen length, however, deviated markedly from this pattern. *M. australis,* one of the smallest species overall, had the largest culmen lengths, followed by *M. serrator,* the approximately equal *M. merganser* and *M. squamatus, M. octosetaceus,* and the much shorter-billed *L. cucullatus* (Table 2); both interspecific (F = 131.29; df = 5, 87; $P < 0.0001$) and intersexual differences (F = 58.99;
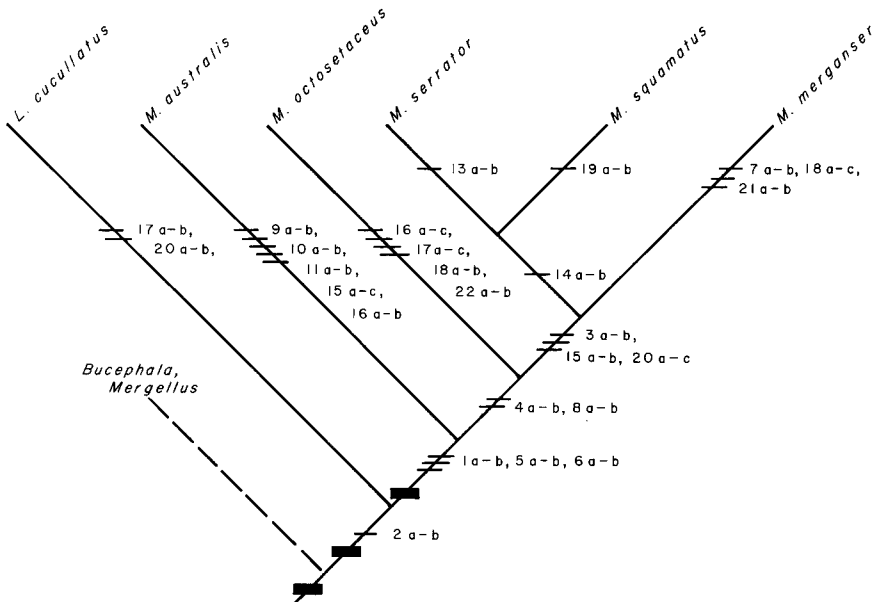
FIG. 1. Phylogenetic tree for Recent mergansers (*Lophodytes* and *Mergus*). Characters (numbers) and states (letters) are defined in Table 1 and compiled in the Appendix; black rectangles indicate skeletal synapomorphies described in Livezey (1986).

df = 1, 87; $P < 0.0001$) in culmen length were significant. Nail width (not tabulated) also differed significantly among species ($F = 15.19$; df = 5, 85; $P < 0.0001$) and sexes ($F = 26.28$; df = 1, 85; $P < 0.0001$); this variable tended to follow body length in interspecific rankings, except that *M. australis* and especially *L. cucullatus* had large nail widths relative to their body size.

Wing lengths showed substantial interspecific ($F = 376.44$; df = 5, 87; $P < 0.0001$) and intersexual variation ($F = 123.78$; df = 1, 87; $P < 0.0001$), and although means tended to follow total body length in interspecific rankings, *M. australis* had disproportionately short wings (Table 2); body lengths of *M. australis* averaged 67 mm longer than those of *L. cucullatus*, but wing lengths of the former averaged 8 mm shorter. All specimens of *M. australis* retained the full complement of primary remiges found in most anseriforms and other mergansers (10 functional plus 1 reduced). Tail lengths also varied significantly among species ($F = 58.90$; df = 5, 86; $P < 0.0001$), and paralleled wing lengths in interspecific differences; *M. australis* had disproportionately short tails (Table 2).

Wing-loadings of the Mergini. — Wing areas were available for all species

TABLE 2
SUMMARY STATISTICS (MEAN ± SD) FOR SELECTED EXTERNAL MEASUREMENTS (MM) OF MERGANSERS, BY SPECIES AND SEX

Species	Sex	N	Total length	Culmen length	Wing length	Tail length	Tarsus length
Lophodytes cucullatus	M	10	424 ± 25	40.7 ± 1.2	193.9 ± 4.2	90.6 ± 5.1	33.6 ± 1.6
	F	10	405 ± 18	39.0 ± 2.1	183.2 ± 3.4	85.7 ± 5.5	32.2 ± 1.1
Mergus australis	M	9	488 ± 63	59.6 ± 3.8	185.1 ± 5.2	69.6 ± 4.9	43.4 ± 1.7
	F	6	475 ± 54	55.0 ± 2.8	175.2 ± 3.5	72.2 ± 2.1	40.5 ± 1.2
M. octosetaceus[a]	M	5	540 ± 55	51.6 ± 1.5	200.2 ± 4.4	93.6 ± 6.6	44.4 ± 2.9
	F	5	480 ± 31	48.6 ± 0.9	193.0 ± 3.9	85.0 ± 10.7	40.8 ± 2.2
M. serrator	M	10	524 ± 45	58.1 ± 1.5	236.3 ± 9.0	78.0 ± 6.1	46.6 ± 1.6
	F	10	506 ± 41	54.4 ± 2.6	216.8 ± 9.1	70.7 ± 6.0	45.1 ± 2.8
M. squamatus	M	8	564 ± 61	55.6 ± 1.4	249.0 ± 6.5	98.5 ± 5.3	46.8 ± 0.7
	F	6	570 ± 53	50.5 ± 2.0	235.5 ± 11.9	94.0 ± 5.8	45.7 ± 2.3
M. merganser	M	10	624 ± 40	55.5 ± 3.6	266.9 ± 5.5	104.2 ± 8.1	51.9 ± 1.7
	F	10	541 ± 33	50.6 ± 2.3	239.0 ± 3.5	92.0 ± 3.5	46.7 ± 1.3

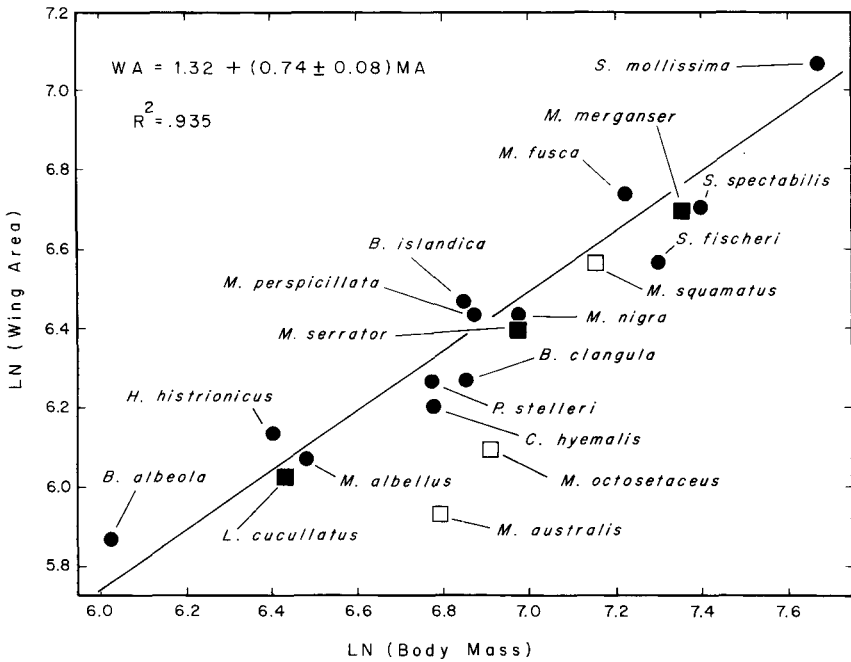a Sample sizes for total length were 3, 4.

FIG. 2.   Logarithmic plot of mean wing areas on mean body masses for extant Mergini; mergansers shown as squares, other species as circles. Regression equation (geometric-mean fit) excludes three estimated points for *Mergus* (hollow squares); slope given ±2 standard errors.

of sea duck except the extinct Labrador Duck (*Camptorhynchus labradorius*) and three species of *Mergus,* including *M. australis.* For the latter, wing areas were estimated using a regression of mean wing areas on mean wing lengths for the three species of merganser for which both data were available (N = 3, log-transformed data, $r = 0.999$). These estimates were 371 cm^2 for *M. australis,* 450 cm^2 for *M. octosetaceus,* and 722 cm^2 for *M. squamatus;* together with the corresponding estimates for body mass (detailed above), rough estimates of wing-loadings (g·cm^{-2}) were 2.42, 2.18, and 1.71, respectively. The estimates for *M. octosetaceus* and especially *M. australis* were high relative to those for other *Mergus* (unweighted mean of species = 1.67, 2 species, N = 4 wing areas), *Lophodytes* (1.50, 1 species, N = 6), *Mergellus* (1.52, 1 species, N = 3), *Bucephala* (1.50, 3 species, N = 20), *Clangula* (1.76, 1 species, N = 5), *Melanitta* (1.62, 3 species, N = 18), *Histrionicus* (1.32, 1 species, N = 8), *Somateria* (1.93, 3 species, N = 6), and *Polysticta* (1.68, 1 species, N = 1).

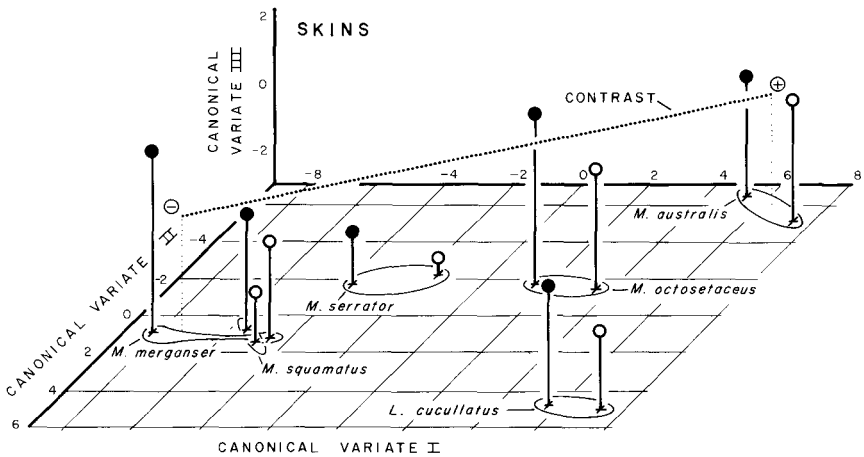A logarithmic plot of mean wing areas and body masses of 16 extant

FIG. 3.   Plot of first three canonical variates of seven external measurements of mergansers. Mean scores of species-sex groups are plotted; males are represented by solid circles, females by hollow circles. Oblique dashed axis labelled "contrast" depicts the approximate orientation of canonical contrast between *M. australis* and other species.

Mergini revealed a strong allometric relationship between the variables (Fig. 2), one which was not significantly different ($P > 0.05$) from that preserving geometric similarity (slope relating an area with mass expected to be 0.67; Gould 1966). the estimated points for the three *Mergus* lacking data were plotted but were not included in the regression. The pronounced negative deviation of *M. australis* (Euclidean distance from line = 0.35) and *M. octosetaceus* (distance = 0.25) from the tribal line reflects their relatively heavy wing-loadings (Fig. 2). The clarity of the allometric relationship indicates that wing-loadings were largely a function of body mass (with the possible exception of the two austral *Mergus*); there was little clustering of congeners, including most mergansers.

   Canonical analysis of external measurements. —A CA of external measurements produced significant dispersion of species-sex groups (Wilks' lambda = 0.0002; df = 6, 11, 87; $P < 0.001$). Stepwise MANOVAs revealed that these multivariate differences involved significant interspecific (Wilks' lambda = 0.11; df = 3, 1, 87; $P < 0.001$) and intersexual (Wilks' lambda = 0.38; df = 2, 1, 87; $P < 0.001$) effects. The first three canonical variates together accounted for over 95% of the total intergroup dispersion and included those dimensions in which *M. australis* differed from the other taxa.

   The first canonical variate (CV-I) encapsulated roughly two-thirds of the total intergroup dispersion in external measurements (Table 3, Fig.

TABLE 3
STANDARDIZED COEFFICIENTS AND SUMMARY STATISTICS FOR CANONICAL VARIATES OF EXTERNAL MEASUREMENTS SEPARATING SPECIES AND SEXES OF MERGANSERS

Character	All-group analysis			Contrast of *Mergus australis*
	CV-I	CV-II	CV-III	
Total length	−0.06	−0.09	0.28	0.04
Culmen length	0.16	−0.77	0.06	0.65
Nail width	0.44	−0.01	0.58	0.43
Wing length	−0.98	0.55	−0.46	−1.10
Tail length	0.11	0.23	0.76	−0.03
Tarsus length	−0.39	−0.41	0.17	−0.03
Middle-toe length	0.02	−0.10	0.34	0.07
Eigenvalue	34.3	13.0	2.3	13.6
Variance (%)	67.0	25.3	4.5	—
Canonical *R*	0.99	0.96	0.83	0.97

3) and involved both interspecific (F = 572.43; df = 5, 87; P < 0.0001) and intersexual differences (F = 90.50; df = 1, 87; P < 0.0001; ANOVA of scores). Canonical coefficients indicate that CV-I primarily contrasted lengths of the wing and tarsus with nail width (Table 3); positions of species and sexes on this axis shows that CV-I is strongly inversely correlated with overall body size (Fig. 3). Large *M. merganser* had the lowest scores on CV-I, followed closely by *M. squamatus* and *M. serrator*, and ultimately the high-scoring *M. octosetaceus, M. australis,* and *L. cucullatus*; males had lower scores than females in all species (Fig. 3).

CV-II described a strikingly different multivariate axis, one involving strong interspecific (F = 215.83; df = 5, 87; P < 0.0001) and less pronounced intersexual differences (F = 7.46; df = 1, 87; P < 0.01; ANOVA of scores). This variate contrasted lengths of the culmen and tarsus with the lengths of the wing and tail (Table 3). *M. australis* had the lowest scores on CV-II, indicating that this species had long bills and tarsi relative to their wing and tail lengths. *L. cucullatus* had opposite proportions, and the remaining *Mergus* had intermediate scores; males tended to have slightly lower scores than females within species (Fig. 3).

The third canonical variate (CV-III) for external measurements incorporated both interspecific (F = 27.96; df = 5, 87; P < 0.0001) and intersexual differences (F = 39.20; df = 1, 87; P < 0.0001; ANOVA of scores). CV-III contrasted wing length with other measurements, especially nail width, tail length, and middle-toe length (Table 3). *M. serrator* had comparatively low scores on this axis, indicating that this species had

long wings relative to their tail lengths, nail widths, and (to a lesser degree) other external measurements (Fig. 3). The high scores of *M. merganser* and *M. octosetaceus* reflected their opposite proportions, and other species were intermediate on this axis; males exceeded females in all species on CV-III.

A canonical contrast between *M. australis* and the other species using external measurements provided good separation of the insular form from other mergansers ($F = 382.30$; df = 3, 85; $P < 0.0001$). Canonical coefficients show that this contrast primarily contrasted wing length with culmen length and nail width (Table 3). Positions of species-sex groups along the contrast indicate that the axis was oriented diagonally with respect to canonical variates I and II and that *M. australis* was distinguished most clearly by its relatively short wings (Fig. 3).

Univariate comparisons of skeletal measurements.—With few exceptions, means of skeletal measurements followed overall body size (total length or body mass) in interspecific rankings (Table 4); *M. squamatus* (not tabulated), represented by a single skeleton, was intermediate between *M. serrator* and *M. merganser* in skeletal measurements. As in external measurements, males exceeded ($P \leq 0.01$) females in skeletal dimensions (Table 4). Several skeletal measurements, however, deviated from the general interspecific size rankings: bill length, scapula length, sternal caudal width, and sternal carina depth (Table 4). Skeletal bill lengths of *M. australis* were disproportionately large, exceeding those of the generally larger *M. serrator, M. squamatus,* and *M. merganser.* Scapula lengths, sternal caudal widths, and sternal carina lengths of *M. australis,* however, were the smallest of all the species compared, including *L. cucullatus* (Table 4).

Intra-alar skeletal proportions.—Mean skeletal wing lengths differed among species ($F = 748.48$; df = 3, 70; $P < 0.0001$) and between sexes ($F = 59.06$; df = 1, 70; $P < 0.0001$) and followed interspecific rankings in body size ($\bar{x} \pm s, n$): *L. cucullatus* (191.5 ± 6.4, 24), *M. australis* (194.6 ± 6.3, 3), *M. serrator* (245.9 ± 9.9, 25), *M. squamatus* (250.6, 1), and *M. merganser* (268.6 ± 15.8, 26). However, the proportions of skeletal wing length contributed by constituent elements differed (ANOVAs of transformed proportions) among species, many of these differences being attributed to the unusual proportions of *M. australis* and, to a lesser degree, overall size; intersexual differences in proportions were not significant in any element ($P > 0.10$). Humeral proportions differed among species ($F = 17.14$; df = 4, 74; $P < 0.0001$), constituted an average of 35.7% of skeletal wing length in *M. australis,* but accounted for only 34.1–34.9% of the wing in the other species compared. Ulnar proportions increased with overall size of species ($F = 14.65$; df = 4, 74; $P < 0.0001$), ranging

TABLE 4

SUMMARY STATISTICS (MEAN ± SD [N]) FOR SELECTED SKELETAL MEASUREMENTS (MM) OF MERGANSERS BY SPECIES AND SEX

Character	L. cucullatus		M. australis		M. serrator		M. merganser	
	Males	Females	Males	Females	Males	Females	Males	Females
Bill length	45.6 ± 1.5 (14)	42.9 ± 1.5 (15)	65.6 (1)	61.3 ± 1.8 (2)	65.0 ± 2.9 (16)	59.0 ± 1.5 (11)	66.8 ± 2.0 (14)	57.7 ± 3.1 (15)
Humerus length	67.8 ± 1.1 (15)	64.9 ± 1.3 (14)	72.1 (1)	68.3 ± 0.7 (2)	88.2 ± 2.4 (16)	81.6 ± 1.7 (12)	96.4 ± 1.8 (14)	88.2 ± 3.2 (16)
Ulna length	55.5 ± 1.3 (14)	53.1 ± 1.2 (14)	57.7 (1)	54.8 ± 0.3 (2)	72.8 ± 1.8 (16)	68.1 ± 0.1 (12)	81.4 ± 1.6 (14)	74.2 ± 2.8 (14)
Carpometacarpus length	40.8 ± 1.0 (15)	39.2 ± 1.2 (15)	40.7 (1)	38.7 ± 0.1 (2)	51.4 ± 1.5 (16)	47.9 ± 0.9 (12)	58.7 ± 1.2 (14)	53.1 ± 2.1 (15)
Digit-II, Ph. 1 length	17.2 ± 0.5 (15)	16.3 ± 0.6 (15)	16.2 (1)	15.5 ± 0.1 (2)	21.8 ± 0.6 (16)	20.0 ± 0.5 (12)	24.0 ± 0.6 (14)	21.6 ± 0.8 (16)
Ph. 2 length	14.5 ± 1.0 (12)	13.5 ± 0.9 (14)	15.1 (1)	13.8 ± 0.3 (2)	18.4 ± 0.7 (15)	17.0 ± 0.5 (10)	20.8 ± 0.7 (14)	18.4 ± 1.1 (15)
Femur length	40.3 ± 0.8 (15)	37.8 ± 1.0 (14)	45.5 (1)	42.8 ± 0.4 (2)	47.0 ± 1.3 (16)	43.6 ± 1.0 (12)	53.7 ± 0.8 (14)	48.3 ± 1.9 (16)
Tibiotarsus length	65.4 ± 1.2 (15)	62.0 ± 1.6 (15)	— (0)	77.3 ± 0.5 (2)	87.1 ± 2.6 (16)	81.3 ± 2.6 (11)	97.2 ± 2.0 (14)	87.9 ± 2.8 (15)
Scapula length	59.4 ± 1.8 (15)	55.8 ± 1.3 (15)	58.6 ± 4.4 (2)	56.0 ± 0.5 (2)	69.7 ± 2.6 (15)	62.5 ± 1.6 (12)	79.5 ± 1.5 (14)	69.5 ± 2.9 (16)
Sternum carina length	83.8 ± 2.5 (15)	78.2 ± 2.0 (15)	89.4 (1)	82.8 ± 0.8 (2)	106.8 ± 4.2 (16)	95.9 ± 2.2 (12)	121.5 ± 3.1 (14)	106.1 ± 3.5 (16)
Caudal width	51.2 ± 2.0 (15)	49.3 ± 1.7 (15)	49.4 (1)	46.6 ± 0.7 (2)	56.8 ± 2.1 (15)	52.6 ± 2.1 (12)	63.7 ± 1.9 (14)	57.2 ± 2.0 (16)
carina depth	22.1 ± 0.8 (15)	20.4 ± 0.8 (15)	19.4 (1)	18.1 ± 0.5 (2)	30.4 ± 1.0 (16)	26.9 ± 0.6 (12)	32.0 ± 1.3 (14)	27.2 ± 1.4 (16)

from 28.4% in *L. cucullatus* to 29.0% in *M. merganser*. Intra-alar proportions of the carpometacarpus ($F = 21.19$; df = 4, 74; $P < 0.0001$) and proximal (first) phalanx of digit-II ($F = 14.65$; df = 4, 74; $P < 0.0001$) opposed those of the humerus, being smaller in *M. australis* (20.2% and 8.1%, respectively) than in the other species (20.4–20.9% and 8.5–8.7%, respectively). The distal (second) phalanx of digit-II had equal ($F = 0.07$; df = 4, 74; $P > 0.95$) proportions in all species (7.3%).

Canonical analysis of complete skeletons. —Suites of 33 skeletal measurements provided the basis for powerful separation of the eight species-sex groups available (Wilks' lambda = 0.0002; df = 10, 7, 83; $P < 0.001$); the single skeleton of *M. squamatus* was plotted on the axes based on the other three species. Stepwise MANOVAs documented significant interspecific (Wilks' lambda = 0.053; df = 13, 1, 83; $P < 0.001$) and intersexual differences (Wilks' lambda = 0.29; df = 5, 1, 83; $P < 0.001$) in these 33-dimensional comparisons. The first three canonical variates accounted for over 95% of the total intergroup variation in skeletons (Table 5).

The first canonical variate (CV-I) displayed significant interspecific ($F = 5079.52$; df = 3, 83; $P < 0.0001$) and intersexual differences ($F = 46.70$; df = 1, 83; $P < 0.0001$; ANOVA of scores) but primarily discriminated *Lophodytes* from *Mergus*; *M. australis* was slightly more similar to *Lophodytes* than its congeners on this axis (Fig. 4). Canonical coefficients for CV-I indicate that *Lophodytes* differed from other mergansers on a complex size-shape axis involving relative proportions of the skull, among elements within the wing and leg, and among dimensions of the pectoral and pelvic girdles (Table 5). Notable proportionalities of *Lophodytes* indicated by the coefficients were: skulls characterized by relatively short bills and long, deep crania; wings with relatively short ulnae and radii; and legs with relatively large femora. Within each species, males and slightly lower scores than females on CV-I (Fig. 4).

CV-II for complete skeletons accounted for an additional 7% of the total intergroup dispersion and included both interspecific ($F = 346.83$; df = 37.41; $P < 0.0001$) and intersexual differences ($F = 37.41$; df = 1, 83; $P < 0.0001$; ANOVA of scores). Mean scores (Fig. 4) indicate that CV-II, together with CV-III (discussed below) primarily discriminated *M. australis* from the other groups (including *Lophodytes*). Because of the small sample available for *M. australis,* interpretation of multivariate differences between *M. australis* and other mergansers must be conservative. Coefficients for CV-II (Table 5), together with the low scores of *M. australis,* primarily indicate that the species was characterized by relatively long bills, relatively short mid-wing elements, legs with relatively robust proximal elements and long tarsometatarsi, and sterna with shallow carinae.

TABLE 5
STANDARDIZED COEFFICIENTS AND SUMMARY STATISTICS FOR CANONICAL VARIATES OF
SKELETAL DIMENSIONS SEPARATING SPECIES AND SEXES OF MERGANSER

| Character	All-group analysis			Contrast of *M. australis*
	CV-I	CV-II	CV-III	
Bill length	−0.48	−0.65	0.15	−0.68
Cranium length	0.55	0.07	0.38	−0.08
Height	0.64	−0.03	0.03	0.03
Width	−0.38	0.12	−0.22	0.18
Humerus length	0.18	−0.26	−1.09	0.36
Head width	0.34	0.35	−0.13	0.39
LWM	0.03	−0.26	−0.28	−0.06
Radius length	−0.51	−0.38	0.13	−0.38
LWM	−0.05	0.17	−0.27	0.29
Ulna length	−0.66	0.24	−0.33	0.25
LWM	−0.48	0.26	0.16	0.08
Carpometacarpus length	0.60	0.87	0.25	0.64
Digit-II, Ph. 1 length	−0.08	0.39	−0.53	0.60
Ph. 2 length	−0.23	−0.53	0.23	−0.58
Femur length	0.65	0.05	0.76	−0.29
Head width	−0.68	−0.39	0.33	−0.59
LWM	0.25	0.23	0.03	0.23
Tibiotarsus length	−0.38	0.07	0.07	0.01
LWM	−0.43	−0.34	0.03	−0.36
Tarsometatarsus length	−0.41	−0.65	−0.23	−0.47
LMW	−0.01	−0.23	0.39	−0.39
Digit-III length	0.30	0.06	0.15	0.02
Scapula length	0.27	0.14	−0.14	0.21
Coracoid length	−0.31	0.24	0.52	−0.08
Basal width	0.20	0.28	0.08	0.23
Sternal carina length	0.14	0.10	0.07	0.05
Basin length	−0.20	0.19	−0.07	0.18
Least width	0.03	−0.29	0.28	−0.39
Caudal width	0.15	0.14	−0.13	0.20
Carina depth	−0.00	0.41	0.02	0.37
Furcula height	−0.16	−0.08	0.39	−0.30
Synsacrum length	−0.15	−0.06	0.07	−0.09
Interacetabular width	0.28	0.13	0.35	−0.05
Eigenvalue	186.8	15.2	11.7	12.7
Variance (%)	84.1	6.8	5.3	—
Canonical *R*	1.00	0.97	0.96	0.96
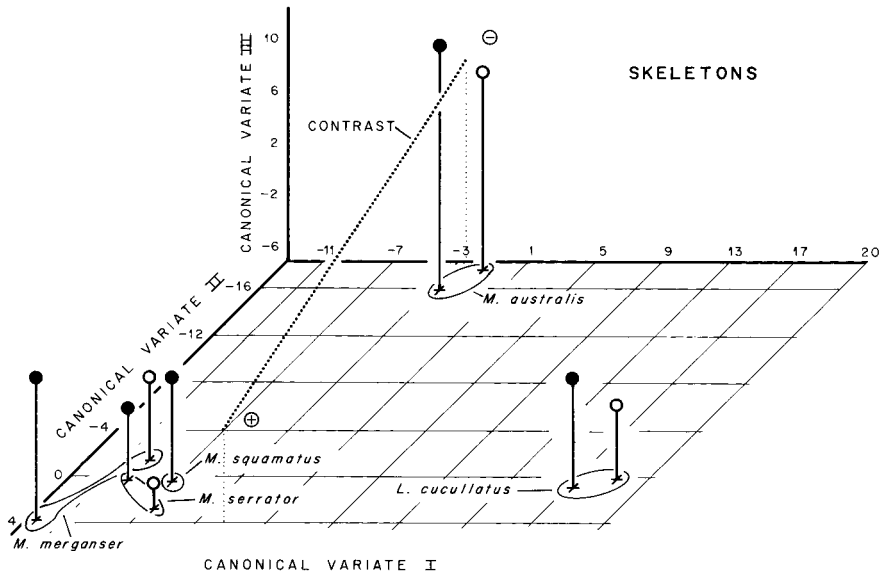
Fig. 4. Plot of first three canonical variates of 33 skeletal measurements of mergansers. Mean scores of species-sex groups are plotted; males are represented by solid circles, females by hollow circles. Oblique dashed axis labelled "contrast" depicts the approximate orientation of canonical contrast between *M. australis* and other species.

The third axis (CV-III) for complete skeletons also incorporated significant interspecific ($F = 227.47$; df $= 3$, 83; $P < 0.0001$) and intersexual differences ($F = 126.26$; df $= 1$, 83; $P < 0.0001$; ANOVA of scores) but mostly represented residual differences between *M. australis* and other species not accounted for by CV-II; CV-III also provided a lesser discrimination of *M. serrator* (Fig. 4). Coefficients for CV-III, together with the high scores of *M. australis,* reflected the small size of most wing elements relative to the lengths of the femur, coracoid, furcula, and interacetabular width (Table 5).

The fourth canonical variate (not tabulated) accounted for another 3.2% of the intergroup variance but served largely to separate further *M. serrator* from its congeners ($F = 73.03$; df $= 3$, 83; $P < 0.0001$) and to discriminate sexes ($F = 97.04$; df $= 1$, 83; $P < 0.0001$) within species (ANOVA of scores). The remaining three variates for complete skeletons together incorporated less than 1% of the total dispersion, contributed mostly to intersexual discrimination, and are not considered further.

The distinctive skeletal proportions of *M. australis* were summarized in a canonical contrast between this species and the other species, which

TABLE 6
STANDARDIZED COEFFICIENTS AND SUMMARY STATISTICS FOR CANONICAL VARIATES OF
STERNAL DIMENSIONS SEPARATING SPECIES AND SEXES OF MERGANSER

Character	All-group analysis			Contrast of *M. australis*
	CV-I	CV-II	CV-III	
Carina length	−0.45	−0.40	−1.06	0.18
Basin length	−0.23	−0.29	1.04	−0.27
Least width	−0.12	−0.39	−0.54	0.40
Caudal width	−0.01	0.22	0.90	−0.43
Carina depth	−0.49	0.90	0.11	−0.92
Eigenvalue	38.6	2.5	1.3	3.2
Variance (%)	90.6	5.9	3.1	—
Canonical *R*	0.99	0.85	0.76	0.87

maximally distinguished *M. australis* from all other groups independently of other interspecific differences and all intersexual differences ($F = 51.00$; df = 15, 69; $P < 0.001$). Mean scores of species and coefficients of variables for the axis showed the contrast to be largely a linear combination of CV-II and CV-III in the all-group analysis, with a lesser contribution from CV-I (Fig. 4). The coefficients for the contrast (Table 5) and the low scores of *M. australis* on this axis primarily reflected the following *relative* proportions: long bills; wing bones generally small, specifically the humerus, carpometacarpus, and proximal phalanx of the major digit; proximal and distal leg elements disproportionately long; and sterna with relatively shallow carinae and small caudal widths.

Canonical analysis of sternal measurements. — A separate CA of the five sternal measurements permitted the plotting of the single specimen of *M. octosetaceus* and a closer examination of this important and relatively complex part of the pectoral girdle. The analysis documented significant differences among groups (Wilks' lambda = 0.003; df = 5, 7, 81; $P < 0.001$), and included both interspecific (Wilks' lambda = 0.39; df = 5, 1, 81; $P < 0.001$) and intersexual differences (Wilks' lambda = 0.38; df = 2, 1, 81; $P < 0.001$). Interspecific differences were significant on each of the first three variates ($F = 895.73$, 64.28, and 30.71, respectively; df = 3, 81; $P < 0.0001$), but sexual differences were limited to the first variate ($F = 134.95$; df = 1, 81; $P < 0.00001$; ANOVA of scores).

Coefficients of CV-I for sterna were of the same sign, suggesting that the axis essentially reflected "sternal size" (Table 6); differences in magnitude among coefficients, however, show that this was not isometric size and that widths contributed little to this axis. CV-I primarily separated
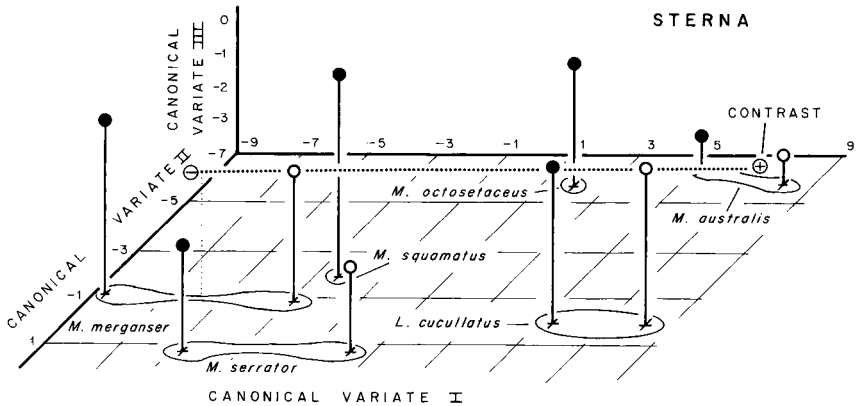
FIG. 5. Plot of first three canonical variates of five sternal measurements of mergansers. Mean scores of species-sex groups are plotted; males are represented by solid circles, females by hollow circles. Oblique dashed axis labelled "contrast" depicts the approximate orientation of canonical contrast between *M. australis* and other species.

the three smaller, "primitive" species (*L. cucullatus, M. australis,* and *M. octosetaceus*) from the larger, more derived species and distinguished sexes within species (Fig. 5). The two austral species were poorly represented, however, and multivariate inferences must be made conservatively. CV-II clearly separated *M. australis* and *M. octosetaceus* from the other mergansers (Fig. 5); coefficients indicate that the former were characterized by sterna with relatively shallow carinae and small caudal widths (Table 6). CV-III provided further separation between *M. australis* and other mergansers, including *M. octosetaceus* (Fig. 5), and primarily reflected the small differences between lengths of the carina and basin and between the two sternal widths in *M. australis* (Table 6). A canonical contrast of *M. australis* (Wilks' lambda = 0.24; df = 3, 1, 81; $P < 0.001$) summarized these sternal differences, and combined the reduced carina depth with the "squarish" ventral and lateral aspects of the sterna of *M. australis* indicated in CV-III of the all-group CA (Table 6, Fig. 5).

DISCUSSION

Phylogenetic and biogeographic inferences. — The evolutionary tree proposed (Fig. 1) differs from previous hypotheses concerning *M. australis*; earlier workers either considered the relationships of *M. australis* to be unresolved (Johnsgard 1961a) or suggested that *M. australis* was an isolated relative of an extant northern-hemisphere congener, most probably *M. squamatus* or *M. merganser* (Humphrey 1955, Johnsgard 1965, Kear and Scarlett 1970, Weller 1980). The tree presented in this paper also

suggests several unexpected historical patterns. First, there is a pronounced trend toward increasing body size, and the relatively small size of *M. australis* is apparently the direct result of phylogeny rather than a secondary (derived) decrease in size. Second, *M. australis* and *M. octosetaceus* are representatives of an early grade of mergansers limited to the southern hemisphere. Although *Mergus* is known from subfossil remains on the mainland of New Zealand, the phylogenetic relationship of these to *M. australis* is not known. It should be noted that a comparatively long (82-mm) subfossil humerus from South Island, New Zealand, attributed by Kear and Scarlett (1970) to a possibly larger congener of *M. australis,* was reidentified by Olson (1977) as that of a coot (*Fulica*). Third, morphological similarities between *M. australis* and *M. octosetaceus* are the result of shared primitive characters (symplesiomorphies; e.g., head color of downy young) or convergence (homoplasies; e.g., sexual monochromatism), and do not reflect close relationship. Fourth, many of the unique plumage characters of *M. australis* are uniquely derived (autapomorphies) and, although not useful for determining relationships, are informative regarding the evolutionary characteristics of this peculiar insular form.

Morphometrics of mergansers. — Mergansers, like all sea ducks, are typical power-fliers, using rapid wing beats in normal flight (Meinertzhagen 1955) and being characterized by moderately high wing-loadings and comparatively pointed wings with reduced slotting between remiges (Raikow 1973; Greenewalt 1962; Livezey and Humphrey 1986, this study). A direct relationship between wing-loading and body size in the Mergini (Fig. 2), a simple outcome of the more rapid increases in mass (a three-dimensional variable) than wing area (a two-dimensional variable), generally produces the greatest wing-loadings in the largest species. A similar allometry of wing area with body mass pertains to birds generally (Poole 1938, Hartman 1961, Greenewalt 1962). Projected estimates for *M. australis* and *M. octosetaceus,* however, suggest that these species possess(ed) wing-loadings comparatively high for the Mergini (Fig. 2). The estimated wing-loading for *M. australis,* roughly 2.4 $g \cdot cm^{-2}$, is especially high (even allowing for possible over-estimation) and approximates the threshold of flightlessness (2.5 $g \cdot cm^{-2}$) hypothesized by Meunier (1951). The estimate for *M. australis* is comparable to the wing-loadings of Flying Steamer-Ducks (*Tachyeres patachonicus*), a species in which flight is heavy in most individuals and impossible for the heaviest males in some marine populations (Humphrey and Livezey 1982). Consequently, it is noteworthy that the *M. australis* observed in flight by Lord Ranfurly was, based on its vocalizations, a female (Kear and Scarlett 1970). I suspect that the heaviest males of *M. australis,* if not permanently flightless, were able to take flight only when aided by the lift provided by a strong head-wind

(presumably common in the Aucklands), and with substantial room for take-off (on water) or from a decline (on land).

Statistical comparisons of external measurements not only confirmed the comparatively small size and relatively short wings of *M. australis* but revealed that the species possessed relatively short tails and exceptionally long bills (Tables 2, 3; Fig. 3). A significant portion of the morphometric differences among mergansers, however, was related to phylogeny in that *L. cucullatus, M. australis,* and *M. octosetaceus* were more similar (symplesiomorphically) to each other than to other *Mergus* on the most important axis of variation (CV-I, Fig. 3). *M. octosetaceus* was most similar to *M. australis* in its external dimensions (Fig. 3). *M. octosetaceus* is specialized for life along fast-flowing tropical rivers (Partridge 1956), and *M. australis* is believed to have inhabited primarily riverine habitats in the Auckland Islands (Delacour 1959, Kear and Scarlett 1970). Therefore, although the riverine habitats of *M. octosetaceus* and *M. australis* differed greatly in ecological characteristics, morphometric similarity between the austral species of *Mergus* may reflect, in part, convergence associated with similar feeding habits.

Analyses of skeletal measurements confirmed the long bills and *relatively* short wing elements of *M. australis* as well as a diversity of other, less obvious differences in proportions (Tables 4, 5; Fig. 4). *Absolute* length of the wing skeleton in *M. australis* was very similar to that in *L. cucullatus*; lengths of the manus (carpometacarpus and major digit) were equal in the two species, indicating that the shorter external wing lengths of *M. australis* result from a roughly 8-mm shortening of the primary remiges. *M. australis* also was characterized by disproportionately short mid-wing elements and relatively weakly keeled, caudally flared sterna (Table 6; Figs. 4, 5). Disproportionately short mid-wing elements and (particularly) reduced sternal carinae are typical of most flight-impaired and flightless species of carinate birds, including those of grebes (Podicipedidae; Livezey 1989), steamer-ducks (Anatidae, *Tachyeres*; Livezey and Humphrey 1986), and rails (Rallidae; Olson 1973). Although not represented by a complete skeleton, *M. octosetaceus* was most similar to *M. australis* in sternal conformation (Fig. 5); given the more typical sterna of *L. cucullatus* and the remaining *Mergus,* the similarity between the two austral species is evidently convergent.

Paedomorphosis in M. australis.—Paedomorphosis, ". . . retention of ancestral juvenile characters in the descendant adult phase . . ." (McNamara 1986), is the result of the alteration of developmental patterns; a frequently cited form of such heterochrony is neoteny, the retardation of the growth of a body part relative to general developmental state (Gould 1977). Neoteny of the pectoral girdle has been inferred as the ontogenetic

basis for the "degenerate" conditions of sterna and wing elements of a number of flightless birds (Lowe 1928, Olson 1973, Diamond 1981, James and Olson 1983) as well as the more subtle changes in skeletal proportions of flightless steamer-ducks (Livezey and Humphrey 1986). The wing skeleton and sternum, and the short primary remiges of *M. australis,* could be characterized similarly. Both sexes of *M. australis* have adult plumages that closely resemble that of juveniles of mergansers generally, and juvenal plumages of *Mergus* can be presumed to be primitive. Therefore, by definition, the adult plumage of male *M. australis* also is paedomorphic; perhaps the condition might be more precisely termed "paedochromatic." Whether this plumage change is the result of neoteny is not known, but such a developmental mechanism may underlie the reduced sexual dichromatism characteristic of many insular populations of anatids (Lack 1970, Weller 1980).

Morphological and ecological correlates of insularity in M. australis.— Weller (1980) described a number of unusual phenotypic features, averred to represent adaptive changes from the ancestral condition, which tend to characterize insular waterfowl: (1) reduced mobility, sometimes flightlessness; (2) reduced body size; (3) reduced sexual dichromatism; (4) development of white eye-rings; (5) comparatively dark natal plumages; (6) exceptional tameness of adults; (7) niche expansion, often to include marine habitats; (8) relaxed seasonality of nesting; (9) long-term pairbonds; (10) small clutch size; and (11) large egg size. Of these, four clearly characterized *M. australis*—reduced flight capacity, reduced sexual dichromatism, dark natal plumages, and tameness (the last based on a virtual lack of escape behavior observed by early collectors). The small size of *M. australis* conforms with the general pattern among insular ducks, but it appears to have been the result of phylogeny (i.e., the species represents a branch from the early grade of smaller mergansers; Fig. 1) instead of representing a decrease in size from a larger "continental" ancestor. The small size of *M. australis* is notable, however, in that *increased* body size is typical of avian lineages undergoing the loss of flight (Pennycuick 1975).

Two other correlates of insularity—increased utilization of marine habitat and long-term pairbonds—find weak support in *M. australis.* Although it is believed to have been primarily reliant on freshwater rivers, *M. australis* were observed on salt water near river mouths, and specimens have contained marine organisms (Kear and Scarlett 1970); given that most mergansers have largely freshwater habitats (the sole exception being *M. serrator*), this evidence suggests a comparatively broad, presumably derived, feeding niche. The disproportionately long bills of *M. australis* also may provide evidence of a diversified, more marine diet; for example, *M. serrator,* a comparatively marine species of moderate size, has a longer

bill than the larger freshwater *M. merganser* (Table 2). Existence of long-term pair bonds in *M. australis* is suggested by the presence of both adults with broods and the observation of paired adults from October to (perhaps) July (Kear and Scarlett 1970). The development of a white eye-ring clearly does not apply to *M. australis,* and the remaining three correlates — relaxed nesting schedule, decreased clutch size, and increased egg size — cannot be evaluated for *M. australis* because of lack of information.

Significance of flight impairment in M. australis. — It appears likely that adults and especially the downy young of *M. australis* were vulnerable, even prior to the arrival of humans, to a variety of avian and subaquatic predators, including Skuas (*Catharacta skua*), Peregrine Falcons (*Falco peregrinus*), predaceous fish, eels, and sea lions (Kear and Scarlett 1970). Although the introduction of exotic predators to the Auckland Islands, notably cats and pigs, posed a significant threat to the endemic birds of the Auckland Islands (Kear and Scarlett 1970), the reduced flight capacity of *M. australis* cannot be considered an evolutionary "response" to a lack of predators. Reduced predation pressure is invoked frequently in discussions of flightlessness in insular birds (e.g., Snow 1966; Weller 1975, 1980); paradoxically, concealment from predators is proposed by some to explain, at least in part, the reduced sexual dichromatism and dark natal plumages of some of these same species (Sibley 1957, Kear and Scarlett 1970, Lack 1970, Weller 1980). It appears that the evolutionary reduction or loss of flight capacity in *M. australis,* a species which did not use its wings in diving, reflects instead the developmentally economical reduction of the pectoral apparatus rendered of decreased selective importance in environments permitting year-round habitation.

LITERATURE CITED

BARTMANN, W. 1988. New observations on the Brazilian Merganser. Wildfowl 39:7–14.

BROOKS, A. 1945. The under-water actions of diving ducks. Auk 62:517–523.

CLARK, R. J. 1971. Wing-loading—a plea for consistency in usage. Auk 88:927–928.

DELACOUR, J. 1959. The waterfowl of the world. Vol. 3. Country Life Ltd., London, England.

DEMENT'EV, G. P. AND N. A. GLADKOV (EDS.). 1967. Birds of the Soviet Union. Vol. IV. Israel Progr. Sci. Trans., Jerusalem, Israel.

DIAMOND, J. M. 1981. Flightlessness and fear of flying in island species. Nature 293:507–508.

DIXON, W. J. (CHIEF ED.). 1985. BMDP statistical software. Univ. California Press, Berkeley, California.

FRANE, J. 1985. PAM: description and estimation of missing data. Pp. 217–234 *in* BMDP statistical software (W. J. Dixon, chief ed.). Univ. California Press, Berkeley, California.

GOULD, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. 41:587–640.

———. 1977. Ontogeny and phylogeny. Belknap, Cambridge, Massachusetts.

GRAY, G. R. 1844. The genera of birds. Vol. 3. Longmans, London, England.

GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. Smithsonian Misc. Coll. 144:1–46.

GREENWAY, J. C., JR. 1967. Extinct and vanishing birds of the world. 2nd ed. Dover Publ., New York, New York.

HARTMAN, F. A. 1961. Locomotor mechanisms of birds. Smithsonian Misc. Coll. 143:1–91.

HUMPHREY, P. S. 1955. The relationships of the sea ducks (Tribe Mergini). Ph.D. diss., Univ. Michigan, Ann Arbor, Michigan.

———. 1957. Observations on the diving of the Surf Scoter (*Melanitta perspicillata*). Auk 74:392–394.

———. 1958. Diving of a captive Common Eider. Condor 60:408–410.

——— AND B. C. LIVEZEY. 1982. Flightlessness in Flying Steamer-Ducks. Auk 99:369–372.

JAMES, H. F. AND S. L. OLSON. 1983. Flightless birds. Natur. Hist. 92:30–40.

JENNRICH, R. AND P. SAMPSON. 1985. P7M: stepwise discriminant analysis. Pp. 519–537 *in* BMDP statistical software (W. J. Dixon, chief ed.). Univ. California Press, Berkeley, California.

JOHNSGARD, P. A. 1960. Classification and evolutionary relationships of the sea ducks. Condor 62:426–433.

———. 1961a. The taxonomy of the Anatidae—a behavioral analysis. Ibis 103a:71–85.

———. 1961b. The behavior and systematic position of the Hooded Merganser. Wilson Bull. 73:227–236.

———. 1965. Handbook of waterfowl behavior. Constable & Co., London, England.

———. 1978. Ducks, geese, and swans of the world. Univ. Nebraska Press, Lincoln, Nebraska.

JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19:497–499.

KEAR, J. AND R. J. SCARLETT. 1970. The Auckland Islands Merganser. Wildfowl 21:78–86.

KELSO, J. E. H. 1922. Birds using their wings as a means of propulsion under water. Auk 39:426–428.

LACK, D. 1970. The endemic ducks of remote islands. Wildfowl 21:5–10.

LIVEZEY, B. C. 1986. A phylogenetic analysis of Recent anseriform genera using morphological characters. Auk 103:737–754.

———. 1988. Morphometrics of flightlessness in the Alcidae. Auk 105:681–698.

———. 1989. Flightlessness in grebes (Aves, Podicipedidae): its independent evolution in three genera. Evolution 43:29–54.

——— AND P. S. HUMPHREY. 1984. Sexual dimorphism in continental steamer-ducks. Condor 86:368–377.

——— AND ———. 1986. Flightlessness in steamer-ducks (Anatidae: *Tachyeres*): its morphological bases and probable evolution. Evolution 40:540–558.

LOWE, P. R. 1928. A description of *Atlantisia rogersi,* the diminutive and flightless rail of Inaccessible Island (southern Atlantic), with some notes on flightless rails. Ibis 70:99–131.

LUTHER, D. 1967. Augestorbene und aussterbende Vogel: V. Falke 14:166–169.

MADGE, S. AND H. BURN. 1988. Waterfowl: an identification guide to the ducks, geese and swans of the world. Houghton Mifflin, Boston, Massachusetts.

MAGNAN, M. A. 1912. Modifications organiques conséctives chez les oiseaux à l'absence de vol. Bull. Mus. Nat. Paris 18:524–530.

———. 1922. Les caracteristiques des oiseaux suivant le mode de vol. Ann. Sci. Nat. (Ser. 10) 5:125–334.

MATHEWS, G. M. AND T. IREDALE. 1913. A reference list to the birds of New Zealand. Ibis 55:402–452.

MCNAMARA, K. J. 1986. A guide to the nomenclature of heterochrony. J. Paleontol. 60:4–13.

MEINERTZHAGEN, R. 1955. The speed and altitude of bird flight (with notes on other animals). Ibis 97:81–117.

MEUNIER, K. 1951. Korrelation und Umkonstruktion in den Grössenbeziehungen zwischen Vogelflügel und Vogelkörper. Biol. Gener. 19:403–443.

———. 1959. Die Grössenabhangigkeit der Korperform bei Vogeln. Z. Wiss. Zool. 162:328–355.

MILLIKEN, G. A. AND D. E. JOHNSON. 1984. Analysis of messy data. Van Nostrand, New York, New York.

MÜLLENHOFF, K. 1885. Die Grosse der Flugflachen. Pflueger's Arch. Ges. Physiol. 35:407–453.

OLSON, S. L. 1973. Evolution of the rails of the South Atlantic islands. (Aves: Rallidae). Smithsonian Contr. Zool. No. 152.

———. 1977. Notes on subfossil Anatidae from New Zealand, including a new species of Pink-eared Duck *Malacorhynchus.* Emu 77:132–135.

PARTRIDGE, W. H. 1956. Notes on the Brazilian Merganser in Argentina. Auk 73:473–488.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pp. 1–75 *in* Avian biology. Vol. 5 (D. S. Farner and J. R. King, eds.). Academic Press, New York, New York.

PHILLIPS, J. C. 1925. A natural history of the ducks. Vol. 3. Houghton Mifflin, Boston, Massachusetts.

PIMENTEL, R. A. 1979. Morphometrics: the multivariate analysis of biological data. Kendall/Hunt Publ. Co., Dubuque, Iowa.

POOLE, E. L. 1938. Weights and wing areas in North American birds. Auk 55:511–517.

RAIKOW, R. J. 1973. Locomotor mechanisms in North American ducks. Wilson Bull. 85:295–307.

RICKER, W. E. 1984. Computation and uses of central trend lines. Can. J. Zool. 62:1897–1905.

SCOTT, P. 1972. A coloured key to the wildfowl of the world. Wildfowl Trust, Slimbridge, England.

SIBLEY, C. G. 1957. The evolutionary and taxonomic significance of sexual dimorphism and hybridization in birds. Condor 59:166–191.

SNOW, B. K. 1966. Observations on the behaviour and ecology of the flightless cormorant *Nannopterum harrisi*. Ibis 108:265–280.

SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman, New York, New York.

TOWNSEND, C. W. 1909. The use of wings and feet by diving birds. Auk 26:234–248.

WELLER, M. W. 1975. Ecological studies of the Auckland Islands Flightless Teal. Auk 92: 280–297.

———. 1980. The island waterfowl. Iowa State Univ. Press, Ames, Iowa.

WILEY, E. O. 1981. Phylogenetics: the theory and practice of phylogenetic systematics. John Wiley and Son, New York, New York.

WILLIAMS, G. R. 1964. Extinction and the Anatidae of New Zealand. Wildfowl 15:140–146.

ERRATUM

In "Song repertoires and the singing behavior of male Northern Cardinals" by Gary Ritchison (Wilson Bull. 100:583–603), the penultimate sentence in paragraph 2 on page 597 should read "Groschupf (1985) reported that male Five-striped Sparrows (*Amphiza quinquestriata*) used more complex songs in intersexual contexts."

APPENDIX I

CHARACTER MATRIX FOR 22 MORPHOLOGICAL CHARACTERS OF *LOPHODYTES* AND *MERGUS*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Outgroups[b]	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
L. cucullatus	a	b	a	a	a	a[c]	a	a	a	a	a	a	a	a	a	a	b	a	a	b	a	a
M. australis	b	b	a	a	b[c]	b	a[d]	a	b	b	b	a	a	a	c	b	—	—	—	a	a	a
M. octosetaceus	b	b	a	b	b[c]	b	a	b	a	a	a	a	a	a	a	c	c	b	a	a	a	b
M. serrator	b	b	b	b	b	b	a	b	a	a	a	b	b	b	b	a	a	a	a	c	a	a
M. squamatus	b	b	b	b	b	b	a	b	a	a	a	b	a	b	b	a	a	a	b	c	a	a
M. merganser	b	b	b	b	b	b	b	b	a	a	a	b	a	a	b	a	a	c	—	c	b	a

a States described in Table 1; dash indicates that state not comparable and treated as "missing" (see text).
b *Bucephala* spp., *Mergellus albellus*.
c Weakly developed, possibly intermediate.
d Vestigial.