

## A CRITICAL EVALUATION OF KENYON'S SHAG (*PHALACROCORAX [STICTOCARBO] KENYONI*)

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**ABSTRACT.**—We examine the validity of *Phalacrocorax [Stictocarbo] kenyoni*, which was described by Siegel-Causey (1991) from the Aleutian Islands using midden remains and existing skeletal specimens. We emphasize a morphometric evaluation of the taxon using 224 skeletal specimens of North Pacific cormorants, but we also evaluate the qualitative characters originally used to characterize *P. kenyoni*. Principal components and discriminant function analyses of 14 skeletal characters failed to support the validity of the species. Similarly, all seven of the character states that Siegel-Causey described as unique to *P. kenyoni* also were found in *P. pelagicus* and *P. urile*. Thus, the three type specimens of *P. kenyoni* appear to be *P. pelagicus*. Although we could not confirm the validity of *P. kenyoni*, our morphometric analyses revealed that *P. pelagicus* individuals from the central Aleutians are smaller than those from surrounding populations. Received 11 December 1998, accepted 20 July 1999.

SIEGEL-CAUSEY (1991) described a new species of cormorant from the Aleutian Islands; he named it *Stictocarbo* (= *Phalacrocorax*) *kenyoni*, reflecting his prior studies of major clades in the Phalacrocoracidae (Siegel-Causey 1988). Siegel-Causey first discovered this bird in midden remains from Amchitka Island in the far western Aleutian Islands but later found three recent skeletal specimens that he ascribed to *kenyoni* and designated as types (Siegel-Causey 1991, Siegel-Causey et al. 1991). No other specimens of this species exist. The external appearance of *P. kenyoni* remains undescribed, and the species was not accepted as valid by AOU (1998).

To facilitate an evaluation of the validity of *P. kenyoni*, the University of Washington Burke Museum (UWBM) salvaged every intact cormorant recovered from the beaches of Prince William Sound, Alaska, following the Exxon Valdez oil spill of 24 March 1989. All were preserved as skeletal specimens, and when carcasses were not too rotten, associated extended wings and flat skins also were preserved. Our analyses focused primarily on a morphometric evaluation of *P. kenyoni* using 224 skeletal specimens of cormorants from the North Pacific. We also evaluated the qualitative characters that Siegel-Causey (1991) used to characterize *P.*

*kenyoni*, based on detailed examinations of a more limited reference series of specimens. Rohwer and Filardi were responsible for the morphometric analyses, and Bostwick and Peterson performed the qualitative analyses.

### METHODS

Hereafter, we refer to the three North Pacific cormorants as *kenyoni*, *pelagicus*, and *urile* for Kenyon's Shag (*P. kenyoni*), Pelagic Cormorant (*P. pelagicus*), and Red-faced Cormorant (*P. urile*), respectively. Table 1 provides general localities and dates of collection for the specimens used in our morphometric analyses. The three *kenyoni* specimens were from Amchitka Island, Alaska; the 25 *urile* specimens were from Prince William Sound, or from other Alaskan localities to the west and north; localities for the 196 *pelagicus* specimens are plotted in Figure 1. About one-third of the 196 *pelagicus* specimens were collected from May to August and thus are likely to be from breeding areas. Although many of the specimens were not yet of breeding age, young *pelagicus* are known to summer near the colonies where they hatched (Palmer 1962).

**Qualitative characters.**—Because Siegel-Causey's diagnosis of *kenyoni* was based on seven autapomorphic skeletal characters (Siegel-Causey 1991: appendix 2) and its small size, we paid special attention to the qualitative characters of skeletal morphology described in his Appendix 1. Our interpretations of Siegel-Causey's characters were based on standard avian anatomical references (Howard 1929, George and Berger 1966, Baumel et al. 1979, Baumel and Witmer

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TABLE 1. Specimens examined by species, locality, and season (breeding = 1 May to 31 August). Map symbols for *pelagicus* refer to Figure 1.

Locality	Map symbol	Breeding season	Nonbreeding season
<i>P. kenyonii</i>			
Aleutian Islands	—	0	3
<i>P. urile</i>			
Alaska	—	15	10
<i>P. pelagicus</i>			
Valdez and Southeast Alaska	V	29	124
Aleutian Islands	A	17	1
Pribilofs and northern Alaska	P	0	3
British Columbia and Washington	W	3	3
California	C	2	6
Russia	R	7	0
Japan	J	1	0
Totals	—	74	150

1993) and on careful inspection of specimens, including one of the paratypes (UWBM 18613). For the purpose of evaluating the validity of each character in diagnosing *kenyonii*, we assembled a reference series of six male (UWBM 22442, 44193, 44194, 44403,

48557, 48617) and six female (UWBM 14484, 38795, 42012, 43071, 44195, 44402) *pelagicus*, and six male (UWBM 48619, 50610, 52084, 52090, 52091, 52094) and six female (UWBM 50611, 50612, 52086, 52089, 52093, 52107) *urile*, the other two "Stictocarbo" shags

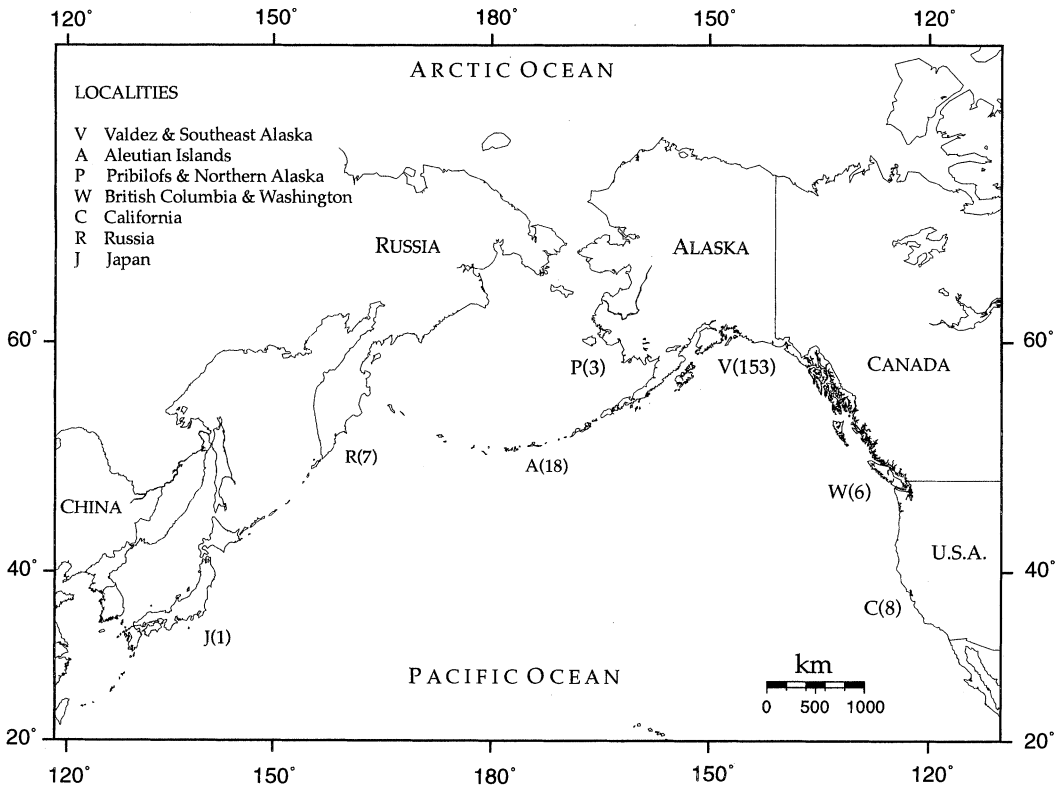


FIG. 1. North Pacific localities for the 196 *pelagicus* specimens used in the morphometric analyses. Symbols for the locality names are followed by sample sizes in parentheses.

TABLE 2. Description of the 14 skeletal characters used in the morphometric analyses. Terminology used in the character descriptions follows Baumel and Witmer (1993).

Character	Description
Cranium depth	Distance from center of external base of cranium to highest point of calvaria (skull cap)
Cranium length	From craniofacial flexion zone (hinge) to dorsal rim of foramen magnum
Maxilla length	From craniofacial flexion zone (hinge) to rostrum of maxilla (tip of premaxilla)
Coracoid length	From acrocoracoid to lateral process of sternal end of coracoid
Humerus length	From head of humerus to ventral condyle at its distal end
Ulna length	From olecranon to ventral condyle at its dorsal end
Carpometacarpus length	From carpal trochlea to distal end of major metacarpal
Sternum length	From dorsal spine of sternal rostrum to caudal border of sternal body at midline
Sternum width	Transverse distance between the first costal processes of each side
Synsacrum length	From corpus (body) of cranial-most synsacral vertebra to that of the caudal-most synsacral vertebra
Pelvis width	Distance between left and right antitrochanters that form the dorsal rims of the acetabula
Femur length	From tip of femoral trochanter to lateral condyle at its distal end
Tibiotarsus length	From patellar articular surface of the cranial cnemial crest to medial condyle at its distal end
Tarsometatarsus length	From the intercondylar eminence at its proximal end to the most distal metatarsal trochlea

in the region. All *urile* reference specimens were from Alaska. It was important that the *pelagicus* reference series included large birds taken outside the Aleutians because *kenyoni* is small and has been reported only from the Aleutians. For *pelagicus* males, these specimens came from Prince William Sound, Alaska ( $n = 2$ ), Russia ( $n = 3$ ), and Washington ( $n = 1$ ); for *pelagicus* females, these specimens came from Russia ( $n = 2$ ), Washington ( $n = 3$ ), and British Columbia ( $n = 1$ ). The birds from Russia and Prince William Sound were large. Each character was scored on each specimen by Bostwick and Peterson to evaluate the hypothesis that these qualitative characters diagnose the species.

**Quantitative characters.**—For our morphometric analyses, we used the 14 skeletal measurements defined in Table 2. All were large enough to be taken accurately with dial calipers. Some of these measurements are difficult to replicate unless other workers first learn to match the measurements we made for individual specimens (available from Rohwer or Filardi). The problem lies not in the repeatability of our measurements, but in interpreting our definitions for them (Table 2). Unless the same measurements are taken, errors between observers seriously affect results. With one exception (see below), Filardi made all measurements.

The holotype specimen for *kenyoni* is housed at the United States National Museum (USNM 431164), and the two paratypes are at the University of Washington Burke Museum (UWBM 18613, 18614). Because the USNM does not lend type specimens, we sent three *pelagicus* measured by Filardi to the

USNM. After using these specimens to learn to repeat our measurements, Brian Schmidt measured the *kenyoni* type for us.

**Resolving problems with the morphometric data.**—Although most of the Valdez birds were in good condition, some were too rotten to be sexed by gonads, and two were initially misidentified to species by their preparators. Additionally, a few specimens from the Valdez collection and from other museums had broken elements that could not be measured. We have dealt with these problems as follows.

Specimens with missing characters were included in the morphometric analyses only if two or fewer characters were missing. Twenty-seven of the 225 specimens we measured had missing characters; 1 with many missing characters was excluded, 23 had a single missing character, and 3 had two missing characters. We estimated values for missing characters in univariate regressions using the character most strongly correlated with the missing character as an estimator. All species and sexes were combined for this regression analysis because sex and species determinations had not yet been evaluated. We later reassessed these estimates using correlations between characters for within-sex and within-species analyses; however, changes in estimates were so small (typically  $<1$  mm) that reestimates were not used. Less than 1% of our 3,136 morphometric values were estimated, making the quality of our data matrix high.

With the full matrix of morphometric measurements, our next step was to resolve problems in sex determination. Several specimens were not sexed by

their preparators, and others apparently were sexed erroneously. In preparing the Valdez series and a group of 23 freshly collected *pelagicus* from Washington, we learned that testes of first-year males are flattened and so little developed that, without carefully checking for paired gonads, testes are easily mistaken for ovaries (S. Rohwer and C. Filardi unpubl. data). For this reason, we felt that correcting the sex on specimens lacking measurements of gonad size was appropriate.

To assign sexes we pooled all sexed specimens ( $n = 214$ ) in a discriminant analysis. We pooled species for this analysis because this analysis needed to precede the evaluation of species identity and because our samples of *urile* and *kenyoni* were too small to be treated separately. Two of the three specimens designated as *kenyoni* by Siegel-Causey (1991) are unsexed, and we measured only 25 specimens of *urile*. We accepted the sexes assigned to specimens by our discriminant analysis except for three University of Kansas Natural History Museum (KUNHM) specimens collected by Siegel-Causey in the Aleutian Islands, each of which had gonad measurements. Finally, we corrected two errors of species identification in which *urile* specimens had been identified as *pelagicus* (UWBM 50583 and 52123). Both were Valdez casualties, presumably encased in tar-like crude oil, which made identification by their preparators difficult.

*Morphometric analyses.*—Terminology surrounding discriminant analysis is confusing because distinctions are often drawn between the two-group case and the case of more than two groups. In two-group comparisons, the new linear combination of the original variables that best separates them is called the discriminant function. When more than two groups are to be discriminated, most references shift names and apply the name canonical analysis. Thus, the first discriminant is called the first canonical axis, or canonical variate 1, and so on for the  $n - 1$  variates needed to plot the  $n$  centroids for the known groups (see Overall and Klett 1972). Both analyses follow the same principle of maximizing the ratio of the between-group variance to the pooled within-group variance. As in principal components analysis (PCA), the canonical axes obtained from a multiple discriminant analysis are orthogonal to each other, with the first axis explaining the greatest difference between the groups, the second the next greatest, and so on.

In all of our multivariate analyses, we used the corrected data matrix (missing measurements replaced, sexes and species assigned or corrected). We evaluated the validity of *kenyoni* using discriminant and canonical analyses. Our first approach was a canonical analysis using *urile* males and females and *pelagicus* males and females as known groups. The three *kenyoni* specimens were then projected onto these axes. In our discussions of discriminant analysis,

posterior probabilities refer to the probabilities of group affiliation assigned by the analysis after the best discrimination had been achieved using the *a priori* groupings.

We also used PCA to evaluate variation in the full matrix of 224 specimens (*kenyoni*, *urile*, *pelagicus*) and in certain subsets of this matrix. Principal components analysis is useful because it economically summarizes variation in morphological data without using information about group membership. We extracted principal components from correlation matrices to avoid weighting larger characters more heavily than small characters, as occurs with covariance matrices. All of our analyses were done using JMP 3.1 and StatView 5.0 from SAS Institute.

## RESULTS

### QUALITATIVE ANALYSES

Here we summarize the results of our inspection of the seven derived characters for *kenyoni* (Siegel-Causey 1991: appendix 2). We first attempt to establish the synonymy of Siegel-Causey's anatomical names with those of Baumel and Witmer (1993), pointing out ambiguities. We then describe the features emphasized in our examination of variation in these qualitative characters; this represents our best attempt to reconstruct what Siegel-Causey (1991) examined. Finally, we report the results of our comparison of the paratype with the reference series. Character descriptions (anatomical names in italics) are followed by a list of possible character states (see Siegel-Causey 1991: appendix 1). See Siegel-Causey (1991: appendix 2) for a description of how the character states apply to the three taxa.

*Character 1 [mandible].*—“*Fossa aditus*: (a) extends usually 1/3 (but no more than 1/2) the length of the insertion of *M. pseudotemporalis*; (b) extends at least 3/4 the length of the insertion” (Siegel-Causey 1991). The fossa aditus canalis mandibulae (Baumel and Witmer 1993) presumably is the same feature as Siegel-Causey's fossa aditus. Its general location is illustrated, but the illustration is insufficient to permit judging its extent with confidence. Baumel et al. (1979) recognized two muscles that create the fossa: *M. pseudotemporalis superficialis* and *M. pseudotemporalis profundus*; they noted that *M. pseudotemporalis profundus* is sometimes synonymous with *M. pseudotemporalis*, but they did not illustrate either. In our reference series, a muscle scar was found near

the fossa aditus, but the nature of that impression varied greatly among specimens, such that comparing its extent among specimens required some subjectivity.

The fossa aditus and the insertion of the *M. pseudotemporalis* were evaluated as follows. The fossa aditus was considered to be the subtle depression at the proximal end of the mandible on the inside of the ramus. The insertion of *M. pseudotemporalis* was assumed to be the long, narrow groove running underneath, and often beyond, the fossa aditus. The extent of the insertion varied among individuals, such that the fossa aditus extended relatively farther in the paratype than in most of the reference series. However, we did not find this character state to be unique to the paratype; at least one *urile* and one *pelagicus* in the reference series were as extreme as the paratype.

*Character 5 [humerus].—“Attachment of M. dorsalis scapulae: (a) proximal most scar lateral to distal scar; (b) both scars in line on bicipital crest”* (Siegel-Causey 1991). *M. dorsalis scapulae* is synonymous with *M. scapulohumeralis posterior* (George and Berger 1966) and *M. scapulohumeralis caudalis* (Baumel and Witmer 1993). George and Berger (1966) describe this muscle in detail. *M. scapulohumeralis caudalis* is a single muscle that inserts onto the humerus by a single tendon, but Siegel-Causey’s (1991) character description refers to the existence of two scars. Furthermore, “lateral” on the bicipital crest is difficult to determine, given the difference of orientation between the bone and the axis of the bird’s body, as well as the curved surface of the bicipital crest. We assumed that Siegel-Causey’s “scars” were equivalent to the two most obvious protuberances on the bicipital crest, and that he used “lateral” in reference to the bird’s body, rather than to the axis of the bone. We found that 33% of *urile* and 42% of *pelagicus* in the reference series exhibited the state that we understood to be derived in *kenyoni*, and that the paratype failed to show the derived state.

*Character 7 [humerus].—“Ligamental furrow: (a) does not reach head; (b) distinctly notches head (Character 64 of Siegel-Causey, 1988)”* (Siegel-Causey 1991). This character is not illustrated and is defined exactly the same way in both references. Baumel et al. (1979) did not recognize a “ligamental furrow,” but referred to a sulcus ligamentus transversus, and Baumel

and Witmer (1993) recognized a sulcus transversus. Siegel-Causey (1988) followed the nomenclature of Owre (1967) and Howard (1929). Howard illustrates the furrow clearly, but from an orientation different from that required to see the character. We looked at the dorsolateral profile of the head of the humerus for a notch and found it on the paratype, although its distinctness depended on the orientation from which the bone was viewed. We then examined the reference series to see if the same notched profile existed. In all, 25% of *pelagicus* and 18% of *urile* showed the notch, although not as noticeably as the paratype.

*Character 13 [femur].—“Attachment of M. obturator externus + internus: (a) elliptical, shallow, indistinct; (b) deeply excavated, broad, subcircular; (c) deeply excavated, narrow (Character 5 of Siegel-Causey and Lefevre, 1989)”* (Siegel-Causey 1991). This illustration of this character was unclear and lacked labels in Siegel-Causey and Lefevre (1989). Baumel and Witmer (1993) did not recognize *M. obturator externus* or *M. obturator internus*, placing them in the synonymy of *M. obturatorius lateralis* and *M. obturatorius medialis*, respectively. We assumed that the impressiones obturatoriae (Baumel et al. 1979) were the attachments to which Siegel-Causey (1991) referred. However, illustrations and descriptions in Baumel et al. (1979) were insufficient to determine to which feature of the femur Siegel-Causey (1991) referred. Scrutiny of the impressiones obturatoriae in our reference series did not reveal the patterns described. The attachment in *urile* was smaller than in the other species, which does not agree with Siegel-Causey’s (1991) general description (“deeply excavated, broad, subcircular”). No discrete variation was observed in the reference series; the paratype may be narrower in a quantitative (but not qualitative) sense.

*Character 14 [femur].—“Attachment of M. flexor perforatus digiti II: (a) indistinct; (b) deeply excavated without noticeable lateral bony margins; (c) deeply excavated with robust lateral bony crest”* (Siegel-Causey 1991). This muscle is synonymous with *M. flexor perforans et perforatus digiti II* (Baumel and Witmer 1993). Neither Baumel and Witmer (1993) nor Howard (1929) described the bony feature attributed to this attachment on the femur. The paratype was indeed deeply excavated with a robust lateral

crest; however, we also found this state on 50% of *pelagicus* and 18% of *urile* in our reference series.

*Character 16 [femur].*—“Attachment of *M. flexor hallucis longis*: (a) medial margin marked by distinct line just adjacent to medial prominence of external condyle; (b) medial margin coincident with medial prominence, causing the superior aspect to appear sharply produced” (Siegel-Causey 1991). Attachment of this muscle was described in detail by George and Berger (1966); its proximity to the external condyle made localization of the features described straightforward. Nevertheless, we found little variation among individuals, and no discrete variation among taxa.

*Character 19 [tibiotarsus].*—“Supratendinal bridge: (a) lateral (inferior) width greater than medial (superior); (b) widths equal” (Siegel-Causey 1991). This feature is the pons supratendineus illustrated by Baumel and Witmer (1993) and was easily identifiable in our reference series. The variation described by Siegel-Causey (1991) was unclear: instead of having a definable width at each extreme, the supratendinal bridge is double-concave in shape, making relative widths difficult to characterize. The paratype and almost all of the reference series are best described as having the medial width greater than the lateral, opposite to the scoring provided by Siegel-Causey (1991). The only individual that was somewhat different, a *pelagicus*, could best be described as having widths equal. Thus, the limited variation we observed in this character did not correspond to Siegel-Causey's (1991) character states, and we found no discrete differences among taxa.

#### QUANTITATIVE ANALYSES

*Determining sex.*—The discriminant analysis for correcting or assigning sex cleanly assigned sex to most of the specimens (see Fig. 2). Only 15 of the 224 specimens had sexes assigned with a probability less than 0.9 of being either male or female. No change in assignment of sex was suggested for any of the 25 *urile* specimens.

Sexing problems occurred for 22 specimens, all *pelagicus* and *kenyoni* (Table 3). Ten of these specimens were not sexed by their preparators. For these 10 specimens, we used the sex they were assigned by our discriminant analysis when our analyses required that we know the

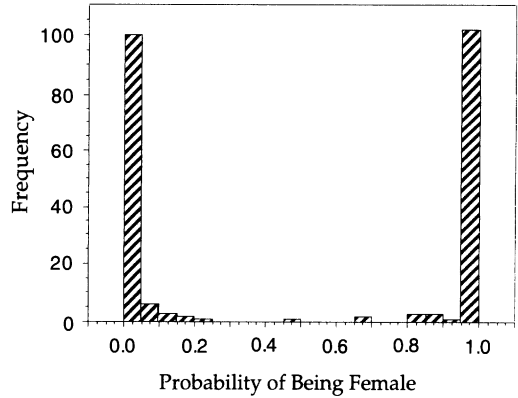


FIG. 2. Posterior probability of sex assignment, as computed from the discriminant analysis using preparator's sexing.

sex; all had posterior probabilities of 0.806 or greater of being either male or female (Table 3). Two of these 10 specimens were the unsexed paratypes of *kenyoni* (UWBM 18613, 18614), whose probabilities of being female exceeded 0.999.

Five specimens in the Valdez sample were sexed as females by their preparators but were suggested to be males by our discriminant analysis. Three of these five specimens were young birds with bursae, and all were listed as having “smooth ovaries” (Table 3). We suspect these birds were young males in which the right testis was not found, either because the carcass was too rotten or because the left testis was mistaken for an ovary, causing the preparator not to look carefully enough for a right gonad. All had posterior probabilities of 0.941 or greater of being males, so we changed their sex assignment accordingly.

Our discriminant analysis challenges the sex assigned to six additional specimens from KUNHM and the Museum of Vertebrate Zoology at Berkeley (MVZ). Three had neither gonad measurements nor age data, so we changed their sex assignments to correspond to those from the discriminant analysis; posterior probabilities for these corrected sexes ranged from 0.691 (a very marginal bird) to more than 0.99 (Table 3). The other three specimens were collected by Siegel-Causey. All had gonad descriptions, so we did not change their sex assignments, despite high posterior probabilities favoring the change (0.872 to 0.998). All of these birds were collected in the Aleutians

TABLE 3. Summary of changes in assignment of sex suggested by discriminant analysis in which the sex assigned by preparators identified known groups (all problems were with *pelagicus* or *kenyoni*). Posterior probabilities are those for predicted sex from the discriminant function analysis. Comments in quotes are from specimen labels.

Museum number	Assigned sex	Predicted sex	Posterior probability	Gonad / age comments
KUNHM 85947	M	F	0.872	Testes (20 × 6 and 26 × 7 mm); no age data
KUNHM 85951	M	F	0.998	Testes (9 × 2 and 8 × 2 mm); no age data
KUNHM 45963	M	F	0.691	No data
KUNHM 85912	F	M	0.979	"Ovary damaged"; no bursa
MVZ 19089	M	F	0.999	No data
MVZ 15184	M	F	0.996	No data
UWBM 17531	F	M	0.968	No data
<b>Miscellaneous sexing problems</b>				
UWBM 52003	F	M	0.941	Smooth ovary (16 × 7 mm); "fleshy bursa"
UWBM 52082	F	M	0.980	Smooth ovary (25 × 7 mm); "no bursa"
UWBM 52088	F	M	0.999	"Smooth ovary"; "deteriorated?"; "pit bursa"
UWBM 52103	F	M	0.982	"Smooth ovary" (12 × 7 mm); "thin-walled bursa"
UWBM 52124	F	M	0.990	"Smooth ovary" (25 × 12 mm); "thin-walled bursa"
<b>Valdez sexing problems</b>				
UWBM 18613 ( <i>kenyoni</i> )	?	F	0.999	No data
UWBM 18614 ( <i>kenyoni</i> )	?	F	0.999	No data
UWBM 21146	?	M	0.994	No data
UWBM 48054	?	M	0.997	Salvaged specimen; "decomposed"
UWBM 50574	?	M	0.999	No gonad data; "fleshy bursa"
UWBM 51966	?	F	0.806	"Sexed by size, no gonads seen"; "no bursa"
KUNHM 88895	?	F	0.999	No data
MVZ 19088	?	M	0.989	No data
MVZ 124050	?	M	0.999	No data
MVZ 17577	?	F	0.995	No data
<b>Specimens not sexed by preparator</b>				

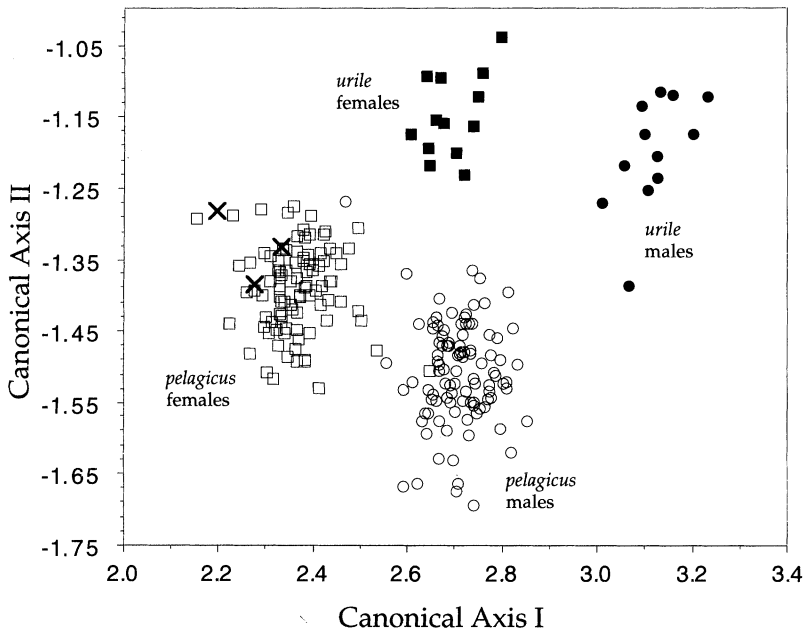


FIG. 3. Multiple discriminant analysis of *urile* and *pelagicus* separated by sex (four groups); each of the three *kenyoni* types that are projected onto the plot are denoted by an X.

where *pelagicus* is small (see below). Small size increases the likelihood of our discriminant analysis classifying a specimen as female.

As a check on the validity of using the discriminant analysis to change assignment of sex, we summarized the morphological variation in all of our *kenyoni* and *pelagicus* specimens using PCA. When we used the assignment changes suggested by the discriminant analysis, the sexes were almost nonoverlapping in a plot of PC I versus PC II. Furthermore, only two of the birds that fell out as intermediates in this PCA (and, thus, whose sex might be questioned) were birds whose sex was assigned using the discriminant analysis. The three Siegel-Causey specimens from the Aleutians were problematic: KUNHM 85912, sexed as female, fell firmly in the male cluster, as the discriminant analysis suggested it should (though its sex was not changed); KUNHM 85947, sexed as male, fell marginally in the male cluster, corroborating Siegel-Causey's sexing; and KUNHM 85951, sexed as male, fell at the edge of the female cluster, as the discriminant analysis suggested it should (although its sex was not changed). To save space, the figure for this analysis is not presented.

*Discriminating pelagicus and urile.*—For this

canonical analysis we used corrected sexes (20 assigned or changed; Table 3) and corrected species identifications (two changed). We excluded *kenyoni* as a known group but projected it onto the canonical axes. Excluding *kenyoni* as a known group was essential to the validity of this analysis because canonical analyses may have little generality when sample sizes are not considerably larger than the number of characters measured (Stevens 1996), especially when the groups being compared are as similar as the sex and species classes of these cormorants. In this four-group analysis (*urile* and *pelagicus*, males and females), the first two canonical axes explained 89% of the variance in the data. Although the measurements for male *pelagicus* and female *urile* specimens overlapped considerably, the four sex-species clusters were clearly discriminated (Fig. 3). When projected onto these axes, the three *kenyoni* specimens fell with *pelagicus* females, suggesting that *kenyoni* may simply be *pelagicus* females (Fig. 3). As was true for the discriminant analysis used to assign sexes, two Aleutian *pelagicus* specimens collected by Siegel-Causey fell in the "wrong" sex class (Fig. 3).

*Discriminating kenyonii and pelagicus.*—Here we present a discriminant analysis attempting



to separate the three *kenyoni* specimens from the 94 *pelagicus* females. This analysis was designed to give the validity of *kenyoni* the benefit of the doubt. All three *kenyoni* specimens appear to be females: one was sexed as such by the preparator, and all three were assigned a sex of female with posterior probabilities greater than 0.999 in our discriminant analysis of sex assignment.

Because we used 14 skeletal characters, and there are only three *kenyoni* specimens, *kenyoni* is almost certain to fall out as correctly identified in a posterior assignment of species identity. Consequently, this result will not reliably assess the validity of *kenyoni*. However, a good ratio of specimens to characters is available for *pelagicus* females. Thus, if this analysis successfully divided the *pelagicus* females clearly into either *kenyoni* or *pelagicus*, without intermediates, then the specific distinctness of *kenyoni* would be supported.

We present the results of this discriminant analysis of female *kenyoni* and *pelagicus* by plotting the posterior probabilities of these specimens being *kenyoni* (Fig. 4). Figure 4 divides birds into *kenyoni* (all from the Aleutians), *pelagicus* females from the Aleutians, and *pelagicus* females from all other localities. The *pelagicus* females from the Aleutians were not identified as a group to be discriminated; instead, they were plotted separately after the two-group discriminant analysis had separated *pelagicus* and *kenyoni* (Fig. 4). Because all three *kenyoni* are from Amchitka Island in the Aleutians, we plotted *pelagicus* from the Aleutians separately to assess their similarity to *kenyoni*. Although the three *kenyoni* specimens are identified as *kenyoni*, only one was identified as such with an extremely high probability (0.999); the other two had posterior probabilities of 0.854 and 0.710 of being *kenyoni*. The looseness of this cluster raises doubt about the validity of *kenyoni*. More important, the combined sample of *pelagicus* and *kenyoni* females does not fall into two clearly separate clusters. This result seriously challenges the validity of *kenyoni* because our sample of female *pelagicus* was large ( $n = 94$ ).

This analysis could be challenged by arguing that determining the sex of *kenyoni* specimens using a generalized discriminant function based on sexes assigned to birds by their preparators for a mixed sample of *kenyoni* ( $n = 1$ ),

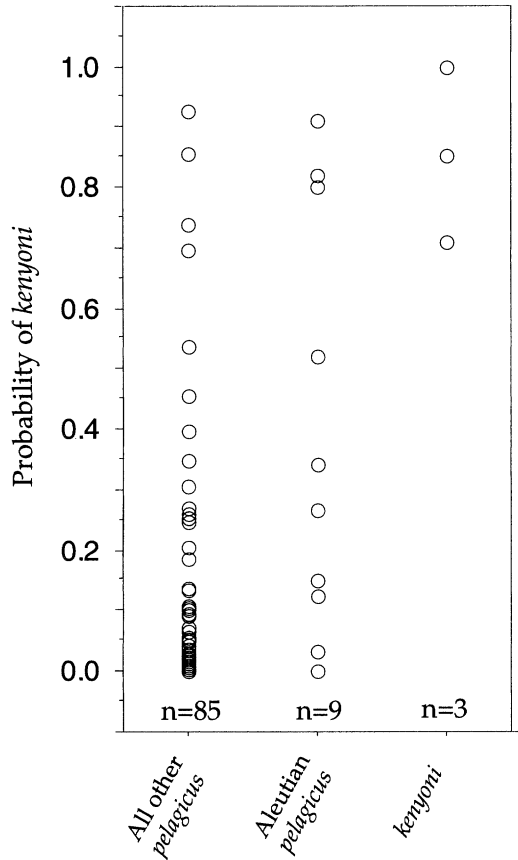


FIG. 4. Posterior probabilities of being *kenyoni*, as computed from the "two-group" discriminant analysis of all *pelagicus* females and *kenyoni*. Aleutian *pelagicus* are identified on the plot but were not an *a priori* group in the analysis.

*urile* ( $n = 25$ ) and *pelagicus* ( $n = 188$ ) is invalid. For this reason, we repeated the analysis using all *pelagicus* ( $n = 196$ ) and the three *kenyoni* specimens, but without assigning sex. The results were similar but, surprisingly, the groups were even less clearly separated because small males from Washington, California, and the Aleutians fell out between the centroids for the two groups.

*Size variation in pelagicus.*—An interesting result of the preceding analysis is that almost half of the *pelagicus* from the Aleutians fell closer to the three specimens Siegel-Causey designated as *kenyoni* than to other *pelagicus*, most of which came from Prince William Sound, Alaska (Fig. 4). This suggests that *pelagicus* from the Aleutians are smaller than those from sur-

TABLE 4. Summary of principal components analysis for *pelagicus* and *kenyoni* ( $n = 199$ ).

Character	PC I loadings	
	Males	Females
Cranium depth	0.629	0.598
Cranium length	0.898	0.904
Maxilla length	0.813	0.888
Coracoid length	0.958	0.964
Humerus length	0.951	0.965
Ulna length	0.949	0.971
Carpometacarpus length	0.929	0.944
Sternum length	0.819	0.854
Sternum width	0.844	0.858
Synsacrum length	0.835	0.846
Pelvis width	0.800	0.837
Femur length	0.921	0.942
Tibiotarsus length	0.934	0.965
Tarsometatarsus length	0.919	0.946

rounding populations. To further explore size variation in *pelagicus*, we summarized the variation in our morphometric measurements using separate PCAs for males and females. By separating the sexes into different analyses, we avoided confusing within-sex size variation with sex differences in the shape of the cranium. In both analyses, loadings for all characters on PC I were strong and positive (Table 4); furthermore, the 14 character coefficients were very strongly correlated between the sexes ( $r = 0.974$ ), indicating that patterns of size variation were comparable in the two sexes. Because these coefficients were so similar (Table 4), we combined the sexes in our plots of results. Thus, the standardized PC scores, computed separately for males and females, were treated as though they were the same measure of size. By combining these independent assessments of size variation, our histograms summarizing information about geographic variation in size are as general as we could make them (Fig. 5).

This analysis shows that most Aleutian specimens are small, including the three designated by Seigel-Causey (1991) as *kenyoni*. The distinction between the Aleutian birds and the other Alaskan specimens, including three *pelagicus* from the Pribilof Islands, is strong and surprising. Specimens of *pelagicus* from the Aleutian Islands do indeed seem to be small birds. In contrast, *pelagicus* from Prince William Sound and from the Pribilofs are large (Fig. 5). Apart from Prince William Sound, we have poor samples from other regions of the west coast of North America. However, most of the 14 *pela-*

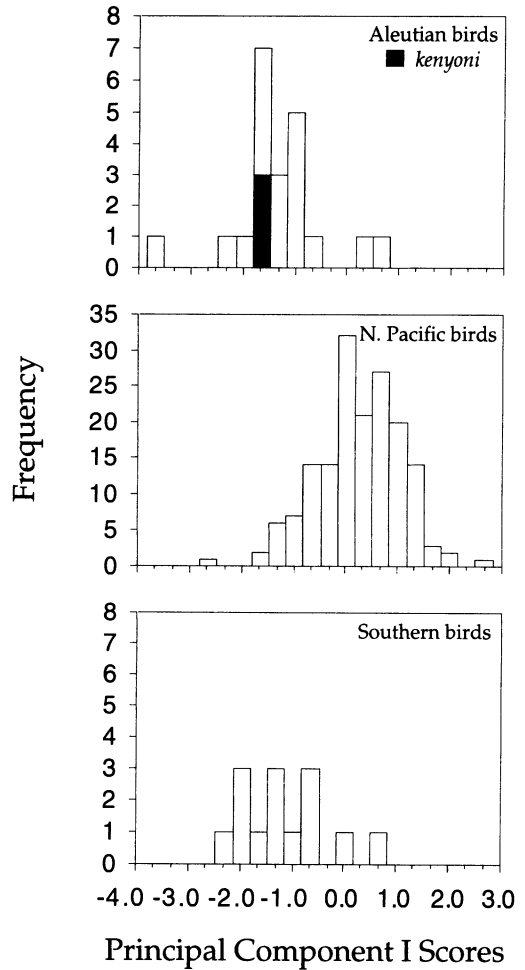


FIG. 5. Principal components scores summarizing size differences among Aleutian (including *kenyoni*), North Pacific, and southern (British Columbia, Washington, and California) *pelagicus*.

*gicus* we measured from British Columbia, Washington, and California were small and were similar in size to birds from the Aleutians (Fig. 5). Although we could have borrowed specimens from more museums, there are probably too few breeding-season specimens to determine if the size transitions in *pelagicus* are gradual or abrupt on the Alaska Peninsula and around the west coast of North America (Campbell et al. 1990, Johnsgard 1993).

DISCUSSION

*Qualitative evaluations.*—The characters used to describe new taxa should be readily acces-

sible to independent investigators. We encountered difficulties in identifying the exact characters on which Siegel-Causey (1991) based his description of *kenyoni*. Because anatomical names were used without an authoritative reference (e.g. Baumel et al. 1979) or an illustration of the features in question, most of the qualitative characters used to identify *kenyoni* were ambiguous.

After making the best judgments possible regarding the interpretation of Siegel-Causey's (1991) characters, we encountered further complications. The discrete taxonomic differences described by Siegel-Causey (1991: appendix 2) could not be confirmed for any of his seven diagnostic characters. Thus, no derived character, or autapomorphy, was verifiable in *kenyoni*. Siegel-Causey (1991) mentioned that several characters showed "modal" variation, although most were not specified and one was referred to in error (Siegel-Causey 1991:11).

Siegel-Causey (1991) stated that *kenyoni* is diagnosable based on "its small size and by six [really seven] autapomorphic skeletal characters." In our reanalysis, none of these seven characters was represented by a derived state in *kenyoni*. If *kenyoni* is a valid biological entity, then differences in size and shape would be the only basis for its diagnosis, a basis that Siegel-Causey (1991) portrayed as unreliable.

*Morphometric analyses.*—Our analyses of skeletal morphometrics also failed to distinguish *kenyoni*. When the three "kenyoni" specimens were plotted on the two canonical axes that cleanly separate *urile* males, *urile* females, *pelagicus* males, and *pelagicus* females, all three fell into the cluster of *pelagicus* females. This result is consistent with our generalized sexing function that identified the *kenyoni* specimens as females.

Assuming that the three *kenyoni* specimens were females, we included them in a discriminant analysis contrasting them with all other *pelagicus* females. Although these specimens were successfully discriminated (an artifact of small sample size), many *pelagicus* females fell into the *kenyoni* cluster. If this analysis had yielded two discrete groups of birds, separated by a gap in morphological space, the validity of *kenyoni* would have been upheld. Instead, specimens from our large sample of *pelagicus* females ( $n = 94$ ) were drawn into the loose cluster of *kenyoni*. No gap divided the specimens

into two clusters, as would be expected if they were different species (Fig. 4). When we repeated this analysis using all *pelagicus* and *kenyoni* specimens, thus making no assumption about sex of the specimens, the separation was even lower. These results suggest that *kenyoni* is a subset of *pelagicus* that cannot be discriminated morphometrically.

Why do our morphometric analyses generate these messy results when Siegel-Causey's (1991) canonical analysis so cleanly separated *kenyoni*, *pelagicus*, and *urile*? The contrast lies in the adequacy of samples. Siegel-Causey included a total of 40 specimens in his analysis (17 *urile*, 20 *pelagicus*, and 3 *kenyoni*). However, he included the measurements of 37 morphometric characters in his canonical analysis. As is true of multiple regression, discriminant and canonical analyses solve a set of  $p$  simultaneous equations (where  $p$  is the number of variables measured) such that the ratio of between-group variance to pooled within-group variance is maximized (Overall and Klett 1972). Because the number of equations in these multivariate analyses equals the number of characters, the number of specimens included in a discriminant analysis must considerably exceed the number of characters. When this is not the case, the solution to these equations risks being unique to the particular set of specimens measured. Only when considerably more specimens than characters are measured can the results of such multivariate analyses be trusted to represent general differences between the groups being discriminated (Stevens 1996:265). Given the similarity of the three cormorants Siegel-Causey (1991) was comparing, he simply did not measure enough specimens for his canonical axes to be generally applicable to other samples representing the same groups.

Although our qualitative and morphometric analyses failed to support the validity of *kenyoni*, our morphometric analyses revealed that *pelagicus* from the Aleutians are quite small, even though they are surrounded by populations that have consistently been characterized as large (Palmer 1962, Hobson 1997). Indeed, we found that the size differences between Aleutian and nearby Alaskan populations (Fig. 5) were as great as those between Alaskan populations and populations to the south, which are treated as *P. p. resplendens* Audubon because of their small size (Palmer 1962). The pattern of

variation that our results revealed for the Aleutians is consistent with the pattern of variation in at least one other Aleutian bird, the Rock Ptarmigan (*Lagopus mutus gabrielsoni*; Jacobsen et al. 1983). Unlike the situation for southeast Alaska and British Columbia (Warner et al. 1982, Rogers et al. 1991), the literature is still controversial concerning ice-free refugia in the western Aleutians. Ager (1983) and Hamilton and Thorson (1983) leave open the possibility of ice-free areas in the westernmost Aleutians at peak glaciation, when the Alaska Peninsula and the eastern Aleutians were fully glaciated.

Our data on the small size of Aleutian *pelagicus* conflict with the pattern of geographic variation summarized in Hobson (1997: appendix 2; based on Siegel-Causey's data for seven major populations of *pelagicus*). We cannot resolve this conflict, but we remain convinced that on the basis of skeletal characters, there is no reason to treat either the *kenyoni* type specimens, or the Aleutian populations of *pelagicus*, as a distinct species. However, both Siegel-Causey's (1991) original description and this evaluation are based only on skeletal characters. Until the behavior, ecology, and external appearance of these small Aleutian cormorants are better known, we see no evidence that *kenyoni* represents a valid taxon, and we suggest that it be considered a synonym of *Phalacrocorax pelagicus*.

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#### LITERATURE CITED

- AGER, T. A. 1983. Vegetational history of western Alaska during the Wisconsin glacial interval and the Holocene. Pages 75–93 in *Late-Quaternary environments of the United States* (H. E. Wright, Jr., Ed.). Volume 1. The late Pleistocene (S. C. Porter, Ed.). University of Minnesota Press, Minneapolis.
- AMERICAN ORNITHOLOGISTS' UNION. 1998. Checklist of North American birds, 7th ed. American Ornithologists' Union, Washington, D.C.
- BAUMEL, J. J., A. S. KING, A. M. LUCAS, J. E. BREAZILE, AND H. E. EVANS. 1979. *Handbook of avian anatomy: Nomina anatomica avium*. Academic Press, London.
- BAUMEL, J. J., AND L. M. WITMER. 1993. Osteologia. Pages 45–132 in *Handbook of avian anatomy: Nomina anatomica avium*, 2nd ed. (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, Eds.). Publications of the Nuttall Ornithological Club No. 23.
- CAMPBELL, R. W., N. K. DAWE, I. McTAGGART-COWAN, J. M. COOPER, G. W. KAISER, AND M. C. E. MCNALL. 1990. *The birds of British Columbia*, Vol. 1. Nonpasserines: Introduction and loons through waterfowl. Royal British Columbia Museum, Victoria.
- GEORGE, J. C., AND A. J. BERGER. 1966. *Avian myology*. Academic Press, New York.
- HAMILTON, T. D., AND R. M. THORSON. 1983. The Cordilleran ice sheet in Alaska. Pages 38–52 in *Late-Quaternary environments of the United States* (H. E. Wright, Jr., Ed.). Volume 1. The late Pleistocene (S. C. Porter, Ed.). University of Minnesota Press, Minneapolis.
- HOBSON, K. A. 1997. Pelagic Cormorant (*Phalacrocorax pelagicus*). In *The birds of North America*, no. 282. (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- HOWARD, H. 1929. *The avifauna of Emeryville Shellmound*. University of California Publications in Zoology 32:301–394.
- JACOBSEN, E. E., JR., C. M. WHITE, AND W. B. EMISON. 1983. Molting adaptations of Rock Ptarmigan on Amchitka Island, Alaska. *Condor* 85:420–426.
- JOHNSGARD, P. A. 1993. *Cormorants, darters and pelicans of the world*. Smithsonian Institution Press, Washington, D.C.
- OVERALL, J. H., AND C. J. KLETT. 1972. *Applied multivariate analysis*. McGraw-Hill, New York.
- OWRE, O. T. 1967. Adaptations for locomotion and feeding in the Anhinga and Double-crested Cormorant. *Ornithological Monographs* No. 6.
- PALMER, R. S. 1962. *Handbook of North American birds*, Vol. 1. Loons through flamingos. Yale University Press, New Haven, Connecticut.
- ROGERS, R. A., L. A. ROGERS, R. S. HOFFMANN, AND L.

- D. MARTIN. 1991. Native American biological diversity and the biogeographic influence of ice age refugia. *Journal of Biogeography* 18:623–630.
- SIEGEL-CAUSEY, D. 1988. Phylogeny of the Phalacrocoracidae. *Condor* 90:885–905.
- SIEGEL-CAUSEY, D. 1991. Systematics and biogeography of North Pacific shags, with a description of a new species. *Occasional Papers of the University of Kansas Museum of Natural History* 140:1–17.
- SIEGEL-CAUSEY, D., AND C. LEFEVRE. 1989. Holocene records of the Antarctic Shag (*Phalacrocorax [Notocarbo] bransfieldensis*) in Fuegian waters. *Condor* 91:408–415.
- SIEGEL-CAUSEY, D., C. LEFEVRE, AND A. B. SAVINETSII. 1991. Historical diversity of cormorants and shags from Amchitka Island, Alaska. *Condor* 93:840–852.
- STEVENS, J. 1996. *Applied multivariate statistics for the social sciences*, 3rd ed. Lawrence Erlbaum Associates, Mahwah, New Jersey.
- WARNER, B. G., R. W. MATHEWES, AND J. J. CLAGUE. 1982. Ice-free conditions on the Queen Charlotte Islands, British Columbia, at the height of late Wisconsin glaciation. *Science* 218:675–677.

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