

# MORPHOMETRIC COMPARISON OF SKELETONS OF THE WESTERN GREBE COMPLEX *AECHMOPHORUS* OF THE UNITED STATES AND CANADA<sup>1</sup>

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**Abstract.** Skeletal specimens of *Aechmophorus*—210 *occidentalis* (dark “phase”) and 77 *clarkii* (light “phase”)—were analyzed morphometrically using univariate and multivariate techniques to assess interspecific and intersexual skeletal variation; variation due to age and locale also was tested. *A. occidentalis* generally exceeded *A. clarkii* in skeletal dimensions; mean differences were less than 1 mm for widths of elements and approximated 5 mm for lengths of major wing elements. Also, 5-vertebral notaria were more frequent in the larger *A. occidentalis* than in *A. clarkii*. Univariate sexual dimorphism was highly significant in all skeletal measurements, dimensions of males exceeding those of females. Stepwise canonical analyses of the four species-sex groups of *Aechmophorus* documented significant interspecific and intersexual differences in skeletons; interspecific differences in proportions within the pelvic limb and bill suggest differential refinement for locomotion and foraging. Multivariate sexual differences were more than twice as great as multivariate differences between species, and sexual dimorphism was significantly greater in *A. clarkii* than in *A. occidentalis*. Classification functions for skeletons of *Aechmophorus* of known sex permitted species identification for 85% of specimens. Identification of single elements to species does not appear to be feasible using mensural criteria. Lesser but significant multivariate variation in skeletons was attributable to age and locale of collection. Magnitude of interspecific differentiation in skeletal dimensions in *Aechmophorus* is small compared to that among species in other genera studied previously.

**Key words:** *Aechmophorus*; *Western grebes*; *sibling species*; *multivariate morphometrics*; *skeletal variation*; *sexual dimorphism*.

## INTRODUCTION

The Western and Clark’s grebes were described as *Podiceps occidentalis* and *P. clarkii*, respectively, by Lawrence (in Baird et al. 1858). Later the genus *Aechmophorus* was established for them by Coues (1862). Coues (1874) and Henshaw (1881) subsequently questioned their treatment as distinct species. In the first edition of the *Checklist of North American Birds* (AOU 1886), the two taxa were combined under the name *Aechmophorus occidentalis*, Clark’s Grebe being considered a light color phase of the Western Grebe. The smaller birds of both forms inhabiting the Mexican Plateau were separated as the subspecies *A. occidentalis clarkii* by Dickerman (1963). Evidence from assortative mating (Storer 1963, 1965; Lindvall 1976; Ratti 1979; Nuechterlein 1981a, 1981b) led to the two forms again being

considered separate species (AOU 1983). This and an earlier study (Dickerman 1973) prompted Dickerman (1986) to propose the subspecific name, *A. o. ephemeralis* for the “dark phase” Mexican birds and *A. c. transitionalis* for the “light phase” northern birds.

Although mensural differences between the Mexican races of the two species are not evident, reports of small differences between the northern forms (Ratti et al. 1983, Storer and Nuechterlein 1985) and differences in foraging behavior (Feerer 1977, Nuechterlein and Buitron 1989) suggest the possibility that the smaller interspecific differences as well as the previously documented sexual dimorphism (Palmer 1962, Storer and Nuechterlein 1985) might be related to foraging behavior.

Of the previous mensural comparisons of the two species, only that by Storer and Nuechterlein (1985) included skeletal measurements and that by Ratti et al. (1983), multivariate techniques.

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This is unfortunate given the utility of multivariate statistics in comparisons of closely related species (e.g., Carter 1984, Livezey and Humphrey 1986, Zink 1986, Atwood 1988).

To provide a morphological background for future studies on ecomorphological differences and possible future morphological divergences between the species, we present morphometric analyses of skeletal variation in the northern races of *Aechmophorus* associated with species and sex, with secondary consideration of latitude and age-related effects (as permitted by the data). Insufficient skeletal material of the Mexican races is available for analyses of these forms. Both univariate and multivariate statistical techniques were used, considering simultaneously the maximal number of sources of variation permitted by the samples available for study.

## MATERIALS AND METHODS

Most available skeletons of *Aechmophorus* in museum collections were taken when *clarkii* was included in *occidentalis* and therefore not identified to species according to the present concept. Hence, we relied primarily on specimens already in the collection of the University of Michigan Museum of Zoology for which such information is available. Most of these were salvaged (Nero 1960) or taken for pesticide studies (Herman et al. 1969, Storer and Nuechterlein 1985). In addition, 13 skeletons accompanied by pelts of the head were borrowed from the National Museum of Natural History. Samples of each species by locality are as follows: CANADA—Alberta; Moose Lake (54.4°N), 1 Western (WN), Lake Newell (50.6°N), 99 WN. Saskatchewan; Pasqua Lake (50.8°N), 4 WN. Manitoba; Pelican Lake (49.6°N), 1 WN. UNITED STATES—Washington; San Juan Island (48.5°N), 1 of unknown species (UNK). Utah; Box Elder Co. (41.5°N), 1 Clark's (CL). California; Eagle Lake (40.7°N), 4 WN, 1 CL; Clear Lake (39°N), 45 WN, 56 CL, 6 UNK; Topaz Lake (38.7°N), 34 WN, 7 CL; Mono Lake (38°N), 1 WN; Marin Co. (38°N), 5 WN; San Francisco Bay (38°N), 1 WN; Monterey Bay (36.7°N), 1 UNK; Santa Barbara (34.4°N), 2 WN, 1 CL, 1 UNK; San Diego (32.8°N), 3 UNK. New Mexico, Sierra Co. (35.9°N), 8 WN, 5 CL. In addition, 5 WN and 4 CL specimens from unspecified localities in California, and 1 WN and 5 CL from unknown localities were included in some analyses.

All Canadian specimens were assumed to be

TABLE 1. Numbers of skeletal specimens of *Aechmophorus* included in this study, by species, sex, and age-group; excludes 15 specimens lacking one or more grouping variables.

Species	Sex	Age group		
		Immature	Adult	Total
<i>A. occidentalis</i> <sup>a</sup>	M	53	85	138
	F	27	45	72
<i>A. clarkii</i> <sup>b</sup>	M	5	37	42
	F	0	35	35
Total	M	58	122	180
	F	27	80	107

<sup>a</sup> In total, 107 specimens (sexed combined) were taken from localities in the U.S., 103 specimens were collected in Canada.

<sup>b</sup> All specimens collected in the U.S.

Western Grebes because of the rareness (<1%) of Clark's Grebes in populations there during the period of collection. Identifications of other specimens were based on the facial pattern and bill color (Storer and Nuechterlein 1985). Flat pelts of most of the other specimens analyzed here were preserved. Specimens were sexed by examination of the gonads, and this was checked by the shape and depth of the bill. Age classes of specimens—"immatures" (fully grown but deemed young of the year) and "adults"—were determined using the size of the bursa cloacalis and relative ossification of the tarsometatarsus and the pons supratendineus of the tibiotarsus (Storer and Nuechterlein 1985). In total, 210 skeletons of *A. occidentalis* and 77 of *A. clarkii* of known sex and locality (Table 1), as well as 15 specimens lacking data on species, sex, or locality were included in this study.

The birds from Moose Lake (Alberta), Saskatchewan, Utah, and Topaz and Eagle lakes (California) were taken on the breeding grounds, as were most of those from Clear Lake (California), although the last were taken throughout the year and may include some migrants or wintering birds. The rest were taken during the migration period or on the wintering grounds. Based on dates of collection, sizes of gonads of collected birds, and the objectives and techniques of collection, we conclude that at least 75% of the total sample was collected on or near the breeding grounds of the specimens.

## MEASUREMENTS

Thirty-eight skeletal measurements were taken with dial calipers to the nearest 0.1 mm by Storer. Most of these are standard and adequately de-

TABLE 2. Summary statistics ( $\bar{x} \pm s$ , [n]) for selected skeletal measurements (mm) of *Aechmophorus*, by species and sex.

Measurement*	<i>A. occidentalis</i>		<i>A. clarkii</i>	
	Males	Females	Males	Females
Mandible length <sup>3,4,2</sup>	110.4 ± 4.0 (130)	95.2 ± 3.4 (60)	110.0 ± 4.1 (37)	91.5 ± 3.0 (30)
Postnarial maxillary length <sup>4,4,0</sup>	25.9 ± 1.3 (134)	21.7 ± 1.3 (71)	24.9 ± 1.1 (40)	20.4 ± 1.2 (34)
Coracoid length <sup>4,4,0</sup>	47.9 ± 1.4 (135)	44.0 ± 1.7 (74)	46.4 ± 1.3 (42)	41.9 ± 1.0 (35)
Humerus length <sup>4,4,2</sup>	122.7 ± 3.8 (116)	114.2 ± 3.8 (60)	119.1 ± 3.1 (26)	107.2 ± 3.4 (21)
Ulna length <sup>4,4,1</sup>	109.9 ± 3.7 (132)	102.5 ± 3.3 (72)	106.6 ± 3.3 (40)	97.0 ± 3.1 (35)
Carpometacarpus length <sup>4,4,1</sup>	54.0 ± 1.7 (133)	50.0 ± 1.8 (74)	52.4 ± 1.7 (41)	47.3 ± 1.6 (35)
Major digit, phalanx I length <sup>4,4,0</sup>	22.5 ± 0.9 (129)	21.3 ± 0.8 (71)	21.9 ± 0.9 (40)	20.4 ± 0.7 (35)
Femur length <sup>4,4,1</sup>	47.0 ± 1.5 (136)	43.8 ± 1.5 (72)	46.4 ± 1.3 (40)	42.2 ± 1.2 (33)
Tibiotarsus shaft length <sup>4,4,1</sup>	124.3 ± 3.7 (133)	115.0 ± 3.1 (74)	123.0 ± 3.5 (38)	111.3 ± 3.4 (31)
Tarsometatarsus length <sup>1,4,0</sup>	78.3 ± 2.5 (135)	72.3 ± 2.3 (74)	78.1 ± 2.3 (42)	70.8 ± 1.8 (35)

\* Significance levels of species, sex, and interaction effects in two-way ANOVAs: 0— $P > 0.05$ ; 1— $P < 0.05$ ; 2— $P < 0.005$ ; 3— $P < 0.0005$ ; 4— $P < 0.0001$ .

scribed by their names (Tables 2, 3), but some require more precise definition. Bill lengths were measured with rhamphotheca removed; "sternum width" was measured between the fourth incisurae intercostales on each side; "carpometacarpus height" was the maximum height of the bone perpendicular to the axis of the bone near the proximal end; widths of the appendicular elements were the maximal (proximal) widths perpendicular to the long axes of the bones; width of shaft of these bones was the least width perpendicular to the axis of the bone; "tibiotarsal shaft length" was the length of the shaft between the proximal articulating surface and the distal end of the bone; the "cnemial crest length" was the difference between the total length of the bone and the tibiotarsal shaft length; "patella length" was measured with the base of the element parallel to one arm of the calipers, and "patella width" was the maximal width at the base. Lengths of the pedal phalanges (excluding the unguis phalanges and digit I) were measured as depicted in Storer (1945); these were summed within digits to produce lengths of digits II, III, and IV. These analytical modifications resulted in the 31 variables used in the analyses.

In addition to these mensural data, the number of fused thoracic vertebrae forming the notarium and the number of free vertebrae between the notarium and the synsacrum were recorded. The numbers of these vertebrae show remarkable interspecific and modest intersexual variation in the Podicipedidae (Storer 1982).

#### STATISTICAL ANALYSES

Univariate comparisons were performed using two-way analyses of variance (ANOVA) based on untransformed data and treating species and sex as fixed effects. If main effects were significant ( $F$ -tests,  $P < 0.05$ ), pairwise differences among groups using  $t$ -tests and Bonferroni critical levels ( $P < 0.05/K$ , where  $K$  is the number of equivalent pairwise comparisons considered) were examined. Variances of species-sex groups in univariate ANOVAs were compared using two-way Levene's tests ( $T$ -values). Comparisons of proportions within the pelvic limb were performed using two-way ANOVA based on log-transformed ratios, the denominator being skeletal leg length (sum of lengths of femur, tibiotarsus, tarsometatarsus, and digit III).

Counts of fused and unfused thoracic verte-

TABLE 3. Correlation coefficients (boldface,  $P < 0.01$ ) between three canonical variates discriminating four species-sex groups of *Aechmophorus* and 34 "sheared" skeletal measurements (see text) and summary statistics.

Measurement*	Canonical variate		
	I	II	III
Mandible length*	<b>0.85</b>	<b>-0.19</b>	<b>0.17</b>
Bill length			
Hinge to tip	<b>0.32</b>	-0.00	0.01
Naris to tip	<b>0.16</b>	-0.02	0.03
Hinge to naris*	<b>0.72</b>	<b>0.20</b>	<b>-0.15</b>
Interorbital width	<b>0.39</b>	-0.10	0.01
Sternum width	0.09	-0.08	-0.12
Coracoid length*	<b>0.29</b>	<b>0.68</b>	-0.00
Humerus head width	0.10	<b>0.29</b>	-0.01
Ulna length*	-0.00	<b>0.75</b>	<b>0.26</b>
Proximal width	0.06	0.13	0.00
Carpometacarpus length*	0.09	<b>0.74</b>	<b>0.26</b>
Height	0.00	<b>0.31</b>	-0.11
Major alar digit, phalanx I length	<b>-0.22</b>	<b>0.49</b>	<b>0.15</b>
Pelvis, preacetabular length	<b>0.17</b>	0.00	0.06
Postacetabular length	0.03	0.12	-0.03
Least interacetabular width	0.09	-0.06	-0.00
Femur length	0.01	<b>0.18</b>	0.11
Proximal width	0.06	0.05	0.00
Least shaft width	0.06	<b>-0.16</b>	<b>-0.19</b>
Distal width	0.10	0.09	-0.07
Tibiotarsus shaft length	0.14	<b>0.19</b>	<b>0.26</b>
Cnemial crest length	-0.07	-0.08	-0.02
Proximal width	0.07	0.05	-0.09
Shaft width*	0.00	-0.10	<b>-0.54</b>
Distal width*	<b>0.19</b>	-0.09	<b>-0.53</b>
Patella length	-0.06	<b>-0.20</b>	0.05
Width*	<b>-0.24</b>	-0.08	<b>0.29</b>
Tarsometatarsus length*	0.11	<b>-0.21</b>	0.04
Proximal width*	<b>0.37</b>	<b>-0.41</b>	-0.02
Shaft width	-0.00	<b>-0.24</b>	-0.14
Distal width	0.08	<b>-0.43</b>	-0.13
Pedal digit II length	<b>-0.37</b>	<b>-0.26</b>	0.01
III length*	<b>-0.48</b>	<b>-0.29</b>	0.00
IV length	<b>-0.43</b>	<b>-0.31</b>	0.01
Eigenvalue	7.05	0.60	0.15
Cumulative variance (%)	90.00	98.10	100.00
Canonical R	0.94	0.61	0.36

\* Variables marked by asterisks were retained significantly ( $F$ -to-remove,  $P < 0.05$ ) in backstep-selected canonical analysis.

brae were compared among species and sexes using  $\chi^2$ -tests.

Prior to multivariate analyses, data from specimens were subjected to a program which replaces missing data (which resulted from bilateral breakage or other damage) with estimates based on stepwise regressions on available measurements for specimens of the same sex. Several measurements originally recorded (e.g., interorbital widths, and pedal digit I) were missing for too many specimens and were excluded from

multivariate analyses. This procedure resulted in 319 estimates (2.8% of the measurements included in 31-variable data set); 213 (67%) of the missing data were lengths of pedal phalanges, which were frequently lost from salvaged specimens.

Canonical analysis, a multivariate technique which defines (sets of) mutually orthogonal axes that maximally separate predefined groups (e.g., species-sex or species-sex-age groups) relative to a pooled estimate of within-group multivariate

variation (Pimentel 1979, Campbell and Atchley 1981), was used to discriminate subsamples of specimens. Canonical analysis also provided associated classification functions which facilitate identification of specimens and permit an alternative assessment of group discrimination through jackknifed classification percentages; efficacy of these classifications (relative to random assignments) was tested using  $\chi^2$ -tests (Titus et al. 1984).

Canonical contrasts, multivariate analyses of variances based on backstep-selected subsets of variables, permitted the quantification of (orthogonal) variance components attributable to particular grouping variables of interest (e.g., species, sex, species-sex interactions). Multivariate separation among groups was tested using Wilks' lambda, a maximum likelihood statistic with  $p$ ,  $g-1$ , and  $n-p$  degrees of freedom (where  $p$  is the number of variables retained significantly in the specific test,  $g$  is the number of groups discriminated, and  $n$  is the total number of specimens in all groups). All canonical analyses (and associated statistics) were based on data transformed to natural logarithms. Corresponding standardized pairwise multivariate distances between group centroids were estimated using Mahalanobis' distances ( $D$ ). Both Wilks' lambda and Mahalanobis'  $D$  were based on "statistically optimal" subsets of the 31 variables analyzed, subsets chosen through a backstep-selection procedure based on sequential  $F$ -tests ( $P < 0.05$ ). Interpretation of the multivariate differences among groups (standardized for within-group covariance structure) was based on correlation coefficients between "sheared" skeletal measurements and scores on the stepwise canonical variates. "Sheared" measurements (Bookstein et al. 1985) are residuals of measurements after variance attributable to the first principal component of the pooled within-group (here, species-sex group) covariance matrix is removed. Relative contributions of interspecific and intersexual differences on each canonical variate were quantified through two-way ANOVAs of scores.

Clinal variation in measurements of *Aechmophorus* (Storer and Nuechterlein 1985) justified preliminary precautions to avoid confounding latitudinal variation with interspecific and intersexual differences. Two approaches were used: (1) a CA and subsequent MANOVAs in which eight sex-age-locale groups of *A. occidentalis* were distinguished; and (2) a CA and MAN-

OVA of the four species-sex groups based on a sample from a single locale—Clear Lake, California.

All statistical procedures were accomplished using algorithms included in the Biomedical Computing Programs (Dixon 1985) and performed on an IBM 3081 KX3 mainframe computer at the University of Kansas.

## RESULTS

### UNIVARIATE COMPARISONS

*Interspecific differences.* Approximately 40% of the skeletal measurements (18 of 45, including combinations of variables described above) differed significantly between *A. occidentalis* and *A. clarkii* in two-way ANOVAs (several are tabulated in Table 2). Interspecific differences in lengths of the postnarial maxilla, coracoid, humerus, ulna, carpometacarpus, proximal phalanx of the major alar digit, femur, and tibiotarsus, widths of the humerus, proximal end of the ulna, and distal end of the femur, and height of the carpometacarpus were highly significant ( $P < 0.0001$ ); those of mandibular lengths, postacetabular lengths, femur widths, and tibiotarsus proximal widths ( $0.0005 < P < 0.005$ ), and interspecific effects in lengths of the cnemial crest and tarsometatarsus were marginal ( $P < 0.05$ ). In all significantly different dimensions, mean lengths of *A. occidentalis* exceeded those for *A. clarkii*. Statistically significant mensural differences between species (within sexes) averaged 2–5%.

Interspecific differences in variances of measurements were few. Within-sex variances were greater in *A. occidentalis* than in *A. clarkii* in coracoid lengths ( $T = 8.81$ ;  $df = 1, 282$ ;  $P < 0.005$ ), patella lengths ( $T = 7.79$ ;  $df = 1, 279$ ;  $P \approx 0.005$ ), and tarsometatarsus distal widths ( $T = 8.39$ ;  $df = 1, 282$ ;  $P < 0.005$ ), and marginally so ( $0.01 < P < 0.05$ ) in tibiotarsus proximal widths and lengths of the proximal phalanx of pedal digit IV. The comparatively high variances in measurements of *A. occidentalis* were due, in part, to the greater geographical diversity represented in the sample. Only preacetabular pelvic length manifested slightly higher within-sex variances in *A. clarkii* than in *A. occidentalis* ( $T = 5.03$ ;  $df = 1, 281$ ;  $P \approx 0.03$ ).

Of all the possible comparisons of counts of fused and unfused thoracic vertebrae among species, sex, and age groups of *Aechmophorus*, only

one pattern showed significant heterogeneity. In neither species were intersexual differences in numbers of fused ( $P > 0.15$ ) or unfused ( $P > 0.08$ ) thoracic vertebrae significant, which contrasts with the intersexual differences reported by Storer (1982). Numbers of fused thoracic vertebrae (i.e., the number incorporated into the notarium) differed, however ( $\chi^2 = 9.75$ ;  $df = 2$ ;  $P < 0.01$ ) between species (sexes pooled). In *A. occidentalis*, 47 (22%), 155 (74%) and 7 (3%) of specimens had four, five, and six fused vertebrae, respectively; in *A. clarkii*, 31 (41%), 44 (58%), and 1 (1%) had corresponding counts. In brief, 4- and 5-vertebral notaria are of roughly equal frequency in *A. clarkii*, whereas 5-vertebral notaria were three times more numerous than 4-vertebral notaria in *A. occidentalis*.

*Intersexual differences.* Intersexual effects in two-way ANOVAs were highly significant ( $P < 0.0001$ ) for all skeletal measurements (Table 2); dimensions of males averaged larger than those of females in both *A. occidentalis* and *A. clarkii*. Magnitudes of mean intersexual differences (within species) generally exceeded those between species (within sexes); species-sex interaction effects were significant in lengths of the humerus ( $F = 8.11$ ;  $df = 1, 219$ ;  $P < 0.005$ ) and mandible ( $F = 9.68$ ;  $df = 1, 259$ ;  $P < 0.005$ ), and marginally indicated ( $P \leq 0.05$ ) in lengths of the ulna, carpometacarpus, femur, tibiotarsus, and second phalanx of pedal digit III, and widths of the sternum, patella, and distal end of the tibiotarsus. These interaction effects reflect a greater sexual dimorphism in *A. clarkii* than in *A. occidentalis*, except in distal widths of the tibiotarsus, in which a weak opposite pattern was suggested.

Intersexual differences in variances were few (two-way Levene's tests). Mandible lengths and preacetabular pelvic lengths of both species, however, were significantly more variable in males than in females ( $P < 0.0005$ ).

#### MULTIVARIATE COMPARISONS

*Species-sex canonical analysis.* A stepwise canonical analysis of 285 skeletons of *Aechmophorus* of known species and sex revealed significant intergroup variation (Wilks' lambda = 0.067;  $df = 11, 3, 281$ ;  $P \ll 0.001$ ) based on 11 variables significantly ( $P < 0.05$ ) retained in the analysis. Subsequent stepwise MANOVAs documented highly significant intergroup variance associated with species effects (Wilks' lambda = 0.565;  $df$

= 8, 1, 281;  $P \ll 0.001$ ), sexual differences (Wilks' lambda = 0.143;  $df = 9, 1, 281$ ;  $P \ll 0.001$ ), and species-sex interactions (Wilks' lambda = 0.867;  $df = 4, 1, 281$ ;  $P \ll 0.001$ ). Mahalanobis' distances (in three-dimensional canonical space based on step-selected variables) show that intersexual differences (within species) were more than twice as great as those between species (within sexes). Intersexual  $D_s$  were 5.12 and 5.97 for *A. occidentalis* and *A. clarkii*, respectively; interspecific  $D_s$  were 1.97 and 2.33 for males and females, respectively. Furthermore, as indicated by the Mahalanobis'  $D_s$  and species-sex interactions, sexual dimorphism is significantly greater in *A. clarkii* than in *A. occidentalis*. Classification functions based on the 11-variable subset achieved 83.5% success in jackknifed assignments of skeletons among the four species-sex groups, a substantial improvement over random assignments ( $\bar{z} = 22.81$ ;  $df = 285$ ;  $P \ll 0.001$ ); all but two of the 47 misclassifications (95.7%) were between species within the same sex. Jackknifed classifications to sex were highly successful: 175 of 176 (99.4%) in males, and 107 of 109 (98.2%) in females.

The first canonical variate (CV-I) accounted for 88.6% of the intergroup variance, and primarily separated the sexes in both species (ANOVA of scores;  $F = 1,803.48$ ;  $df = 1, 281$ ;  $P \ll 0.0001$ ), with slightly greater sexual dimorphism indicated for *A. clarkii* (ANOVA of scores, interaction effects;  $F = 6.39$ ;  $df = 1, 281$ ;  $P \approx 0.01$ ). A lesser but highly significant separation of species also was achieved on CV-I (ANOVA of scores;  $F = 33.70$ ;  $df = 1, 281$ ;  $P < 0.0001$ ). Correlation coefficients (Table 3) reveal that CV-I primarily contrasted bill length, interorbital width, coracoid length, and proximal width of the tarsometatarsus with length of the distal alar phalanx, width of the patella, and lengths of pedal digits II-IV. Positions of the species-sex clusters on CV-I indicate that males tend to have long bills, skulls with broad frontal regions, long coracoids, and robust tarsometatarsi relative to the distal-most element of the manus, patellar width, and lengths of their toes; opposite proportions characterized females (Fig. 1).

The second axis (CV-II) contributed another 9% of the intergroup variance, and primarily separated the two species of *Aechmophorus* (ANOVA of scores;  $F = 221.07$ ;  $df = 1, 281$ ;  $P < 0.0001$ ); minor intersexual differences also evident on CV-II ( $F = 6.93$ ;  $df = 1, 28$

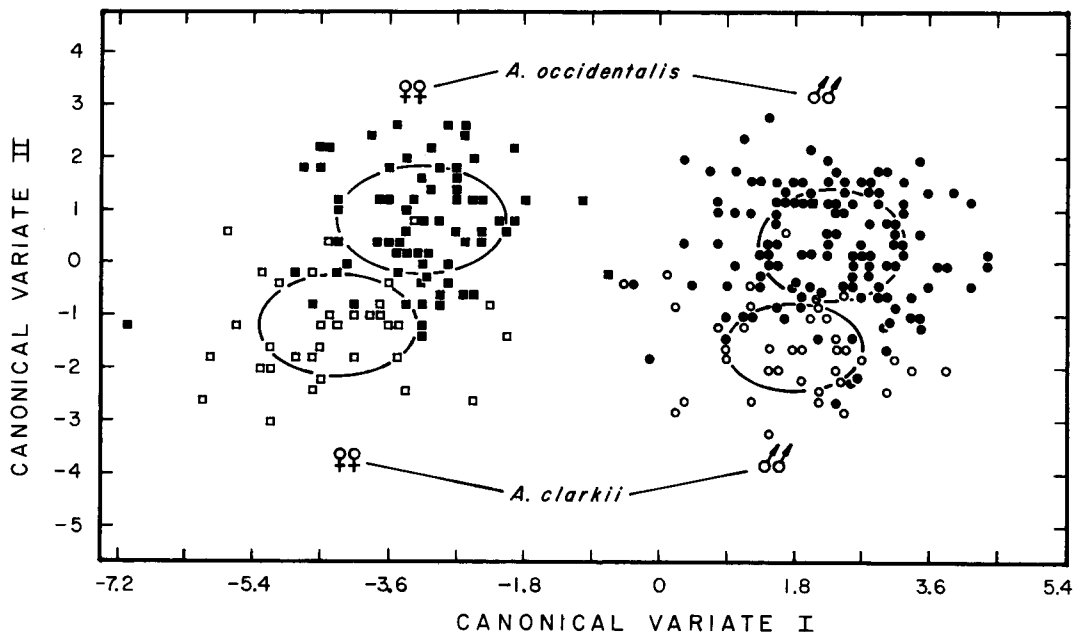


FIGURE 1. Plot of skeletal specimens of *Aechmophorus* on first two canonical variates. *A. occidentalis* is represented by solid symbols and *A. clarkii* by hollow symbols; males are shown as circles, females as squares. Ellipses represent group centroids  $\pm$  one standard deviation for scores.

0.01) differences which were common to both species (interaction effects;  $F = 0.22$ ;  $df = 1, 281$ ;  $P > 0.60$ ). Moreover, scores for *A. occidentalis* on CV-II were more variable (Levene's  $T = 5.19$ ;  $df = 1, 281$ ;  $P < 0.05$ ) than those for *A. clarkii*. Correlation coefficients for CV-II indicate that the axis essentially contrasted basal length of the bill, coracoid length, dimensions of the humeral head, ulna, manus, and lengths of the femur and tibiotarsus with lengths of the mandible and patella, and most dimensions of the tarsometatarsus and pedal digits (Table 3). Mean scores show that *A. occidentalis* had relatively great basal lengths of the bill, long pectoral elements, and long femora, tibiotarsi, and patellae and small tarsometatarsi and toes, compared to *A. clarkii* (Fig. 1). The slight (<1%) but significant interspecific differences in intra-appendicular proportions were confirmed by ANOVAs of proportions (transformed to arcsines of square-roots); femoral ( $F = 11.63$ ;  $df = 1, 225$ ;  $P < 0.001$ ) and tibiotarsal proportions ( $F = 6.91$ ;  $df = 1, 225$ ;  $P < 0.01$ ) were greater in *A. occidentalis* than in *A. clarkii*, whereas tarsometatarsal proportions showed an opposite pattern ( $F = 5.02$ ;  $df = 1, 225$ ;  $P < 0.05$ ).

The third and last canonical variate (CV-III,

not shown in Fig. 1) accounted for the remaining 2.3% of the intergroup variance, contributing additional intersexual differences (ANOVA of scores;  $F = 8.64$ ;  $df = 1, 281$ ;  $P < 0.005$ ). These intersexual effects differed interspecifically (interaction effects;  $F = 57.90$ ;  $df = 1, 281$ ;  $P < 0.0001$ ), being in opposite directions in the two species. Scores for *A. clarkii* were more variable (Levene's  $T = 7.85$ ;  $df = 1, 281$ ;  $P = 0.005$ ) than those for *A. occidentalis*, but no additional separation of species means was achieved on CV-III ( $F = 0.70$ ;  $df = 1, 281$ ;  $P > 0.40$ ). Correlations between "sheared" measurements and scores on CV-III revealed that the axes contrasted lengths of the distal wing elements, mandible, and tibiotarsus, and patella width with widths of the major leg elements (Table 3).

Discrimination among species-sex groups remained significant if the analyses were confined to adult specimens. MANOVAs documented highly significant multivariate differences attributable to species (Wilks' lambda = 0.598;  $df = 13, 3, 196$ ;  $P \ll 0.001$ ), sexes (Wilks' lambda = 0.121;  $df = 7, 1, 196$ ;  $P \ll 0.001$ ) and species-sex interactions (Wilks' lambda = 0.821;  $df = 6, 1, 196$ ;  $P < 0.001$ ). Once again, mean intersexual differences (within species) were twice as great

(Mahalanobis'  $\bar{D} = 4.20$ ) as those between species within sexes ( $\bar{D} = 1.95$ ).

*Single-sex classification functions.* Stepwise discriminant analyses for males and females separately achieved jackknifed classification successes of 84.1% ( $\bar{Z} = 9.05$ ;  $df = 174$ ;  $P \ll 0.001$ ) and 86.2% ( $\bar{Z} = 7.56$ ;  $df = 107$ ;  $P \ll 0.001$ ). The associated classification functions (Table 4) for these single-sex models permit identifications of species for a high percentage of skeletons of *Aechmophorus* of known sex using relatively few measurements.

*Latitudinal and age-related differences.* A canonical analysis and seven related MANOVAs were performed on the eight groups of 207 *A. occidentalis* defined by sex, locale of collection (U.S. vs. Canada), and age (yearling vs. adult). The overall CA documented highly significant intergroup dispersion (Wilks' lambda = 0.017;  $df = 15, 7, 199$ ;  $P \ll 0.001$ ). Subsequent stepwise MANOVAs (orthogonal contrasts) indicated significant variance attributable to sex (Wilks' lambda = 0.292;  $df = 6, 1, 199$ ;  $P \ll 0.001$ ), locale (Wilks' lambda = 0.790;  $df = 8, 1, 199$ ;  $P < 0.001$ ), age (Wilks' lambda = 0.654;  $df = 6, 1, 199$ ;  $P < 0.001$ ), sex-locale interactions (Wilks' lambda = 0.977;  $df = 1, 1, 199$ ;  $P < 0.05$ ), sex-age interactions (Wilks' lambda = 0.920;  $df = 5, 1, 199$ ;  $P < 0.01$ ), locale-age interactions (Wilks' lambda = 0.864;  $df = 4, 1, 199$ ;  $P < 0.001$ ), and sex-locale-age interactions (Wilks' lambda = 0.887;  $df = 5, 1, 199$ ;  $P < 0.001$ ). The significant and complex interaction-effects reflect the non-additivity of variances associated to the three factors, and therefore there was significant but unavoidable redundancy of variances attributed to each factor and the significance of the separate MANOVAs are therefore inflated. Pairwise *F*-statistics based on the overall CA revealed that six pairs of groups did not differ significantly (Bonferroni level for 28 comparisons;  $df = 15, 185$ ;  $P > 0.002$ ), including differences between age classes of males and females from the U.S. and between locale-groups of males and females. The comparatively small differences due to locale and age are indicated by the mean *F*-values of the four pairwise comparisons in which the other two factors are invariant;  $\bar{F} = 3.10$  for locale and  $\bar{F} = 2.87$  for age, whereas  $\bar{F} = 17.85$  for sex.

Analysis of the 101 specimens collected from Clear Lake, California substantiated significant overall dispersion of species-sex groups (Wilks'

TABLE 4. Non-standardized classification coefficients for identification of skeletons of *Aechmophorus* of known sex;<sup>a</sup> these functions achieved jackknifed classification successes of 84.1% and 86.2%, respectively, of 176 males and 109 females.

Variable	Coefficients	
	Males	Females
Mandible length	-22.458	41.397
Postnarial premaxillary length	13.173	—
Coracoid length	52.288	—
Ulna length	-41.479	52.653
Carpometacarpus length	63.752	57.600
Height	21.292	—
Pelvis, preacetabular length	-11.141	—
Femur length	27.368	—
Proximal width	—	-53.488
Tibiotarsus, proximal width	-42.365	—
Shaft width	14.079	-17.193
Distal width	21.690	—
Digit II length	-53.112	-40.533
Constant	-68.863	-328.328

<sup>a</sup> Specimens are scored by summing the products of log-transformed measurements and their corresponding coefficients and adding the constant given; for either sex, negative scores classify the specimen as *clarkii*, positive as *occidentalis*.

lambda = 0.060;  $df = 7, 3, 97$ ;  $P \ll 0.001$ ), including interspecific differences (Wilks' lambda = 0.554;  $df = 9, 1, 97$ ;  $P \ll 0.001$ ), intersexual differences (Wilks' lambda = 0.091;  $df = 7, 1, 98$ ;  $P \ll 0.001$ ), and species-sex interactions (Wilks' lambda = 0.799;  $df = 4, 1, 97$ ;  $P < 0.001$ ).

Age effects also were assessed through MANOVA of age and age-sex interactions for *A. occidentalis* collected in Canada. Overall separation of sex-age groups remained highly significant (Wilks' lambda = 0.031;  $df = 10, 3, 98$ ;  $P \ll 0.001$ ) as did discrimination of sexes (Wilks' lambda = 0.148;  $df = 5, 1, 98$ ;  $P \ll 0.001$ ). Discrimination of age groups was clarified further (Wilks' lambda = 0.358;  $df = 4, 1, 98$ ;  $P \ll 0.001$ ); multivariate distances and substantial sex-age interaction effects (Wilks' lambda = 0.792;  $df = 5, 1, 98$ ;  $P \ll 0.001$ ) indicated that age-related differences in Canadian *A. occidentalis* were roughly twice as great in males than in females.

## DISCUSSION

### INTERSPECIFIC DIFFERENTIATION

In spite of the confounding effects of age and geographic variation, there is strong evidence of significant differences between mean skeletal di-



mensions of *A. occidentalis* and *A. clarkii* (Fig. 1). There is considerable overlap between the species, however, and only 85% of sexed skeletons can be identified correctly using the measurements analyzed here; Ratti et al. (1983) achieved comparable success using external measurements and discriminant functions. Hybridization between the species of *Aechmophorus* could further complicate identification of skeletons. Skeletal morphometrics based on complete skeletons are of little or no use for analyses of fossil *Aechmophorus* because virtually all known fossils of this genus consist of single, unassociated bones (e.g., Murray 1967). In large samples of Pleistocene material, sex can be assigned provisionally to most individual bones on the basis of evident bimodalities in measurements (Storer 1989). Whether such samples include one or more species might be inferred through the use of statistical methods and clustering algorithms designed for mixture distributions (Titterton et al. 1985, McLachlan and Basford 1988, Kaufman and Rousseeuw 1990), but uncertainty concerning the possible number of species represented and small interspecific differences in measurements documented for extant *Aechmophorus* (Table 2) make such determinations unlikely. There are no strictly comparable morphometric studies of avian skeletons, but the interspecific Mahalanobis' distances separating species of *Aechmophorus* are less than those between most other congeners of Podicipedidae (Livezey 1989), a finding concordant with the far greater interspecific divergences in plumage and other morphological characters in the latter.

Morphometric differentiation between closely related species is not necessarily an accurate reflection of genetic divergence (Zink 1982, 1986, 1988; Zink and Avise 1990). This discrepancy may be caused, at least in part, by the nongenetic effects of different environmental conditions during development (James 1983, Zink 1986). Generally, such phenotypic variation among populations exceeds genetic variation (cf. Barrowclough 1983, Zink 1986). In *Aechmophorus*, interspecific genetic distance based on DNA hybridization (0.57) is less than that (0.7) between two subspecies of Brown Kiwi (*Apteryx australis*) and in the lower part of the range of distances between congeners (Ahlquist et al. 1987). A definitive test will require genetic comparisons of several populations of both species of *Aechmophorus*, preferably based on the more rapidly evolving mitochondrial genome (Avise and Zink 1988).

An improved assessment of morphometric variation in *Aechmophorus* will require skeletal samples of both species which include adequate subsamples of both sexes of adults from breeding populations at a range of different latitudes. Such sampling would permit several more comprehensive statistical analyses, including: (1) a two-way multivariate analysis of covariance (MANCOVA), treating species and sex as main effects and latitude (or possibly longitude) as a covariate; or (2) a canonical analysis of four species-sex groups based on residual data after the common variance attributable to latitude has been partitioned. In *Aechmophorus*, the morphometric effects of latitude are of particular importance if the populations of comparatively small *A. occidentalis* and *A. clarkii* from Mexico are to be included (Dickerman 1963, 1973, 1986; Storer and Nuechterlein 1985).

#### FUNCTIONAL IMPLICATIONS OF INTERSPECIFIC DIFFERENCES

Pursuit divers like *Aechmophorus* are highly specialized for foot-propelled locomotion and capturing their prey under water (Lawrence 1950, Storer 1960, Raikow 1985). In both foot-propelled and wing-propelled diving birds, body mass is directly correlated with maximal depths attained during dives (Piatt and Nettleship 1985, Cooper 1986), although amounts of subcutaneous fat (which can vary from none to 280 g in breeding female *Aechmophorus*; R. W. Storer, unpubl. data) and behavioral accommodations (compression of feathers and exhalation prior to submergence) can further affect buoyancy and therefore diving capacity. Consequently, the finding that the mean body mass of *A. occidentalis* (sex for sex) exceeds that of *A. clarkii* (Ratti et al. 1983, Storer and Nuechterlein 1985) may have implications for the relative diving capacities of the two species. More precisely, the resistance of a bird moving through water is proportional to its cross-sectional area (Stonehouse 1967; a function of body mass among closely related, similarly shaped species), and power of propulsion (in foot-propelled species) is proportional to the area of the feet (Raikow 1973); a relative change in this proportion would alter the power of propulsion of which the bird is capable. Multivariate comparisons indicate that *A. clarkii* has relatively longer tarsometatarsi and toes than the generally larger *A. occidentalis* (Table 3, Fig. 1); these differences may permit *A. clarkii* to swim faster under water, thereby enabling birds to at-

tain greater depths within a given time period than *A. occidentalis*. Nuechterlein (1981a) found that *A. clarkii* performed more "spring" dives than "level" dives and tended to feed relatively far from shore, whereas feeding *A. occidentalis* were characterized by more "level" dives performed closer to shore; Nuechterlein (1981a) suggested that *A. clarkii* may forage in deeper water than the larger *A. occidentalis*. Further evidence that *A. clarkii* performs "spring" dives more frequently and tends to forage in deeper water than *A. occidentalis* was reported by Nuechterlein and Buitron (1989).

Although *A. occidentalis* exceeds *A. clarkii* in all mean dimensions (Table 2), the magnitudes of these differences are not equal, resulting in subtle but reasonably consistent interspecific differences in skeletal proportions. These slight differences in relative sizes form the basis for multivariate discrimination (Tables 3, 4; Fig. 1), especially because canonical analysis standardizes among-group differences by pooled within-group variance (which is predominantly "size" variation), but render confident functional interpretation difficult. In particular, the slight interspecific differences in proportions within the pelvic limb of *Aechmophorus* suggest differences in aquatic locomotion (Stolpe 1932, Storer 1971, Raikow 1985). It is tempting to interpret the skeletal proportions of *A. clarkii*, most importantly the relatively longer tarsometatarsi and pedal digits of the species (Table 3, CV-II), as "shape-specialized" for deeper dives, but the functional importance of these slight proportional differences may be overwhelmed by the differences in size and behavior in the two species (Table 1). Moreover, these interspecific differences in skeletal proportions may be the simple developmental correlate of ontogenetic allometry and differences in adult body size (Gould 1966). Similarly, the tendency for comparatively extensive fusion of thoracic vertebrae in *A. occidentalis*, a feature which undoubtedly favors spinal strength over flexibility, may simply be a reflection of a family-wide trend toward increased fusion with increasing body size (Storer 1982).

#### SEXUAL DIMORPHISM

Sexual dimorphism in *Aechmophorus*, earlier noted by Rand (1952), Selander (1966), Ratti et al. (1983), and Storer and Nuechterlein (1985), was the primary source of skeletal variation in this analysis, significantly exceeding that attrib-

utable to interspecific differences (Table 2, Fig. 1). Rising and Schueler (1980) found the sexual dimorphism exceeded interspecific differences in wood-pewees (*Contopus*), and suggested that "sibling species" be defined as reproductively isolated populations in which this relationship obtains. The selection regime that underlies sexual dimorphism in *Aechmophorus* is not known, but a combination of generally hypothesized sources may apply, e.g., sexual selection (Selander 1972, Trivers 1972, West-Eberhard 1983), differential thermodynamic optima (Johnston et al. 1972, Johnston and Fleischer 1981, Fleischer and Johnston 1982), constraints related to mobilization of resources for reproduction (Downhower 1976), or intersexual partitioning of feeding niche (Selander 1966, Shine 1989).

The likelihood of intersexual differences in feeding niche is supported by the importance of relative bill size and curvature in sexual dimorphism of *Aechmophorus* (Rand 1952, Selander 1966) and the observation that male *A. occidentalis* tend to catch and provide to chicks larger prey than their mates (Forbes and Sealy 1990). Equivocal observational evidence for intersexual differences in foraging, at least in *A. clarkii*, also has been reported (Forbes and Sealy 1988, Nuechterlein and Buitron 1989). Much of the skeletal dimorphism documented here was common to both species and summarized on the first canonical variate (Fig. 1). The large, positive coefficients for the two bill measurements (Table 3) and the positive scores of males indicate that the bills of males are not only larger than those of female conspecifics, but *disproportionately* so. This sexual difference in shape of the feeding apparatus, the significantly greater skeletal sexual dimorphism of *A. clarkii* (largely reflected by the third canonical variate; Table 3), the comparatively local and semicolonial distribution of *A. clarkii* (Ratti 1979, 1981), and the possibility that *A. clarkii* routinely performs deeper dives than *A. occidentalis* (Nuechterlein 1981a; but see Ratti 1985), suggest that Clark's Grebe may be more specialized in feeding niche than its larger congener.

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