MORPHOMETRICS OF FLIGHTLESSNESS IN THE ALCIDAE

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ABSTRACT.—Data collected from skin specimens of the 23 Recent species of Alcidae, skeletal material for Recent and fossil alcids, and published data on body mass and wing area were used to describe the morphometric characteristics of flightlessness in the Great Auk (*Pinguinus impennis*) and the fossil mancalline auks. A regression equation confirmed a body-mass estimate (5 kg) for *P. impennis* (Bédard 1969). The size and relatively small wings produced wing-loadings of roughly 22 $g \cdot cm^{-2}$, comparable to those of medium-sized penguins. Multivariate analysis of external measurements underscored the uniquely large size, relatively short wings, and moderately deep bill of *Pinguinus* compared to other Recent alcids. Analysis of skeletal measurements revealed that the genera of flightless Alcidae (*Pinguinus, Mancalla, Praemancalla,* and *Alcodes*) were characterized by relatively short distal wing elements and dorsoventral flattening of all major wing elements, in combination with relatively large core and pelvic dimensions. These differences were most pronounced in *Mancalla*, moderately developed in *Praemancalla*, and smallest in *Pinguinus*. Estimated body mass (1-4 kg) for selected fossil mancallines exceeded the largest flighted alcids (*Uria*) but was less than for *Pinguinus*. *Pinguinus* was a comparatively large piscivore sharing many morphological features with the Razorbill (*Alca torda*) and murres (*Uria* spp.). Its flightlessness evidently was a consequence of extreme specialization for pursuit diving, convergent with that of the Spheniscidae. Loss of flight imposed significant requirements on breeding sites and foraging habitats of the Great Auk and presumably the mancallines, and rendered *Pinguinus* exceptionally vulnerable to human exploitation. *Received 30 December 1987, accepted 23 May 1988.*

THE Great Auk (*Pinguinus impennis*), a flightless alcid of the North Atlantic, is remembered most for its extinction in the 19th century. This is understandable, for the demise of the Great Auk remains one of the most dramatic extirpations in historical times, one related to human exploitation for food (Grieve 1885, Nettleship and Evans 1985) and possibly to long-term climatic trends (Bengtson 1984). Superstition also took a toll: the last Great Auk taken in Great Britain reportedly was killed as a tempest-conjuring witch (Ley 1935, Greenway 1967). The extermination of the species was complete by 1844 (Greenway 1967), despite the prediction of this eventuality in the late 18th century (Nettleship and Evans 1985).

Flightlessness of the Great Auk, traditionally less compelling to ornithologists than the demise of the species, is of comparable importance to evolutionary biology. Although the flightless condition of *Pinguinus* was noted frequently by early naturalists, particularly with respect to its vulnerability to hunters on land, the anatomical correlates of flightlessness in the Great Auk have received relatively little attention. Existing anatomical studies consist of basic descriptive osteology (Owen 1879, Wiman and Hessland 1942) and limited mensural comparisons (Lucas 1890, Blanc 1927, Storer 1945, Miller and Howard 1949, Verheyen 1958). Even compilations of standard external measurements for the Great Auk are not available (cf. Coues 1868, Forbush 1912). The situation is related to the rarity of skin specimens and the variable distribution of the abundant skeletal material of *Pinguinus* in museums.

The fossil flightless mancalline alcids of coastal California are morphologically similar but less well known. Hundreds of elements of the group have been recovered, and 8 species in 3 genera are recognized from the late Miocene through the early Pleistocene: *Praemancalla lagunensis, P. wetmorei, Mancalla californiensis, M. diegensis, M. milleri, M. cedrosensis, M. emlongi,* and *Alcodes ulnulus* (Lucas 1901; Miller 1933; Howard 1947, 1966, 1968, 1970, 1971, 1976, 1978, 1982, 1983; Miller and Howard 1949; Olson 1981; Howard and Barnes 1987). The Miocene genus *Praemancalla* is considered to be a possible ancestor of the largely Pliocene genus *Mancalla* (Howard 1966, 1976.) Neither genus is thought to be closely related to *Pinguinus*. The Pacific genera generally are placed in a separate family or subfamily (Howard 1966, 1983) and may be related most closely to the puffins (Fraterculini; R. M. Chandler unpubl. data). *Pinguinus* is judged to be closely related to the Razorbill (*Alca torda*)

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and murres (*Uria* spp.) on behavioral and morphological grounds (Storer 1945, Strauch 1985).

Alcids are wing-propelled diving birds. Strokes of the partly folded wings provide virtually all of the propulsion and much of the maneuverability for submarine locomotion (Townsend 1909, Kelso 1922, Storer 1945). Structural convergences between the Great Auk and the similarly flightless, wing-propelled penguins (Spheniscidae) have received considerable attention (e.g. Owen 1879, Wiglesworth 1900, Storer 1945). Aerial flight and submarine propulsion clearly impose different selective pressures on alar structure and the morphology of *Pinguinus* reflects the evolutionary substitution of aerial flight for extreme specialization for diving (Wiglesworth 1900; Bent 1919; Storer 1960, 1971; Bédard 1969; Bengtson 1984). *Mancalla* was probably at least as specialized osteologically for diving as *Pinguinus* (Wiman and Hessland 1942, Miller and Howard 1949, Howard 1970).

I compared flightless and flighted alcids, emphasizing multivariate morphometric analyses. Data from study skins and skeletons of all 22 extant alcid species, the Great Auk, and the fossil mancalline auks were included. My objectives were: to describe quantitatively the morphological characteristics associated with loss of flight in the Alcidae; to estimate the body mass of adequately represented mancalline auks; and, using available ecological and biogeographical information, to consider selected aspects of the evolution of flightlessness in alcids.

METHODS

Specimens and related data.—I collected data from 11 mounted skin specimens of the Great Auk. In addition, colleagues provided comparable data from an additional 14 mounted *Pinguinus* skins (see Acknowledgments). At least 20 study skins (usually 10 of each sex) of each of the 22 extant species of Alcidae were sampled for comparisons. I measured total length (extended specimens only, from bill to tail, feet excluded), culmen length (exposed, on midline), bill height (at gonys), wing length (chord of unflattened wing), tarsus length (cranial surface), digit-III (middle-toe) length (excluding nail), and tail length (medial arc) (Baldwin et al. 1931).

Data on body mass of extant alcids were collected from specimen labels and published compilations (Johnson 1935, 1944; Belopol'skii 1961; Bédard 1967, 1969; Kuroda 1967; Dement'ev and Gladkov 1968; Sealy 1976; Threlfall and Mahoney 1980; Vermeer and Cullen 1982; Murray et al. 1983; Dunning 1984). Wing areas were traced (Raikow 1973), from fresh birds or thawed, fresh-frozen specimens, and the resultant areas were measured with a compensating polar planimeter. Additional wing areas were taken from Magnan (1912, 1922), Poole (1938), Kuroda (1967), Spring (1971), Stempniewicz (1982), and Pennycuick (1987); several tracings were provided by R. M. Chandler. Wing-loading was calculated as the ratio of body mass divided by total wing area ($g \cdot cm^{-2}$; Clark 1971).

Associated skeletal material of the Great Auk is not available. One possible exception is an apparently complete, largely articulated skeleton of an immature bird at the British Museum. Mounted skeletons of *Pinguinus* are composites of unassociated skeletal elements. Extensive series of disassociated skeletal elements are held at the U.S. National Museum of Natural History, American Museum of Natural History, and Museum of Comparative Zoology (Harvard University). Anatomical nomenclature follows Baumel (1979).

I sought to measure at least 40 unworn specimens of each major skeletal element of *P. impennis*. The more fragile scapula, furcula, and distal phalanges were not available in such numbers. Comparable data were collected from all available material of *Mancalla*, *Praemancalla*, and *Alcodes*. Limited mensural data also were collected from a new species of *Mancalla* (here referred to as *Mancalla* lg. sp.; Chandler unpubl. data) and *Australca* sp. (Brodkorb 1955, Olson 1977). *Pinguinus alfrednewtoni*, a poorly represented Pliocene form similar to *P. impennis* in its measurements (Olson 1977), was excluded from study. I also sampled 10 complete skeletons (5 of each sex) of each of the 22 extant species of alcid, although complete samples were not available for several species (e.g. *Cepphus carbo*, *Synthliboramphus wumizusume*, *Aethia pygmaea*).

Forty-six skeletal measurements were employed, most of which were described previously (Livezey and Humphrey 1984, 1986) and 11 of which were illustrated by Spring (1971; measurements 2, 6, 7, 12, 13, 14, 16, 38, 39, 40, 41). All skeletal measurements were made with dial calipers to 0.1 mm. Sexual dimorphism was considered to be small in extant species of alcid (Storer 1952), and in this study sexual differences were found to be negligible. This similarity of the sexes, and the lack of information on sex for specimens of *Pinguinus* and the fossil species, prompted the pooling of the sexes in the morphometric comparisons.

Statistical analyses.—Linear measurements and log-transformed (base *e*) wing-loadings and skeletal ratios were compared using analysis of variance (ANOVA) and analysis of covariance (ANCOVA). Spearman correlation coefficients (*r*) were used to measure bivariate associations.

Allometry of body dimensions, i.e. the relative rates of size change among variables, was quantified using bivariate allometric equations (Gould 1966). I based these estimates on linear regressions on log-transformed data, using "geometric mean" estimates to accommodate error in both variables (Livezey and Humphrey 1986).

Stepwise linear regressions of log-transformed data were used to estimate the body mass of *P. impennis* based on species means of external measurements of skins. Body mass of fossil *Mancalla* and *Praemancalla* was estimated from stepwise regressions of log-transformed body mass on significantly correlated ($P < 0.05$) principal components of available skeletal measurements. Components were derived from covariance matrices based on log-transformed data.

For external measurements that involved associated measurements for samples of skins of Great Auks, canonical analyses of log-transformed data for Recent species of alcid were used. Canonical analysis (CA) is a multivariate technique that is robust to moderate departures from the assumptions of multivariate normality and homogeneity of covariance matrices of groups. CA provides multivariate axes that maximally discriminate predefined groups (Pimentel 1979). CAs were also used for interspecific comparisons of associated measurements of humeri, ulnae, and sterna. Variables included in each CA were backstep-selected from the complete suites of measurements using F-statistics ($P < 0.05$).

I used principal component analyses (PCAs) of mean measurements for the species of flightless auks (sexes pooled) to assess multivariate skeletal variation among taxa. Components were extracted by singular value decompositions of covariance matrices based on log-transformed data. *Pinguinus* and the extant Alcidae were compared using 46 skeletal measurements, and a reduced data set of 23 measurements was used to include fossil species in the comparisons. Because of poor representation of the similarly sized *Mancalla californiensis, M. cedrosensis,* and *M. diegensis,* the three species were pooled to derive a single mean vector representing "medium-sized" *Mancalla.* My primary objectives for the PCAs were to determine the multivariate axis or axes of changes associated with flightlessness, and to determine the relative positions of flightless species on the major axes of variation for alcids generally. The flightless species, because of their large size and exceptional shape, acted as influential outliers in the definition of axes in normal PCAs. This seriously confounded "size" with the shape correlates of flightlessness on PC-I and adversely affected the definition of subsequent axes. Therefore, I excluded the flightless species for the definition of the first principal component. The flightless species were projected onto this PC-I *a posteriori,* and the residuals for *all species* were subjected to another PCA to extract the subsequent axes. I refer to these modified components as PC-I*, PC-II*, and PC-III*. Because the flightless species were not used in the derivation of PC-I* but were considered in subsequent components, the latter axes were correlated with PC-I* (but were mutually orthogonal). Despite this sacrifice of orthogonality, this approach was preferable to a standard PCA. It produced a virtually isometric "size" axis for PC-I*, defined a single important "shape" PC-II* for alcids generally (using complete skeletons), and isolated the morphometric changes associated with flightlessness on separate axes (PC-III* and PC-II*, for complete and reduced data sets, respectively). Total variances incorporated on the standard principal components and corresponding modified components were virtually identical. The standard PCs exceeded the modified axes by less than 0.05% of the total variance in the subspaces discussed.

I use the term "size" in its traditionally broad sense, i.e. in reference to spatial extent or dimension. Various measures of "size," none perfect for all purposes, emerged from the morphometric comparisons; and rationales for considering them as representative of "size" are given. Correlations between mean body mass (using log-transformed data) and these emergent "size" measures are probably the most useful direct measure of overall size (Clark 1979), and are given to facilitate interpretation. I estimated divergences between multivariate "size" axes and hypothetical axes of isometric size using direction cosines between vectors (Pimentel 1979).

For CAs of skins and separate skeletal elements, specimens lacking a minority of measurements were subjected to missing-data estimation. Missing data were estimated from stepwise regressions on available measurements for specimens grouped by genus. These estimates comprised 0.9% of the skin and 1.5% of the skeletal data sets.

Statistical procedures used were part of the Biomedical Computing Programs (Dixon 1985) and performed on an IBM computer at the University of Kansas.

RESULTS

EXTERNAL CHARACTERS

Univariate comparisons.—External measurements demonstrate the substantially larger size of the Great Auk compared with other Recent alcids (Table 1), including the large extant piscivorous genera *Cepphus, Uria,* and *Alca. Alca* is considered to be the closest extant relative of *Pinguinus* (Storer 1945, Strauch 1985). *Pinguinus* shared with *Alca* its deep, laterally compressed bill and, despite its much larger body size, had wing lengths comparable to those of *Cepphus* (Table 1).

Despite the thousands of Great Auks slaughtered during the eighteenth and nineteenth centuries, the only putative datum for body mass was the report by Feilden (1872) of a *Pinguinus* killed in 1808 which weighed nine Danish

TABLE 1. External measurements (mm, g) of three flighted alcids and the Great Auk ($\bar{x}$ ± SD [n]).

Species	Total length	Total mass[a]	Culmen length	Bill height	Wing length	Tail length	Tarsus length	Middle-toe length
Cepphus grylle	309 ± 18 (20)	427 (155)	30.6 ± 1.4 (20)	7.3 ± 0.6 (20)	159 ± 5 (19)	46 ± 3 (20)	32.7 ± 1.4 (20)	36.4 ± 1.6 (20)
Uria aalge	423 ± 25 (20)	1,030 (613)	44.9 ± 1.7 (20)	13.3 ± 0.8 (20)	200 ± 6 (20)	44 ± 3 (20)	38.7 ± 2.1 (20)	43.8 ± 2.5 (20)
Alca torda	403 ± 29 (20)	722 (217)	34.7 ± 1.7 (20)	21.9 ± 1.7 (20)	197 ± 10 (20)	79 ± 7 (20)	33.7 ± 1.6 (20)	41.9 ± 2.3 (20)
Pinguinus impennis	786 ± 58 (24)	[5,000]	84.7 ± 4.3 (25)	39.3 ± 2.4 (25)	160 ± 9 (23)	73 ± 13 (17)	59.6 ± 11.2 (22)	70.2 ± 5.1 (24)

[a] Means based on published data and specimen labels; standard deviations not available. Mass of *Pinguinus* estimated (see text).

pounds (4.5 kg). Bédard (1969) estimated the body mass of *Pinguinus* to be "c. 5000 [g]" but provided no details concerning this estimate. I attempted an independent approximation of the mass of *Pinguinus* from a regression equation that related body mass to six non-alar external measurements for the 22 extant species of alcids, using log-transformed means. I excluded wing length because its relationship to body size is obviously atypical in *Pinguinus*. Despite the small number of data (n necessarily being 22), all six remaining variables entered significantly ($P <$ 0.10). The resulting regression model was:

$$\begin{aligned} \mathrm{M} = & -7.909 + 2.344(\mathrm{TOTLEN}) \\ & + 0.991(\mathrm{LDIGIT3}) - 0.325(\mathrm{LTARSUS}) \\ & - 0.508(\mathrm{LTAIL}) + 0.172(\mathrm{HTBILL}) \\ & - 0.121(\mathrm{LCULMEN}). \end{aligned}$$

The variables are listed in order of entry into the model; adjusted R^2 for the model was 98.8%. Substituting log-transformed mean measurements for the Great Auk into this equation (Table 1) and taking the antilog provided an estimated body mass of 4,999 g, almost identical to the value of Bédard (1969).

Relative wing size.—The extremely small relative wing lengths of *Pinguinus* was conspicuous in a bivariate plot of wing lengths on body mass for 23 species of alcids, using the estimated body mass of 5,000 g for *Pinguinus* (Fig. 1). The allometric coefficient for the flighted species, $\hat{b}$ = 0.322 (SE [$\hat{b}$] = 0.001), was significantly less (P < 0.001) than the coefficient for isometry between a linear variate with mass (b = 0.333). The relatively shorter wings of *Pinguinus* retained the 10 functional primary remiges typical of the Alcidae (6 specimens examined), although the remiges were substantially shorter than in extant species.

Wing areas of 10 flighted species of the Alcidae are available, and the resultant estimates of wing-loading closely mirrored the negative allometry of wing length with body size. This relationship produced progressively greater wing-loadings as body mass increased. Wing-loadings were, from smallest to largest mean body mass (n = sample sizes for wing areas): *Aethia pusilla*, 0.71 (n = 2); *Alle alle*, 0.94 (113); *Synthliboramphus antiquus*, 1.02 (2); *Aethia cristatella*, 1.32 (1); *Cyclorrhynchus psittacula*, 1.11 (1); *Cepphus columba*, 1.23 (1); *Fratercula arctica*, 1.34 (21); *Alca torda*, 1.63 (4); *Uria lomvia*, 1.69 (2); and *U. aalge*, 2.06 (20). The allometric coefficient for wing area on body mass for flighted alcids was $\hat{b}$ = 0.632 (SE [$\hat{b}$] = 0.003; regression significant, $P < 0.001$; $R^2 = 0.99$), significantly less ($P <$ 0.001) than that for isometry of wing area with body mass (b = 0.667). The estimated wing area for *Pinguinus* was 230 cm^2, based on the doubled area of a tracing of a partially folded wing that was "corrected" graphically to approximate an extended wing. Together with the 5-kg estimate for body mass, this indicates that the wing-loading of *Pinguinus* was roughly 22 g·cm^{-2}. This estimate was much higher than one from an allometric extrapolation of a "flighted" alcid to a body mass of 5 kg, which yielded a wing-loading of 3.26 g·cm^{-2}. This projection, and the empirical estimate of 22 g·cm^{-2} for *Pinguinus*, exceed the threshold of flightlessness of 2.5 g·cm^{-2} hypothesized by Meunier (1951).

Multivariate patterns.—A CA of the external measurements from 481 skin specimens defined three important axes of interspecific variation. All seven variables entered the model significantly (P < 0.001), and provided highly signif-

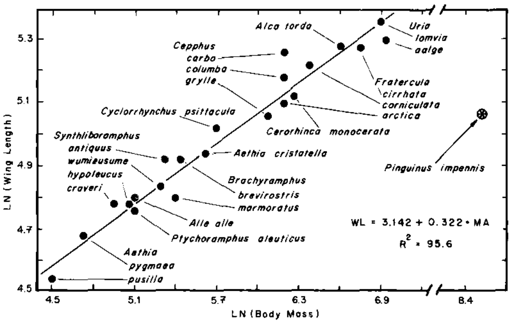

Fig. 1. Log of the mean body mass and wing length of the 23 Recent species of alcid. Regression line (Type-II) was fitted for 22 flighted species, and mass of *Pinguinus impennis* was estimated. The abscissa was broken to accommodate *Pinguinus.*

TABLE 2. Standardized coefficients and associated statistics for canonical variates of seven external measurements of 23 alcid species ($n = 481$).

	Canonical variate		
Character	I	II	III
Total length	−0.26	0.24	−0.31
Culmen length	−0.64	0.48	−0.34
Bill height	−0.25	−0.99	0.15
Wing length	−0.18	0.39	0.97
Tail length	−0.11	−0.17	0.07
Tarsus length	−0.03	0.24	−0.18
Middle-toe length	−0.27	−0.24	−0.12
Eigenvalue	152.6	26.5	13.2
Variance (%)	73.3	12.7	6.4
Canonical *R*	1.00	0.98	0.96

icant discrimination of the 23 Recent species of alcid (Wilks' lambda $< 10^{-7}$; df = 7, 22, 458; $P \ll 0.001$) All pairwise interspecific differences were significant ($P < 0.001$).

The first canonical variate (CV-I) had coefficients of like sign for all measurements and reflects in large part "general size," although the relatively great contribution of culmen length and small contributions of tail and tarsus lengths resulted in an approximate 35° divergence from isometry. Mean scores on CV-I were strongly correlated with mean body mass ($r = -0.91$ for flighted species, $r = -0.95$ including estimated mass for *Pinguinus*). CV-I incorporated almost three-fourths of the total interspecific variance (Table 2), and scores on the axis differed significantly among species (ANOVA of scores; $F = 3177.6$; df = 22, 458; $P < 0.0001$). Small species (e.g. *Aethia, Alle, Brachyramphus*) were scored highly on this axis (reflecting the negative coefficients), whereas species with large overall size (*Uria, Fratercula,* and especially *Pinguinus*) had low scores (Fig. 2).

The second most important axis (CV-II) was in large part a measure of "relative bill height," with a lesser, correlated contribution from lengths of the tail and middle toe (Table 2). Interspecific differences in scores on CV-II were highly significant ($F = 551.6$; df = 22, 458; $P < 0.0001$). Species with relatively deep bills and, to a lesser extent, relatively long tails and middle toes (e.g. *Fratercula, Cyclorrhynchus, Aethia*) had low scores on CV-II, and groups with opposite proportionalities (e.g. *Uria, Cepphus*) had high scores (Fig. 2). The Great Auk was intermediate on CV-II, with a score similar to those of *Alca, Ptychoramphus,* and *Alle* (Fig. 2).

The third variate (CV-III) reflected "relative wing length" (Table 2), and once again underscored the unique body form of *Pinguinus* compared to other Recent alcids. The highly significant interspecific differences in scores on CV-III ($F = 295.1$; df = 22, 458; $P < 0.0001$) resulted largely from the extremely low mean score of *Pinguinus,* and reflected its relatively short wings (Fig. 2). Of the 22 flighted species, only the two endomychurine *Synthliboramphus* and *Aethia pusilla* showed any tendency toward relative shortening of the wing.

SKELETAL CHARACTERS

Univariate comparisons of species.—Most skeletal measurements also reflected the large size of *Pinguinus* (Tables 3, 4). Except for distal wing elements, *Pinguinus* exceeded all other Alcidae, *Mancalla* and *Praemancalla,* in its skeletal dimensions. Measurements of the trunk and leg demonstrated the difference most clearly, e.g. tibiotarsi of *Pinguinus* averaged 4 cm (45%) longer than those of *Uria aalge* (Table 4). Although the humeri of *Pinguinus* were the longest in the Alcidae, they averaged only 22% longer than those of *Uria.* That is, the *relative* length of the humerus of *Pinguinus* was less than in *Uria, Alca,* and *Cepphus,* but was approached by those of *Mancalla* and *Praemancalla* (Tables 3, 4). The tendency toward alar shortening in the flightless auks is more pronounced in the mid-wing elements, especially lengths of the radius, ulna, and carpometacarpus, which were absolutely

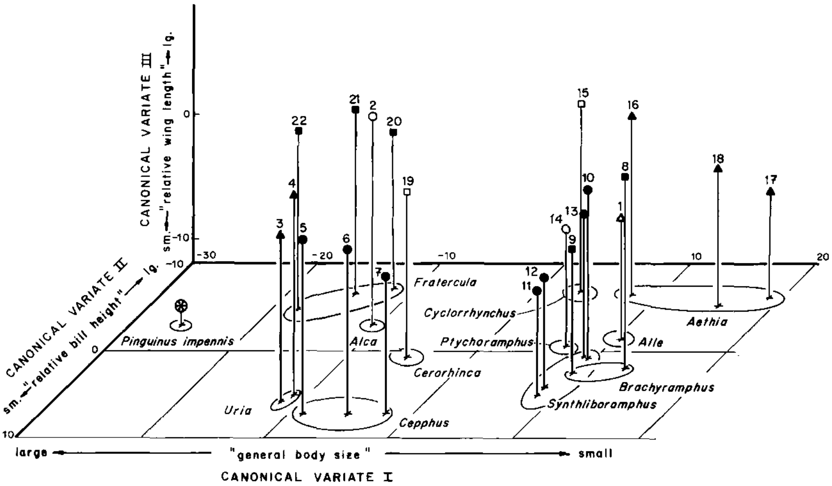

Fig. 2. Plot of mean scores of 23 species of alcid on the first 3 canonical variates based on seven external measurements. Flighted species are numbered as follows: (1) *Alle alle*, (2) *Alca torda*, (3) *Uria aalge*, (4) *U. lomvia*, (5) *Cepphus carbo*, (6) *C. columba*, (7) *C. grylle*, (8) *Brachyramphus brevirostris*, (9) *B. marmoratus*, (10) *Synthliboramphus antiquus*, (11) *S. craveri*, (12) *S. hypoleucus*, (13) *S. wumizusume*, (14) *Ptychoramphus aleuticus*, (15) *Cyclorrhynchus psittacula*, (16) *Aethia cristatella*, (17) *A. pusilla*, (18) *A. pygmaea*, (19) *Cerorhinca monocerata*, (20) *Fratercula arctica*, (21) *F. corniculata*, and (22) *F. cirrhata*.

shorter in *Pinguinus* than in the much smaller *Uria* (Table 3). Reductions in the lengths of the mid-wing elements were even greater in *Praemancalla* and *Mancalla*.

Greater shaft widths also characterized the wing elements of the three flightless genera (Table 3), as demonstrated by their comparatively large maximal widths (MWMs). An ANCOVA of "relative flatness" (ratios of maximal and least shaft widths) confirmed these shape differences in humeri ($F = 84.8$; df = 6, 113; $P < 0.001$) and ulnae ($F = 24.1$; df = 6, 120; $P <$

TABLE 3. Summary statistics ($\bar{x}$ ± SD [n]) for selected measurements of major skeletal wing elements of three flighted and 6 flightless alcids. MWM = maximal width at midpoint.

	Humerus		Ulna		
Species	Length	MWM	Length	MWM	Carpometacarpus length
Cepphus grylle	59.6 ± 1.6 (11)	4.4 ± 0.2 (11)	51.4 ± 1.7 (11)	4.2 ± 0.3 (11)	34.0 ± 1.3 (11)
Uria aalge	87.3 ± 2.4 (12)	7.9 ± 0.5 (12)	65.9 ± 1.6 (12)	6.3 ± 0.3 (12)	43.3 ± 2.8 (12)
Alca torda	75.5 ± 3.0 (10)	6.9 ± 0.3 (10)	60.1 ± 2.6 (10)	5.8 ± 0.3 (10)	40.2 ± 1.8 (10)
Pinguinus impennis	106.1 ± 7.3 (69)	12.3 ± 0.7 (69)	57.4 ± 1.8 (59)	8.6 ± 0.4 (59)	42.7 ± 1.4 (59)
Mancalla diegensis	72.9 ± 6.9 (12)	9.7 ± 1.0 (15)	29.3 ± 1.7 (15)	6.0 ± 0.6 (15)	35.7 ± 2.4 (7)
M. cedrosensis	71.7 ± 2.3 (2)	9.6 ± 1.3 (2)	30.0 ± 1.0 (9)	6.2 ± 0.3 (9)	35.8 (1)
M. milleri	63.0 ± 2.8 (18)	8.3 ± 0.8 (24)	26.4 ± 1.3 (21)	5.5 ± 0.4 (21)	31.6 ± 1.7 (12)
M. emlongi	87.1 ± 4.4 (2)	11.3 ± 0.1 (2)	—	—	40.6 ± 1.1 (2)
Praemancalla spp.	78.0 ± 5.3 (4)	9.8 ± 1.1 (5)	40.6 ± 5.2 (2)	7.3 ± 0.0 (2)	36.3 (1)

TABLE 4. Summary statistics ($\bar{x}$ ± SD [n]) for lengths of two trunk and three leg elements of three flighted and six flightless alcids.

Species	Sternal carina length	Coracoid length	Femur length	Tibiotarsus length	Tarsometatarsus length
Cepphus grylle	81.2 ± 3.0 (11)	30.4 ± 0.9 (11)	36.2 ± 1.0 (11)	64.5 ± 1.9 (11)	31.3 ± 1.2 (11)
Uria aalge	122.5 ± 5.8 (12)	40.1 ± 1.1 (12)	47.8 ± 1.5 (12)	91.1 ± 2.9 (12)	38.0 ± 1.3 (12)
Alca torda	108.7 ± 2.8 (10)	36.3 ± 1.2 (10)	41.2 ± 1.9 (10)	76.1 ± 1.4 (10)	33.2 ± 1.0 (10)
Pinguinus impennis	189.7 ± 11.3 (28)	60.3 ± 2.8 (62)	73.0 ± 2.4 (62)	132.8 ± 4.6 (62)	52.2 ± 1.8 (60)
Mancalla diegensis	—	47.8 ± 4.6 (6)	52.3 ± 5.5 (3)	89.3 ± 8.7 (7)	41.4 ± 2.7 (5)
M. cedrosensis	—	—	54.8 (1)	87.0 (1)	41.2 (1)
M. milleri	—	42.8 ± 5.1 (6)	48.3 ± 2.9 (8)	78.4 ± 4.5 (5)	35.2 ± 2.3 (10)
M. emlongi	—	58.6 (1)	65.7 ± 2.3 (3)	—	47.3 (1)
Praemancalla spp.	—	—	68.8 (1)	108.0 (1)	47.6 (1)

0.001). This "flattening" of the wing bones in flightless auks also was confirmed by an ANCOVA of maximal shaft widths (MWMs) for the species tabulated (excluding the inadequate samples of *M. emlongi* and *Praemancalla*), while correcting for interspecific differences in lengths of elements, for both the humerus ($F = 194.6$; df = 6, 113; $P < 0.001$) and ulna ($F = 334.2$; df = 6, 120; $P < 0.001$).

Canonical analyses of single elements.—Separate CAs of humeri, ulnae, and sterna of flightless and selected flighted alcids permitted a multivariate assessment of morphological differences among a maximal number of taxa (Fig. 3). The CA of 125 humeri of 10 species of alcid incorporated all four measurements significantly ($P < 0.001$), and effectively discriminated the six adequately sampled species (Wilks' lambda = 0.0009; df = 4, 5, 113; $P < 0.001$) and five additionally plotted taxa (*Australca* sp., *Mancalla cedrosensis, M. emlongi, M.* lg. sp., *Praemancalla* spp.). The first axis (CV-I) reflected the lengths, head widths, and maximal shaft widths of humeri (Table 5), and interspecific differences in scores were significant ($F = 518.6$; df = 8, 115; $P < 0.0001$). Species with large measurements had low scores (*P. impennis*), smaller species incurred higher scores (*Cepphus grylle*), and the remaining taxa (e.g. *Alca, Uria,* and *Mancalla*) were intermediate (Fig. 3A). CV-II contrasted lengths and maximal shaft widths of humeri, i.e. measured "relative shaft width" (Table 5). Species differed significantly in scores on CV-II ($F = 135.6$; df = 8, 115; $P < 0.0001$). Those with comparatively narrow humeri (*Uria, Alca,* and *Cepphus*) scored highly; *P. impennis* was in-

TABLE 5. Standardized coefficients and summary statistics for canonical variates of humeri, ulnae, and sterna of selected Recent and fossil alcids.

Element	Variable	CV-I	CV-II
Humerus (n = 125)	Length	−0.55	1.01
	Head width	−0.18	−0.12
	LWM	0.06	0.11
	MWM	−0.50	−1.08
	Eigenvalue	36.7	9.1
	Variance (%)	77.4	19.2
	Canonical R	0.99	0.95
Ulna (n = 131)	Length	1.19	0.15
	LWM	0.02	−0.15
	MWM	−0.55	−0.98
	Eigenvalue	125.8	13.7
	Variance (%)	90.0	9.8
	Canonical R	1.00	0.97
Sternum (n = 43)	Carina length	−0.44	1.14
	Basin length	−0.54	−0.79
	Least width	−0.34	−0.39
	Caudal width	0.15	−0.52
	Eigenvalue	86.5	3.4
	Variance (%)	94.9	4.8
	Canonical R	0.99	0.89

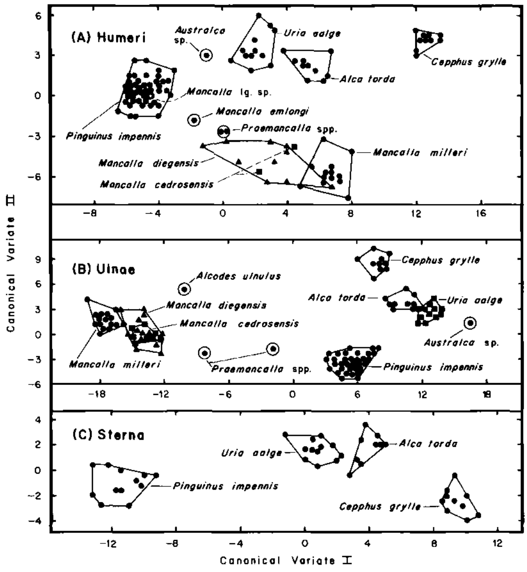

Fig. 3. Plots of first 2 canonical variates for flightless and selected flighted alcids of: (A) 4 measurements of humeri, (B) 3 measurements of ulnae, and (C) 4 sternal measurements. Polygons connect extreme individuals in each taxon.

termediate; and the mancallines had the broadest humeral shafts and lowest scores (Figs. 3A, 4). The undescribed, large *Mancalla* ("*M.* lg. sp.") closely resembled *Pinguinus* in its humeral dimensions. A third variate (CV-III, not figured) contributed only 3% of total intergroup variance, but provided significant interspecific differences in scores ($F = 30.0$; df = 8, 115; $P < 0.0001$). CV-III primarily separated *Alca, Uria,* and *M. milleri* from *Cepphus, Pinguinus,* and the larger mancallines by relative least shaft width and relative head width.

A CA of ulnae of selected alcids significantly separated the seven species analyzed (Wilks' lambda = 0.0004; df = 3, 6, 121; $P < 0.001$); an additional three taxa were plotted on the axes (*Australca, Alcodes, Praemancalla*) which were represented by small samples (Fig. 3B). The three variables entered the model significantly (Table 5; $P < 0.001$) and contributed to two axes incorporating interspecific differences in scores; (ANOVA of scores; $F = 1669.8$ and 213.2, respectively; df = 8, 122; $P < 0.0001$). CV-I contrasted lengths and maximal shaft widths of the ulna (Table 5). *Mancalla* had short, wide ulnae and hence low scores, *Praemancalla* and *Pinguinus* were intermediate, and the three flighted genera and the fossil *Australca* had high scores which reflected their comparatively long, slender ulnae (Figs. 3B, 4). The vertical axis (CV-II) implied residual robustness of the ulnar shafts, which was greatest in the stout bones of *Pinguinus* and progressively less so in *Mancalla* and the flighted genera (Fig. 3B).

Sterna of the Great Auk, similar in overall conformation to that of *Uria* (*Pinguinus* illustrated in Eyton 1875, Wiman and Hessland 1942; *Uria* in Kuroda 1954), were contrasted with those of three flighted species of alcid using a CA of five measurements, four of which entered the model significantly ($P < 0.01$; Table 5). No sternum of the fossil species was preserved adequately for analysis. The resultant CA significantly differentiated the four species (Wilks' lambda = 0.003; df = 4, 3, 39; $P < 0.001$). CV-I for sterna essentially ordinated the taxa by general sternal size, exclusive of caudal width (Table 5). Taxa differed significantly on this axis ($F = 864.1$; df = 3, 39; $P < 0.0001$), and the low scores for *Pinguinus* on this axis reflect their large sterna (Fig. 3C). CV-II contrasted carina length with the remaining sternal dimensions (Table 5). Scores differed among taxa ($F = 43.7$; df = 3, 39; $P < 0.0001$), and indicated that *Alca* and *Uria* slightly exceeded *Pinguinus* and *Cepphus* in "relative carina length" (Fig. 3C).

PCA of complete skeletons.—A modified PCA of mean vectors of 46 skeletal measurements

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Fig. 4. Illustrations of major wing elements of (A) *Alca torda* (Univ. S. Florida 4358), (B) *Pinguinus impennis* (U.S. Nat. Mus. 1285, Los Angeles County Mus. 90055, 90057), and (C) *Mancalla diegensis* (San Diego Nat. Hist. Mus. 24868, 21044, 28603, 25002); dorsal views of left elements in probable positions used in submarine propulsion with diagrams of mean intra-alar skeletal proportions (H = humerus, U = ulna, C = carpometacarpus, M = proximal phalanx of digiti majoris, not illustrated). Note the comparatively great extension of distal elements (positions inferred from qualitative osteology) and dorsoventral flattening of alar elements in flightless *Pinguinus* and *Mancalla*; *Mancalla* is further derived in the proximal position of the processus supracondylaris dorsalis or "ectepicondylar process" (ep), shortening of the forewing, and curvature of the humerus.

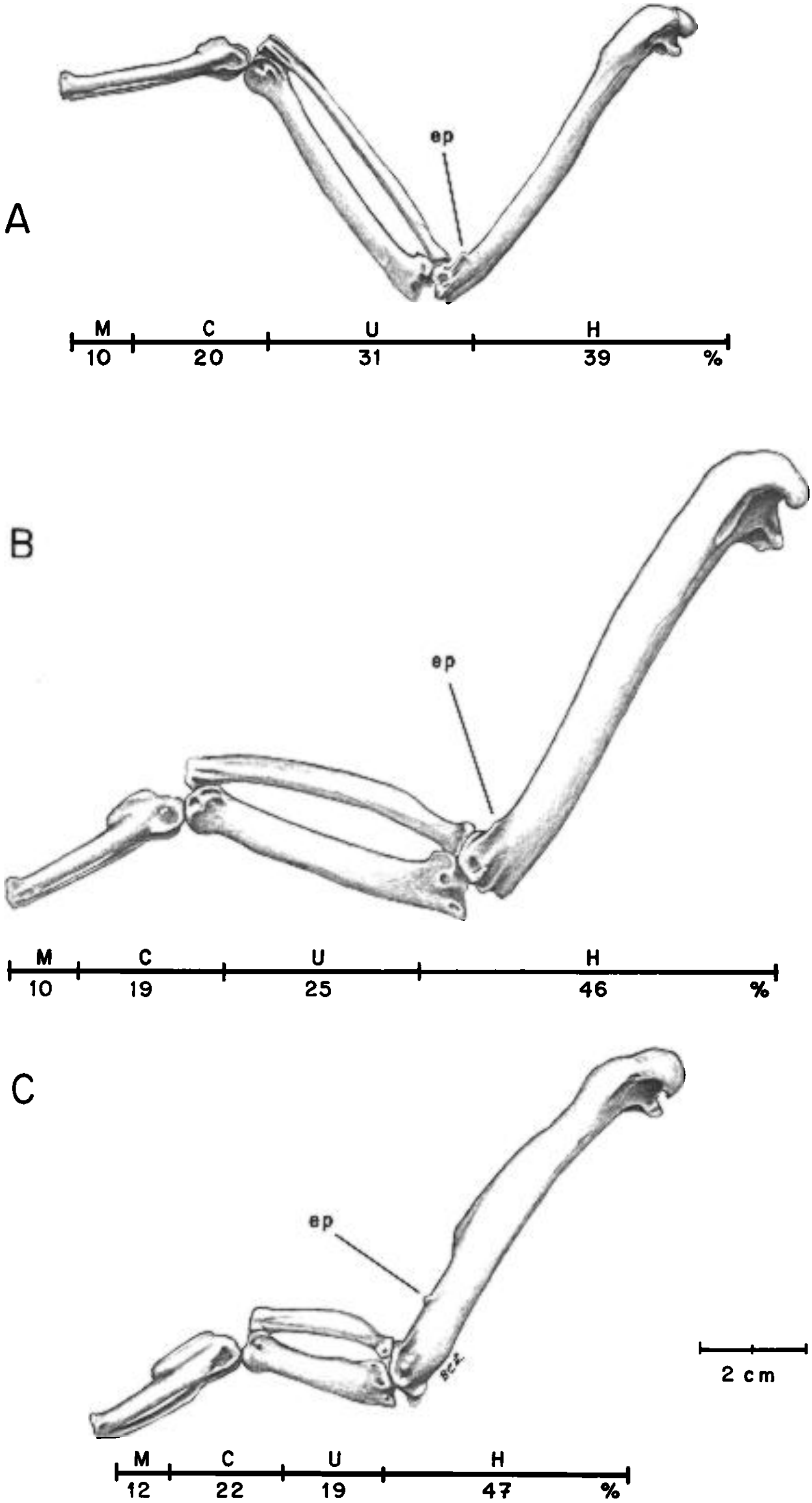
A
ep
M
C
U
H
10
20
31
39
%
B
ep
M
C
U
H
10
19
25
46
%
C
ep
M
C
U
H
12
22
19
47
%
2 cm

TABLE 6. Correlation coefficients of 46 original skeletal variables with first (modified) principal component (PC-I*, see text), and the first and second principal components of the residual variance from PC-I* for 23 Recent alcids (PC-II*, PC-III*). Signs to right of coefficients for PC-III* indicate variables so correlated with residuals from PC-I* ($|r| \geq 0.20$).

Variable	PC-I*	PC-II*	PC-III*		Variable	PC-I*	PC-II*	PC-III*	
Bill length	0.95	0.30	−0.48		Tibiotarsus length	0.98	−0.03	−0.52	−
Cranium length	0.99	0.18	−0.48		LWM	0.97	−0.08	−0.54	−
Height	0.95	0.07	−0.59	−	Tarsometatarsus length	0.89	−0.11	−0.42	
Width	0.96	0.01	−0.50		APW	0.96	−0.07	−0.54	−
Humerus length	0.99	0.15	−0.39	+	LMW	0.94	−0.11	−0.61	−
Head width	0.99	0.10	−0.39	+	Digit III, Ph. 1 length	0.96	−0.13	−0.51	−
LWM	0.98	0.08	−0.37	+	Ph. 2 length	0.98	−0.08	−0.50	
MWM	0.96	0.35	−0.51	−	Ph. 3 length	0.95	−0.15	−0.55	−
Radius length	0.92	−0.02	−0.15	+	Scapula length	0.98	0.24	−0.44	
LWM	0.98	0.11	−0.33	+	Blade width	0.91	0.29	−0.61	−
MWM	0.99	0.21	−0.52	−	Coracoid length	0.99	0.02	−0.50	
Ulna length	0.92	−0.02	−0.14	+	Basal width	0.95	0.36	−0.41	
LWM	0.99	0.13	−0.37	+	Sternal carina length	0.93	0.44	−0.44	
MWM	0.99	0.18	−0.46	+	Basin length	0.98	0.20	−0.51	−
Carpometacarpus					Least width	0.98	0.21	−0.39	+
length	0.95	0.06	−0.21	+	Caudal width	0.95	0.05	−0.38	+
APW	0.98	0.13	−0.35	+	Carina depth	0.97	0.14	−0.53	−
DVW	0.98	0.16	−0.33	+	Furcula height	0.97	−0.06	−0.55	−
Digit II, Ph. 1 length	0.97	0.07	−0.29	+	LWM	0.96	0.29	−0.46	
Ph. 1 MWM	0.97	−0.01	−0.33	+	MWM	0.93	0.40	−0.47	
Ph. 2 length	0.95	−0.01	−0.26	+	Synsacrum length	0.98	0.21	−0.50	−
Femur length	0.96	−0.15	−0.54	−	Interacetabular width	0.89	0.07	−0.40	
Head width	0.97	−0.11	−0.57	−	Eigenvalue[a]	3.90	0.12	0.06	
LWM	0.98	−0.04	−0.55	−	Percentage of variance	91.9	2.8	1.9	
MWM	0.99	0.12	−0.53	−					

[a] Eigenvalues and percentages of variance include contributions from all 23 species; variance shared between PC-I* and PC-II* attributed to PC-I*.

(see methods) concisely summarized the multivariate differences among Recent species (Table 6, Fig. 5). The first three components together incorporated 96.7% of the total interspecific skeletal variation. Loadings of variables on the first component (PC-I*) were all positive and of high magnitude ($r \geq 0.89$, 38 $r_i \geq 0.95$), and identified PC-I* as a measure of "general skeletal size" (Table 6). Scores on this component were highly correlated with mean body mass ($r = 0.99$ for extant species, $r = 0.98$ including estimate for *Pinguinus*), and the axis deviated from strict isometric size by only 8°. Small species (e.g. *Aethia, Alle, Synthliboramphus*) had low scores in PC-I*, whereas the largest taxa (*Uria, Pinguinus*) had the highest scores (Fig. 5).

The second axis (PC-II*) for complete skeletons was a shape variable, characterized by loadings of varying magnitude and sign (Table 6). Bill length, maximal humeral shaft width, sternal carina length, and widths of the coracoid and furcula had relatively large loadings, whereas dimensions of leg elements, especially lengths, had negative correlations with PC-II*. PC-II* contrasted bill length and the size of the pectoral girdle with the pelvic limb. Genera characterized by long bills and robust pectoral girdles relative to their leg measurements (e.g. *Brachyramphus*, subgenus *Endomychura* of *Synthliboramphus*) had high scores on this axis, and genera with opposite proportions (e.g. *Aethia, Cyclorrhynchus*) had low scores (Fig. 5). *Pinguinus* was moderately high in this dimension, as were *Uria* and *Alca*.

The third modified component (PC-III*) summarized the unique morphometric characteristics of *Pinguinus impennis* relative to other Recent alcids, notably the skeletal correlates of flightlessness (Fig. 5). This axis contrasted least shaft widths and lengths (to a lesser extent) of wing elements, and widths of the sternum with cranial height, maximal shaft widths of the humerus and radius, scapular blade width, basin length and carina depth of the sternum, most dimensions of the pelvic limb, and synsacrum length (Table 6). The large negative score for *Pinguinus* revealed that, compared with flighted alcids, the Great Auk had flattened humeri and

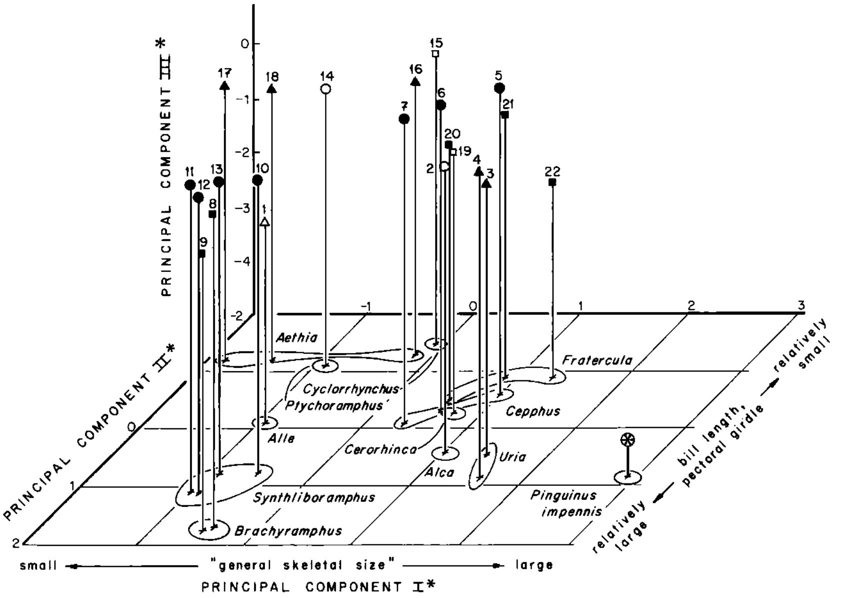

Fig. 5. Trivariate plot of mean scores of Recent species of alcid on first 3 (modified) principal components of 46 skeletal measurements; PC-III*, the axis which separates *Pinguinus* from flighted alcids, is explained in text. Flighted species are numbered as in Fig. 2.

radii, was (slightly) shortened in the mid-wing and manus, and had comparatively large leg elements (except tarsometatarsus length), broad scapulae, long and narrow pelvises, and sterna that were long and narrow with relatively deep carina. Although none approached the extreme position of *Pinguinus* on PC-III*, the Dovekie (*A. alle*) and puffins (*Cerorhinca, Fratercula*) had the lowest scores on this axis of the flighted Alcidae (Fig. 5).

PCA of reduced skeletal vectors.—A PCA of mean vectors for the reduced data sets for "medium-sized" *Mancalla, M. milleri, Praemancalla* spp., and 23 Recent species identified two major axes of skeletal variation. Together, these accounted for 96.1% of the interspecific dispersion in the reduced morphometric space (Table 7). As in the PCA of complete skeletal vectors, PC-I* of the reduced data set largely reflected "general skeletal size" (Table 7). Mean body mass was strongly correlated with scores on this component ($r = 0.99$ for flighted species, $r = 0.98$ including the estimate for *Pinguinus*), and the axis deviated from strict isometric size by only 5°. PC-I* indicated *M. milleri* was comparable in "general skeletal size" to *Alca*; the medium-sized *Mancalla* spp. were similar to *Uria*; and *Praemancalla* and *Pinguinus* were progressively larger (on this axis) than any flighted alcid (Fig. 6).

The second component (PC-II*) contrasted lengths and least shaft widths of wing elements (especially humeri and radii) with maximal widths of wing elements, lengths and widths of leg elements, and synsacrum length (Table 7). This axis corresponded closely with PC-III* for complete skeletons (Table 6). The 4 flightless species or species-groups had extremely low scores on PC-II*, whereas the flighted alcids varied little in this dimension. The low scores of the flightless species reflect their relatively short, flattened wing elements, and their relatively long leg elements and long synsacra. Scores on PC-II* indicate that, of the flightless genera, *Mancalla* was most extreme in these proportions, *Praemancalla* was next most distinctive, and *Pinguinus* was the least modified in this dimension (Fig. 6).

Estimated body masses of mancalline auks.—Regressions of total body mass on principal components of mean skeletal measurements for Recent alcids (including the estimated body mass of 5 kg for *Pinguinus impennis*) provided estimates of body masses for selected fossil mancalline species. For each taxon, principal com-

TABLE 7. Correlation coefficients of 23 skeletal variables with first (modified) principal component (PC-I*, see text) and the first principal component of the residual variance from PC-I* for Recent and fossil alcids (PC-II*). Signs to right of coefficients of PC-II* indicate variables so correlated with residuals from PC-I* ($|r| \geq 0.20$).

Variable	PC-I*	PC-II*	
Humerus length	0.99	−0.42	+
Head width	0.99	−0.41	+
LWM	0.98	−0.39	+
MWM	0.94	−0.55	−
Radius length	0.94	−0.14	+
LWM	0.98	−0.35	+
MWM	0.98	−0.55	−
Ulna length	0.93	−0.14	+
LWM	0.99	−0.40	+
MWM	0.99	−0.48	
Carpometacarpus length	0.96	−0.23	+
APW	0.97	−0.35	
DVW	0.98	−0.35	+
Femur length	0.97	−0.51	−
Head width	0.98	−0.56	−
LWM	0.99	−0.57	−
MWM	0.99	−0.57	−
Tibiotarsus length	0.99	−0.54	−
LWM	0.98	−0.56	−
Tarsometatarsus length	0.91	−0.50	−
APW	0.97	−0.56	−
LMW	0.94	−0.54	−
Synsacrum length	0.97	−0.55	−
Eigenvalue[a]	2.23	0.22	
Percentage of variance	87.6	8.5	

[a] Eigenvalues and percentages of variances include contributions from all 26 species. Variance shared between PC-I* and PC-II* attributed to PC-I*; r (PC-I*, PC-II*) = −0.48.

ponents of available skeletal measurements which were significantly correlated ($P < 0.05$) with body masses were used as estimator variables. However, unlike the rough "size" comparisons permitted by PC-I* for the reduced skeletal data set (Fig. 6), these regression estimates also incorporated "shape" variables that distinguished the larger flightless alcids from flighted confamilials (Table 8). My estimates indicate that the mancalline auks were more massive than the flighted alcids and less than *P. impennis*, varying between 1 and 4 kg in total mass. An estimate was not attempted for the very large, as yet undescribed species of *Mancalla* (Fig. 3A). Furthermore, the estimates confirmed that *M. milleri* was the smallest of the group, followed by the "medium-sized" *Mancalla* and *Praemancalla*, and the largest was the relatively poorly represented *M. emlongi* (Table 8).

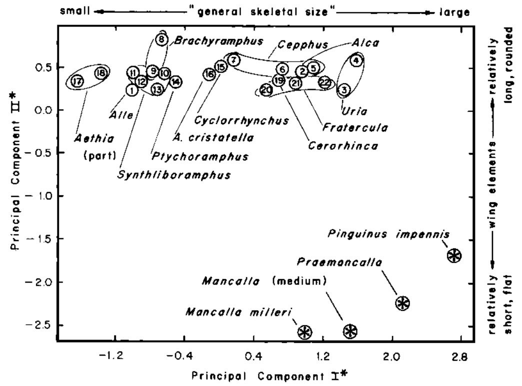

Fig. 6. Plot of mean scores of Recent and selected fossil alcids on first 2 (modified) principal components of 23 skeletal measurements. Flighted species are numbered as in Fig. 2; "medium" *Mancalla* represents mean vector for pooled data of similarly sized *M. californiensis, M. cedrosensis,* and *M. diegensis.*

DISCUSSION

Locomotor compromise and convergence.—The Alcidae are morphologically committed to a largely aquatic existence. The compromise in wing shape necessary for wing-propelled diving is substantial (Storer 1960, 1971; Pennycuick 1975, 1987), and in flighted alcids is associated with their comparatively heavy wing-loadings (Greenewalt 1962; this study) and high wing-beat frequencies (Meinertzhagen 1955). Wing-loadings of murres (*Uria*) are moderately high, but do not approach closely the threshold of flightlessness of 2.5 $g \cdot cm^{-2}$ (Meunier 1951). Using available wing areas, allometric extrapolations of wing-loadings of flighted alcids to greater body masses yielded estimates of 2.10

TABLE 8. Estimated body masses for fossil alcids, based on regressions of body masses of 23 Recent species on principal components of (p) skeletal measurements available for each fossil taxon.[a]

Species	Mass[b]	p	R^2 (%)	Components entered
Mancalla (intermediate)[c]	2,400	38	99.1	I, III, IV
M. milleri	1,650	29	99.2	I, III, IV
M. emlongi	3,800	24	98.9	I, IV, V
Praemancalla spp.	3,050	23	98.8	I, III, IV

[a] Included estimated mass for *Pinguinus impennis* (5,000 g, see text).

[b] Estimates rounded to nearest 50 g.

[c] Pooled for similarly sized *M. californiensis, M. diegensis,* and *M. cedrosensis.*

at 1,500 g, 2.33 at 2,000 g, and 2.53 at 2,500 g. Allometric enlargement probably would result in impaired flight, and might compromise the wing-body proportions optimal for submarine propulsion (Bédard 1969). The mean area of two half-folded wings (the position used for diving; Spring 1971) of *Pinguinus* was 77 cm^2. Doubled and divided into the estimated 5-kg body mass, this yields a "flipper-loading" of 32 g$\cdot$cm^{-2}, a value comparable to those of the spheniscid genera *Megadyptes, Pygoscelis,* and some *Spheniscus* (Stonehouse 1967). This reduction in wing area, and other morphological characteristics of the flightless alcids, are aptly termed "specializations." They are of obvious adaptive significance for one function (diving), limiting with respect to another (aerial flight), and uniquely associated with flightlessness, unquestionably a derived condition in carinate birds.

Parallels have been drawn between the diving petrels (Pelecanoididae) and flighted alcids (Verheyen 1958, Kuroda 1967, Harrison 1977), and between the flightless alcids and the penguins (Storer 1960, 1971; Pennycuick 1975; Feduccia 1980; Sparks and Soper 1987) and the fossil Plotopteridae (Olson and Hasegawa 1979, Olson 1980). Despite these notable convergences in pectoral anatomy, obvious differences in locomotor adaptations and diagnostic osteological synapomorphies demonstrate their homoplasious nature (e.g. Harrison 1977), the predictions by Olson (1980) concerning the fallibility of a cladistic analysis of such groups notwithstanding. Particularly manifest are the numerous and extreme morphological novelties of the penguins, which include significantly reduced mobility of the wing articulations and radical modifications of the remiges (Coues 1872, Owen 1879, Sparks and Soper 1987, Raikow et al. 1988).

Alcine vs. mancalline flightlessness.—Members of different suprageneric groups within the Alcidae, *Pinguinus* (Tribe Alcini) and the subfamily Mancallinae share several morphological correlates of flightlessness. Those include large size (Tables 1, 2, 8), relatively short wings (Figs. 1, 2), and dorsoventrally flattened skeletal wing elements (Figs. 3–6). These characteristics were among the first to be recognized, largely because of similarities to the anatomy of penguins (Newton 1861, Owen 1879, Lucas 1901). Raikow et al. (1988) concluded that in flighted, wing-propelled diving birds the functional demands of aerial flight preclude the skeletal and myological modifications observed in flightless alcids and penguins. There also is osteological evidence that the remiges of *Mancalla* were at least as reduced as those of *Pinguinus* (Miller and Howard 1949). Other unusual characters of *Pinguinus*—sequential molt of the primary remiges (Storer 1960), comparatively extensive fusion and short transverse processes of vertebrae (Storer 1945), and a large number of caudal vertebrae (Owen 1879)—may also have been convergent with the mancallines, but currently available material does not permit such inferences. Contrary to the reference to ". . . degeneration of the wing and keel . . ." in *Pinguinus* by Greenway (1967), the flightless auks had robust wing elements and deep sternal carinae.

Pinguinus was unique among the Alcidae for its large size, exceeding the described mancallines in skeletal dimensions (Tables 2, 3; Fig. 6) and in estimated body mass (Table 8). The mancallines were more specialized than *Pinguinus* in morphometric shape characters (Figs. 3, 4, 6), and had wing elements that more closely approached those of the penguins in relative length, flatness, curvature, and articulative rigidity (Lucas 1901, Miller 1933, Wiman and Hessland 1942, Miller and Howard 1949). The exceptional modification of the wing for submarine propulsion in *Mancalla* is indicated by the degree of shaft compression of major elements, well developed sulcus musculus scapulotrioipitis, the proximal position of the humeral processus supracondylaris dorsalis, and by the obsolete processus pisiformis, distally extended processus extensorius, and dorsoventral compression of the trochlea carpalis of the carpometacarpus (Fig. 4; Howard 1966). There is also significant qualitative variation in skeletons within *Mancalla* (Howard 1970). The geologically older *Praemancalla*, as confirmed by its morphometric intermediacy (Figs. 3, 6), was not as specialized as *Mancalla* osteologically (Howard 1966, 1976, 1978; Howard and Barnes 1987). The poorly known mancalline genus *Alcodes*, described by Howard (1968: 19) as "progressing towards flightlessness," appears on the basis of its ulnar proportions to have been completely flightless (Fig. 3B).

Ontogenetic considerations.—The likely importance of heterochrony, specifically neoteny, in the evolution of avian flightlessness has been suggested (Lowe 1928, Olson 1973, James and Olson 1983) largely on the basis of morphological similarities between the wing and pectoral girdle of adults of flightless species and juveniles of flighted relatives. However, the obvious locomotor specializations of *Pinguinus* and the Spheniscidae led Olson (1973: 31) to recommend that these groups ". . . not be included in discussions of flightlessness." Olson (1977: 690) also stated: "The great modifications seen in the wing of *Pinguinis* [*sic*] are not the result of neoteny, as seen in many other flightless birds . . . . Instead, these modifications represent highly derived specializations for wing-propelled diving."

Implicit in this conclusion are the assumptions that "neotenic" flightlessness is *necessarily* "degenerate," pervasive in its impact on the pectoral girdle, and not associated with locomotor specialization. Although the compression and curvature of wing elements cannot be attributed to neoteny because neither characterizes developing alcids, the relatively short distal wing elements of flightless auks resemble the intra-alar proportions of embryonic alcids and other nonpasserines (Böker 1927, Marples 1930). Hence, they are by definition paedomorphic (Gould 1977). Definitive support for heterochrony in the extinct auks is probably unattainable, but Livezey and Humphrey (1986) presented evidence of a heterochronic basis for flightlessness in the pectorally "nondegenerate" steamer-ducks (Anatidae: *Tachyeres*).

Ecological implications.—The Great Auk is probably related most closely to *Alca* and *Uria* (Strauch 1985), and all three genera are considered to be comparatively specialized for piscivory (Storer 1945, Bédard 1969, Hudson et al. 1969). Although *Pinguinus* is morphologically specialized (Figs. 2, 3, 5), the genus and its close relatives are characterized by only moderate proportions on several major axes of skeletal variation in the Alcidae (Figs. 2, 5). *Pinguinus* had only moderate scores on PC-II* for complete skeletons (Fig. 5), an axis with profound locomotory and ecological implications and which reflects, in part, the patterns in pelvic proportions (Storer 1945). Hudson et al. (1969) concluded that the close relatives of *Pinguinus* (*Alca* and *Uria*) were myologically "specialized," whereas the puffins were "primitive." The myological details of *Pinguinus* will in all probability never be known; although it seems likely that the genus was at least as specialized in its pectoral musculature as its close relatives (Miller and Howard 1949).

Probably the most conspicuous characteristic shared by *Pinguinus, Alca,* and *Uria* is comparatively large size (Figs. 1, 2, 5). Large body mass is an advantage for diving birds, especially marine pursuit-divers, because it reduces buoyancy and makes available a greater range of water depths for foraging (Sparks and Soper 1987). A direct relationship between body mass and maximal diving depth was documented in alcids (Piatt and Nettleship 1985), and the diving ability of *Uria* appears to be comparable to that of medium-sized penguins (Burger and Simpson 1986).

Avian flightlessness generally is associated with large, often absolute, increases in body size (Pennycuick 1975), and it is probable that the exceptionally large size of flightless alcids represents an adaptive body form for submarine foraging (Storer 1960, Bédard 1969). Although Olson et al. (1979) presented evidence that breeding Great Auks at Funk Island, Newfoundland, may have fished primarily in water less than 18 m deep, it is agreed generally that *Pinguinus* typically foraged in deeper waters (Bradstreet and Brown 1985, Brown 1985). A related advantage of large body size is the ability to capture and swallow larger prey, also inferred for *Pinguinus* (Bradstreet and Brown 1985). The relatively large contribution of culmen length to the size-related first canonical variate (Table 2, Fig. 2) underscores the important relationship between body size and the size of the feeding apparatus in alcids (Bédard 1969).

Although sexual differences in skeletal measurements were negligible in extant species of alcid, samples of *Pinguinus* from Funk Island indicated bimodality in sample distributions of several measurements, especially bill length. The larger samples ($n = 200$) of *Pinguinus* measured by Lucas (1890) suggest that sexual differences in length of the femur were present, although Lucas (1890: 523) concluded otherwise. The likelihood of sexual dimorphism of bill length in *Pinguinus* is enhanced by the importance of bill size in the feeding niches of alcids (Bédard 1969), wherein sexual differences in bill size may reflect intersexual niche differences. Increased sexual dimorphism in flightless species characterizes at least one other family of diving birds, the grebes (Podicipedidae; Livezey in press).

Another benefit of large body size is a thermodynamically efficient surface : volume ratio (Calder 1974, Sparks and Soper 1987). This advantage would be greater in colder waters at high latitudes, and probably contributed to the extreme size of *Pinguinus* compared with the mancallines. Furthermore, the larger body size of *Pinguinus* may have compensated, in part, for its only moderate skeletal specializations, rendering it comparable in diving ability to the osteologically more extreme *Mancalla.*

In spite of these advantages of large size and specialized wing morphology, the resultant flightlessness imposed significant ecological constraints on the Great Auk. Inability to fly undoubtedly limited the foraging radius of adults during nesting and its large size probably increased incubation and developmental periods, thus making the species more vulnerable to climatic variations in the lengths of breeding seasons (Bengtson 1984). Even more important was the requirement for nesting sites that were free from terrestrial predators, sufficiently near rich food supplies, and accessible to flightless birds (Bengtson 1984, Harris and Birkhead 1985). Similar nesting habitats were inferred for the mancallines (Miller and Howard 1949). In addition to rendering *Pinguinus* more vulnerable to human exploitation, these requirements, in combination with other breeding constraints and long-term fluctuations in climate in the North Atlantic, may have predisposed the Great Auk to a natural decline (Bengtson 1984).

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