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RESEARCH ARTICLE

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ABSTRACT
Flight ability has been lost many times in the family Anatidae (ducks, geese, swans, and allies), and this provides unique insights into the morphological and ecological evolution of the family. Although ~15 fossil anatids have been reported to be flightless or possibly so, there has not been an established criterion that is widely applicable to assessing flight ability in fossil anatids. In this study, discriminant rules for the presence–absence of flight ability were constructed by linear discriminant analysis (LDA) based on 7 skeletal measurements in 93 modern anatids in order to set a basis for the inference of flight ability in fossil anatids. Model selection for LDA was conducted by a high-dimensional modification of Akaike's Information Criterion, and selected models discriminated the volant and flightless groups with only one misclassification (*Tachyeres patachonicus*). Flight abilities of fossil anatids were assessed by the constructed rules, supplemented by resampling experiments that were designed to assess the uncertainty in estimating skeletal proportions of fossil anatids in the absence of associated skeletons. The flightless condition was strongly supported for *Cnemiornis* spp., *Branta rhuax*, Hawaiian moa-nalos, *Chenonetta finschi*, *Anas chathamica*, *Chendytes* spp., *Shiriyanetta hasegawai*, *Cayaoa bruneti*, and the "Annaka Short-winged Swan," whereas the volant condition was supported for *Mergus milleneri* and *Bambolinetta lignitifila*. Results were ambiguous for *Branta hylobadistes* and *Anas marecula*. The constructed rules can easily be applied to new observations in the future, although limitations in the inference of ecological traits in fossil species from morphological measurements, including the risk of extrapolations, should be appreciated.

Keywords: Anatidae, discriminant analysis, flightlessness, limb proportion, multivariate morphometrics

Discriminación cuantitativa de la ausencia del vuelo en fósiles de Anatidae a partir de las proporciones del esqueleto

RESUMEN
La habilidad del vuelo se ha perdido muchas veces en la familia Anatidae (patos, gansos, cisnes y aliados), brindando ideas únicas sobre la evolución morfológica y ecológica de la familia. Aunque unos 15 anátidos fósiles han sido reportados como no voladores o posiblemente no voladores, no ha habido un criterio establecido ampliamente aplicable a los anátidos fósiles para evaluar sus habilidades de vuelo. En este estudio, se elaboraron reglas discriminantes para la presencia/ausencia de la habilidad del vuelo mediante análisis discriminantes lineales (ADL) basados en 7 medidas del esqueleto provenientes de 93 anátidos modernos, con el propósito de establecer una base para la inferencia de la habilidad del vuelo en los anátidos fósiles. La selección del modelo de ADL fue realizada por una modificación alta-dimensional del criterio de información de Akaike, y los modelos selectos discriminaron los grupos voladores y no voladores con un solo error de clasificación (*Tachyeres patachonicus*). La habilidad del vuelo de los anátidos fósiles fue evaluada por medio de las reglas construidas, suplementadas por experimentos de remuestreo que fueron diseñados para evaluar la incertidumbre para estimar las proporciones del esqueleto de los anátidos fósiles en ausencia de esqueletos asociados. La condición no voladora fue apoyada fuertemente por *Cnemiornis* spp., *Branta rhuax*, los moa-nalos de Hawái, *Chenonetta finschi*, *Anas chathamica*, *Chendytes* spp., *Shiriyanetta hasegawai*, *Cayaoa bruneti* y el "Cisne de alta-corta de Annaka," mientras que la condición voladora fue apoyada para *Mergus milleneri* y *Bambolinetta lignitifila*. Los resultados fueron ambiguos para *Branta hylobadistes* y *Anas marecula*. Las reglas construidas pueden ser aplicadas fácilmente a nuevas observaciones en el futuro, aunque existen limitaciones de las inferencias de los rasgos ecológicos que pueden hacerse a partir de las medidas morfológicas de las especies fósiles, incluyendo el riesgo de las extrapolaciones, que deben ser apreciadas.

Palabras clave: análisis discriminante, Anatidae, ausencia de vuelo, morfométrica multivariada, proporción de los miembros

INTRODUCTION

Flight ability is a key feature of the evolutionary diversification of birds, but it also places various constraints on their anatomy and physiology (e.g., body size, energy allocation; Storer 1971, Pennycuick 1996). The loss of flight ability, which has occurred numerous times in the evolutionary history of birds (Raikow 1985, Feduccia 1999, Livezey 2003), may lead to morphological specialization, recent studies on which have provided novel insights into avian biology. Examples include use of the wing as a weapon (Longrich and Olson 2011, Hume and Steel 2013, Williams 2015a, Pavia et al. 2017), neuroanatomical modifications (Iwaniuk et al. 2004, 2009, Smith and Clarke 2012), and structural and histological modifications of bones (Habib and Ruff 2008, Habib 2010, Smith and Clarke 2014, De Mendoza and Tambussi 2015).

The family Anatidae (ducks, geese, swans, and allies) is characterized by the frequent loss of flight ability. Among ~160 modern species of Anatidae, 5 species are known to be flightless. *Anas aucklandica* and *A. nesiotis* from the Auckland and Campbell Islands are small-bodied flightless teals (Weller 1980, Livezey 1990) that are closely related to each other and to volant *A. chlorotis* from New Zealand (Kennedy and Spencer 2000, Mitchell et al. 2014). *Tachyeres pteneres*, *T. brachypterus*, and *T. leucocephalus* from South America are large-bodied, flightless diving ducks (Livezey and Humphrey 1986, 1992) closely related to volant *T. patachonicus* (which has a broader distribution; Bulgarella et al. 2010) and probably have lost flight ability independently (Fulton et al. 2012; but see below). Recently extinct *Mergus australis* has occasionally been regarded as flightless or in an incipient stage of the loss of flight (Livezey 1989), but this may not be the case because Livezey's (1989) estimation of body mass may have been too high (Williams 2012). Apart from these modern examples, ~15 species of fossil anatids have been reported to be flightless or possibly so (reviewed by Watanabe and Matsuoka 2015, Pavia et al. 2017). Fossil flightless anatids have provided unique opportunities to investigate consequences of evolutionary diversifications that are not exemplified by modern species (e.g., Iwaniuk et al. 2009, Olsen 2015, Li and Clarke 2016).

To date, flight ability of extinct anatids has been assessed in various ways, often with limited comparative data and subjective criteria, which sometimes led to incongruence of ideas regarding whether an extinct anatid could fly or not. For example, *A. chathamica*, an extinct duck from the Chatham Islands, was described as flightless by some authors (Millener 1999, Williams 2015b) but as volant by others (Worthy and Holdaway 2002, Mitchell et al. 2014). An objective criterion that is widely applicable to various fossil anatids would be useful. One potential candidate is the inference of flight ability from estimated wing loadings, as used in extinct seaducks of the genus *Chendytes* by Livezey (1993c), who estimated body mass and wing area of *Chendytes lawi* from scaling relationships of those variables with skeletal dimensions in modern Mergini and then estimated the wing loading of *C. lawi* by taking a fraction of those values. He concluded that the species was flightless because the estimated wing loading was greater than a postulated threshold of the flightlessness in modern *Tachyeres* (Humphrey and Livezey 1982, Livezey and Humphrey 1986). Although Livezey's (1993c) conclusion may be right for that particular case, such a quotient of 2 variables can be statistically intractable due to the deviation from normality (e.g., Atchley et al. 1976), which renders the method less reliable in general.

Many fossil anatids are known only from unassociated skeletal elements. Apart from the difficulty of assigning different skeletal elements to a particular species in such cases, the lack of associated skeletons (i.e. specimens representing multiple skeletal elements from single individuals) may pose another difficulty in quantifying skeletal proportions by adding errors due to intraspecific variation. In order to solve the problem, potential effects of intraspecific variation should be taken into account when assessing skeletal proportions of such species.

In this study, classification rules for the presence–absence of flight ability were constructed with discriminant analyses of skeletal dimensions in modern anatids, and the rules were then applied to assess the putative flightlessness of selected fossil anatids. Quantitative assessments of skeletal proportions have been used to infer locomotor modes of extinct birds (e.g., Hinić-Frlog and Motani 2010, Wang et al. 2011). Given the limited variation of skeletal proportions of wings and the strong correlation between body size and skeletal wing length in volant birds (Olmos et al. 1996, Middleton and Gatesy 2000, Nudds 2007), it can be postulated that there are functional constraints in the skeletal proportions in volant anatids, possibly within the wing skeleton or between skeletal wing size and overall body size. If there are consistent patterns of deviation in skeletal proportions in flightless anatids from those in volant ones, it would be possible to infer the flight ability of fossil anatids from their skeletal proportions. I included leg bones because they are generally considered good indicators of body mass in birds (Campbell and Tonni 1983, Campbell and Marcus 1992). One dimension of the sternal carina was also included as an indicator of the amount of pectoral muscles. Given the small sample size, especially for modern flightless anatids, the linear discriminant analysis was chosen as a classification rule that gives relatively stable results in such cases (see below). To avoid overfitting for the modern training sample, variable selection was performed with an information-theoretic approach. A resampling experiment was

conducted to explore the reliable assessments for fossil taxa in the absence of associated skeletons.

METHODS

Target Taxa and Measurement Data

Measurement data for modern anatids were taken from skeletal specimens of 787 individuals representing 103 modern species or subspecies (Appendix Table 10 and Supplemental Material Table S13). Taxonomy follows del Hoyo and Collar (2014). Subspecies were distinguished for the *Branta canadensis–hutchinsii* complex to accommodate great intraspecific size variation but were pooled for other species. All these species and subspecies are referred to as "species" for convenience. They were assigned to 2 groups defined a priori: the flightless group, which consists of 4 species, *T. leucocephalus*, *T. pteneres*, *T. brachypterus*, and *A. aucklandica*; and the volant group, which includes all other species. Measurements of limb bones of another flightless species, *A. nesiotis*, were taken from Williams (2015b) and were used for a posteriori evaluations of classification rules. Some specimens of *Tachyeres* spp. were identified from osteological keys given by Livezey and Humphrey (1992). Fulton et al. (2012) considered that the volant Falkland Islands population formerly identified as *T. patachonicus* was probably conspecific with the parapatric flightless population of *T. brachypterus*, which together would form a partially flightless species. For the purposes of the present study, individuals of *T. patachonicus* from the Falkland Islands were excluded from analysis and *T. brachypterus* was treated as a totally flightless species. Only skeletally mature specimens, as assessed by surface textures of long bones (Tumarkin-Deratzian et al. 2006, Watanabe and Matsuoka 2013), were included in the analysis. Specimens of captive individuals were measured, but all bones showing signs of pathology were excluded from the analysis. When available, the means of dimensions of left and right sides were used as individual values. For each species and for each variable, a species mean value was calculated from all available individual values, including those from individuals lacking some dimensions (i.e. incomplete skeletons), pooling sexes and localities. The modern sample covers all extant subfamilies and tribes recognized by Kear (2005) and spans almost the entire range of body size of modern anatids, from the smallest *Nettapus auritus* (mean body mass 266 g) to the largest *Cygnus buccinator* (mean body mass 11,110 g; body mass data from Dunning 2008).

Skeletal measurements were also taken on 365 specimens of 11 species of fossil anatids (Appendix Table 11 and Supplemental Material Table S13). Measurement data for 5 additional species were taken from the literature and included in the analyses (Worthy and Holdaway 2002, Matsuoka et al. 2004, Mayr and Pavia 2014, Williams et al.

2014, Williams 2015b), although it should be noted that these measurements may have been taken in different ways. Several putatively flightless fossil anatids, including *Garganornis ballmanni*, *Megalodytes morejohni*, *Cygnus falconeri*, *Chelychelynechen quassus*, *Thambetochen xanion*, and *Talpanas lippa*, were not included in this study because of the unavailability of measurements of most major limb bones (at least from published materials).

Measurements were taken with a Mitutoyo digital caliper to 0.01 mm and rounded to ±0.1 mm for bones up to ~200 mm, and with a metal ruler with a finite end and rounded to ±1 mm for those >200 mm. The following 7 dimensions were measured (Figure 1; anatomical terminology follows Baumel and Witmer 1993): carinal height, the dorsoventral depth of carina sterni measured along the cranial margin (pila carinae); humerus length, the greatest length from caput humeri to condylus ventralis; ulna length, the greatest length from olecranon to condylus dorsalis ulnae; carpometacarpus length, the greatest length from trochlea carpalis to facies articularis digitalis major; femur length, the greatest length from trochanter femoris to condylus lateralis; tibiotarsus length, length from facies articularis lateralis (not from crista cnemialis cranialis) to condylus lateralis; and tarsometatarsus length, greatest length from eminentia intercotylaris to trochlea metatarsi III. The area of the sternal carina and the length of the entire manus might better represent functional units than the carinal height and carpometacarpus length, respectively, but the former measurements are rarely available for fossil species, so ones were employed as proxies. In some instances (e.g., in *Ptaiochen pau*), the sternal carina was virtually absent (height ~0 mm). In such individuals, the carinal height was arbitrarily set to 0.1 mm to allow log transformation.

Multivariate Allometry

The interspecific variation of limb dimensions in Anatidae was investigated with principal component analysis (PCA) from a variance-covariance matrix of log-transformed variables. It is of interest to this study to examine whether there is a general trend of deviation of flightless anatids from volant ones in limb proportion (shape), which is represented by the principal components (PCs) other than the first one (which represents the size component; Jolicoeur 1963a, 1963b, Klingenberg 1996). All statistical analyses were conducted in R 3.2.0 (R Core Team 2015).

In order to estimate PCs while incorporating phylogenetic nonindependence, the phylogenetic principal component analysis (pPCA; Revell 2009) was conducted. Pagel's (1999) lambda statistic was used to adjust the effect of phylogenetic correction and was optimized with maximum likelihood estimation. Hypothetical ancestral states of log-transformed variables at nodes of the phylogenetic tree were reconstructed with the function
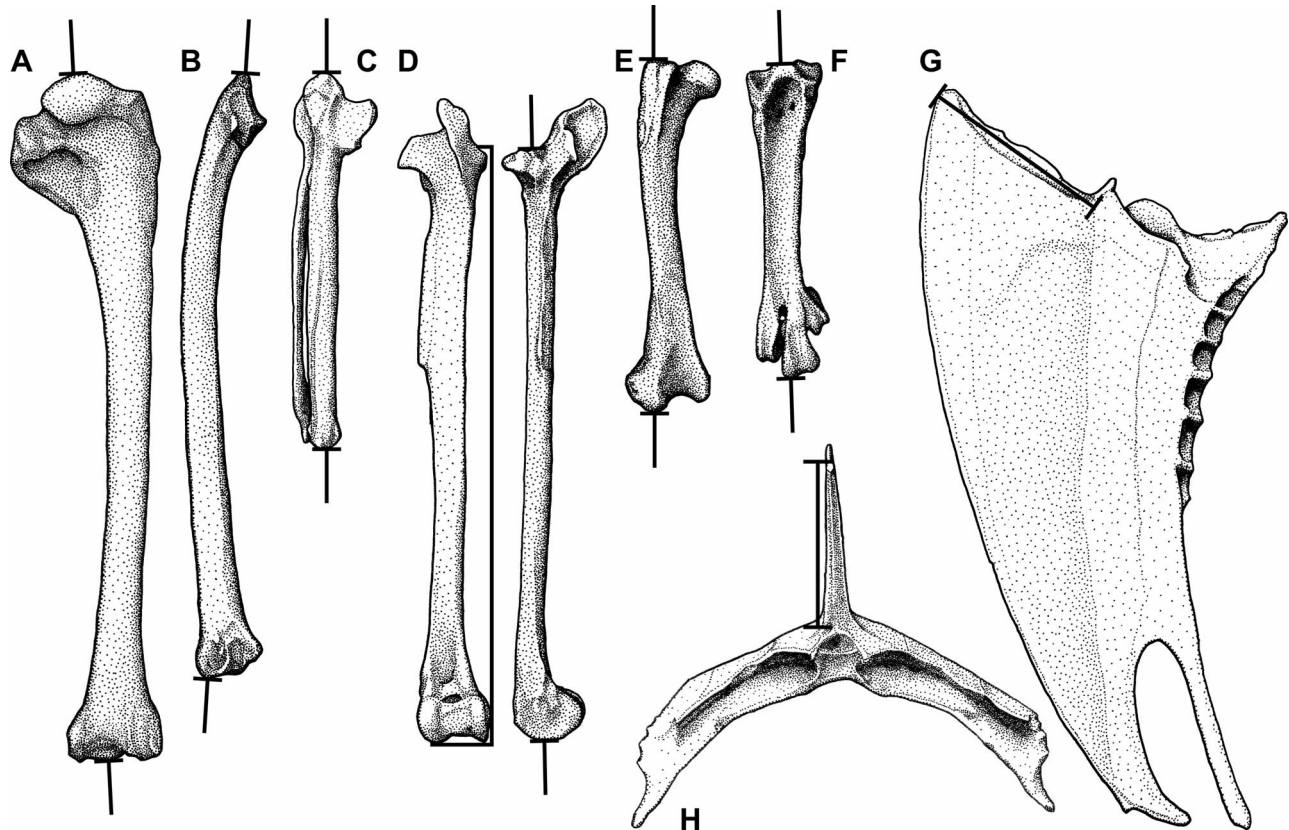
FIGURE 1. Osteological measurements taken in this study. (**A**) Humerus in caudal view. (**B**) Ulna in dorsal view. (**C**) Carpometacarpus in dorsal view. (**D**) Tibiotarsus in cranial (left) and lateral (right) views. (**E**) Femur in cranial view. (**F**) Tarsometatarsus in dorsal view. (**G**) Sternum in left lateral view. (**H**) Sternum in cranial view. See text for detailed definition of measurements. Drawings based on *Aythya valisineria* (USNM 288639).

fastAnc in the package phytools (Revell 2012), which reconstructs ancestral states utilizing Felsenstein's (1985) contrast algorithm (see also Rohlf 2001). The reconstruction was performed for all variables on a tree scaled with the optimal Pagel's lambda, and corresponding pPC scores were calculated. Although only species with phylogenetic information can be included in pPCA, pPC scores for those without phylogenetic information were plotted a posteriori for visual presentation. pPCA was performed with the package phytools (Revell 2012).

The topology of the working phylogeny was taken mainly from Gonzalez et al. (2009), and some taxa not sampled by those authors were grafted according to several other phylogenies (Sorenson et al. 1999, Paxinos et al. 2002, Fulton et al. 2012, Liu et al. 2014, Mitchell et al. 2014). Nodes with incongruent branching orders were collapsed into a polytomy. All branch lengths were first calculated with Grafen's (1989) method and were subsequently scaled using the function chronos in the package ape (Paradis et al. 2004), which estimates a chronogram with the penalized likelihood, using each branch length as the number of substitutions per character, with the

smoothing parameter $\lambda = 1$ and age constraints taken from previous studies (Gonzalez et al. 2009, Fulton et al. 2012, Mitchell et al. 2014). Because all extinct taxa represented in the tree were quite young in geological age (Late Pleistocene–Holocene), branch lengths were not scaled for their tip ages. The working phylogeny includes 76 modern and 4 fossil species (Supplemental Material Figure S1). Grafting of missing taxa onto a phylogeny based on taxonomic information is often used in the literature, but it is not employed here because the method is suboptimal in estimating phylogenetic signals of traits and, possibly, evolutionary correlations between traits (Rabosky 2015).

Linear Discriminant Analysis

Classification rules of the linear discriminant analysis (LDA) of skeletal dimensions were constructed from measurement data of modern anatids and subsequently applied to fossil anatids. LDA extracts a linear combination of variables that maximizes the discrimination between each pair of groups, assuming multivariate normal distributions with a common variance-covariance matrix

across groups. Group assignments of observations are based on posterior probabilities, relative likelihoods of assignments given prior probabilities for groups. Values of the linear combination can be used to represent classification results, when adjusted so that zero corresponds to the discriminant boundary (so-called discriminant score). In this study, 2 groups (volant and flightless) based on 7 skeletal dimensions were considered, and 93 species means (89 volant and 4 flightless) with complete sets of variables were used to construct rules.

Raw variables were log transformed before the analysis to conform to allometric analyses. Although there is slight evidence of asymmetric distribution of data points, LDA is known to be reasonably robust to the deviation from multivariate normality (McLachlan 1992) and gives a quite stable classification rule (Hastie et al. 2009).

The sample prior proportions (89/93 for volant vs. 4/93 for flightless species) were used as prior probabilities in the analysis, which resulted in adding 3.10 [= log(89 / 4)] for all discriminant scores (not included in the constant term shown in tables). This practice renders inference of flightlessness more conservative than when equal prior probabilities (0.5 vs. 0.5) are used. Such a practice may be justified when observations are assumed to come from groups of different sizes (see also Angielczyk and Schmitz 2014). The extant proportions of Anatidae (~160 volant vs. 5 flightless) appear to be less realistic than the sample proportions, because the former values are likely to have been biased by selective extinctions of flightless species in the Holocene (e.g., Duncan and Blackburn 2004).

The precision of classification rules was assessed by the bootstrap cross-validation (BCV) error rate estimation (Fu et al. 2005) with 10,000 bootstrap replications. The bootstrap resampling was conducted in a stratified manner (i.e. the subsample number for each group in a bootstrap replicate was fixed as in the original sample). The confidence intervals of discriminant coefficients were constructed from bootstrap percentiles that were constructed in the same manner. In order to examine the effect of intraspecific variation in classification results, all available individual values were evaluated with the constructed rules. When possible, species means with incomplete sets of variables, which were not used to construct rules, were also evaluated.

A statistical classification method that takes phylogenetic correlation between organisms into account has been proposed by Motani and Schmitz (2011). However, its statistical properties and underlying models are not well understood, and there seem to be several methodological issues in the application. Thus, I decided not to employ this method in the present study.

Model selection. In order to seek the best compromise between goodness-of-fit and model simplicity in LDA, a model selection based on Akaike's Information Criterion

(AIC) was performed. Specifically, an asymptotically unbiased high-dimensional modification of AIC (HAIC) for LDA in normal populations derived by Sakurai et al. (2013) was employed in this study (see also Fujikoshi 1985, Fujikoshi et al. 2010). HAIC values were calculated for all the 120 possible models with more than one variable and were compared; models with only one variable are of little interest and hence are not considered. Akaike weights (w_i) were calculated from ΔHAIC values. The relative importance of each variable was assessed by summing Akaike weights across models that include the variable (Burnham and Anderson 2002, Symonds and Moussalli 2011) and by taking a weighted mean (with w_i) of coefficients scaled with within-group standard deviation of the variable.

Size correction. Size-independent discrimination rules were explored in the context of multivariate allometry. As noted above, the PC1 of log-transformed variables represents an allometric size component, and the remaining PCs represent shape components. Hence, LDA based on PC scores excluding PC1 gives a discriminant rule on the shape space. The discriminant coefficient vector for the original variables can be obtained by retransforming the one for PC scores by simple matrix algebra. For the size-correction in LDA, PCs were extracted from the pooled variance-covariance matrix of variables centered at group means (i.e. within-group variance-covariance matrix in LDA), without phylogenetic correction. This procedure is equivalent to the size correction with back projection along the common PC1 axis (Burnaby 1966, Reyment and Banfield 1976, McCoy et al. 2006). In the context of the present study, the allometric size is more appropriate than the isometric one, because the allometric changes of skeletal proportions probably reflect the functional demand of flight at varying sizes. This procedure is hereafter referred to as the "size-corrected LDA," whereas that based on original variables is referred to as the "ordinary LDA."

Resampling experiment. Because some fossil anatids are known only from isolated skeletal elements, errors due to intraspecific variation in skeletal dimensions should be taken into account in work with those species. In order to simulate the potential errors from intraspecific variation in applying LDA to such species, hypothetical distributions of discriminant scores under a constructed classification rule were generated by resampling individual dimensions of modern species, which were subsequently compared with a discriminant score corresponding to the species mean of a fossil species. For each fossil species to be considered, the resampling method includes the following steps: (1) a classification rule and several modern comparative species are selected; (2) for each modern comparative species and for each element, individual values (as many as are available for the fossil species under consideration) are resampled, from which a pseudo-species mean is taken; (3) discriminant scores under the predefined classification

TABLE 1. Results of a phylogenetic principal component analysis (pPCA) including 75 modern anatids. Coefficients of first 3 pPCs and phylogenetic means (p-mean) of log-transformed variables are shown, as well as eigenvalues and percent of phylogenetic variance explained (PVE) by each pPC. Abbreviations of variables: CAR = carinal height; HUM = humerus length; ULN = ulna length; CMC = carpometacarpus length; FEM = femur length; TIB = tibiotarsus length; TMT = tarsometatarsus length.

Variable	pPC1	pPC2	pPC3	p-mean
CAR	0.3424	−0.5869	−0.6537	3.173
HUM	0.4003	−0.0462	0.2307	4.646
ULN	0.4252	−0.2124	0.6055	4.601
CMC	0.3790	−0.3273	0.0800	4.047
FEM	0.3376	0.4892	−0.3672	3.998
TIB	0.3670	0.4113	−0.1068	4.545
TMT	0.3865	0.3045	0.0177	4.022
Eigenvalues	1.997×10^{-2}	0.114×10^{-2}	0.030×10^{-2}	
PVE	92.0%	5.3%	1.4%	

rule are calculated for the pseudo-species mean; and (4) steps 2–3 are repeated many (e.g., 10,000) times for every comparative species to obtain resampled distributions of discriminant scores. The obtained distributions can be used to assess whether the score for the fossil species could be obtained from a population similar to the modern comparative species by chance. This procedure assumes that the extent of intraspecific variation in the fossil species does not exceed those of modern species compared. Obviously, the dispersion of resampled discriminant scores is largest when only a single value for each variable is resampled in the step 2, leading to a conservative inference. The more samples that are available for a fossil species, the more precise the inference. In the assessment of fossil species with LDA, 10 volant species with sufficient sample size (*Biziura lobata*, *Cygnus columbianus*, *Anser albifrons*, *A. rossii*, *Branta sandvicensis*, *Melanitta deglandi*, *Mergus merganser*, *Netta rufina*, *Aythya marila*, and *Tachyeres patachonicus*) and 2 flightless species (*T. brachypterus* and *T. patachonicus*) were included in the resampling experiment, and resampling was performed 10,000 times for each case. R codes used for LDA and associated analyses, along with data files, are available in the Supplemental Material R Codes Data file.

RESULTS

Multivariate Allometry
The pPCA was first performed with the dataset of 7 log-transformed variables for both modern and fossil anatids. The inspection of pPC plots clearly indicated that several fossil species have extreme skeletal proportions and perform as outliers in the estimation of pPCs, masking general patterns of interspecific variation (results not shown). In order to more closely inspect variations between modern volant and flightless species, the dataset including only modern species was analyzed (Table 1 and Figure 2). pPC1 was strongly positively correlated with all 7 variables, explaining 92.0% of the total variance, and

hence can be interpreted as the general skeletal size axis, whereas other pPCs can be interpreted as shape axes. pPC2 is negatively correlated with the carinal height and lengths of 3 wing bones and positively with 3 leg bones and, thus, can be interpreted as the contrast between pectoral and pelvic elements. pPC3 can be interpreted as an additional contrast between ulna length vs. carinal height and femur length. Modern flightless species were characterized by high pPC2 scores and low pPC3 scores, indicating that, not unexpectedly, they have relatively small wings for their size. The results of ancestral state reconstructions at nodes differed substantially, depending on whether fossil species were included in the analysis, probably because the fossil species included had extreme skeletal proportions (Figure 2). It is notable that modern flightless species occupy a distinct region of the morphospace from volant ones (Figure 2), especially in the "shape" subspace (i.e. subspace perpendicular to pPC1). Furthermore, the ancestral state reconstruction demonstrated that such characteristic skeletal proportions in flightless anatids had been obtained independently in 2 lineages, *Anas* and *Tachyeres* (Figure 2). These results suggest that discrimination of fossil crown-group flightless anatids from skeletal proportions is feasible, as long as the assumption that the form–function relationship is common within Anatidae holds.

Linear Discriminant Analysis
Full model. An LDA discriminant rule with all the 7 log-transformed variables (full model) clearly separated volant and flightless anatids (Figure 3A). All training cases, or modern species means, were correctly assigned to their original group with posterior probabilities >0.97, except for volant *T. patachonicus*, which was assigned to the flightless group with a posterior probability of 0.81, resulting in an apparent error rate of 1.08% (= 1/93). Classification results of the leave-one-out cross-validation were identical to those of the original analysis, only *T. patachonicus* being misidentified. The estimated BCV
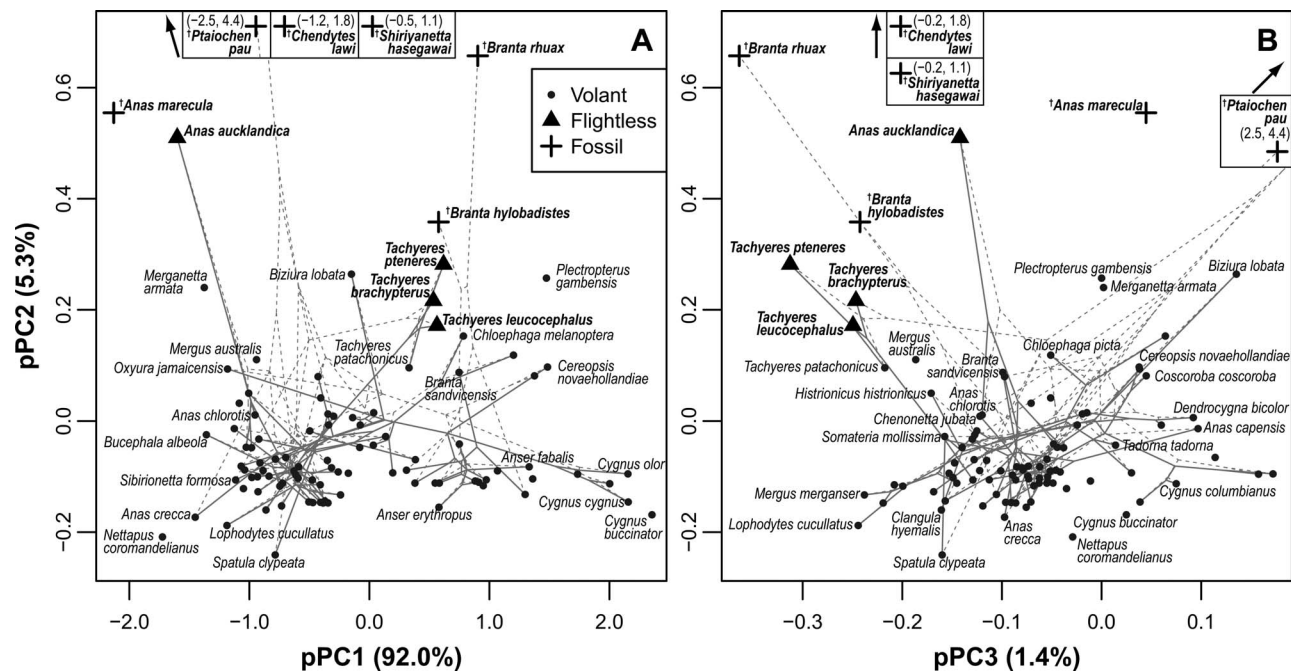
FIGURE 2. Phylogenetic principal component (pPC) plots of 7 log-transformed variables, based on modern species alone. (**A**) pPC1 vs. pPC2. (**B**) pPC3 vs. pPC2. Solid branching lines connect hypothetical ancestral states at nodes reconstructed with states in modern species, and broken ones are those reconstructed with both modern and fossil species. pPC scores for species without phylogenetic information were also plotted a posteriori. Note that some fossil species have extreme pPC scores, which are shown in insets. Legend: circles = modern volant species; triangles = modern flightless species; crosses = fossil species.
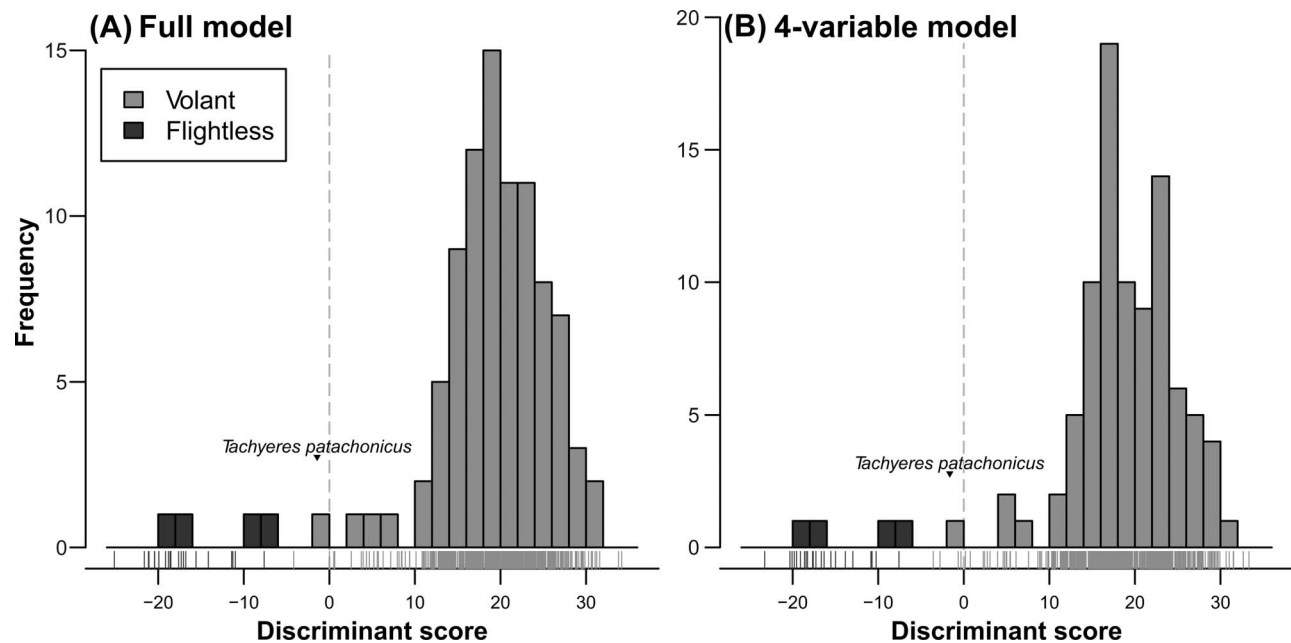
FIGURE 3. Summary of discriminant scores in linear discriminant analysis. (**A**) The full model. (**B**) The 4-variable model. Distributions of discriminant scores corresponding to species means of modern anatids are shown as histograms. Distributions of scores calculated for individuals are shown by rugs at the bottom. Flightless species are denoted by darker gray. Discriminant score for the species mean of *Tachyeres patachonicus* is indicated by a black triangle.

TABLE 2. Coefficients of variables used in linear discriminant analysis. For each of the full and 4-variable models, coefficients are shown with bootstrap 95% confidence intervals in parentheses. Note that the constant does not include the adjustment term for prior probabilities. Abbreviations are defined in Table 1.

Variable	Full model		4-variable model	
CAR	−6.07	(−32.83 to 23.22)	−	
HUM	−63.30	(−161.79 to −13.59)	−48.88	(−113.53 to −11.75)
ULN	75.49	(39.91 to 166.03)	61.64	(35.31 to 120.99)
CMC	50.13	(18.65 to 109.43)	40.11	(14.88 to 85.23)
FEM	−60.40	(−123.48 to −20.83)	−71.22	(−117.46 to −50.04)
TIB	−0.36	(−76.30 to 61.57)	−	
TMT	−13.59	(−57.03 to 21.87)	−	
Constant	79.62	(47.05 to 170.55)	84.33	(53.48 to 152.28)

error rate was 1.13%. With the classification rule, most of 477 individuals of modern species were correctly assigned to their group, except for 2 out of 4 individuals of *T. patachonicus*. Despite these misclassifications, discriminant scores did not overlap between volant and flightless groups, for both species means and individual values (Supplemental Material Table S1). Altering prior probabilities from the sample values of 0.95:0.05 (= 89:4) to the equal 0.50:0.50 and to 0.97:0.03 (= 160:5) prior probabilities would move the discriminant boundary by 3.10 and −0.36, respectively, and does not qualitatively affect assignments of any modern species means.

Discriminant coefficients were large positive values for the ulna and carpometacarpus, large negative values for the humerus and femur, and relatively small in magnitude for the remaining 3 variables (carinal height, tibiotarsus, and tarsometatarsus length; Table 2). The 95% bootstrap confidence intervals (CIs) of coefficients for the last 3 variables overlapped zero, whereas those of the other 4 variables did not (Table 2).

Model selection. HAIC was evaluated for all possible combinations of 7 variables that include more than 1 variable (120 models). The results of model selection are summarized in Table 3. The full model ranked 16th with a ΔHAIC value of 6.64 (w_i = 0.009), showing high redundancy among variables. All models with substantial model weights (w_i > 0.01) included ulna length and femur length, along with several or none of the other variables, which suggests the importance of these 2 variables in assessing flight ability in anatids, as confirmed by the Akaike weights and model-averaged scaled discriminant coefficients of variables (Table 4). The carpometacarpus length and humerus length follow the 2 variables, whereas the other 3 variables were much less important for these measures.

Across all models with more support than the full model (Table 3), signs and magnitudes of discriminant coefficients were quite similar, except that the signs were variable for tibiotarsus and tarsometatarsus length. Classification results for all species mean and individual values

TABLE 3. Results of model selection by HAIC (see text). Doubled negative log likelihood (−2 log L), doubled estimated bias (2 b), ΔHAIC, model weight (w_i), and model formula are shown for those with HAIC smaller than that of the full model. Abbreviations are defined in Table 1.

−2 log L	2 b	ΔHAIC	w_i	Model formula
−1,597.54	85.91	0.00 [a]	0.261	∼ HUM + ULN + CMC + FEM ("4-variable model")
−1,598.74	88.56	1.44	0.127	∼ HUM + ULN + CMC + FEM + TMT
−1,593.08	83.34	1.88	0.102	∼ ULN + CMC + FEM ("3-variable model")
−1,598.10	88.55	2.08	0.092	∼ HUM + ULN + CMC + FEM + TIB
−1,597.66	88.40	2.36	0.080	∼ CAR + HUM + ULN + CMC + FEM
−1,599.11	91.17	3.69	0.041	∼ CAR + HUM + ULN + CMC + FEM + TMT
−1,593.62	85.79	3.80	0.039	∼ ULN + CMC + FEM + TIB
−1,593.24	85.73	4.11	0.033	∼ CAR + ULN + CMC + FEM
−1,598.74	91.39	4.27	0.031	∼ HUM + ULN + CMC + FEM + TIB + TMT
−1,593.08	85.76	4.30	0.030	∼ ULN + CMC + FEM + TMT
−1,598.34	91.14	4.42	0.029	∼ CAR + HUM + ULN + CMC + FEM + TIB
−1,593.90	88.27	5.99	0.013	∼ CAR + ULN + CMC + FEM + TIB
−1,593.90	88.29	6.01	0.013	∼ ULN + CMC + FEM + TIB + TMT
−1,585.94	80.90	6.59	0.010	∼ ULN + FEM ("2-variable model")
−1,593.26	88.24	6.61	0.010	∼ CAR + ULN + CMC + FEM + TMT
−1,599.11	94.12	6.64	0.009	∼ CAR + HUM + ULN + CMC + FEM + TIB + TMT ("full model")

[a] HAIC value: −1,511.62.

TABLE 4. Variable weights and averaged coefficients based on ΔHAIC (see text). Averaged coefficients and those scaled with within-group standard deviation of variables are shown for the ordinary linear discriminant analysis. Abbreviations are defined in Table 1.

Variable	Weight	Averaged coefficient	Scaled coefficient
CAR	0.256	−0.697	−0.225
HUM	0.715	−37.370	−14.545
ULN	0.996	57.669	24.864
CMC	0.936	36.680	13.004
FEM	0.979	−66.663	−20.549
TIB	0.272	−5.217	−1.810
TMT	0.287	−2.464	−0.958

of both modern and fossil species were also consistent across those models wherever applicable, except for some individuals of *T. patachonicus* and the species mean of *Anas marecula*, which generally lie near the discriminant boundary. Models with the smallest HAIC within models including each of 4 variables, 3 variables, and 2 variables are referred to, respectively, as the "4-variable model" (humerus, ulna, carpometacarpus, and femur length), "3-variable model" (ulna, carpometacarpus, and femur length), and "2-variable model" (ulna and femur length) in the following analyses (Table 3).

Reduced models. In the 4-variable model, signs of discriminant coefficients of retained variables were the same as in the full model, and the bootstrap 95% CI of coefficients did not overlap zero, indicating the stability of the discriminant rule (Table 2). Group assignments were the same as the full model for the species mean values of modern species (only *T. patachonicus* is misclassified). As in the full model, ranges of discriminant scores were well separated between groups in the 4-variable model (Figure 3B; Supplemental Material Table S1). The estimated BCV error rate was slightly improved from the full model, being 0.95%. These results indicate that the 4-variable model performs as well as the full model, and perhaps better than that model for future observations. For comparison, see Supplemental Material Table S2 for coefficients in the 3-variable and 2-variable models.

Because only measurements of wing elements are available for one of the putatively flightless fossil anatids analyzed (*Bambolinetta lignitifila*), LDA models with wing elements were also evaluated, although all 4 models got relatively little support from HAIC ($w_i < 0.001$). The one including the humerus, ulna, and carpometacarpus lengths and another including the humerus and ulna lengths gained more supports from HAIC and apparently performed much better than the other 2. The signs and relative magnitudes of discriminant coefficients in the former 2 models were similar to the full model. In these models, all the species means in the training sample were correctly assigned to their original groups, giving an apparent error rate of 0%. However, some individual values were misclassified in these models: In the model with humerus, ulna, and carpometacarpus lengths, 7 out of 11 individuals of *Biziura lobata* and 1 out of 7 individuals of *Aythya nyroca* were misclassified; in the model with humerus and ulna lengths, 1 individual for each of *B. lobata*, *A. nyroca*, and *Anas aucklandica* and the species mean for *A. nesiotis* were misclassified.

Size correction. A discriminant rule of size-corrected LDA based on all 7 variables (size-corrected full model) was constructed from scores of PC2 to PC7 extracted from the within-group variance-covariance matrix of the variables as described above. The discriminant rule of the size-corrected full model was quite similar to that in the ordinary LDA, as indicated by the small angle between 2 discriminant coefficient vectors (Table 5). This is because the contrast vector between the group mean vectors in the original space happened to be nearly perpendicular to the within-group PC1 axis in this case. Group assignments in the size-corrected full model were identical to those in the ordinary full model for all species means (only *T. patachonicus* is misclassified) and for all individuals except one individual of *T. patachonicus*, which lies near the discriminant boundaries in both rules (Supplemental Material Figure S2A). The estimated BCV error rate was 1.14%.

As for the full model, the size-corrected LDAs corresponding to reduced models were quite similar to corresponding

TABLE 5. Coefficients of size-corrected models in linear discriminant analysis. For each of the full and 4-variable models, coefficients are shown with bootstrap 95% confidence intervals in parentheses. The angle between the discriminant coefficient vectors in the ordinary and size-corrected LDAs (degrees) is shown in parentheses at the heading. Note that the constant does not include the adjustment term for prior probabilities. Abbreviations are defined in Table 1.

Variable	Full model (0.07°)		4-variable model (0.03°)	
CAR	−6.02	(−32.73 to 23.02)	−	
HUM	−63.24	(−161.96 to −13.43)	−48.84	(−113.49 to −11.63)
ULN	75.56	(40.12 to 166.11)	61.68	(35.43 to 121.12)
CMC	50.19	(18.76 to 109.44)	40.14	(15.20 to 84.92)
FEM	−60.35	(−123.53 to −20.73)	−71.19	(−117.48 to −49.84)
TIB	−0.30	(−76.34 to 61.68)	−	
TMT	−13.52	(−57.20 to 22.00)	−	
Constant	77.90	(44.66 to 168.81)	83.78	(52.03 to 152.73)

TABLE 6. Classification results of species mean values of fossil anatids. For each species and each model, a discriminant score calculated from species means and posterior probability for the assignment to the flightless group is shown. A positive discriminant score and a posterior probability <0.50 indicate assignment to the volant group, whereas a negative score and a posterior probability >0.50 indicate assignment to the flightless group. All values were adjusted for the sample prior probabilities of 89/93 vs. 4/93. Posterior probabilities >0.995 are shown as "~1.00."

Species	Full model		4-variable model		3-variable model		2-variable model	
Cnemiornis calcitrans	–		−49.43	~1.00	−49.22	~1.00	−36.74	~1.00
C. gracilis	–		−51.91	~1.00	−50.25	~1.00	−35.09	~1.00
Branta hylobadistes	−8.37	~1.00	−4.57	0.99	−7.18	~1.00	−4.77	0.99
B. rhuax	−42.78	~1.00	−36.45	~1.00	−33.92	~1.00	−23.88	~1.00
Chenonetta finschi	–		−11.35	~1.00	−12.19	~1.00	−7.46	~1.00
Ptaiochen pau	−77.72	~1.00	−96.22	~1.00	−95.83	~1.00	−69.01	~1.00
Thambetochen chauliodous	–		−94.06	~1.00	−92.12	~1.00	−64.70	~1.00
Chendytes lawi	−107.66	~1.00	−95.19	~1.00	−72.54	~1.00	−62.85	~1.00
Shiriyanetta hasegawai	−57.61	~1.00	−51.63	~1.00	−40.22	~1.00	−32.67	~1.00
Mergus milleneri	–		4.79	0.008	5.11	0.006	5.39	0.005
Anas chathamica	–		−14.63	~1.00	−12.14	~1.00	−11.52	~1.00
A. marecula	0.69	0.33	0.74	0.32	−1.66	0.84	2.99	0.05
"Annaka Short-winged Swan"	–		−35.34	~1.00	−15.43	~1.00	−9.65	~1.00

ordinary LDAs, as indicated by small angles between discriminant vectors (Table 5). For the 4-variable model, all group assignments of modern species mean and individual values in size-corrected LDA were identical with those in the ordinary LDA (Supplemental Material Figure S2B). The estimated BCV error rate was 0.97% for the size-corrected 4-variable model. Additional information on size-corrected LDA is given in Supplemental Material Tables S3–S5.

Inference of fossil species. LDA discrimination rules constructed with species means of modern anatids were applied to species means and individuals of fossil anatids to infer the presence–absence of flight ability. For species means, discriminant scores and posterior probability for the assignment of flightless group in the full, 4-variable, 3-variable, and 2-variable models are shown in Table 6. When available for prediction, species means of *Cnemiornis calcitrans*, *C. gracilis*, *Branta hylobadistes*, *B. rhuax*, *Chenonetta finschi*, *P. pau*, *Thambetochen chauliodous*, *Chendyes lawi*, *Shiriyanetta hasegawai*, *Anas chathamica*, and "Annaka Short-winged Swan" were invariably assigned to the flightless group with high posterior probabilities (~1.00), whereas *Mergus milleneri* was always assigned to the volant group with high posterior probabilities (>0.99). The species mean for *A. marecula* was assigned to the volant group in the 3-variable model, but to the flightless group in the others, with relatively ambiguous posterior probability values.

Only limited sets of variables are available for *Bambolinetta lignitifila*, *Cayaoa bruneti*, and *Chendytes milleri*, precluding application of most highly supported models. The flight ability of these species was assessed by ad hoc models with the highest HAIC support within sets of applicable models (Table 7). As a result, *B. lignitifila* was assigned to the volant group with a discriminant score well within the range of the volant group's score (4.12) and a high posterior probability (0.98). *Cayaoa bruneti* and *Chendytes milleri* were assigned to the flightless group with high posterior probabilities (~1.00).

For species for which more than one associated skeleton was available, results of the group assignment for individual values are summarized in Table 8. Individuals of *Branta rhuax*, *P. pau*, and *T. chauliodous* were consistently assigned to the flightless group. One individual of *B. hylobadistes* was, unlike other individuals of the same species, assigned to the volant group in the 4-variable model (Table 8).

Resampling experiment. Resampling experiments were conducted for the full, 4-variable, 3-variable, and 2-variable models to examine possible effects of varying numbers of variables. First, resampling was performed by randomly choosing a single individual value independently for every element to form a hypothetical distribution of species "means" for each species, from which resampled distribu-

TABLE 7. Classification results for *Bambolinetta lignitifila*, *Cayaoa bruneti*, and *Chendytes milleri*, including variables available, the model formula of the ad hoc model with highest HAIC support within those applicable, corresponding model weight (w_i'), discriminant score calculated from species means, and posterior probability (pp) for the assignment to the flightless group. For further information, see Tables 1 and 6.

Species	Variables available	Model	w_i'	Score	pp
Bambolinetta lignitifila	HUM, ULN, and CMC	~ HUM + ULN + CMC	0.664	4.12	0.02
Cayaoa bruneti	CMC, FEM, TIB, and TMT	~ CMC + FEM	0.356	−34.22	~1.00
Chendytes milleri	HUM, ULN, TIB, and TMT	~ HUM + ULN + TIB	0.449	−79.66	~1.00

TABLE 8. Classification results for individuals of fossil anatids. For each species and each model, the range of discriminant scores is shown, with individual numbers available for the prediction with the model in parentheses. All values were adjusted for the sample prior probabilities of 89/93 vs. 4/93.

Species	Full model	4-variable model	3-variable model	2-variable model
Branta hylobadistes	−13.34 to −13.07 (2)	−9.30 to 0.81 (4)	−10.91 to −4.37 (4)	−6.71 to −0.79 (4)
B. rhuax	−37.86 (1)	−40.17 to −31.10 (8)	−40.20 to −28.85 (10)	−30.93 to −18.47 (10)
Ptaiochen pau	–	−97.61 to −86.40 (3)	−95.53 to −89.36 (3)	−71.30 to −64.93 (3)
Thambetochen chauliodous	–	–	–	−65.29 to −55.98 (2)

tions of discriminant scores were obtained (Figure 4; Supplemental Material Table S7). The resampled distributions were widely dispersed and in some cases spanned the discriminant boundary, although the dispersion tends to be smaller for models with fewer variables (Table 9). Dispersion of the resampled distributions of discriminant

scores also varies among species and is relatively small for *Aythya marila*, *Netta rufina*, *Melanitta deglandi*, and *Tachyeres* spp., whereas it is quite large for *Biziura lobata*.

Discriminant scores for fossil species known only from unassociated bones were compared with the resampled distributions. More specifically, resampled distributions
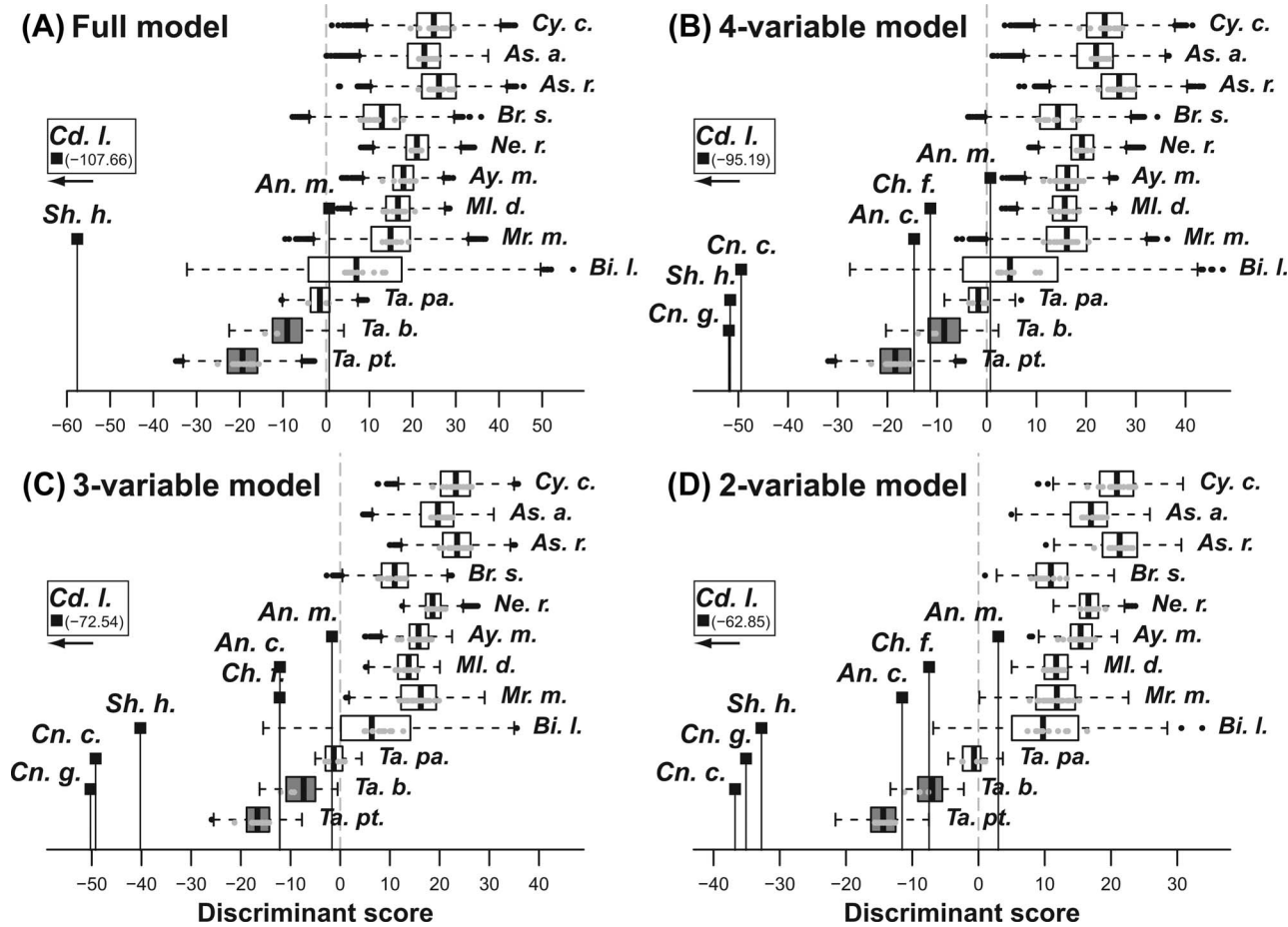

FIGURE 4. Distribution of discriminant scores from resampled experiments. (**A**) The full model. (**B**) The 4-variable model. (**C**) The 3-variable model. (**D**) The 2-variable model. Discriminant scores were calculated from a resampled distribution; a single individual value for every element was randomly chosen 10,000 times for each species. Distributions of resampled species means are shown as box plots, whereas original individual values for each species are indicated by gray circles. Vertical positions stand only for graphical purpose. Note that *Chendytes lawi* has extreme discriminant scores, which are shown in insets. Abbreviations for species labels: *An. c.* = *Anas chathamica*; *An. m.* = *Anas marecula*; *As. r.* = *Anser rossii*; *As. a.* = *Anser albifrons*; *Ay. m.* = *Aythya marila*; *Bi. l.* = *Biziura lobata*; *Br. s.* = *Branta sandvicensis*; *Cd. l.* = *Chendytes lawi*; *Ch. f.* = *Chenonetta finschi*; *Cn. c.* = *Cnemiornis calcitrans*; *Cn. g.* = *Cnemiornis gracilis*; *Cy. c.* = *Cygnus columbianus*; *Ml. d.* = *Melanitta deglandi*; *Mr. m.* = *Mergus merganser*; *Ne. r.* = *Netta rufina*; *Sh. h.* = *Shiriyanetta hasegawai*; *Ta. b.* = *Tachyeres brachypterus*; *Ta. pa.* = *Tachyeres patachonicus*; *Ta. pt.* = *Tachyeres pteneres*.

TABLE 9. Scaled standard deviation of discriminant scores from resampling experiments. For each species, a single individual value was randomly chosen for every element 10,000 times, and corresponding discriminant scores were calculated for each model. For comparison among models, standard deviations of resampled discriminant scores were scaled for within-group standard deviation of discriminant scores corresponding to original species means in each model. Only results for ordinary LDA are shown, because those for size-corrected LDA were almost identical to them. For other statistics, see Supplemental Material Table S7.

Species	Full model	4-variable model	3-variable model	2-variable model
Cygnus columbianus	1.01	0.92	0.78	0.72
Anser albifrons	0.97	0.93	0.87	0.79
A. rossii	1.00	0.90	0.75	0.72
Branta sandvicensis	1.08	0.94	0.72	0.69
Netta rufina	0.61	0.55	0.49	0.45
Aythya marila	0.68	0.62	0.53	0.51
Melanitta deglandi	0.69	0.62	0.51	0.49
Mergus merganser	1.15	1.05	0.91	0.85
Biziura lobata	2.53	2.25	1.84	1.75
Tachyeres patachonicus	0.56	0.50	0.39	0.41
T. brachypterus	0.84	0.78	0.70	0.61
T. pteneres	0.88	0.78	0.63	0.59

were treated as null distributions for the test of flightless hypothesis of such fossil species. In all models considered, discriminant scores for species means of *Cnemiornis calcitrans*, *C. gracilis*, *Chendytes lawi*, and *Shiriyanetta hasegawai* were much smaller than the resampled distributions of modern volant species, indicating that small discriminant scores for those species are unlikely to have been extracted from populations similar to volant species by chance alone (Figure 4). By contrast, discriminant scores for *Anas chathamica* and *Chenonetta finschi*, which unambiguously lie in the region assigned to the flightless group in most models applicable (the full model was not applicable to these species), were within the resampled range of volant *Biziura lobata* in the 4-variable and 3-variable models (Figure 4B, 4C). In order to more closely examine these species, another set of resampling was conducted for each species, by resampling as many individual values for every element as were available for those species and taking their means, which is expected to reflect a similar degree of precision of estimation of species means in the fossil species. Results with the 4-variable model for *A. chathamica* and *C. finschi*, whose data were taken from Williams (2015b) and Worthy (1988), respectively, are shown in Figure 5, along with those with ad hoc models for *Chendytes milleri* and *Cayaoa bruneti*. For *C. finschi*, the sample size in this study was too small to allow further comparisons; hence, data reported by Worthy (1988) for 2 localities (Graveyard layer 2 and Martinborough) were examined separately instead. For each species, perhaps except for *C. finschi* from Graveyard layer 2, the species mean was clearly lying below resampled distributions of any modern volant species compared, indicating that the species mean is unlikely to have come from distributions similar to modern volant species by sampling error due to the lack of associated skeletons.

Results for inference of fossil species and resampling with size-corrected LDAs were quite similar to those with ordinary LDAs (see Supplemental Material Figures S3 and S4 and Tables S8–S12).

DISCUSSION

Applicability and Limitation of the Method

Modern anatids are diverse both taxonomically and morphologically. Some species can vertically take off from the water or from the land, whereas others need to taxi for a long distance on the water before taking off (Raikow 1973). In addition, although most anatids are suited to foraging on the water surface, some specialize in feeding on the ground, and some others regularly dive into the water column to obtain food items (e.g., Hughes and Green 2005). Given the morphological and ecological diversity of modern anatids, one might doubt whether there could be a universal criterion to assess flight ability in fossil anatids. However, it is notable that the 2 lineages of modern flightless anatids, the diminutive *A. aucklandica* and the large-bodied, diving *Tachyeres* spp., appear to have undergone similar modifications of limb skeletal proportions, as demonstrated by the ordination of pPCA and ancestral state reconstruction (Figure 2); in short, the flightless species have relatively short wing elements, especially distal ones, compared to their ancestral states. In addition, a few sedentary insular species with disparate ecologies, including *Branta sandvicensis* and *Mergus australis* (see Miller 1937, Livezey 1989), appear to have shifted in a similar direction. These facts suggest the presence of a certain component in limb proportion that responds to the evolution of reduced flight ability, which justifies the assessment of flight ability in fossil anatids from limb proportion.
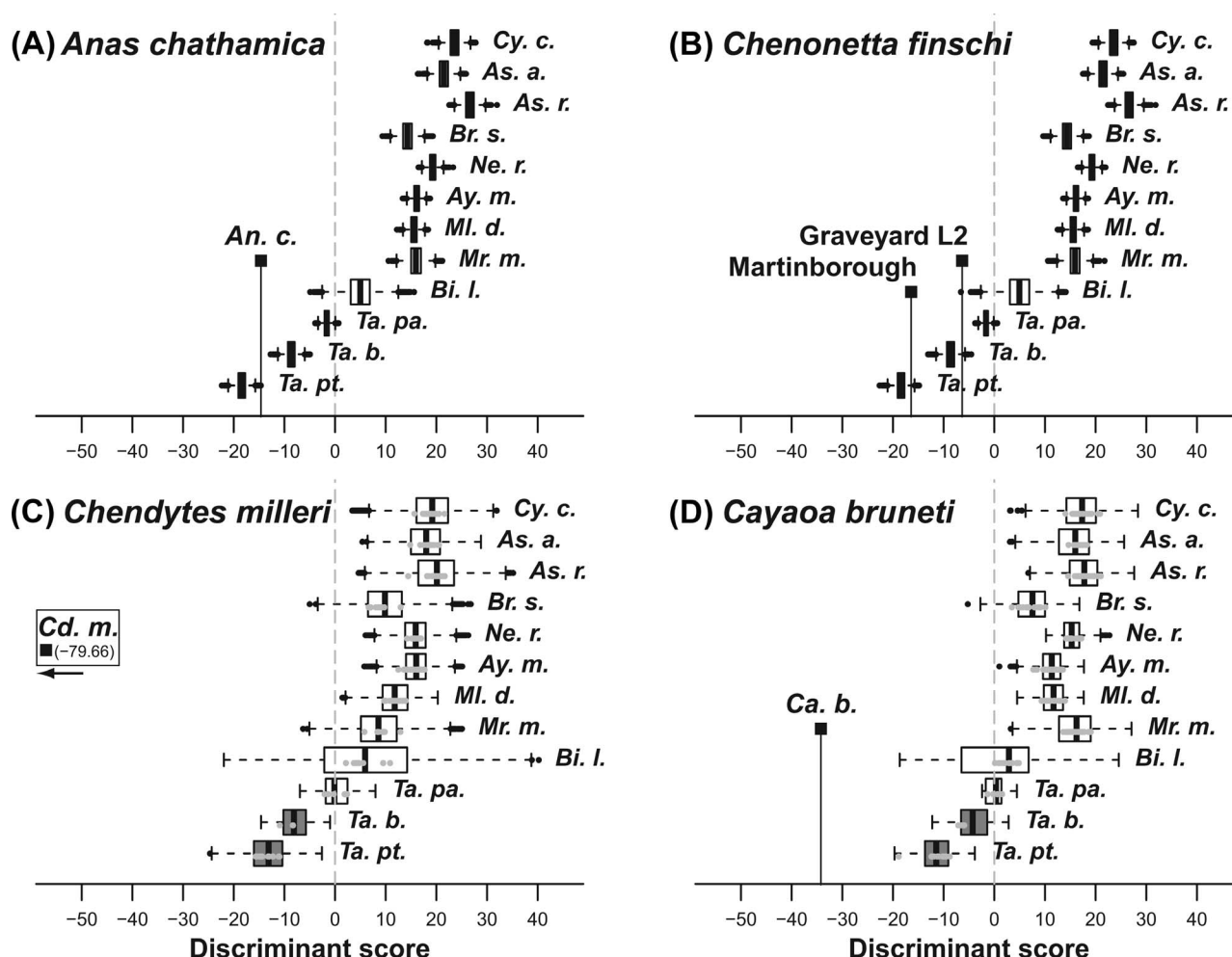
FIGURE 5. Distribution of discriminant scores from resampled experiments for *Anas chathamica* (**A**) and *Chenonetta finschi* (**B**) based on the 4-variable model, and for *Chendytes milleri* (**C**) and *Cayaoa bruneti* (**D**) based on ad hoc models. Discriminant scores were calculated from the simulated distribution for each fossil species, which is a resampled distribution of 10,000 mean vectors of randomly chosen individual values of the same number as available for every element of that species. For *C. finschi*, values from 2 localities (Graveyard layer 2 and Martinborough) studied by Worthy (1988) are shown, and the smaller set of sample sizes was used. Distribution of resampled species means are shown as box plots. Vertical positions are for graphical purposes only. Note that *Chendytes milleri* has extreme discriminant scores, which are shown in insets. Abbreviations for species labels: *Ca. b.* = *Cayaoa bruneti*; *Cd. m.* = *Chendytes milleri* (see Figure 4 for other abbreviations).

LDA models constructed from skeletal measurements in modern anatids gave reasonable separation and classification results for the volant and flightless groups. In all models that attained substantial support from HAIC ($w_i >$ 0.01) as well as in the full model, all species means were correctly assigned to their original group except for *T. patachonicus*, whose discriminant scores tend to be distributed around discriminant boundaries. Misclassifications of *T. patachonicus* were not completely unexpected, however, since that species is known to have the highest wing loading among volant anatids and to be "partially flightless," in that some of the heaviest males are (at least temporarily) not capable of becoming airborne (Humphrey and Livezey 1982). *Tachyeres patachonicus* would have

been under selection for large body size and small wings, which resulted in its specialized morphological traits (Livezey and Humphrey 1986). Apart from the interpretability of misclassified cases, it should be noted that the inference based on LDA is only in a statistical sense; the actual functional threshold for flightlessness, if one exists, may lie somewhere else than the discriminant boundary. Although the separation of ranges of discriminant scores between groups may be satisfactory for a descriptive purpose, it can raise a practical problem in prediction when a discriminant score for a fossil anatid falls between the 2 ranges. Although the discriminant rule would strongly suggest that the species would be flightless in such cases, the inference should be made with caution

since the position of the actual functional boundary is not clear. The inference of the actual boundary is inevitably prohibited by the scarcity of the training sample or by the low diversity of modern flightless anatids that form the basis for construction of discriminant rules. Nevertheless, the discriminant rules presented here incorporated most of the information available at present and would represent an objective basis for inferring the presence–absence of flight ability in fossil anatids.

In the models considered above, discriminant scores for individuals were distributed around corresponding species mean values and mostly assigned to the same group with them (see also Figure 4), which suggests that classification results for individuals of fossil anatids would be largely consistent within species, except when they lie near discriminant boundaries. For fossil species known only from isolated bones, the resampling procedure described above can be used to assess the reliability of assignments based on species means by evaluating the extent of possible errors due to intraspecific variation.

Classification results for both species means and individuals in models with smaller HAIC values than the full model were almost consistent with those in the full model, indicating that little information is lost by dropping some variables (carinal height, tibiotarsus length, and tarsometatarsus length) and that these models are more preferable than the full model on the grounds of parsimony. Indeed, the estimated BCV error rates for models with smaller HAIC values (range: 0.86–1.09%, mean = 0.96%) were slightly lower than that for the full model (1.13%), which suggests that the reduced models may perform better in prediction. One of the largest advantages of reduced models, along with avoidance of overfitting to training sample, is that the inferences are less likely to be affected by sampling errors (intraspecific variations) in estimating species means when only a small number of isolated specimens are available for measurement, as is true for many fossil anatids. This is because errors in estimating the species mean for each element are amplified by multiplications of discriminant coefficients and are summed in calculating discriminant scores. When more variables are included, more errors are included in the calculation. Such inflations of discriminant scores were exemplified by the resampling experiments, in which dispersions of discriminant scores were larger in models with more variables (Figure 4 and Table 9; Supplemental Material Figure S3 and Tables S7 and S10).

One peculiarity observed in the resampling experiment was that dispersions of resampled distributions of discriminant scores were quite large for *Biziura lobata* compared to other species considered (Figure 4 and Table 9), whereas those for original individual values were not so large. It is likely that this is largely due to the pronounced sexual dimorphism of body size in *B. lobata*, which is

among the most extreme within Anatidae (Livezey and Humphrey 1984, McCracken et al. 2000); when the intraspecific variation in body size and, hence, in morphological variables is large, the dispersion of a linear combination or proportion of resampled individual measurements is expected to be large.

Some previous studies have explored correlations between morphological and ecological traits by explicitly controlling for the effect of size (e.g., Simons 2010, Hughes 2013). In the present study, size-corrected LDAs were conducted by removing allometric size represented by PC1 of the within-group variance-covariance matrix for each variable set. The resultant classification rules of size-corrected LDAs were quite similar to those of the corresponding ordinary LDAs, largely because the contrast vector between the 2 group means happened to be nearly perpendicular to the size axis. The motivation for the allometric size correction was that skeletons may change in proportions while varying in size in order to retain similar performance, which is expected to be reflected in the allometric scaling of skeletal proportions. Unfortunately, however, current observations are likely to be largely constrained by the availability of the modern sample, and it is not clear whether the allometric scaling trends observed in the sample and the apparent threshold perpendicular to it hold for birds with larger or smaller body size than observed in the current sample, which spans almost the entire range of body-size variation in modern Anatidae. For example, Northcote (1982) estimated the body mass of an extinct swan (*Cygnus falconeri*) as ~16 kg from the dimensions of tarsometatarsus, assuming elastic similarity to recent *C. cygnus* and considered that such a large anatid might have a limited flight ability or even be flightless. In the absence of appropriate modern species of comparable size, it is not clear whether such an assertion based solely on body mass can be justified or whether statistical classification methods like LDA constructed from modern samples can be applied to such a large species. Another problem is exemplified by a small extinct species, *Anas marecula* (see below). Inferences of flight ability based on estimation of kinematic parameters of flight (e.g., Campbell and Tonni 1983, Pennycuick 1996, Ksepka 2014) have the same fundamental difficulties of extrapolations, among others (Alexander 2003). Issues concerning size-related variation in flight ability and extrapolations clearly require further theoretical and empirical studies.

Functional Interpretation
Functional interpretations of discriminant coefficients and relative importance of variables would be useful in assessing functional bases underpinning discriminant rules. Discriminant coefficients in this case correspond to hypothetical marginal effects of changes in skeletal

dimensions while other dimensions are held constant. In almost all models, the discriminant axes represent a contrast between relative sizes of wing and leg elements, and flightless species were characterized by relatively small wing elements (especially the ulna and carpometacarpus) and large leg elements, as expected from the results of PCA. It might be less intuitive that the coefficients for humerus length are negative (in contrast to the other wing elements) whenever it is included in models with ulna length (see also Table 2 and Supplemental Material Table S2). Statistically speaking, such a contrast in signs of coefficients for 2 variables with apparently similar roles might arise as an artifact due to the high correlation between the humerus length and ulna length (i.e. when they are redundant). However, the fact that many models including both of these variables attain relatively large supports from HAIC (Table 3) suggests that they are not completely redundant in discriminating the 2 groups. Rather, it is more likely that the contrast between humerus and ulna lengths is associated with a functional constraint in skeletal proportions of wings in volant birds. The ratio between the humerus (upper arm) and the ulna (forearm) is known to be correlated with various morphological traits relevant to flight mechanics, and to show a strong phylogenetic signal (Rayner and Dyke 2003, Nudds et al. 2004, 2007). Rayner and Dyke (2003) postulated that a relatively short humerus is beneficial in reducing wing inertia during flapping flight, and that there are constraints in the position of the wrist joint in the upstroke and various morphological traits in the shoulder joint complex that are affected by a modification of the ratio. It is likely that the ratio is under such constraints imposed by flapping flight in volant anatids, whereas it is free to vary in flightless anatids that have been released from those constraints. Relative shortenings of distal wing elements, especially the ulna and radius, have been repeatedly observed in flightless anatids (Livezey and Humphrey 1986, Livezey 1990, 1993c), as well as in other avian groups (e.g., Gadow 1902, Livezey 1992, 1993a, Middleton and Gatesy 2000, Smith 2011). Given that skeletal proportions of modern flightless anatids appear to have been shifted in similar directions, it is conceivable that functional demands other than flight (e.g., combating or steaming) or developmental constraints may affect skeletal proportions of flightless species. At present, however, little information is available to further discuss effects of such factors on avian skeletal proportion.

Among the 3 variables taken from leg bones (femur, tibiotarsus, and tarsometatarsus lengths), femur length is by far the most important by means of both model weights and magnitudes of scaled coefficients (Table 4). It can be concluded that the tibiotarsus and tarsometatarsus lengths are largely redundant in discriminating the 2 groups when femur length is taken into account. It is notable that femur length has a different scaling pattern than other limb bones and shows strong negative allometry in relation to the length of the other 2 leg bones (Table 1). Zeffer et al. (2003) found that femur length is the most strongly correlated with body mass among the lengths of the 3 leg elements (both log transformed). The avian femur in general is tightly connected to the trunk and plays an important role in placing the horizontal (anteroposterior) position of the center of mass above the knee joint (Campbell and Marcus 1992, Hertel and Campbell 2007). Given these facts, it is not surprising that the femur is a better indicator of body size than the 2 distal leg bones and acts in the discrimination of the 2 groups as such.

The height of the sternal carina was expected to be correlated with flightlessness through the amount of major flight muscles (mm. pectoralis et supracoracoideus). However, it turned out to be one of the least important variables in discriminating the 2 groups (Table 3). Although there was a tendency for flightless anatids to have a relatively small sternal carina compared to body mass, the variation within each group was so large as to obscure the difference between the groups. For example, the sternum and pectoral muscles of flightless *Tachyeres* species are not quite diminutive because the wings are utilized in other activities than flight, including underwater diving and combating (Livezey and Humphrey 1986). Among volant anatids, the carina is relatively small in *B. lobata*, perhaps as part of the extreme streamlining of the body related to the specialization for underwater diving (see also Raikow 1970). *Cygnus* spp., which are also characterized by relatively small carinae, have specialized sterna, including the intrusion of the trachea (e.g., Johnsgard 1961, Humphrey and Clark 1964) and the modification of attachment sites of pectoral muscles (see Woolfenden 1961, Matsuoka and Hasegawa 2007). Such variations due to specializations not directly related to flight ability might affect the morphology of the sternum in Anatidae.

Assessment of Flight Ability in Fossil Anatids

Discriminant rules constructed in this study can be used to infer the presence–absence of flight ability in fossil anatids, with the limitations mentioned above. *Cnemiornis calcitrans* and *C. gracilis* from the the Quaternary of New Zealand, *Chendytes lawi* and *C. milleri* from the Quaternary of California, and *Shiriyanetta hasegawai* from the Pleistocene of Japan were assigned to the flightless group (Figure 4 and Table 6). Indeed, *Chendytes* is characterized by diminutive wing bones (Howard 1947, Livezey 1993c), perhaps more extremely so than any other anatids except *Chelychelynechen quassus*, although known wing bones are rather fragmentary for the latter species (Olson and James 1991).

Among the Quaternary anatids from Hawaii, *Branta rhuax*, *P. pau*, and *Thambetochen chauliodous* were

assigned to the flightless group (Tables 6 and 8). Results are more ambiguous for another Hawaiian anatid *B. hylobadistes* from Maui Island, which has been described as "at best a weak flyer" (Paxinos et al. 2002:1399). Although it was assigned to the flightless group, discriminant scores for the species mean fall between the ranges of the 2 groups in some models (Table 6 and Supplemental Material Table S1). It seems likely that Hawaiian *Branta* populations were "at a stage in the evolution of flightlessness" as suggested by Olson and James (1991:43). More detailed investigation is required for this species, possibly incorporating variations among individuals from various localities (see Olson and James 1991).

The result for *Anas marecula* from the Holocene of Amsterdam Island was somewhat problematic. Discriminant scores were distributed around the discriminant boundaries (Figure 4 and Table 6). Although Livezey (1993b) and Olson and Jouventin (1996) considered the species to be almost certainly flightless from the skeletal proportion and the morphology of the sternum, the skeletal proportions considered in this study were found to be inconclusive in confirming the presence–absence of flight ability in this species. This result was largely attributable to the fact that the distal wing elements are relatively long compared to the humerus, despite the relatively small sternum and wing elements compared to leg elements. One perplexing factor is that the species is smaller than any modern anatids (Figure 2; Olson and Jouventin 1996); it is not certain whether the discriminant boundary constructed in this study can be extended beyond the observed range of body size in the modern sample.

Chenonetta finschi from the Quaternary of New Zealand has been considered as either possibly flightless (Holdaway et al. 2002) or facultatively flightless (Worthy and Olson 2002), but most authors remained inconclusive about whether the species was flightless. On the basis of measurements collected during the present study from a limited number of specimens from the Earnscleugh Cave, stored at the Natural History Museum (London, UK), the species was assigned to the flightless group. Worthy (1988, 1997) gave measurements from a large number of specimens collected in various localities and demonstrated that the species have undergone a reduction of wing elements during the period from 14,000–20,000 yr BP to 1,000–2,000 yr BP. Results using some measurement data given by Worthy (1988) for this species from Graveyard layer 2 (11,000–14,000 yr BP) and Martinborough Cave (~1,500 yr BP) indicate that *C. finschi* was flightless (Figure 5), at least after the reduction of pectoral elements in that period.

Anas chathamica from the Holocene of Chatham Islands has been described as either flightless (Millener 1999, Williams 2015b) or not (Worthy and Holdaway 2002,

Mitchell et al. 2014). The discriminant rules and resampling experiments in the present study assigned it to the flightless group (Figure 5 and Table 6). *Mergus milleneri* from the Chatham Islands was first stated as being flightless by Millener (1999), but Williams et al. (2014) concluded that the species was volant. Based on measurements given by Williams et al. (2014) and discriminant rules constructed in our study, there seems to be little evidence suggesting the flightlessness of this species (Table 6).

Bambolinetta lignitifila, an anatine of uncertain affinity known from an incomplete skeleton from the Miocene of Italy, was redescribed by Mayr and Pavia (2014). They considered the relatively shortened forearm of the species to be indicative of reduced flight ability, and the flattened wing bones as a possible specialization for wing-propelled diving. From the estimated lengths of wing bones given by them, the species was assigned to the volant group in ad hoc LDA models with dimensions of wing bones (Table 7). At least, it can be concluded that the proportion of wing skeleton alone provides only ambiguous evidence for the reduced flight ability of *B. lignitifila*.

Cayaoa bruneti, known from isolated bones from the Miocene of Argentina, was considered to be flightless and adapted to foot-propelled diving by Noriega et al. (2008). The loss of flight was considered an important factor that enabled the species to attain extremely thick bone walls (De Mendoza and Tambussi 2015). In the present study, the flightless condition of this species was confirmed by an ad hoc model that includes carpometacarpus and femur length (Table 7). The resampling experiment showed that such an extreme proportion was unlikely to be obtained from a volant anatid (Figure 5D).

The "Annaka Short-winged Swan," a large unnamed anatid of uncertain affinity from the Miocene of Japan, has quite peculiar skeletal proportions and thick bone walls (Matsuoka et al. 2001, 2004). Analysis of the measurements given by Matsuoka et al. (2004) confirmed the flightlessness of that species.

Conclusion

Discriminant rules to assess the presence–absence of flight ability from skeletal measurements in fossil anatids were constructed and were applied to selected fossil anatids. Variable selection based on HAIC gave high support to models including ulna length and femur length, suggesting the usefulness of these variables in discriminating the 2 groups. Apart from the merit of avoiding overfitting, variable selection procedure appears to be useful in reducing the undesired effect of intraspecific variation in inferring ecological traits from limb proportions when only a small number of isolated bones are available for measurements, as is true for many fossil birds.

The discriminant rules of LDA described here can easily be applied to a future observation by calculating its

discriminant score—that is, the sum of natural-log-transformed measurements multiplied by corresponding discriminant coefficients (plus the constant term) as shown in Tables 2 and 5 and in Supplemental Material Tables S2 and S4. Adjustment for prior probabilities can be made by adding the log-transformed value of the ratio of prior probabilities for volant over flightless groups (3.10 in the present study). A positive score indicates classification to the volant group, and a negative one indicates classification to the flightless group. The use of a (size-corrected) 4-variable model is recommended, although ad hoc models may be required when some of the variables are lacking. Custom-made analyses can be conducted with R codes and data available in the Supplemental Material.

Although a simple dichotomy between volancy and flightlessness might seem too simplistic given various transitional cases toward flightlessness in Anatidae (Humphrey and Livezey 1982, Worthy 1988, Guillemette and Ouellet 2005a, 2005b, Fulton et al. 2012), the classification rules given in the present study would at least form an objective basis for ecological and evolutionary studies on fossil anatids. Nevertheless, it should be remembered that inferences based on rules constructed from modern samples are generally constrained by the availability of modern samples and that one should be cautious in extrapolating the rules to fossil species that show departures from morphological variations observed in modern species. At present, it is not certain whether the discriminant rules constructed from modern anatids can be applied to other avian groups such as Rallidae. It might be possible that various patterns of skeletal proportions are realized to perform a similar functional performance of flight (many-to-one mapping; Wainwright et al. 2005). Patterns of correspondence between form and function in the avian skeleton, and to what extent phylogenetic signals may affect them, are under active research (Stoessel et al. 2013, Wang and Clarke 2014). A few methods have been proposed to infer functional signals in morphology while incorporating phylogenetic signals (Motani and Schmitz 2011, Cooper et al. 2014), but much remains to be explored in regard to the theoretical and practical aspects. In order to further explore morphological aspects of avian flightlessness and other ecological traits in general, more empirical and theoretical investigations into biomechanics and evolutionary patterns are required.

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LITERATURE CITED

Alexander, R. M. (2003). Achievements and limitations in the mechanics of extinct animals. In Vertebrate Biomechanics and Evolution (V. L. Bels, J.-P. Gasc, and A. Casinos, Editors). BIOS, Oxford, UK. pp. 11–21.

Angielczyk, K. D., and L. Schmitz (2014). Nocturnality in synapsids predates the origin of mammals by over 100 million years. Proceedings of the Royal Society B 281: 20141642.

Atchley, W. R., C. T. Gaskins, and D. Anderson (1976). Statistical properties of ratios. I. Empirical results. Systematic Zoology 25:137–148.

Baumel, J. J., and L. M. Witmer (1993). Osteologia. In Handbook of Avian Anatomy: Nomina Anatomica Avium, second edition (J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans, and J. C. Vanden Berge, Editors). Publications of the Nuttall Ornithological Club 23. Nuttall Ornithological Club, Cambridge, MA, USA. pp. 45–132.

Bulgarella, M., M. D. Sorenson, J. L. Peters, R. E. Wilson, and K. G. McCracken (2010). Phylogenetic relationships of *Amazonetta*, *Speculanas*, *Lophonetta*, and *Tachyeres*: Four morphologically divergent duck genera endemic to South America. Journal of Avian Biology 41:186–199.

Burnaby, T. P. (1966). Growth-invariant discriminant functions and generalized distances. Biometrics 22:96–110.

Burnham, K. P., and D. R. Anderson (2002). Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second edition. Springer, New York, NY, USA.

Campbell, K. E., Jr., and L. Marcus (1992). The relationship of hindlimb bone dimensions to body weight in birds. In Papers in Avian Paleontology Honoring Pierce Brodkorb (K. E. Campbell, Jr., Editor). Natural History Museum of Los Angeles County Science Series 36:395–412.

Campbell, K. E., Jr., and E. P. Tonni (1983). Size and locomotion in teratorns (Aves: Teratornithidae). The Auk 100:390–403.

Cooper, L. N., T. L. Hieronymus, C. J. Vinyard, S. Bajpai, and J. G. M. Thewissen (2014). New applications for constrained ordination: Reconstructing feeding behaviors in fossil Remingtonocetinae (Cetacea: Mammalia). In Experimental Approaches to Understanding Fossil Organisms: Lessons from

the Living (D. I. Hembree, B. F. Platt, and J. J. Smith, Editors). Springer Science + Business Media, Dordrecht, The Netherlands. pp. 89–107.

del Hoyo, J., and N. J. Collar (2014). HBW and BirdLife International Illustrated Checklist of the Birds of the World, vol. 1. Lynx Edicions, Barcelona, Spain.

De Mendoza, R. S., and C. P. Tambussi (2015). Osteosclerosis in the extinct *Cayaoa bruneti* (Aves: Anseriformes): Insights on behavior and flightlessness. Ameghiniana 52:305–313.

Duncan, R. P., and T. M. Blackburn (2004). Extinction and endemism in the New Zealand avifauna. Global Ecology and Biogeography 13:509–517.

Dunning, J. B., Jr. (Editor). (2008). CRC Handbook of Avian Body Masses, second edition. CRC Press, Boca Raton, FL, USA.

Feduccia, A. (1999). The Origin and Evolution of Birds, second edition. Yale University Press, New Haven, CT, USA.

Felsenstein, J. (1985). Phylogenies and the comparative method. The American Naturalist 125:1–15.

Fu, W. J., R. J. Carroll, and S. Wang (2005). Estimating misclassification error with small samples via bootstrap cross-validation. Bioinformatics 21:1979–1986.

Fujikoshi, Y. (1985). Selection of variables in discriminant analysis and canonical correlation analysis. In Multivariate Analysis, vol. 6: Proceedings of the Sixth International Symposium on Multivariate Analysis (P. R. Krishnaiah, Editor). Elsevier Science, Amsterdam, The Netherlands. pp. 219–236.

Fujikoshi, Y., V. V. Ulyanov, and R. Shimizu (2010). Multivariate Statistics: High-Dimensional and Large-Sample Approximations. Wiley, Hoboken, NJ, USA.

Fulton, T. L., B. Letts, and B. Shapiro (2012). Multiple losses of flight and recent speciation in steamer ducks. Proceedings of the Royal Society B 279:2239–2346.

Gadow, H. (1902). The wings and the skeleton of *Phalacrocorax harrisi*. Novitates Zoologicae 9:169–176 [plates 14 and 15].

Gonzalez, J., H. Düttmann, and M. Wink (2009). Phylogenetic relationships based on two mitochondrial genes and hybridization pattern in Anatidae. Journal of Zoology 279:310–318.

Grafen, A. (1989). The phylogenetic regression. Philosophical Transactions of the Royal Society of London, Series B 326:119–157.

Guillemette, M., and J.-F. Ouellet (2005a). Temporary flightlessness as a potential cost of reproduction in pre-laying Common Eiders *Somateria mollissima*. Ibis 147:301–306.

Guillemette, M., and J.-F. Ouellet (2005b). Temporary flightlessness in pre-laying Common Eiders *Somateria mollissima*: Are females constrained by excessive wing-loading or by minimal flight muscle ratio? Ibis 147:293–300.

Habib, M. B. (2010). The structural mechanics and evolution of aquaflying birds. Biological Journal of the Linnean Society 99:687–698.

Habib, M. B., and C. B. Ruff (2008). The effects of locomotion on the structural characteristics of avian limb bones. Zoological Journal of the Linnean Society 153:601–624.

Hastie, T., R. Tibshirani, and J. Friedman (2009). The Elements of Statistical Learning: Data Mining, Inference, and Prediction, second edition. Springer Science + Business Media, New York, NY, USA.

Hertel, F., and K. E. Campbell, Jr. (2007). The antitrochanter of birds: Form and function in balance. The Auk 124:789–805.

Hinić-Frlog, S., and R. Motani (2010). Relationships between osteology and aquatic locomotion in birds: Determining modes of locomotion in extinct Ornithurae. Journal of Evolutionary Biology 23:372–385.

Holdaway, R. N., M. D. Jones, and N. R. Beavan Athfield (2002). Late Holocene extinction of Finsch's Duck (*Chenonetta finschi*), an endemic, possibly flightless, New Zealand duck. Journal of the Royal Society of New Zealand 32:629–651.

Howard, H. (1947). Wing elements assigned to *Chendytes*. The Condor 49:76–77.

Hughes, A. L. (2013). Indices of Anseriform body shape based on the relative size of major skeletal elements and their relationship to reproductive effort. Ibis 155:835–846.

Hughes, B., and A. J. Green (2005). Food and feeding ecology. In Ducks, Geese and Swans, vol. 1 (J. Kear, Editor). Oxford University Press, Oxford, UK. pp. 27–56.

Hume, J. P., and L. Steel (2013). Fight club: A unique weapon in the wing of the solitaire, *Pezophaps solitaria* (Aves: Columbidae), an extinct flightless bird from Rodrigues, Mascarene Islands. Biological Journal of the Linnean Society 110:32–44.

Humphrey, P. S., and G. A. Clark, Jr. (1964). The anatomy of waterfowl. In The Waterfowl of the World, vol. 4 (J. Delacour, Editor). Country Life, London, UK. pp. 167–232.

Humphrey, P. S., and B. C. Livezey (1982). Flightlessness in flying steamer-ducks. The Auk 99:368–372.

Iwaniuk, A. N., J. E. Nelson, H. F. James, and S. L. Olson (2004). A comparative test of the correlated evolution of flightlessness and relative brain size in birds. Journal of Zoology 263:317–327.

Iwaniuk, A. N., S. L. Olson, and H. F. James (2009). Extraordinary cranial specialization in a new genus of extinct duck (Aves: Anseriformes) from Kauai, Hawaiian Islands. Zootaxa 2296:47–67.

Johnsgard, P. A. (1961). Tracheal anatomy of the Anatidae and its taxonomic significance. Wildfowl 12:58–69.

Jolicoeur, P. (1963a). The degree of generality of robustness in *Martes americana*. Growth 27:1–27.

Jolicoeur, P. (1963b). The multivariate generalization of the allometry equation. Biometrics 19:497–499.

Kear, J. (Editor). (2005). Ducks, Geese and Swans. Oxford University Press, Oxford, UK.

Kennedy, M., and H. G. Spencer (2000). Phylogeny, biogeography, and taxonomy of Australasian teals. The Auk 117:154–163.

Klingenberg, C. P. (1996). Multivariate allometry. In Advances in Morphometrics (L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor, and D. E. Slice, Editors). Plenum Press, New York, NY, USA. pp. 23–49.

Ksepka, D. T. (2014). Flight performance of the largest volant bird. Proceedings of the National Academy of Sciences USA 111:10624–10629.

Li, Z., and J. A. Clarke (2016). The craniolingual morphology of waterfowl (Aves, Anseriformes) and its relationship with feeding mode revealed through contrast-enhanced X-ray computed tomography and 2D morphometrics. Evolutionary Biology 43:12–25.

Liu, G., L. Zhou, B. Li, and L. Zhang (2014). The complete mitochondrial genome of *Aix galericulata* and *Tadorna ferruginea*: Bearings on their phylogenetic position in the Anseriformes. PLOS One 9:e109701. doi:10.1371/journal.pone.0109701

Livezey, B. C. (1989). Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands Merganser. The Wilson Bulletin 101:410–435.

Livezey, B. C. (1990). Evolutionary morphology of flightlessness in the Auckland Islands Teal. The Condor 92:639–673.

Livezey, B. C. (1992). Flightlessness in the Galápagos Cormorant (Compsohalieus [Nannopterum] harrisi): Heterochrony, giantism and specialization. Zoological Journal of the Linnean Society 105:155–224.

Livezey, B. C. (1993a). An ecomorphological review of the dodo (Raphus cucullatus) and solitaire (Pezophaps solitaria), flightless Columbiformes of the Mascarene Islands. Journal of Zoology 230:247–292.

Livezey, B. C. (1993b). Comparative morphometrics of Anas ducks, with particular reference to the Hawaiian Duck Anas wyvilliana, Laysan Duck A. laysanensis, and Eaton's Pintail A. eatoni. Wildfowl 44:75–100.

Livezey, B. C. (1993c). Morphology of flightlessness in Chendytes, fossil seaducks (Anatidae: Mergini) of coastal California. Journal of Vertebrate Paleontology 13:185–199.

Livezey, B. C. (2003). Evolution of flightlessness in rails (Gruiformes: Rallidae): Phylogenetic, ecomorphological, and ontogenetic perspectives. Ornithological Monographs 53.

Livezey, B. C., and P. S. Humphrey (1984). Sexual size dimorphism in continental steamer-ducks. The Condor 86:368–377.

Livezey, B. C., and P. S. Humphrey (1986). Flightlessness in steamer-ducks (Anatidae: Tachyeres): Its morphological bases and probable evolution. Evolution 40:540–558.

Livezey, B. C., and P. S. Humphrey (1992). Taxonomy and identification of steamer-ducks (Anatidae: Tachyeres). University of Kansas Museum of Natural History Monographs 8.

Longrich, N. R., and S. L. Olson (2011). The bizarre wing of the Jamaican flightless ibis Xenicibis xympithecus: A unique vertebrate adaptation. Proceedings of the Royal Society B 278:2333–2337.

Matsuoka, H., and Y. Hasegawa (2007). Myology and osteology of the Whooper Swan Cygnus cygnus (Aves: Anatidae) part 1. Muscles attached to the sternum, coracoid, clavicle, scapula and humerus. Bulletin of the Gunma Museum of Natural History 11:7–14.

Matsuoka, H., Y. Hasegawa, and Y. Takakuwa (2004). Osteological note on the completely prepared fossil "Annaka Short-winged Swan" from the Miocene Tomioka Group, Japan. Bulletin of the Gunma Museum of Natural History 8:35–56 [in Japanese with English summary].

Matsuoka, H., H. Nakajima, Y. Takakuwa, and Y. Hasegawa (2001). Preliminary note on the Miocene flightless swan from the Haraichi Formation, Tomioka Group of Annaka, Gunma, Japan. Bulletin of the Gunma Museum of Natural History 5:1–8.

Mayr, G., and M. Pavia (2014). On the true affinities of Chenornis graculoides Portis, 1884, and Anas lignitifila Portis, 1884—an albatross and an unusual duck from the Miocene of Italy. Journal of Vertebrate Paleontology 34:914–923.

McCoy, M. W., B. M. Bolker, C. W. Osenberg, B. G. Miner, and J. R. Vonesh (2006). Size correction: Comparing morphological traits among populations and environments. Oecologia 148:547–554.

McCracken, K. G., D. C. Paton, and A. D. Afton (2000). Sexual size dimorphism of the Musk Duck. The Wilson Bulletin 112:457–466.

McLachlan, G. J. (1992). Discriminant Analysis and Statistical Pattern Recognition. Wiley, New York, NY, USA.

Middleton, K. M., and S. M. Gatesy (2000). Theropod forelimb design and evolution. Zoological Journal of the Linnean Society 128:149–187.

Millener, P. R. (1999). The history of the Chatham Islands' bird fauna of the last 7000 years—A chronicle of change and extinction. Smithsonian Contributions to Paleobiology 89:85–109.

Miller, A. H. (1937). Structural modifications in the Hawaiian Goose (Nesochen sandvicensis): A study in adaptive evolution. University of California Publications in Zoology 42:1–80.

Mitchell, K. J., J. R. Wood, R. P. Scofield, B. Llamas, and A. Cooper (2014). Ancient mitochondrial genome reveals unsuspected taxonomic affinity of the extinct Chatham Duck (Pachyanas chathamica) and resolves divergence times for New Zealand and sub-Antarctic brown teals. Molecular Phylogenetics and Evolution 70:420–428.

Motani, R., and L. Schmitz (2011). Phylogenetic versus functional signals in the evolution of form–function relationships in terrestrial vision. Evolution 65:2245–2257.

Noriega, J. I., C. P. Tambussi, and M. A. Cozzuol (2008). New material of Cayaoa bruneti Tonni, an Early Miocene anseriform (Aves) from Patagonia, Argentina. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 249:271–280.

Northcote, E. M. (1982). Size, form and habit of the extinct Maltese Swan Cygnus falconeri. Ibis 124:148–158.

Nudds, R. L. (2007). Wing-bone length allometry in birds. Journal of Avian Biology 38:515–519.

Nudds, R. L., G. J. Dyke, and J. M. V. Rayner (2004). Forelimb proportions and the evolutionary radiation of Neornithes. Proceedings of the Royal Society B:S324–S327.

Nudds, R. L., G. J. Dyke, and J. M. V. Rayner (2007). Avian brachial index and wing kinematics: Putting movement back into bones. Journal of Zoology 272:218–226.

Olmos, M., A. Casinos, and J. Cubo (1996). Limb allometry in birds. Annales des Sciences Naturelles–Zoologie et Biologie Animale 17:39–49.

Olsen, A. M. (2015). Exceptional avian herbivores: Multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. Ecology and Evolution 5:5016–5032.

Olson, S. L., and H. F. James (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part 1. Non-Passeriformes. Ornithological Monographs 45.

Olson, S. L., and P. Jouventin (1996). A new species of small flightless duck from Amsterdam Island, southern Indian Ocean (Anatidae: Anas). The Condor 98:1–9.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. Nature 401:877–884.

Paradis, E., J. Claude, and K. Strimmer (2004). APE: Analyses of phylogenetics and evolution in R language. Bioinformatics 20:289–290.

Pavia, M., H. J. M. Meijer, M. A. Rossi, and U. B. Göhlich (2017). The extreme insular adaptation of Garganornis ballmanni Meijer, 2014: A giant Anseriformes of the Neogene of the Mediterranean Basin. Royal Society Open Science 4:160722.

Paxinos, E. E., H. F. James, S. L. Olson, M. D. Sorenson, J. Jackson, and R. C. Fleischer (2002). mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the

Canada Goose (*Branta canadensis*). Proceedings of the National Academy of Sciences USA 99:1399–1404.

Pennycuick, C. J. (1996). Stress and strain in the flight muscles as constraints on the evolution of flying animals. Journal of Biomechanics 29:577–581.

Rabosky, D. L. (2015). No substitute for real data: A cautionary note on the use of phylogenies from birth–death polytomy resolvers for downstream comparative analyses. Evolution 69: 3207–3216.

Raikow, R. J. (1970). Evolution of diving adaptations in the stifftail ducks. University of California Publications in Zoology 94.

Raikow, R. J. (1973). Locomotor mechanisms in North American ducks. The Wilson Bulletin 85:295–307.

Raikow, R. J. (1985). Locomotor system. In Form and Function of Birds, vol. 3 (A. S. King and J. McLelland, Editors). Academic Press, London, UK. pp. 57–147.

Rayner, J. M. V., and G. J. Dyke (2003). Origins and evolution of diversity in the avian wing. In Vertebrate Biomechanics and Evolution (V. L. Bels, J.-P. Gasc, and A. Casinos, Editors). BIOS, Oxford, UK. pp. 297–317.

R Core Team (2015). R: A Language and Environment for Statistical Computing 3.2.0. R Foundation for Statistical Computing, Vienna, Austria.

Revell, L. J. (2009). Size-correction and principal components for interspecific comparative studies. Evolution 63:3258–3268.

Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). Methods in Ecology and Evolution 3:217–223.

Reyment, R. A., and C. F. Banfield (1976). Growth-free canonical variates applied to fossil foraminifers. Bulletin of the Geological Institutions of the University of Uppsala, New Series 7:11–21.

Rohlf, F. J. (2001). Comparative methods for the analysis of continuous variables: Geometric interpretations. Evolution 55:2143–2160.

Sakurai, T., T. Nakada, and Y. Fujikoshi (2013). High-dimensional AICs for selection of variables in discriminant analysis. Sankhyā A 75:1–25.

Simons, E. L. R. (2010). Forelimb skeletal morphology and flight mode evolution in pelecaniform birds. Zoology 113:39–46.

Smith, N. A. (2011). Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). ZooKeys 91.

Smith, N. A., and J. A. Clarke (2012). Endocranial anatomy of the Charadriiformes: Sensory system variation and the evolution of wing-propelled diving. PLOS One 7:e49584. doi:10.1371/journal.pone.0049584

Smith, N. A., and J. A. Clarke (2014). Osteological histology of the Pan-Alcidae (Aves, Charadriiformes): Correlates of wing-propelled diving and flightlessness. The Anatomical Record 297:188–199.

Sorenson, M. D., A. Cooper, E. E. Paxinos, T. W. Quinn, H. F. James, S. L. Olson, and R. C. Fleischer (1999). Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. Proceedings of the Royal Society of London, Series B 266:2187–2193.

Stoessel, A., B. M. Kilbourne, and M. S. Fischer (2013). Morphological integration versus ecological plasticity in the avian pelvic limb skeleton. Journal of Morphology 274:483–495.

Storer, R. W. (1971). Adaptive radiation of birds. In Avian Biology, vol. 1 (D. S. Farner and J. R. King, Editors). Academic Press, New York, NY, USA. pp. 149–188.

Symonds, M. R. E., and A. Moussalli (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behavioral Ecology and Sociobiology 65:13–21.

Tumarkin-Deratzian, A. R., D. R. Vann, and P. Dodson (2006). Bone surface texture as an ontogenetic indicator in long bones of the Canada Goose *Branta canadensis* (Anseriformes: Anatidae). Zoological Journal of the Linnean Society 148:133–168.

Wainwright, P. C., M. E. Alfaro, D. I. Bolnick, and C. D. Hulsey (2005). Many-to-one mapping of form to function: A general principle in organismal design? Integrative and Comparative Biology 45:256–262.

Wang, X., and J. A. Clarke (2014). Phylogeny and forelimb disparity in waterbirds. Evolution 68:2847–2860.

Wang, X., A. J. McGowan, and G. J. Dyke (2011). Avian wing proportions and flight styles: First step towards predicting the flight modes of Mesozoic birds. PLOS One 6:e28672. doi: 10.1371/journal.pone.0028672

Watanabe, J., and H. Matsuoka (2013). Ontogenetic change of morphology and surface texture of long bones in the Gray Heron (*Ardea cinerea*, Ardeidae). In Paleornithological Research 2013: Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna, 2012 (U. B. Göhlich and A. Kroh, Editors). Naturhistorisches Museum Wien, Vienna, Austria. pp. 279–306.

Watanabe, J., and H. Matsuoka (2015). Flightless diving duck (Aves, Anatidae) from the Pleistocene of Shiriya, northeast Japan. Journal of Vertebrate Paleontology 35:e994745.

Weller, M. W. (1980). The Island Waterfowl. Iowa State University Press, Ames, IA, USA.

Williams, M. (2012). A merganser at Auckland Islands, New Zealand. Wildfowl 62:3–36.

Williams, M. (2015a). Formidable carpal weaponry of *Anas chathamica*, Chatham Island's extinct flightless duck. Notornis 62:113–120.

Williams, M. (2015b). Size and flight capability of *Anas chathamica*, an extinct duck from Chatham Island, New Zealand. Wildfowl 65:75–99.

Williams, M., A. J. D. Tennyson, and D. Sim (2014). Island differentiation of New Zealand's extinct mergansers (Anatidae: Mergini), with description of a new species from Chatham Island. Wildfowl 64:3–34.

Woolfenden, G. E. (1961). Postcranial osteology of the waterfowl. Bulletin of the Florida State Museum, Biological Science 6:1–129.

Worthy, T. H. (1988). Loss of flight ability in the extinct New Zealand duck *Euryanas finschi*. Journal of Zoology 215:619–628.

Worthy, T. H. (1997). Fossil deposits in the Hodges Creek Cave System, on the northern foohills of Mt Arthur, Nelson, South Island, New Zealand. Notornis 44:111–124.

Worthy, T. H., and R. N. Holdaway (2002). The Lost World of the Moa: Prehistoric Life of New Zealand. Indiana University Press, Bloomington, IN, USA.

Worthy, T. H., R. N. Holdaway, M. D. Sorenson, and A. C. Cooper (1997). Description of the first complete skeleton of the extinct New Zealand goose *Cnemiornis calcitrans* (Aves:

Anatidae), and a reassessment of the relationships of *Cnemiornis*. Journal of Zoology 243:695–723.

Worthy, T. H., and S. L. Olson (2002). Relationships, adaptations, and habits of the extinct duck '*Euryanas*' *finschi*. Notornis 49:1–17.

Zeffer, A., C. Johansson, and Å. Marmebro (2003). Functional correlation between habitat use and leg morphology in birds (*Aves*). Biological Journal of the Linnean Society 79: 461–484.

APPENDIX

APPENDIX TABLE 10. List of modern species included in the analysis. The group membership (volant or flightless) and species means of variables (mm) are shown, with sample number in parentheses. Abbreviations are defined in Table 1.

Species	Group	CAR	HUM	ULN	CMC	FEM	TIB	TMT
Dendrocygna viduata	Volant	23.0 (2)	98.2 (2)	102.1 (2)	53.7 (2)	49.8 (1)	89.5 (2)	59.1 (1)
D. autumnalis	Volant	24.7 (3)	100.2 (3)	102.5 (3)	55.8 (3)	54.4 (3)	95.9 (3)	60.4 (3)
D. bicolor	Volant	21.8 (11)	97.5 (10)	102.8 (11)	51.9 (10)	50.2 (11)	87.3 (10)	55.2 (11)
Thalassornis leuconotus	Volant	18.8 (3)	86.3 (3)	84.6 (3)	40.3 (3)	41.3 (3)	70.0 (3)	39.3 (3)
Heteronetta atricapilla	Volant	19.9 (1)	76.0 (1)	–	–	39.3 (1)	–	–
Oxyura jamaicensis	Volant	14.7 (10)	70.0 (9)	60.7 (10)	34.7 (10)	39.7 (10)	62.6 (10)	33.3 (10)
Biziura lobata	Volant	17.3 (13)	110.4 (12)	92.8 (12)	51.9 (11)	58.8 (13)	102.0 (13)	48.9 (12)
Malacorhynchus membranaceus	Volant	18.1 (15)	66.1 (10)	60.8 (14)	40.0 (14)	36.7 (14)	64.2 (14)	35.7 (14)
Stictonetta naevosa	Volant	20.4 (3)	89.3 (3)	78.2 (3)	50.9 (3)	50.5 (3)	82.2 (3)	46.7 (3)
Cereopsis novaehollandiae	Volant	36.2 (9)	183.4 (9)	184.8 (9)	101.0 (9)	92.2 (9)	162.4 (9)	108.9 (9)
Coscoroba coscoroba	Volant	35.0 (1)	183.7 (1)	177.8 (1)	96.3 (1)	89.8 (1)	157.3 (1)	97.6 (1)
Cygnus atratus	Volant	41.3 (6)	241.4 (6)	227.0 (6)	111.6 (6)	88.2 (6)	170.8 (6)	100.1 (6)
C. olor	Volant	46.4 (12)	291.8 (11)	272.8 (11)	134.9 (10)	105.8 (11)	196.2 (11)	111.2 (11)
C. buccinator	Volant	58.0 (5)	290.6 (4)	286.0 (4)	144.2 (4)	114.5 (5)	209.7 (4)	120.1 (4)
C. cygnus	Volant	53.1 (4)	264.0 (2)	261.8 (2)	133.7 (2)	105.6 (2)	194.0 (1)	118.0 (1)
C. columbianus	Volant	48.0 (38)	248.8 (21)	248.4 (21)	126.7 (21)	100.5 (36)	187.4 (21)	110.7 (21)
Branta bernicla	Volant	30.3 (13)	122.9 (10)	116.4 (11)	66.6 (11)	59.8 (13)	104.3 (11)	61.6 (11)
B. leucopsis	Volant	32.8 (1)	–	–	–	72.1 (1)	–	–
B. ruficollis	Volant	28.8 (3)	118.7 (1)	110.8 (1)	65.9 (1)	58.0 (3)	101.7 (1)	62.5 (1)
B. hutchinsii leucopareia	Volant	30.3 (2)	–	–	–	64.9 (2)	–	–
B. h. minima	Volant	32.6 (13)	130.0 (9)	125.0 (9)	73.1 (9)	62.9 (13)	112.2 (9)	69.4 (9)
B. h. taverneri	Volant	36.9 (5)	151.1 (4)	145.3 (4)	85.2 (4)	71.9 (5)	128.6 (4)	78.3 (4)
B. canadensis moffitti	Volant	42.2 (3)	180.6 (3)	170.9 (3)	99.4 (3)	83.7 (3)	150.3 (3)	91.0 (3)
B. c. interior	Volant	44.2 (1)	173.7 (1)	–	–	85.8 (1)	149.0 (1)	–
B. c. canadensis	Volant	42.8 (5)	175.6 (5)	163.9 (4)	97.9 (5)	82.3 (5)	143.7 (5)	88.5 (5)
B. sandvicensis	Volant	31.6 (17)	131.0 (19)	126.3 (16)	72.6 (15)	72.3 (17)	129.6 (14)	83.2 (14)
Anser canagicus	Volant	32.2 (7)	140.9 (3)	134.6 (4)	78.5 (4)	72.5 (7)	123.1 (2)	69.2 (4)
A. caerulescens	Volant	38.7 (15)	147.4 (9)	145.6 (7)	82.7 (8)	73.1 (12)	130.5 (9)	81.9 (9)
A. rossii	Volant	32.0 (22)	126.6 (22)	125.2 (22)	71.9 (21)	61.5 (24)	111.1 (20)	69.2 (22)
A. indicus	Volant	34.4 (3)	151.4 (2)	146.2 (2)	83.2 (1)	70.9 (3)	123.4 (2)	74.7 (2)
A. anser	Volant	31.9 (4)	158.0 (2)	149.7 (2)	–	71.1 (3)	130.1 (2)	79.6 (2)
A. cygnoid	Volant	38.4 (3)	158.9 (2)	148.6 (1)	88.7 (1)	78.7 (3)	132.3 (2)	82.3 (2)
A. fabalis	Volant	40.5 (6)	179.5 (5)	168.7 (4)	99.7 (4)	85.4 (7)	148.0 (6)	88.8 (6)
A. albifrons	Volant	35.7 (40)	150.3 (20)	144.5 (19)	85.0 (19)	73.1 (38)	125.3 (19)	74.9 (20)
A. erythropus	Volant	33.6 (2)	131.5 (2)	126.9 (2)	73.7 (2)	64.1 (2)	110.3 (2)	64.8 (2)
Clangula hyemalis	Volant	21.2 (9)	72.2 (10)	64.6 (11)	45.0 (11)	41.6 (10)	66.9 (10)	34.7 (11)
Somateria mollissima	Volant	27.1 (10)	108.4 (10)	95.0 (10)	65.0 (10)	63.6 (10)	100.6 (10)	51.8 (10)
Melanitta perspicillata	Volant	21.8 (14)	82.5 (13)	75.1 (13)	48.6 (13)	48.7 (14)	80.5 (13)	43.5 (13)
M. stejnegeri	Volant	25.7 (3)	96.4 (1)	87.2 (1)	56.2 (1)	55.2 (3)	90.0 (1)	43.6 (1)
M. deglandi	Volant	25.7 (15)	98.8 (17)	88.8 (17)	57.7 (17)	55.9 (16)	93.0 (17)	49.7 (17)
M. nigra	Volant	21.2 (2)	92.5 (2)	84.6 (2)	52.7 (2)	51.4 (2)	84.1 (2)	44.4 (2)
M. americana	Volant	20.7 (11)	91.9 (10)	83.4 (11)	53.1 (11)	51.5 (11)	84.0 (10)	45.2 (11)
Bucephala albeola	Volant	16.3 (3)	59.4 (3)	51.6 (4)	35.1 (4)	37.1 (3)	55.3 (2)	32.2 (4)
B. clangula	Volant	22.0 (13)	75.5 (9)	66.3 (11)	45.7 (11)	46.6 (10)	67.2 (10)	37.2 (11)
B. islandica	Volant	21.1 (1)	77.4 (1)	68.6 (1)	47.6 (1)	46.8 (1)	68.0 (1)	36.5 (1)
Mergellus albellus	Volant	19.6 (2)	72.3 (1)	59.5 (1)	41.6 (1)	40.6 (1)	63.4 (1)	34.9 (1)
Lophodytes cucullatus	Volant	20.5 (1)	64.4 (1)	53.2 (1)	38.9 (1)	37.5 (1)	58.4 (1)	30.9 (1)
Mergus merganser	Volant	27.3 (31)	91.8 (28)	77.4 (27)	55.7 (28)	50.9 (28)	84.6 (11)	48.1 (11)
M. squamatus	Volant	24.9 (1)	85.7 (1)	73.3 (1)	52.6 (1)	48.4 (1)	80.0 (1)	44.8 (1)
M. serrator	Volant	26.3 (3)	87.8 (1)	73.5 (1)	51.4 (1)	45.6 (2)	82.5 (1)	46.3 (1)
M. australis	Volant	18.1 (3)	69.6 (3)	55.8 (3)	39.4 (3)	43.7 (3)	71.8 (2)	40.6 (2)
Histrionicus histrionicus	Volant	17.8 (8)	65.9 (8)	56.2 (6)	41.1 (6)	42.4 (8)	69.5 (6)	37.0 (5)
Camptorhynchus labradorius	Volant	22.4 (1)	–	69.7 (1)	48.7 (1)	–	–	48.2 (1)
Chloephaga melanoptera	Volant	27.0 (3)	137.5 (3)	139.8 (3)	76.9 (3)	75.2 (3)	131.6 (3)	80.6 (3)
C. picta	Volant	34.2 (9)	158.9 (9)	154.5 (9)	90.8 (9)	87.4 (8)	152.6 (8)	95.9 (7)
Tadorna tadorna	Volant	23.9 (8)	105.7 (8)	99.0 (8)	63.2 (8)	53.5 (8)	94.1 (8)	55.5 (8)

APPENDIX TABLE 10. Continued.

Species	Group	CAR	HUM	ULN	CMC	FEM	TIB	TMT
T. ferruginea	Volant	25.5 (4)	113.4 (2)	107.2 (2)	69.7 (2)	55.1 (4)	96.7 (2)	58.5 (2)
Plectropterus gambensis	Volant	33.4 (3)	184.9 (5)	167.2 (5)	97.6 (5)	98.3 (5)	175.0 (5)	115.4 (5)
Cairina moschata	Volant	29.5 (7)	122.6 (7)	105.1 (6)	73.2 (7)	65.8 (7)	103.4 (7)	60.3 (7)
Sarkidiornis sylvicola	Volant	21.9 (1)	–	–	–	53.2 (1)	–	–
Nettapus auritus	Volant	19.4 (1)	69.4 (1)	60.1 (1)	45.0 (1)	41.3 (1)	64.5 (1)	38.8 (1)
N. coromandelianus	Volant	15.1 (5)	56.0 (5)	48.5 (5)	31.7 (5)	28.6 (4)	46.3 (5)	24.9 (5)
Aix sponsa	Volant	19.9 (18)	70.9 (9)	59.1 (9)	46.2 (10)	41.2 (16)	64.3 (9)	35.4 (10)
A. galericulata	Volant	18.5 (6)	69.3 (5)	59.6 (5)	45.2 (5)	42.0 (7)	65.8 (5)	38.4 (5)
Chenonetta jubata	Volant	22.7 (7)	86.5 (8)	78.8 (8)	54.5 (8)	51.0 (8)	86.2 (8)	51.2 (8)
Hymenolaimus malacorhynchos	Volant	20.7 (3)	83.6 (3)	74.4 (3)	49.4 (3)	48.9 (3)	85.3 (3)	50.5 (3)
Merganetta armata	Volant	13.0 (2)	59.3 (2)	51.5 (2)	31.4 (2)	36.3 (2)	64.5 (2)	37.1 (2)
Marmaronetta angustirostris	Volant	18.6 (3)	71.9 (3)	63.6 (3)	43.7 (3)	38.5 (3)	63.8 (3)	38.1 (3)
Netta rufina	Volant	23.1 (15)	98.9 (12)	87.0 (12)	55.4 (11)	50.9 (12)	84.4 (11)	43.6 (11)
N. erythrophthalma	Volant	20.7 (5)	86.5 (5)	74.4 (4)	46.6 (3)	45.0 (5)	73.5 (2)	38.0 (3)
N. peposaca	Volant	24.1 (10)	94.5 (9)	82.1 (9)	53.6 (8)	47.6 (11)	79.5 (9)	43.7 (9)
Aythya ferina	Volant	21.6 (7)	84.7 (13)	74.8 (13)	45.9 (13)	45.3 (13)	75.8 (13)	37.9 (13)
A. americana	Volant	22.6 (10)	90.0 (10)	79.3 (9)	49.1 (10)	47.8 (10)	78.0 (9)	39.8 (10)
A. valisineria	Volant	23.7 (11)	93.3 (10)	81.5 (9)	50.2 (10)	50.4 (11)	83.1 (10)	43.4 (10)
A. australis	Volant	22.6 (1)	89.4 (1)	77.7 (1)	49.9 (1)	45.1 (1)	74.0 (1)	41.4 (1)
A. nyroca	Volant	18.4 (8)	73.5 (7)	61.8 (7)	39.2 (7)	39.5 (8)	64.3 (6)	31.9 (6)
A. novaeseelandiae	Volant	16.8 (1)	70.3 (1)	59.6 (1)	37.0 (1)	41.1 (1)	64.0 (1)	34.4 (1)
A. collaris	Volant	20.0 (10)	75.3 (10)	65.5 (10)	41.3 (10)	42.9 (10)	67.1 (10)	34.3 (10)
A. fuligula	Volant	19.7 (14)	79.1 (14)	68.8 (14)	42.3 (14)	42.9 (15)	68.0 (14)	34.1 (14)
A. marila	Volant	21.4 (10)	86.1 (29)	75.4 (30)	46.8 (30)	47.1 (30)	75.6 (29)	37.7 (30)
A. affinis	Volant	19.4 (10)	79.5 (10)	70.5 (9)	43.6 (10)	43.8 (10)	70.1 (10)	35.7 (9)
Rhodonessa caryophyllacea	Volant	21.1 (1)	98.0 (1)	85.6 (1)	–	49.2 (1)	78.1 (1)	48.2 (1)
Tachyeres patachonicus	Volant	28.6 (5)	117.7 (5)	97.4 (5)	63.3 (5)	72.0 (6)	114.5 (5)	59.4 (5)
T. leucocephalus	Flightless	30.1 (1)	126.7 (1)	103.0 (1)	68.4 (1)	81.6 (1)	127.9 (1)	67.6 (1)
T. pteneres	Flightless	30.1 (18)	128.7 (17)	98.8 (17)	66.1 (17)	89.0 (18)	138.1 (17)	71.5 (17)
T. brachypterus	Flightless	28.9 (5)	124.4 (3)	100.0 (4)	67.4 (4)	81.0 (4)	130.9 (3)	68.3 (3)
Spatula querquedula	Volant	20.0 (1)	–	–	–	35.9 (1)	–	–
S. clypeata	Volant	22.9 (1)	76.5 (3)	65.9 (3)	47.3 (3)	39.3 (3)	66.6 (3)	36.6 (3)
Sibirionetta formosa	Volant	18.5 (2)	64.8 (1)	58.1 (1)	40.5 (1)	38.4 (2)	61.1 (1)	33.3 (1)
Mareca strepera	Volant	22.6 (2)	88.1 (2)	76.9 (2)	54.3 (2)	47.0 (2)	75.6 (2)	40.5 (2)
M. falcata	Volant	21.2 (3)	80.9 (2)	67.1 (2)	48.1 (2)	42.6 (3)	69.3 (3)	36.7 (3)
M. penelope	Volant	20.6 (4)	84.1 (1)	71.6 (1)	52.2 (1)	44.0 (4)	74.7 (1)	40.3 (1)
M. americana	Volant	18.7 (1)	–	–	–	44.9 (1)	–	–
Anas zonorhyncha	Volant	22.5 (10)	92.1 (8)	80.5 (7)	58.3 (7)	50.8 (9)	80.5 (7)	45.1 (8)
A. platyrhynchos	Volant	24.3 (4)	90.8 (4)	76.0 (4)	56.1 (4)	49.3 (5)	78.0 (4)	43.3 (4)
A. gibberifrons	Volant	17.3 (5)	70.9 (4)	61.9 (5)	43.6 (5)	39.4 (5)	64.7 (5)	36.3 (5)
A. castanea	Volant	17.2 (1)	69.8 (1)	60.2 (1)	42.4 (1)	38.7 (1)	62.3 (1)	36.9 (1)
A. chlorotis	Volant	18.0 (2)	69.8 (2)	59.0 (2)	42.2 (2)	41.4 (2)	67.7 (2)	38.4 (2)
A. aucklandica	Flightless	10.8 (5)	54.5 (2)	39.5 (1)	28.1 (1)	44.2 (3)	65.2 (1)	33.0 (1)
A. nesiotis [a]	Flightless	–	48.2 (12)	36.5 (7)	24.9 (6)	39.4 (13)	62.6 (8)	32.0 (8)
A. capensis	Volant	15.0 (1)	68.8 (1)	62.2 (1)	40.3 (1)	34.8 (1)	61.9 (1)	36.6 (1)
A. acuta	Volant	23.3 (6)	88.7 (2)	78.0 (2)	55.1 (2)	46.2 (6)	77.9 (2)	44.0 (2)
A. eatoni	Volant	17.8 (1)	70.2 (1)	62.3 (1)	42.3 (1)	37.6 (1)	61.7 (1)	33.5 (1)
A. crecca	Volant	16.6 (8)	58.7 (6)	50.9 (5)	36.8 (5)	33.2 (7)	49.0 (5)	30.1 (5)

[a] Data from Williams (2015b).

APPENDIX TABLE 11. List of fossil species included in the analysis. Availability of at least one associated skeleton and species means of variables (mm) are shown, with sample number in parentheses. Abbreviations are defined in Table 1.

Species	Associated	CAR	HUM	ULN	CMC	FEM	TIB	TMT
Cnemiornis calcitrans	Yes [a]	–	163.1 (3)	129.5 (3)	68.7 (3)	151.0 (3)	270.5 (2)	144.4 (1)
C. gracilis [b]	No	–	134.6 (23)	104.0 (20)	52.1 (19)	126.2 (25)	225.1 (26)	118.0 (34)
Branta hylobadistes	Yes	28.1 (4)	113.7 (6)	100.2 (5)	62.0 (11)	77.9 (11)	141.0 (6)	89.7 (8)
B. rhuax	Yes	29.5 (1)	133.8 (11)	103.0 (11)	56.5 (13)	105.9 (12)	181.2 (11)	108.2 (12)
Chenonetta finschi	Yes [c]	–	88.7 (7)	73.3 (1)	45.5 (1)	65.1 (2)	95.7 (10)	52.7 (1)
Ptaiochen pau	Yes	0.1 (1)	53.1 (17)	35.3 (7)	18.8 (4)	98.3 (18)	145.9 (14)	83.1 (12)
Thambetochen chauliodous	Yes	–	58.9 (27)	39.1 (8)	19.5 (6)	99.1 (12)	154.5 (5)	85.4 (15)
Chendytes lawi	No [d]	5.8 (5)	67.8 (13)	25.5 (3)	24.2 (2)	71.3 (83)	140.9 (21)	68.2 (15)
C. milleri	No	–	69.5 (2)	31.2 (1)	–	–	127.2 (1)	59.1 (1)
Shiriyanetta hasegawai	No	11.9 (2)	87.6 (1)	49.6 (2)	36.2 (3)	72.4 (2)	144.8 (1)	62.9 (1)
Mergus milleneri [e]	No	–	66.6 (47)	53.5 (43)	37.3 (41)	43.0 (44)	72.2 (47)	39.9 (51)
Anas chathamica [f]	No	–	94.7 (16)	69.7 (24)	51.4 (20)	66.8 (18)	105.4 (15)	57.5 (22)
A. marecula	No	7.9 (2)	42.4 (6)	35.1 (5)	23.4 (5)	33.1 (11)	55.2 (12)	29.8 (16)
Bambolinetta lignitifila [g]	Yes	–	76.8 (1)	∼62 (1)	∼47 (1)	–	–	–
Cayaoa bruneti	No	–	–	–	32.4 (1)	68.5 (1)	161.5 (1)	70.4 (3)
"Annaka Short-winged Swan" [h]	Yes	–	222.0 (1)	126.4 (1)	69.4 (1)	98.7 (1)	203.6 (1)	102.5 (1)

[a] Not examined in this study. See Worthy et al. (1997).
[b] Data from Worthy and Holdaway (2002).
[c] Not examined in this study. See Worthy and Olson (2002).
[d] One partial skeleton (Santa Barbara Museum of Natural History 624) includes HUM, FEM, TIB, and TMT.
[e] Data from Williams et al. (2014).
[f] Data from Williams (2015b).
[g] Data from Mayr and Pavia (2014). Ulna and carpometacarpus lengths were estimated by those authors.
[h] Data from Matsuoka et al. (2004).