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Mitogenomics supports an unexpected taxonomic relationship for the extinct diving duck *Chendytes lawi* and definitively places the extinct Labrador Duck

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ABSTRACT

Chendytes lawi, an extinct flightless diving anseriform from coastal California, was traditionally classified as a sea duck, tribe Mergini, based on similarities in osteological characters. We recover and analyze mitochondrial genomes of *C. lawi* and five additional Mergini species, including the extinct Labrador Duck, *Camptorhynchus labradorius*. Despite its diving morphology, *C. lawi* is reconstructed as an ancient relictual lineage basal to the dabbling ducks (tribe Anatini), revealing an additional example of convergent evolution of characters related to feeding behavior among ducks. The Labrador Duck is sister to Steller's Eider which may provide insights into the evolution and ecology of this poorly known extinct species. Our results demonstrate that inclusion of full length mitogenomes, from taxonomically distributed ancient and modern sources can improve phylogeny reconstruction of groups previously assessed with shorter single-gene mitochondrial sequences.

1. Introduction

True ducks (subfamily Anatinae) are a distinct clade of birds whose evolutionary history is valuable for understanding past and present environments. Unfortunately, the phylogenetic relationships within this group remain problematic, making it difficult to reconstruct the life history of several interesting but extinct duck species. We reconstruct the Anatinae phylogeny to systematically place the extinct diving duck *Chendytes lawi*. Miller (1925) erected the genus *Chendytes* based on Holocene fossil material from the California coast and nearby Channel Islands (Fig. 1). Two species are known. The goose-sized *C. lawi* has more degeneration of the wing elements than the smaller *C. milleri,* which may represent an intermediate form between a flying ancestor and the flightless *C. lawi* (Howard, 1955). Known only from the Pleistocene of San Nicolás Island, *C. milleri* is more limited in abundance and geography than *C. lawi,* which has an extensive Holocene record extending from northern Baja to southern Oregon (Jones et al., 2008a; Gruhn and Bryan, 2006). Carbon dating and the frequent recovery of material from middens suggest that the latter species was eventually lost to human exploitation, but unlike many other extinct Pleistocene lineages it persisted until as recently as 2400 years ago (Jones et al., 2008a; Grayson, 2008).

Chendytes was traditionally classified as a sea duck, tribe Mergini. Miller (1925) allied it with the Surf scoter (*Melanitta perspicillata*), but an extended study by Livezey (1993) suggested placement in the eider genus *Somateria*. Despite uncertainty regarding the modern genus closest to *Chendytes,* previous authors consistently placed it amongst the Mergini based on osteological characters and proportions (Howard, 1947, 1955, 1964; Livezey, 1993; Miller, 1930; Miller et al., 1961). Nevertheless, several characters used for phylogenetic placement of *Chendytes* were found to be convergent, as they also occur in other diving Anatinae clades such as *Tachyeres* (steamer ducks) and Aythyini (scaups/pochards), as well as in more basal diving anseriforms such as *Oxyura* (e.g. Ruddy duck) (Livezey, 1993; Miller, 1930).

Here, we address the systematic placement of *Chendytes lawi* using molecular data. We generated mitochondrial genome sequences for *C. lawi* and five additional sea duck species, including the extinct Labrador Duck, *Camptorhynchus labradorius*. We analyzed these in combination with other anatid mitochondrial sequences. Using maximum likelihood and Bayesian inference methods, we compare phylogenetic results from three alternative data matrices: (1) maximized taxonomic sampling with missing data (2) mitogenomes only with limited taxonomic sampling and (3) a two-gene matrix with maximized taxonomic sampling and zero missing data. Our results consistently indicate that *Chendytes lawi* is not a member of any currently recognized diving duck clade but is a stem dabbling duck with convergent osteological adaptations for diving. *Camptorhynchus labradorius* is an eider that is sister to *Polysticta stelleri* (Steller's Eider) within the sea-duck tribe Mergini. The

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combination of mitogenomic and single mitochondrial gene sequences improve estimates of phylogeny within the Anatinae.

2. Methods

2.1. Sample collection

In this study, we follow the binomial list of Clements et al. (2017) for species – eBird/Clements checklist of birds of the world – supplemented by the higher taxonomic classifications outlined by Cracraft (2013). Samples of *Chendytes lawi* bone fragments were provided by TLJ. The bones were recovered from archaeological site, CA-SLO-2, on the central California coast in San Luis Obispo County, midway between Avila Beach and Morro Bay (Jones et al. 2008b).[1] Two toe pad samples from separate individuals of *Camptorhynchus labradorius* (Labrador Duck) were lent by the American Museum of Natural History (AMNH). One toe pad sample from each of the extant species of Mergini (*Mergus serrator*, *Mergus merganser americanus*, *Melanitta nigra* and *Melanitta fusca deglandi*) were provided by the Donald R. Dickey Collection of Birds and Mammals at the University of California, Los Angeles (UCLA DC). All other mitochondrial sequences for anatid species were acquired from Genbank. See S1 for catalog numbers, accession numbers and species information.

2.2. DNA extraction, library preparation and target enrichment

DNA was extracted from a left tibiotarsus shaft of *Chendytes lawi* in a dedicated ancient DNA facility at UCLA. Prior to extraction the outer surface of the bone was removed with a sterilized dremel tool and a new, disposable rotary head to reduce exogenous contamination. The sample was subsequently ground into a coarse powder. This powder was then incubated in a solution of EDTA pH 8.0 and proteinase-K for 24 h on a rotator followed by 3 h of incubation at 56 °C. DNA was then treated to the silica-adhesion protocol described in Rohland and Hofreiter (2007). The resulting DNA extract was quantified using an Agilent 2100 Bioanalyzer (Agilent Technologies, Santa Clara, California, USA) and then stored at –20 °C prior to downstream application.

DNA extraction from all toe pads was performed in a dedicated hood for historic DNA extraction in a pre-PCR DNA free laboratory. We followed the manufacturer's protocol for the Qiagen DNEasy extraction kit (Qiagen Inc., Valencia, California, USA) with the following modifications: adding 40 uL proteinase K and 20 uL of 1 M dithiothreitol (DTT) to the extraction buffer and incubating the sample at 50 °C until completely digested, about 48 h (Fulton et al., 2012a). Qubit (ThermoFisher) fluorometric quantification of double stranded DNA followed extraction and all subsequent steps of the protocol.

After extraction, we prepared libraries from all DNA extracts with end-repair and dual-indexed adapter ligation using the Kapa Biosystems LTP Library Preparation Kit and custom indexes from BadDNA UGA oligos, respectively, following the manufacturers' protocols. Resulting DNA was size selected with Seramag Speedbeads to exclude fragments less than 150 base pairs (bp) (Rohland and Reich, 2012). Note: Though libraries were prepared in the same way for all samples, the extraction and library preparation (indexing) of the *Chendytes lawi* specimen was completed in the dedicated ancient DNA facility before any handling or processing of the historic toe pad samples.

We synthesized an 80mer bait set with 8× tiling at MYcroarray based on eight published anatid mitogenomes (*Dendrocygna javanica, Cygnus atratus, Mergus squamatus, Cairina moschata, Aythya americana, Anas formosa, Anas crecca, Anas platyrhynchos*) to target the full mitochondrial genome (see S1 for accession numbers). Following library preparation and quantification, we performed target capture of mitogenomes following the manufacturer's protocol except that hybridization and subsequent washes were carried out at a temperature of 55 °C. Dual-end sequencing (2 × 300 bp) was performed on the pooled, enriched libraries on a MiSeq instrument (Illumina Inc., San Diego, California, USA).

2.3. Read processing

Reads were de-multiplexed and sequence quality was evaluated using FastQC (Andrews, 2010). As the insert lengths from our ancient and historic DNA were on average several base pairs shorter than our read length, we created a first set of "QC reads" by cutting the sequences down to the first 70 bp. We also used the Trimmomatic pipeline enabled on the online platform Galaxy (version 0.32.3) on the raw reads to remove adapter contamination and sequencing artifacts to create a second set of QC reads (Bolger et al., 2014). Poor quality leading and trailing ends were removed and sequences were trimmed based on a sliding window of 5 base pairs where windows with an average quality less than 30 were removed. Reads from Trimmomatic of fewer than 30 bp were excluded. We mapped these two sets of processed reads for each of our museum samples from extant species as well as the Labrador Duck to the single published mitogenome for a Mergini species, *Mergus squamatus,* using Geneious Pro 9.0.5 (Kearse et al., 2012). Reads from *Chendytes lawi* were verified by eye and suspected contaminants were identified using NCBI's nucleotide BLAST and removed. Once all samples were processed, contigs were assembled to produce two mitogenome sequences for each species based on the 70mer and Trimmomatic processed reads. We compared the mappings for the two datasets for each species visually by aligning the assembled contigs and looking for discrepancies. When discrepancies were found, the highest base call quality was used to decide between nucleotides. When there was no difference in base call quality, the Trimmomatic mappings were chosen over the 70mer mappings.

2.4. Validation of historic DNA

We used mapDamage 2.0 (Jónsson et al., 2013) to identify nucleotide mis-incorporations in our ancient and historic DNA samples (S2). Such damage patterns are typical and expected from these historical sources of genetic data and thus also serve as a method of confirming that ancient DNA (aDNA) sequences are from the target specimen and not from modern contaminants. We used Bowtie (Langmead et al., 2009) to map the MiSeq reads back to the assembled mitogenomes of *C. lawi* and *M. f. deglandi*. The resulting alignment (BAM) files were used as input files for mapDamage.

2.5. Phylogenetic reconstruction

We aligned mitogenome data to previously published Anatid mitogenomes and mitochondrial gene sequences available from GenBank using the MUSCLE algorithm in Geneious Pro 9.0.5. Each taxon had between one and four gene fragments, or a complete mitogenome, represented in the alignment. In all, 32 taxa had complete mitogenomes, 14 had four gene fragments, 17 had three fragments, 30 had two fragments and 11 taxa had one fragment and were present in the combined matrix (matrix A) of 104 total taxa (S1). Two additional partial matrices of 32 taxa with complete genomes (matrix B), and 72 taxa with both Cyt b and COI fragments without missing data (matrix C) were generated. In matrix C, one taxon with missing data was included, *Polysticta stelleri*, in order to confirm relationships to extinct species recovered from analyses of matrix A. Note that the control region was

[1] [1]The *C.lawi* fossils were excavated in 1968 (Greenwood, 1972) from a 3.4 m deep shell midden deposit, and were identified in 2007 by Judy Porcasi who relied on comparative materials at Los Angeles County Museum of Natural History (Paleontology Department.) and the Department of Biology at California State University, Long Beach. Thirty-three radiocarbon determinations show that the archaeological site was occupied from 10,300 to 300 cal BP. The specimen that produced the sequence was recovered from unit S4/W2, from a depth of 270–280 cm (Jones et al., 2008b). Eight radiocarbon determinations show that the levels between 280 and 200 cm date between 9000 and 5000 cal BP.

Table 1
Summary of mitogenome sequencing amount and coverage.

Species	Sequence length	Total reads in contig	Total bases	Avg. bp coverage	Min. bp coverage	Max bp coverage
C. lawi	16,647	2867	217,221	12.1	0	40
C. labradorius (45802)	16,624	1,074,706	75,245,945	4631.4	26	11,988
C. labradorius (45803)	16,611	654,259	45,814,655	2819.8	12	8225
M. f. deglandi	16,608	841,326	58,909,345	3605.7	15	8832
M. nigra	16,625	219,134	15,355,905	942.6	6	3711
M. m. americana	16,613	439,024	30,748,205	1874.6	35	5080
M. serrator	16,632	575,166	40,278,145	2470.9	40	8055

not included in any of the three matrices to mitigate issues related to ambiguous alignment.

Using k-means clustering in R (Ellingson et al., 2014), each of the sequence alignments were binned into five rate classes according to per-site relative rates as estimated in HyPhy (Kosakovsky Pond et al., 2005). Sites that evolve quickly—particularly at deeper nodes of a phylogeny—potentially lead to long-branch attraction if substitution models cannot accurately account for homoplasy. It is not uncommon to omit such rapidly evolving sites from phylogenetic analyses (Pisani, 2004), a procedure analogous to (but more precise than) choosing loci based on the optimal rate of molecular evolution for a given phylogeny. In matrix A sites of the two highest rate classes (n = 4 bp total) were removed and in matrix B sites of the single highest rate class (n = 5 bp total) were removed as they were most likely to exhibit homoplasy. In matrix C, no sites were evolving especially rapidly to warrant removal from the alignment (S3).

We reconstructed the phylogenetic relationships of Anatidae with all three matrices using Mr.Bayes 3.2.6 (Huelsenbeck and Ronquist, 2001) and performed two runs of the analysis for 50 million generations, with four chains (3 heated, one cold) and Beagle options enabled on CIPRES (Miller et al., 2010). The data in matrix A were partitioned into three rate categories, in matrix B four categories and in matrix C five categories. We applied a mixed nucleotide substitution model with gamma rate heterogeneity. We also reconstructed the phylogenies under maximum likelihood using RAxML 8.2.10 (Stamatakis, 2014) under the default settings enabled on CIPRES.

3. Results

We recovered complete mitochondrial genomes for the four extant species and two individual Labrador Duck specimens. Excluding the control region, only *Mergus serrator* was missing a total of two bases in the alignment among historic samples. We recovered a near complete mitogenome (45 missing bases, not including missing bases in the control region) for *Chendytes lawi* with 12X average coverage. The mitogenomic sequences from the two Labrador Duck toe pads were identical, we therefore include only the highest quality sequence (determined by read depth) in the phylogeny. Further details of the quality of assembly are included in Table 1. Data matrix A included a total of 15,513 sites, 5778 of which were variable (37.2%). Data matrix B

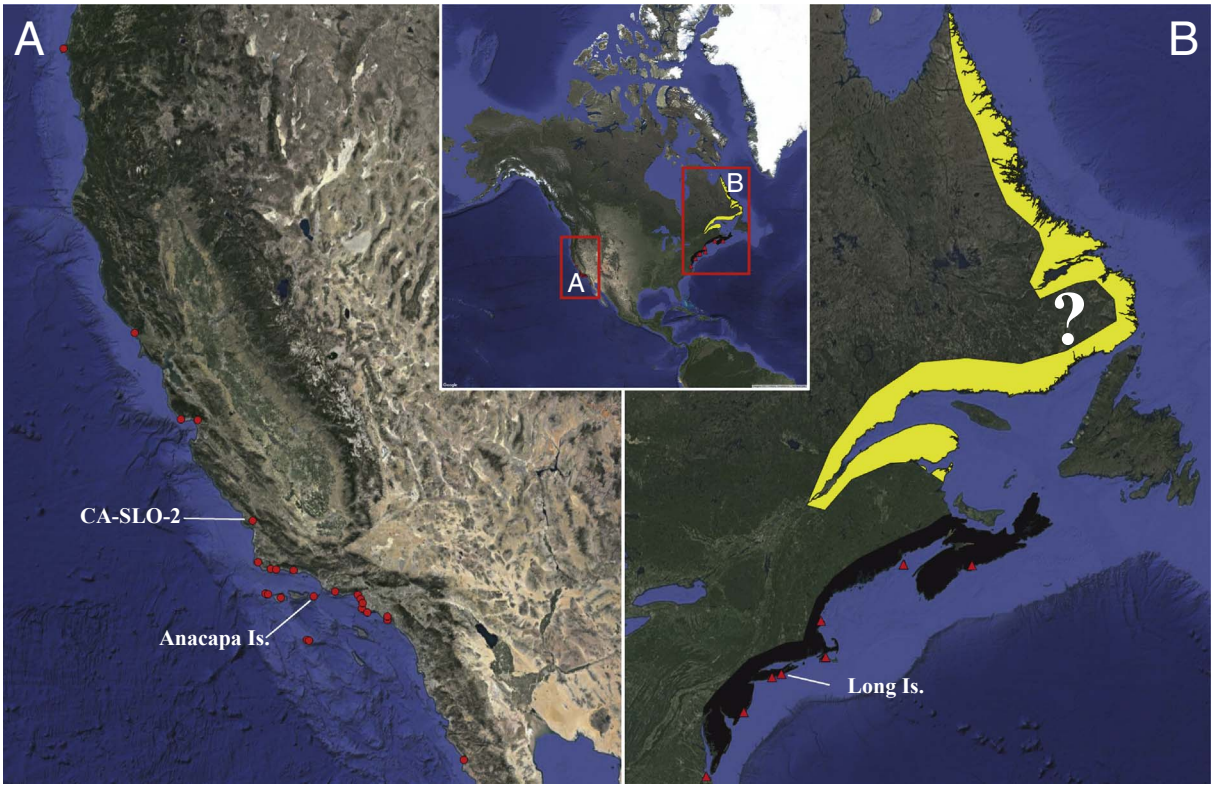

Fig. 1. Distribution maps for *Chendytes* sp. (A) and *Camptorhynchus labradorius* – Labrador Duck (B). Red circles demarcate localities of fossil recovery for *Chendytes lawi* and *Chendytes milleri.* The locality (CA-SLO-2) for the sample used in this study is labelled. The only known locality for *C. milleri* (Anacapa Island) is also labelled. Red triangles demarcate verified locality records of the Labrador Duck. However, these are all winter records. The reconstructed breeding range (yellow) and wintering range (black) according to www.birdlife.org is shown. Note that the breeding and molting ranges of this taxon are necessarily speculative as indicated by the question mark (see Discussion). The locality (Long Island, NY) for the two sampled Labrador ducks used in this study is labelled. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

included a total of 15, 512 sites, 5662 of which were variable (36.5%). Data matrix C included a total 1093 sites, 464 of which were variable (42.5%).

The topologies from our maximum likelihood (ML) and Bayesian trees based on matrix A were largely congruent. With geese and swans constrained as the outgroup, the Tadornini branch first, followed by the Mergini, then the Aythyini and finally the Anatini (Fig. 2). Within the tribe Anatini, the topologies differ in that there is a polytomy at the base of this clade in the Bayesian tree while in the ML tree *Spatula/Sibirionetta* branch first, leaving the South American dabblers sister to *Mareca/Anas*. Consequently, placement of the South American clade consisting of *Amazonetta*, *Speculanas* and *Tachyeres* is uncertain (bootstrap support (bs) = 39) and differs between the two methods (Fig. 2).

The extinct Labrador Duck, *Camptorhynchus labradorius*, is strongly supported—bs = 100; posterior probability (pp) = 1.0—as sister to Steller's Eider, *Polysticta stelleri*, consistent with previous placement of the Labrador Duck within the Mergini based on morphology (Livezey, 1995). This *Polysticta/Camptorhynchus* grouping falls within a monophyletic eider group, and all modern sea ducks sampled form a well-supported (bs = 66; pp = 1.0) monophyletic tribe Mergini (Fig. 2). Sea duck genera are monophyletic except for *Mergus,* which includes *Lophodytes* but with low support in the maximum likelihood tree

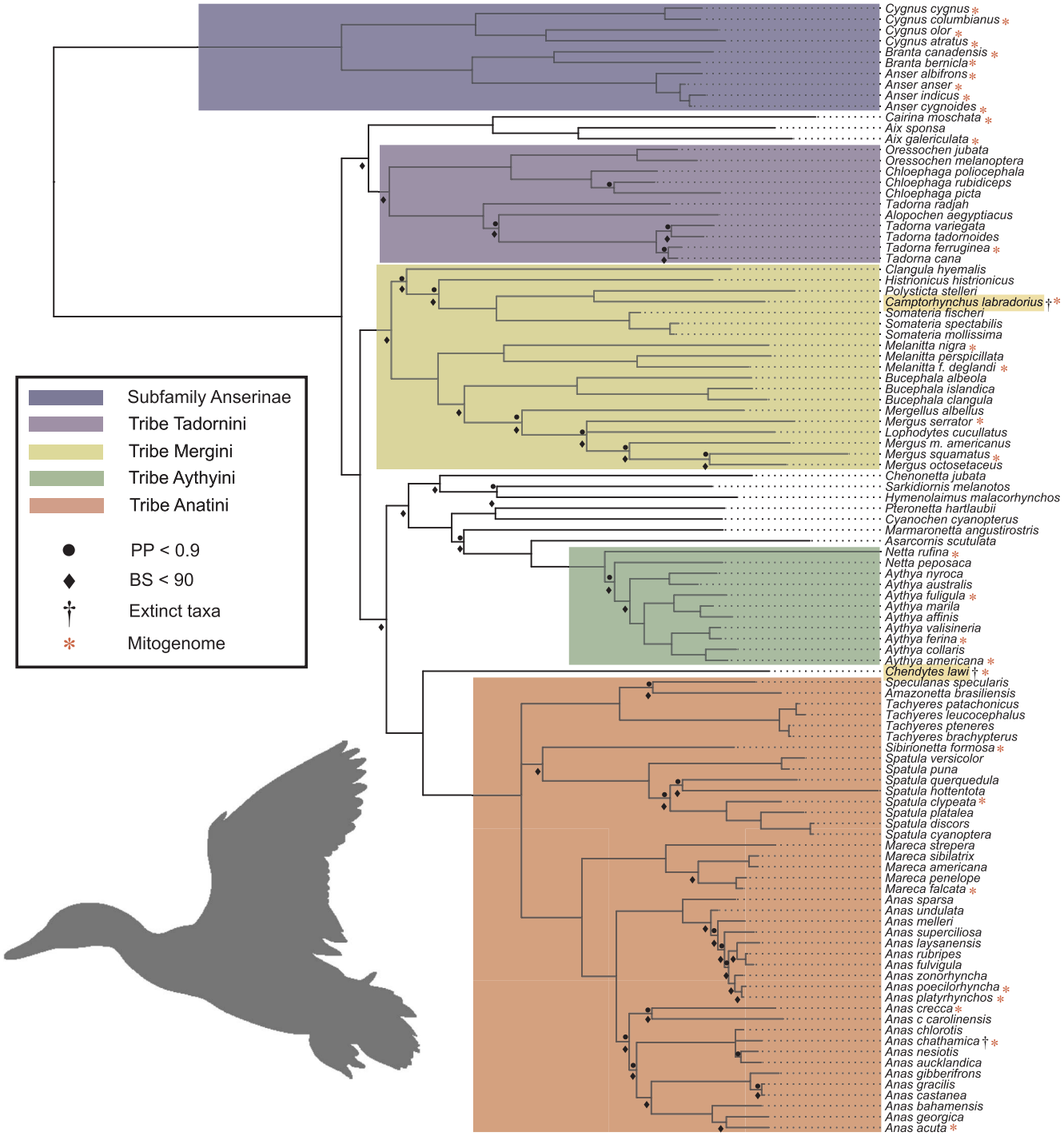

Fig. 2. Bayesian inference tree based on the combined data matrix A. Circles above nodes represent low posterior probabilities from the MrBayes analysis (< 0.9). Diamonds below nodes represent low bootstrap values from the RAxML analysis (< 90). *Chendytes lawi* and *Camptorhynchus labradorius* (Labrador Duck) are marked with an asterisk (*). A dagger (†) indicates an extinct species. Major subfamilies and tribes are color coded (see legend).

(bs = 42) and forming a polytomy in our Bayesian tree (Fig. 2).

The topologies resulting from matrix B (mitogenomes only) support the relationships among tribes obtained from analyses of matrix A and the placement of *Chendytes lawi* (S4). The Labrador Duck remains closely related to the Mergini, but more specific comment on this relationship is not possible with this reduced taxonomic sampling. In the analyses of matrix C (Cyt b and COI, no missing data), taxonomic placement of both extinct species is largely maintained (S5). The Labrador Duck is again confirmed as sister to Steller's eider (*P. stelleri*) with high support (bs = 96; pp = 0.99). *Chendytes lawi* is maintained as basal to the Anatini (bs = 71; pp = 0.93). However, while matrix C contained almost no missing data, there is substantial degradation of resolution in terms of the relationships among the duck tribes and significant decreases in statistical support generally across nodes relative to analyses of the combined matrix A. Assessment of missing data and addititional analyses of the submatrices are provided (S6–12).

4. Discussion

4.1. *Anatinae phylogeny*

Our approach to the overall topology of the Anatinae phylogeny involved (1) combining a well-supported backbone of complete mitogenomes from a limited number of taxa across true ducks with (2) shorter single-gene sequences representing more thorough taxonomic sampling (Fig. 2). Analysis of this whole matrix compared with analyses of each of the reduced matrices shows the importance of the mitogenomic backbone in generating strong support for the basal arrangement of tribes as well as many internal nodes of the tree. Further evidence of the utility of analyzing a patchwork of gene fragments with the aid of a strong mitogenomic backbone is shown by the inability to place the South American duck clade (*Amazonetta, Tachyeres, Speculanus*). There are no mitogenomes available for any member of this group, or an apparent close relative. Beyond resolution of the base of the Anatinae phylogeny and placement of the extinct taxa, our effort produced a comprehensive and well-supported hypothesis that bears some similarity to previous studies.

Our work is largely in agreement with Mitchell et al. (2014) although they did not include representatives of Mergini. Our basal topology contrasts with Fulton et al. (2012b), where the first split among the subfamily Anatinae is between Anatini and the remaining tribes. Within the latter, Mergini branches first leaving Aythini sister to Tadornini. Our results resemble those of Gonzalez et al. (2009) with the exception that in their phylogeny the branching order of Tadornini and Mergini are reversed: Mergini branches first, followed by Tadornini, then Aythyini and finally Anatini. This latter relationship is also recovered in the two-gene phylogeny presented in Sun et al. (2017), however in the same publication the authors recover a branching order equivalent to ours in their mitogenome only tree, supporting our contention that inclusion of these complete mitogenomes provides important resolution in the base of the tree. Our own two-gene phylogenies, where the data are most like previous mitochondrial (mtDNA) gene-based studies, did not support any hypothesis of relationships among major tribes (S4).

The implication then is that the mitogenomes we included in our combined matrix (A) provide a strongly supported backbone. This topology is also recovered from the mitogenome data matrix with virtually no missing data and a much larger number of variable sites than would be available from any two-gene alignment. Inclusion of two genes has been the dominant pattern among published anatid phylogenies. Inclusion of additional fragmented mtDNA sequence data with this strong backbone then allows a better supported phylogeny with more species aiding in the placement of our extinct ducks. Weins (2006) demonstrated that inclusion of more taxa often benefits phylogenetic results even at the cost of including large amounts of missing data, consistent with our results. Thus, sequencing of more anatid mitogenomes may improve our understanding of their evolutionary history with minimal cost, while allowing the effective inclusion of samples from a variety of source material. This approach does have limits where whole genomes are poorly distributed or where gene fragments are too small to allow effective inclusion of taxa in the analyses. Thus, researchers must always take care to evaluate the effect of varying configurations of data on analyses and results. Additionally, mitochondria provide an important but limited basis for phylogenetic analysis, which should ultimately be compared to other data sources. However, such alternative data may be less easily obtained from degraded material such as fossil bone or museum specimens.

4.2. *Phylogenetics and inferred ecology of C. lawi and C. labradorious*

In previous phylogenetic studies of Anseriformes, non-monophyletic assemblages share morphological adaptations for diving, dabbling, or grazing, indicating convergence of these feeding modalities (Faith, 1989; Gonzalez et al., 2009; McCracken et al., 1999; Olsen, 2015). Molecular phylogenetics strongly supports placement of *Chendytes lawi* in a novel position as sister to the Anatini, not with Mergini or any other diving clade within Anatidae (Fig. 2). Thus, this lineage likely represents a fourth independent evolution of diving within true ducks and *C. lawi* appears hyper-adapted to this feeding modality.

Head and beak morphology suggest *C. lawi* was an invertivore (Miller et al., 1961). Based on the large, robust morphology of the cervical vertebrae, skull, and bill, Miller further argued that *C. lawi* specialized on sessile invertebrates commenting that the species likely possessed "a remarkable ability to wrench off invertebrate animals attached to hard substrate" (Miller et al., 1961). The lack of obvious adaptations for piscivory and the presence of a robust supraorbital process, which likely protects the eyes and salt glands during benthic foraging, further support such an invertebrate diet (Livezey, 1993; Raikow, 1970). Mussels and urchins are often abundant on the California coast and are amongst the diverse invertebrate prey of other large diving ducks (Lovvorn et al. 2003; Savard and Petersen 2015). The largest modern sea ducks regularly dive to 60-m depths (Žydelis & Richman, 2015) and with its larger body size, *C. lawi* presumably could have taken advantage of prey in deeper habitats (Miller et al., 1961).

Larger body size and foot-propelled diving were achieved at the expense of wing degeneration and likely resulted in high wing loadings in *C. lawi* (Howard, 1947; Livezey, 1993). The close relationship between *C. lawi* and the Pleistocene *C. milleri* with its intermediate reduction in flight (Howard, 1955) appears comparable to the differential loss of flight in lineages of South American Steamer ducks *(Tachyeres* – Fulton et al., 2012b). This may suggest a dynamic or iterative late-Pleistocene evolution of a flightless form in the *Chendytes* lineage facilitated by their presence on islands. Flightlessness has strong implications for reproductive biology in birds, rendering them obligate residents and typically ground-nesting species. In *Chendytes*, extensive recovery of fossil birds and eggshells from the Channel Islands confirms ground nesting and further suggests that they mainly bred on offshore islands (Guthrie, 1992; Miller et al., 1961). *Tachyeres* species display a similar pattern where they are distributed in southern South America and offshore on the Falkland Islands, displaying the inferred reproductive behavior evident in the fossil record for *Chendytes*.

Steamer ducks (*Tachyeres*) are the only extant flightless diving anseriforms, and *Chendytes lawi* and *Shiriyanetta hasegawai* are the only flightless divers reported from the fossil record. The latter is described as a large sea duck of the tribe Mergini but given the emphasis of its morphological similarity to *Chendytes* (Watanabe and Matsuoka, 2015), it could represent a third example of a derived Anatinae lineage. Molecular systematics are required to support or refute this hypothesis. However, if *S. hasegawai* is indeed more closely related to *Chendytes* than to Mergini, a repeated pattern could emerge of resident, large, flightless Anatinae on mid-latitude insular coasts. Competition in species-rich habitats might have driven repeated adaptation of diving

specialists capable of exploiting deep-water resources inaccessible to their primarily dabbling sister species. Thus, our result that *Chendytes* spp. are not sea ducks (Mergini) but dabbling ducks (Anatini) with derived anatomical features specialized for diving could be the beginning of broader evolutionary interpretation if more data can be generated.

Although *Chendytes lawi* is known exclusively from fossil material and has been extinct for millennia, aspects of its biology and ecology, (e.g., breeding range) are more easily established than those of the much more recently extinct (c. 1875) Labrador Duck. Relatively specific locality data are only established for a small number of the roughly forty known museum specimens and these appear to pertain exclusively to wintering birds (see Fig. 1). Purported eggs of the species were later shown through genetic analyses to be those of other ducks (Chilton and Sorenson, 2007). Given the lack of verified information on the Labrador Duck beyond the winter range, an improved understanding of Mergini relationships may help interpret its biology.

In contrast with our result for *C. lawi*, the Labrador Duck (*Camptorhynchus labradorius*) does fall within the Mergini as previously argued. However, it is sister to Steller's Eider, not a scoter of the genus *Melanitta* as suggested by Livezey (1995). Similarities of the bill and plumage reflect this sister taxon relationship. Steller's Eider, Long-tailed Duck (*Clangula hymelis*) and Harlequin Duck (*Histrionicus histrionicus*), which are basal to the remaining eiders, have more sensitive bills to feed on aquatic insects in the breeding season and feed more extensively on softer bodied arthropod (amphipod) prey in the winter than *Somateria* or scoters. Steller's Eider also appears to have a lower dependence on bivalves and a greater dependence on gastropods than these larger invertivore Mergini (Cottam, 1939; Bustnes & Systad, 2001; Lovvorn et al., 2003; Ouellet et al., 2013). Studies further suggest that Steller's Eider feeds extensively in kelp and eelgrass beds (Bustnes et al., 2000; Metzner, 1993).

Steller's Eider use of distinct breeding, molting and wintering habitat may allow us to generate more informed hypotheses regarding the Labrador Duck range and biology. Steller's Eider breeding occurs around freshwater ponds in the arctic coastal plains of the Alaskan North Slope and in Siberia; they then migrate to shallow protected embayments to molt in the autumn (Petersen et al., 2006; Martin et al., 2015), and ice free shallow water habitats in winter. A major Steller's Eider molting ground on Novoya Zemla (Petersen et al., 2006), has extensive shallow glacial formed embayments very similar to those of the Labrador coast potentially suggesting that Labrador was a significant molting area. Coastal plain breeding may then have occurred further north in coastal plain ponded habitats in the Fox Basin or Eastern Ungava as suggested by some earlier authors (Audubon, 1843; Cottam, 1939). Labrador Ducks recovered from the sea bird markets suggest the south shore of Long Island as the most extensive source of known specimens (Dutcher, 1891; 1894). This coast has large bay/lagoon systems behind barrier islands, such as Great South Bay that once contained vast eel grass beds (Cottam & Addy, 1947; Jones & Schubel, 1978). This and similar habitats in other shallow vegetated marine bays along the coast were likely winter habitats of the Labrador duck given the Steller's eider analogue.

5. Conclusion

Our phylogenetic analyses placed *C. lawi* as sister to the dabbling group Anatini, contrary to its traditional morphology-based placement within the Mergini (sea ducks). Its large body size, exaggerated hind limbs, robust head and neck, high degree of wing degeneration and inability to fly point to an emphasis on foot-propelled diving to procure invertebrate prey. Its taxonomic placement and adaptations to dive-foraging suggest an evolutionary pattern more similar to steamer ducks (*Tachyeres*) than any other living anatid group. The sister taxon relationship between the extinct Labrador Duck and Steller's Eider may ultimately help clarify ecological evolution of eiders while permitting the reconstruction of aspects of Labrador Duck biology. Our study emphasizes the need, where possible, to use molecular phylogenetics to corroborate morphological systematic studies, particularly in groups prone to convergent evolution such as the Anseriformes. It also strongly suggests that inclusion of taxa with incomplete sequence representation is beneficial if there is a sufficient backbone of shared data across the taxa included.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ympev.2017.12.008.

References to data sources (S1)

Bulgarella et al. (2010), Chaves et al. (2015), Ding et al. (2016), Donne-Gousse et al. (2002), Hebert et al. (2004), Jiang et al. (2010), Johnson and Sorenson (1998), Kennedy and Spencer (2000), Kerr et al. (2007), Kerr et al. (2009), Lee et al. (2012), Liu et al. (2012), Liu et al. (2014), Livezey (1989), Meng et al. (2016), Mindell et al. (1997), Mindell et al. (1998), Pan et al. (2014), Park et al. (2016), Pearce et al. (2005), Ryu and Hwang (2011), Schindel et al. (2011), Slack et al. (2003), Sorenson et al. (1999), Sun et al. (2016), Tavares et al. (2011), Tu et al. (2014), Zhou et al. (2015), Zhou et al. (2016).

References

Andrews, S., 2010. FastQC: A Quality Control Tool for High Throughput Sequence Data. Retrieved from: < http://www.bioinformatics.babraham.ac.uk/projects/fastqc/ > .

Audubon, J.J., 1843. The birds of America: from Drawings Made in the United States and their Territories, vol 6. Audubon, New York, NY & Philadlphia, PA. https://doi.org/10.5962/bhl.title.61411.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30 (15), 2114–2120. http://dx.doi.org/10.1093/bioinformatics/btu170.

Bulgarella, M., Sorenson, M.D., Peters, J.L., Wilson, R.E., McCracken, K.G., 2010. Phylogenetic relationships of *Amazonetta*, *Speculanas*, *Lophonetta* and *Tachyeres*: four morphologically divergent duck genera endemic to South America. J. Avian Biol. 41 (2), 186–199. http://dx.doi.org/10.1111/j.1600-048X.2009.04819.x.

Bustnes, J.O., Systad, G.H., 2001. Comparative feeding ecology of Steller's eider and long-tailed ducks in winter. Waterbirds 24 (3), 407–412. http://dx.doi.org/10.2307/1522072.

Bustnes, J.O., Asheim, M., Bjørn, T.H., Gabrielsen, H., Systad, G.H., 2000. The diet of Steller's Eiders wintering in Varangerfjord, northern Norway. Wilson Bull. 112 (1), 8–13. http://dx.doi.org/10.1676/0043-5643(2000) 112[0008:TDOSSE]2.0;2.

Chaves, B.R., Chaves, A.V., Nascimento, A.C., Chevitarese, J., Vaconcelos, M.F., Santos, F.R., 2015. Barcoding Neotropical birds: assessing the impact of nonmonophyly in a highly diverse group. Molecul. Ecol. Resource 15 (4), 921–931. http://dx.doi.org/10.1111/1755-0998.12344.

Chilton, G., Sorenson, M.D., 2007. Genetic identification of eggs purportedly from the extinct Labrador Duck (*Camptorhynchus labradorius*). Auk 124 (3), 962–968. http://dx.doi.org/10.1642/0004-8038(2007) 124[962:GIOEPF]2.0.CO;2.

Clements, J.F., Schulenberg, T.S., Iliff, M.J., Roberson, D., Fredericks, T.A., Sullivan, B.L., Wood, C.L., 2017. The eBird/Clements Checklist of Birds of the World: v2016.

Retrieved from < http://www.birds.cornell.edu/clementschecklist/download/ > .
Cottam, C., 1939. Food habits of North Amercian ducks. United States Depart. Agri. Tech. Bull. 643, 1–129.
Cottam, C., Addy, C.E., 1947. Present eelgrass condition and problems on the Atlantic coast of North America. In: Proc. 12th North Amer. Wildlife Conference. San Antoniao, Texas, pp. 387–398.
Cracraft, J., 2013. Avian higher-level relationships and classification: nonpasseriforms. In: Dickinson, E.C., Remsen, J.V. (Eds.), The Howard and Moore Complete Checklist of the Birds of the World, 4th edn. Non-passerines, vol. 1. Aves Press Limited, Eastbourne, UK, pp. 21–47.
Ding, L., Zhang, C., Chang, Q., Yan, L., Zhang, B., 2016. The complete mitochondrial genome of Aythya fuligula (Anatidae: Aythya). Mitochondrial DNA 27 (2), 1003–1004. http://dx.doi.org/10.3109/19401736.2014.926525.
Donne-Gousse, C., Laudet, V., Hanni, C., 2002. A molecular phylogeny of Anseriformes based on mitochondrial DNA analysis. Molecul. Phylogenet. Evolut. 23 (3), 339–356. http://dx.doi.org/10.1016/S1055-7903(02)00019-2.
Dutcher, W., 1891. The Labrador Duck: a revised list of the extant specimens in North America, with some historical notes. Auk 8 (2), 201–216. http://dx.doi.org/10.2307/4068077.
Dutcher, W., 1894. The Labrador Duck: another specimen, with additional data respecting extant specimens. Auk 11 (1), 4–12. http://dx.doi.org/10.2307/4067622.
Ellingson, R.A., Swift, C.C., Findley, L.T., Jacobs, D.K., 2014. Convergent evolution of ecomorphological adaptations in geographically isolated Bay gobies (Teleostei: Gobionellidae) of the temperate North Pacific. Molecul. Phylogenet. Evolut. 70, 464–477. http://dx.doi.org/10.1016/j.ympev.2013.10.009.
Faith, D.P., 1989. Homoplasy as pattern: multivariate analysis of morphological convergence in Anseriformes. Cladistics 5 (3), 235–258. http://dx.doi.org/10.1111/j.1096-0031.1989.tb00488.x.
Fulton, T.L., Wagner, S.M., Shapiro, B., 2012a. Case study: recovery of ancient nuclear DNA from Toe Pads of the extinct passenger pigeon. In: In: Shapiro, B., Hofreiter, M. (Eds.), Ancient DNA Methods in Molecular Biology (Methods and Protocols), vol 840. Humana Press, New York, NY, pp. 29–35.
Fulton, T.L., Letts, B., Shapiro, B., 2012b. Multiple losses of flight and recent speciation in steamer ducks. Proc. Royal Soc. B 279, 2339–2346. http://dx.doi.org/10.1098/rspb.2011.2599.
Gonzalez, J., Düttman, H., Wink, M., 2009. Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. J. Zool. 279 (3), 310–318. http://dx.doi.org/10.1111/j.1469-7998.2009.00622.x.
Grayson, D.K., 2008. Holocene underkill. Proc. Nation. Acad. Sci. 105 (11), 4077–4078. http://dx.doi.org/10.1073/pnas.0801272105.
Gruhn, R., Bryan, A., 2006. An interim report on two rockshelter sites with early holocene occupation in the Northern Baja California Peninsula. Pacific Coast Archaeol. Soci. Quart. 42 (2), 1–16.
Guthrie, D.A., 1992. A late Pleistocene avifauna from San Miguel Island, California. Paper Avian Paleontol. Sci. Ser 36, 319–327.
Hebert, P.D., Stoeckle, M.Y., Zemlak, T.S., Francis, C.M., 2004. Identification of birds through DNA Barcodes. PLoS Biol. 2 (10), E312. http://dx.doi.org/10.1271/journal.pbio.0020312.
Howard, H., 1947. Wing elements assigned to *Chendytes*. Condor 49 (2), 76–77.
Howard, H., 1955. New records and a new species of *Chendytes*, an extinct genus of diving geese. Condor 57 (3), 135–143. http://dx.doi.org/10.2307/1364861.
Howard, H., 1964. Futher discoveries concerning the flightless “diving geese” of the genus *Chendytes*. Condor 66 (5), 372–376. http://dx.doi.org/10.2307/1365429.
Huelsenbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogeny. Bioinformatics 17 (8), 754–755.
Jiang, F., Miao, Y., Liang, W., Ye, H., Liu, H., Liu, B., 2010. The complete mitochondrial genomes of the whistling duck (*Dendrocygna javanica*) and black swan (*Cygnus atratus*): dating evolutionary divergence in Galloanserae. Molecul. Biol. Rep. 37 (6), 3001–3015. http://dx.doi.org/10.1007/s11033-009-9868-9.
Johnson, K.P., Sorenson, M.D., 1998. Comparing molecular evolution in two mitochondrial protein coding genes (cytochrome b and ND2) in the dabbling ducks (Tribe: Anatini). Molecul. Phylogenet. Evolut. 10 (1), 82–94.
Jones, C.R., Schubel, J.R., 1978. Distribution of surficial sediments and eelgrass in New York's south shore bays: an assessment from the literature. Marine Science Resources Center Spec. Rep., No. 13, Stony Brook, New York.
Jones, T.L., Porcasi, J.F., Erlandson, J.M., Dallas Jr., H., Wake, T.A., Schwaderer, R., 2008a. The protracted Holocene extinction of California's flightless sea duck (*Chendytes lawi*) and its implications for the Pleistocene overkill hypothesis. Proc. Nation. Acad. Sci. 105 (11), 4105–4108. http://dx.doi.org/10.1073/pnas.0711140105.
Jones, T.L., Porcasi, J.F., Gaeta, J., Codding, B.F., 2008b. Diablo Canyon Fauna: a course-grained record of trans-Holocene foraging from the central California mainland coast. Am. Antiquity 73 (2), 289–316.
Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P.L., Orlando, L., 2013. mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. Bioinformatics 29 (13), 1682–1684. http://dx.doi.org/10.1093/bioinformatics/btt193.
Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Mentjies, P., Drummond, A., 2012. Geneious basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28 (12), 1647–1649. http://dx.doi.org/10.1093/bioinformatics/bts199.
Kennedy, M., Spencer, H.G., 2000. Phylogeny, biogeography, and taxonomy of Australasian teals. Auk 117 (1), 154–163.
Kerr, K.C., Stoeckle, M.Y., Dove, C.J., Wigt, L.A., Francis, C.M., Hebert, P.D., 2007. Comprehensive DNA barcode coverage of North American birds. Molecul. Ecol. Notes 7 (4), 535–543. http://dx.doi.org/10.1111/j.1471-8286.2007.01670.x.
Kerr, K.C., Lijtmaer, D.A., Barreira, A.S., Hebert, P.D., Tubaro, P.L., 2009. Probing evolutionary patterns in neotropical birds through DNA barcodes. PLoS ONE 4 (2), E4379. http://dx.doi.org/10.1371/journal.pone.0004379. doi:10.1371/journal.pone.0004379.
Kosakovsky Pond, S.L., Frost, S.D.W., Muse, S.V., 2005. HyPhy: hypothesis testing using phylogenies. Bioinformatics 21 (5), 676–679. http://dx.doi.org/10.1093/bioinformatics/bti079.
Langmead, B., Trapnell, C., Pop, M., Salzberg, S.L., 2009. Ultrafast and memory-efficient alignment of short DNA sequences to the human genome. Genome Biol. 10 (3), R25. http://dx.doi.org/10.1186/gb-2009-10-3-r25.
Lee, J.H., Ryu, S.H., Kang, S.G., Hwang, U.W., 2012. Complete mitochondrial genome of the Bewick’s swan *Cygnus columbianus bewickii*. Mitochondrial DNA 23 (2), 129–130. http://dx.doi.org/10.3109/19401736.2011.653808.
Liu, G., Zhou, L.Z., Gu, C.M., 2012. Complete sequence and gene organization of the mitochondrial genome of scaly-sided merganser (*Mergus squamatus*) and phylogeny of some Anatidae species. Molecul. Biol. Rep. 39 (3), 2139–2145. http://dx.doi.org/10.1007/s11033-011-0961-5.
Liu, G., Zhou, L., Li, B., Zhang, L., 2014. The complete mitochondrial genome of *Aix galericulata* and *Tadorna ferruginea*: bearings on their phylogenetic position in the Anseriformes. PLoS ONE 9 (22), E109701. http://dx.doi.org/10.1371/journal.pone.0109701.
Livezey, B.C., 1989. Phylogenetic relationships and incipient flightlessness of the extinct Auckland Islands merganser. Wilson Bull. 101 (3), 410–435.
Livezy, B.C., 1993. Morphology of flightlessness in *Chendytes*, fossil seaducks (Anatidae: Mergini) of coastal California. J. Vertebr. Paleontol. 13 (2), 185–199.
Livezey, B.C., 1995. Phylogeney and evolutionary ecology of modern seaducks (Anatidae: Mergini). Condor 97 (1), 233–255.
Lovvorn, J.R., Richman, S.E., Grebmeier, J.M., Cooper, L.W., 2003. Diet and body condition of spectacled eiders wintering in pack ice of the Bering Sea. Polar Biol. 26 (4), 259–267.
Martin, P.D., Douglas, D.C., Obritschkewitsch, T., Torrence, S., 2015. Distribution and movements of Alaska-breeding Steller's Eiders in the nonbreeding period. Condor 117 (3), 341–353.
McCracken, K.G., Harshman, J., McClellan, D.A., Afton, A.D., 1999. Data set incongruence and correlated character evolution: an example of functional convergence in the hind-limbs of stifftail diving ducks. Systema. Biol. 48 (4), 683–714.
Meng, S., Wu, Z., Pan, T., Yan, Ls, Bei, Y., Li, G., Zhang, B., 2016. Mitochondrial genome of the *Aix galericula* (Anatidae: Aix). Mitochondrial DNA 27 (1), 318–319. http://dx.doi.org/10.3109/19401736.2014.892096.
Metzner, K.A., 1993. Ecological strategies of wintering Steller’s Eider on Izembek Lagoon and Cold Bay. Master’s thesis. Univ of Missouri, AlaskaColumbia.
Miller, L., 1925. *Chendytes*, a diving goose from the California Pleistocene. Condor 27, 145–147.
Miller, L., 1930. Further bird remains from the upper San Pedro Pleistocene. Condor 32 (2), 116–118. http://dx.doi.org/10.2307/1363530.
Miller, L., Mitchell, E.D., Lipps, J.H., 1961. New light on the flightless goose *Chendytes lawi*. Los Angeles County Museum Contribut. Sci. 43, 3–10.
Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1–8.
Mindell, D.P., Sorenson, M.D., Huddleston, C.J., Miranda Jr., H.C., Knight, A., Sawchuk, S.J., Yuri, T., 1997. Phylogenetic relationships among and within select avian orders based on mitochondrial DNA. In: Mindell, D.F. (Ed.), Avian Molecular Evolution and Systematics. Academic Press, Cambridge, MA, pp. 211–245.
Mindell, D.P., Sorenson, M.D., Dimcheff, D.E., Hasegawa, M., Ast, J.C., Yuri, T., 1998. Interordinal relationships of birds and other reptiles based on whole mitochondrial genomes. Systema. Biol. 48 (1), 138–152.
Mitchell, K.J., Wood, J.R., Scofield, R.P., Llamas, B., Cooper, A., 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. Molecul. Phylogenet. Evolut. 70, 420–428. http://dx.doi.org/10.1016/j.ympev.2013.08.017.
Olsen, A.M., 2015. Exceptional avian herbivores: multiple transitions toward herbivory in the bird order Anseriformes and its correlation with body mass. Ecol. Evolut. 5 (21), 5016–5032. http://dx.doi.org/10.1002/ece3.1787.
Ouellet, J.F., Vanpé, C., Guillemette, M., 2013. The body size-dependent diet composition of North American sea ducks in winter. PloS one 8 (6), e65667. http://dx.doi.org/10.1371/journal.pone.0065667.
Pan, T., Ren, L., Wang, H., Chen, J., zhang, B., 2014. Mitochondrial genome of the *Anas falcata* (Anatidae: Anas). Mitochondrial DNA 25 (2), 111–112. http://dx.doi.org/10.3109/19401736.2013.786709.
Park, C.E., Park, G.S., Kwak, Y., Hong, S.J., Rahim Khan, A., Kwon Jung, B., Park, Y.J., Kim, J., Cheon Park, H., Shin, J.H., 2016. Complete mitochondrial genome of *Cygnus cygnus* (Aves, Anseriformes, Anatidae). Mitochondrial DNA 27 (4), 2907–2908. http://dx.doi.org/10.3109/19401736.2015.1060433.
Pearce, J.M., Talbot, S.L., Petersen, M.R., Rearick, J.R., 2005. Limited genetic differentiation among breeding, molting, and wintering groups of the threatened Steller’s eider: the role of historic and contemporary factors. Conserv. Genet. 6 (5), 743–757. http://dx.doi.org/10.1007/s10592-005-9034-4.
Petersen, M.R., Bustnes, J.O., Systad, G.H., 2006. Breeding and moulting locations and migration patterns of the Atlantic population of Steller's eiders *Polysticta stelleri* as determined from satellite telemetry. J. Avian Biol. 37 (1), 58–68. http://dx.doi.org/10.1111/j.2005.0908-8857.03472.x.
Pisani, D., 2004. Identifying and removing fast-evolving sites using compatibility analysis: an example from the Arthropoda. Systema. Biol. 53 (6), 978–989. http://dx.doi.

org/10.1080/1063515049088877.
Raikow, R.J., 1970. The function and evolution of the supraorbital process in ducks. Auk 87 (3), 568–572. http://dx.doi.org/10.2307/4083799.
Rohland, N., Hofreiter, M., 2007. Comparison and optimization of ancient DNA extraction. BioTechniques 42 (3), 343–352.
Rohland, N., Reich, D., 2012. Cost-effective, high-throughput DNA sequencing libraries for multiplexed target capture. Genome Res. 22 (5), 939–946. http://dx.doi.org/10.1101/gr.128124.111.
Ryu, S.H., Hwang, U.W., 2011. Complete mitochondrial genome of the Baikal teal *Anas formosa* (Aves, Anseriformes, Anatidae). Mitochondrial DNA 22 (4), 74–76. http://dx.doi.org/10.3109/19401736.2011.624600.
Savard, J.P.L., Petersen, M.R., 2015. Remigial molt of sea ducks. In: Savard, J.L., Derksen, D.V., Esler, D., Eadie, J.M. (Eds.), Ecology and Conservation of North American Sea Ducks. Studies in Avian Biology. CRC Press, Boca Raton, FL, pp. 305–336.
Schindel, D.E., Stöckle, M.Y., Milensky, C., Trizna, M., Schmidt, B., Gebhard, C., Graves, G., 2011. Project description: DNA barcodes of bird species in the national museum of natural history, Smithsonian institution, USA. Zookeys 152, 87–92. http://dx.doi.org/10.3897/zookeys.152.2473.
Slack, K.E., Janke, A., Penny, D., Arnason, U., 2003. Two new avian mitochondrial genomes (penguin and goose) and a summary of bird and reptile mitogenomic features. Gene 302 (1–2), 43–52.
Sorenson, M.D., Cooper, A., Paxinos, E.E., Quinn, T.W., James, H.F., Olson, S.L., Fleischer, R.C., 1999. Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. Proc. R. Soc. Lond., B, Biol. Sci. 266 (1434), 2187–2193. http://dx.doi.org/10.1098/rspb.1999.0907.
Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30 (9), 1312–1313. http://dx.doi.org/10.1093/bioinformatics/btu033.
Sun, Z., Wang, B., Sun, X., Yan, L., Pan, T., Zhang, B., 2016. Phylogenetic studies of *Anas clypeata* (Anatidae: Anas) based on complete mitochondrial DNA sequences. Mitochondrial DNA A DNA Map Seq. Anal. 27 (6), 4320–4321. http://dx.doi.org/10.3109/19401736.2015.1089482.
Sun, Z., Pan, T., Hu, C., Sun, L., Ding, H., Wang, H., Zhang, C., Jin, H., Chang, Q., Kan, X., Zhang, B., 2017. Rapid and recent diversification patterns in Anseriformes birds: inferred from molecular phylogeny and diversification analyses. PloS ONE 12 (9), e0184529. http://dx.doi.org/10.1371/journal.pone.0184529.
Tavares, E.S., Gonçalves, P., Miyaki, C.Y., Baker, A.J., 2011. DNA barcode detects high genetic structure within neotropical bird species. PLoS One 6 (12), e28543. http://dx.doi.org/10.1371/journal.pone.0028543.
Tu, J., Si, F., Wu, Q., Cong, B., Xing, X., Yang, F.H., 2014. The complete mitochondrial genome of the Muscovy duck, *Cairina moschata* (Anseriformes, Anatidae, Cairina). Mitochondrial DNA 25 (2), 102–103. http://dx.doi.org/10.3109/19401736.2013.784756.
Watanabe, J., Matsuoka, H., 2015. Flightless diving ducks (Aves, Anatidae) from the Pleistocene of Shiriya, northeast Japan. J. Vertebr. Paleontol. 35 (6), e994745. http://dx.doi.org/10.1080/02724634.2014.994745.
Weins, J.J., 2006. Missing data and the design of phylogenetic analyses. J. Biomed. Inform. 39 (1), 34–42. http://dx.doi.org/10.1016/j.jbi.2005.04.001.
Zhou, W., Zhang, C., Pan, T., Yan, L., Hu, C., Sue, C., Can, Q., Zhang, B., 2015. The complete mitochondrial genome of *Anas poecilorhyncha* (Anatidae: Anas). Mitochondrial DNA 26 (2), 265–266. http://dx.doi.org/10.3109/19401736.2013.823191.
Zhou, W., Zhang, C., Chang, Q., Yan, L., Pan, T., Zhang, B., 2016. The complete mitochondrial genome of *Aythya ferina* (Anatidae: Aythya). Mitochondrial DNA A DNA Mapp Seq. Anal. 27 (2), 968–969. http://dx.doi.org/10.3109/19401736.2014.926509.
Žydelis, R., Richman, S.E., 2015. Foraging behavior, ecology, and energetics of sea ducks. In: Savard, J.L., Derksen, D.V., Esler, D., Eadie, J.M. (Eds.), Ecology and Conservation of North American Sea Ducks. Studies in Avian Biology. CRC Press, Boca Raton, FL, pp. 243–268.