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GENETIC IDENTIFICATION OF EGGS PURPORTEDLY FROM THE EXTINCT LABRADOR DUCK (*CAMPTORHYNCHUS LABRADORIUS*)

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Abstract.—Material extracted from inside the shells of nine purported Labrador Duck (*Camptorhynchus labradorius*) eggs was subjected to DNA extraction and polymerase chain reaction (PCR) amplification. For each egg, partial sequences of one to three mitochondrial genes (12S, ND2, and control region) were compared with sequences derived from a Labrador Duck specimen and representatives of several other waterfowl species. Sequences from six eggs were consistent with those of the Red-breasted Merganser (*Mergus serrator*), whereas the sequences from one egg was most consistent with that of the Common Eider (*Somateria mollissima*). The remaining two eggs yielded sequences consistent with that of the Mallard (*Anas platyrhynchos*) or a domestic duck. Regrettably, none of the eggs provided additional information about the breeding grounds of the extinct Labrador Duck. To our knowledge, this is the first report of DNA extraction and amplification from old eggshells of birds.
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Key words: *Camptorhynchus labradorius*, DNA analysis, eggs, Labrador Duck.

Identification génétique d'œufs présumés provenir de l'espèce disparue *Camptorhynchus labradorius*

Résumé.—Le matériel extrait de la paroi intérieure des coquilles de neuf oeufs présumés provenir de *Camptorhynchus labradorius* a été soumis à l'extraction d'ADN et à l'amplification en chaîne par polymérase (PCR). Pour chacun des oeufs, des séquences partielles d'un à trois gènes mitochondriaux (12S, ND2 et région de contrôle) ont été comparées avec des séquences dérivées d'un spécimen de *Camptorhynchus labradorius* et des représentants de plusieurs autres espèces de sauvagine. Les séquences de six oeufs correspondaient à celles de *Mergus serrator*, alors que les séquences de l'un des oeufs correspondaient davantage à celles de *Somateria mollissima*. Les deux oeufs restants ont produit des séquences correspondant à celles d'*Anas platyrhynchos* ou d'un canard domestique. Malheureusement, aucun des oeufs n'a fourni d'information additionnelle sur les aires de reproduction de *Camptorhynchus labradorius*, une espèce maintenant disparue. D'après nos connaissances, ceci est la première mention de l'extraction et l'amplification d'ADN à partir de vieilles coquilles d'oiseaux.

The Labrador Duck (*Camptorhynchus labradorius*) is among the most enigmatic of all North American birds. Having become extinct late in the 19th century, the species is now represented by just 55 specimens in museums in Europe, North America, and the Middle East (Hahn 1963, G. Chilton unpubl. data). Most of these specimens were collected during migration or on the wintering grounds, particularly

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around Long Island, New York. The breeding biology of the Labrador Duck is essentially unknown (Chilton 1997). They presumably bred somewhere in Labrador and northern Quebec, though no reliable records exist. The frequently cited description of Labrador Duck nests in Blanc Sablon, Quebec, by Audubon is not consistent with the journal he kept of his 1833 journey (Chilton 2004).

We are aware of shells of nine putative Labrador Duck eggs. Because we know where some of these eggs were collected, they might help clarify the breeding distribution of the species. None of these eggs, however, is supported by credentials that make their identity a certainty. Recent advances in molecular methods have made it possible to subject small quantities of biological material to genetic analysis, allowing us to determine which of these eggs, if any, were produced by Labrador Ducks.

Methods

The shells of six eggs in the Staatliche Naturhistorische Saamlungen, Museum für Tierkunde, Dresden, are catalogued as Labrador Duck eggs. These have catalogue numbers 3597-1 through 3597-6. Each egg is light green to light brown, smooth and slightly glossy. The smallest egg is 59 × 42 mm, and the largest two are 60 × 44 mm and 62 × 42 mm, respectively (Eck 1970). Otherwise, these eggs are very similar in dimension and appearance, and it is likely that they were collected from a single clutch. These eggs are from the collection of Thienemann and were purchased by the Dresden museum in July 1901. No other details of their provenance are known.

Two specimens in The Natural History Museum, Tring, are catalogued as possible Labrador Duck eggs. Claims of a third egg, catalogue number E.1962.1.560, by Knox and Walters (1994) were the result of a clerical error. The Tring egg, catalogue number 1901.11.15.226, is from the collection of Canon H. B. Tristram and measures 61.8 × 44.1 mm (M. Walters pers. comm.). The shell is olive-green, smooth and glossy, with a slightly soapy surface. It is inscribed in ink with the words "Fuligula Labradora Disco 1855" and four faint letters that may represent initials. In a letter dated 4 April 1901 or 1907, Tristram wrote to Oates concerning this egg, explaining that it was collected by his cousin Henry Piers, Assistant Surgeon on the *HMS Investigator*. According to Tristram's letter, Piers collected the egg on the ship's first spring voyage. This would indicate that the egg was collected in the western Canadian Arctic in the spring of 1851. However, the collection locality of this egg is given as "Disco," which almost certainly refers to Disco (also spelled "Disko") Island (69°15′N, 54°33′W) off the west coast of Greenland in Baffin Bay. Hence, the collection locality is not absolutely clear.

The Tring egg, catalogue number 1962.1.559, is from the collection of Count Roedern and was purchased by Walter Rothschild in 1889; it measures 61.5 × 43.8 mm (M. Walters pers. comm.). The shell is very pale grayish-cream, smooth and glossy, with a slightly soapy surface. It is inscribed with "Canard Labrador" in ink, and with "Labrador 8 Juin" in pencil. No other details of its provenance are known.

A private collection in Scotland contains a single putative Labrador Duck egg. The shell is grayish-white and measures 61.9 × 44.4 mm. The shell is inscribed in ink with the words "Labrador Duck" and "Calton," and the initials "H.S." The egg came to its current owner from a large worldwide collection with an emphasis on North American eggs. Its owner believed that "Calton" might refer to the place in Canada where the egg was collected. Two localities in Canada have the name "Calton." The first is a point of land on the Beaufort Sea (69°30′N, 139°09′W). The other is a small community in southern Ontario (42°43′N, 80°52′W). The second locality was not named until after the Labrador Duck became extinct.

From each of these nine egg shells, material was extracted from the interior through their blowholes using fine probes. This material included shell membranes and debris that was not removed when the eggs were first "blown." Two of the Dresden eggs (3597-5 and 3597-6) provided less material than the other eggs, making genetic analyses more difficult.

Samples from the above eggs were collected by G.C. and provided to M.D.S. without information about the source of each sample. A small sample of dried membrane from a Mallard (*Anas platyrhynchos*) egg was also included as an additional positive control. The DNA extraction and polymerase chain reaction (PCR) setups were conducted in a separate laboratory reserved for work on samples from museum specimens. The

laboratory is stocked with dedicated equipment and supplies, and access is strictly controlled. Genomic DNA was extracted using a DNeasy Tissue Kit (Qiagen, Valencia, California) following the manufacturer's protocol. Great care was taken to avoid cross-contamination of samples, including the use of a new aerosol filter pipette tip for each pipetting operation. A negative extraction control and negative PCR controls were completed to ensure that reagents were not contaminated with avian DNA. The PCR products were removed for processing in another room.

In retrospect, a recently collected egg was not a good choice for a positive control because it may have increased the risk of cross-contamination, though the use of a very small sample of dried membrane perhaps mitigated this risk. Because initial sequences for two of the old egg samples were identical to those of the positive control, we amplified and sequenced portions of the mitochondrial DNA (mtDNA) control region to test for differences between these samples and to rule out cross-contamination (see below).

The PCR reactions included 25 μL AmpliTaq Gold PCR Master Mix (Applied Biosystems, Foster City, California), 2.5 μL of each primer (0.5 μM final concentration), 10 μL water, and 10 μL DNA extract (or water as a negative control). We amplified short segments of mtDNA using primers for the small subunit rRNA gene (12S) and NADH dehydrogenase subunit 2 (ND2). Primers L1936 (5′-CAGCCTAYATACCGCCGTC-3′) and H1993 (5′-DDGCTATACCTYGACCTGTC-3′) or L1936 and H2084 (5′-NTTTACTDCTAAATCCDCCTT-3′) were used to amplify regions of ~56 and ~148 base pairs (bp), respectively, from the 12S gene. Primers L5216 (5′-GGCCCATACCCCGRAAATG-3′) and H5292 (5′-CAGTGGTTGCTRGARAT TGTGATYGT-3′) were used to amplify 75 bp spanning the end of tRNA-Met and the beginning of ND2. All these primers, except H5292, were designed to be broadly applicable to birds (Sorenson et al. 1999a, Sorenson and Payne 2005). Primer H5292 was designed specifically for this study on the basis of ND2 sequences of other waterfowl. Subsequent amplification and sequencing of the control region used waterfowl-specific primer pairs L78 (5′-GTTA-TTTGGTTATGCATATCGTG-3′) with H768 (5′-TATACGCMAACCGTCTCATYGAG-3′); L78 with C1R2 (5′CGATTAGTAAATCCATCTGGTAC - 3′); CDF1 (5′-GTACACCTCACGTGAAATCAG-3′) with H768; and MallAB2F (5′-CCAA-CCACAACCCCACAATA-3′) with MallAB2R (5′-TATGTGGACGGGGCAGGT-3′), the latter pair designed for Mallards and close relatives (*Anas* spp.).

Products were gel-purified in 1% agarose and prepared for sequencing using a QIAquick Gel Extraction Kit (Qiagen). Sequencing reactions used the BigDye Terminator chemistry, version 3.1 (Appied Biosystems), and products were separated on an ABI3100 capillary sequencer (Applied Biosystems).

We compared the sequences derived from eggs with those obtained from a feather taken from the stuffed Labrador Duck drake at the Museum of Zoology, University of Michigan, catalogue number 152253. Extraction of DNA from the feather was completed before work on any of the eggs and followed protocols previously described for older museum specimens (Sefc et al. 2003, Sorenson and Payne 2005). Sequences from eggs were also compared with 12S and ND2 sequences from most other waterfowl species (Johnson and Sorenson 1999, Sorenson et al. 1999b, McCracken and Sorenson 2005, M. D. Sorenson et al. unpubl. data), including all species of seaduck (tribe Mergini). New sequence data collected in this study have been deposited in GenBank (accession numbers DQ831199–DQ831216).

RESULTS

We obtained PCR products and sequences for all 10 eggs (9 putative Labrador Duck eggs and 1 control) using primers for the beginning of the ND2 gene. We also obtained PCR products for the longer 12S gene fragment for eight eggs. For the remaining two eggs, we amplified and sequenced the shorter fragment from 12S. Most of these products yielded a single unambiguous sequence matching known sequences of waterfowl species, whereas a few showed evidence either of coamplification of nonspecific products or of contamination with human or perhaps other avian DNA. Sequences from the latter samples included smaller secondary peaks, representing the nonspecific product or contaminating DNA. In two cases (the two Dresden eggs for which very little material was available), the principal signal for the longer 12S fragment matched the published sequence

for human mtDNA. Despite these issues, interpretable sequences were obtained for both ND2 and 12S for seven of the nine old eggs. In all cases, the two sequences were consistent in identifying the species of each egg.

Of the six Dresden eggs, three yielded ND2 sequences identical to that of the Red-breasted Merganser (*Mergus serrator*). Two of these three eggs yielded clean results for the longer 12S fragment, and these sequences also were identical to that of the Red-breasted Merganser. For both genes, the Red-breasted Merganser sequence differs from all other waterfowl species for which data are available. A sequence for the shorter 12S product was obtained for the third egg, and this too was consistent with Red-breasted Merganser, though a second species (Bufflehead [*Bucephala albeola*]) has an identical sequence over this short fragment. The three remaining Dresden eggs yielded ND2 sequences (and in one case, the shorter 12S sequence) with a low level of coamplified nonspecific product or contamination, but each sequence was consistent with that of the Red-breasted Merganser. Where double-peaks occurred, one of the bases was always the same as that in the Red-breasted Merganser, and these sequences also included unambiguous positions that were inconsistent with Labrador Duck, which suggests that this entire set of six eggs is from a Red-breasted Merganser.

For the first Tring egg, catalogue number 1901.11.15.266, a clean ND2 sequence was identical to those of the Common Eider (*Somateria mollissima*) and King Eider (*S. spectabilis*). The two eider species differ at a single position in the longer 12S fragment, and although this sample yielded a 12S sequence with some underlying contamination (or nonspecific product), the sequence was consistent with that of *S. mollissima*, but not with *S. spectabilis*, in having only a G peak and no evidence of A at position 100 of this sequence (Fig. 1). In addition, the sequence clearly differed from that of Labrador Duck in at least eight positions.

For the second Tring egg, catalogue number 1962.1.559, both the ND2 sequence and the longer 12S fragment matched sequences for those of Mallard and closely related species, such as the American Black Duck (*A. rubripes*) and Spot-billed Duck (*A. poecilorhyncha*). These sequences were also identical to those of the various breeds of domestic duck that have been derived from Mallards. Likewise for the Scottish egg, both the ND2 sequence and the larger 12S fragment were identical to those of Mallard and related species.

Because our positive control was from a recently collected domestic duck egg, we must consider the possibility that our results for the second Tring egg and the Scottish egg were the result of cross-contamination. To rule this out, we amplified and sequenced portions of the mtDNA control region. Three clear differences between the domestic duck egg and the two old eggs were found in the region amplified with primers L78 and H768. Sequences for the two old eggs also included possible artifacts of DNA damage (see Pääbo and Wilson 1988, Pääbo et al. 1990), as might be expected given the relatively long fragment that was amplified (655 bp). We therefore sequenced this same region in two smaller pieces and obtained clean sequences for the older samples while also replicating the three differences between the old eggs and the recent egg sample: two differences in the fragment amplified using primers L78 and C1R2 (278 bp) and one difference in the region between CDF1 and H768 (334 bp). Thus, the Mallard sequences obtained from the old eggs do not reflect cross-contamination from the recent sample. These additional control-region sequences also allow us to exclude American Black Duck and other North American monomorphic species as the likely source of the two old eggs; both old eggs had "Type A" haplotypes that are characteristic of Eurasian Mallards and domestic ducks (see Avise et al. 1990, Johnson and Sorenson 1999). A control-region sequence also was obtained for one of the Dresden eggs and confirmed our identification of Red-breasted Merganser.

The ND2 and 12S sequences we obtained from the Labrador Duck museum skin were similar to but uniquely different from those of all other sea ducks (M. D. Sorenson et al. unpubl. data). None of the sequences we obtained from eggs matched those of the Labrador Duck specimen (Fig. 1).

Discussion

None of the nine putative Labrador Duck eggs we subjected to DNA analysis was produced by that species. This is regrettable, given that this material therefore provides no additional information concerning the breeding distribution of this enigmatic bird.

tMet/ND2

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Labrador Duck          ATGGTTCAACCCCCTCCCCTACTAATGAACCCCCATGCCACCCCAATCCTAGTCCTCAGTCTCGCATTGGGCACG
R.B. Merganser            .................................A.................C...ATGC.A.....A
*Dresden.3597-1           .................................A.................C...ATGC.A.....A
*Dresden.3597-2           .................................A.................C...ATGC.A.....A
*Dresden.3597-3           .................................A.................C...ATGC.A.....A
Bufflehead                .................................A.....................ATG........
Common Eider              .................................A............C...........T.........A
King Eider                .................................A............C...........T.........A
*Tring.1901.11.15.266     .................................A............C...........T.........A
Spectacled Eider          ............................T.....A............C...........T.........A
Mallard                   ..............T..................A......G.....................A.....A
Spot-billed Duck          ..............T..................A......G.....................A.....A
American Black Duck       ..............T..................A......G.....................A.....A
*Tring.1962.1.559         ..............T..................A......G.....................A.....A
*Scotland                 ..............T..................A......G.....................A.....A
*domestic duck            ..............T..................A......G.....................A.....A
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12S

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Labrador Duck          TCGAATGAGAGCACAACAGTGGACGCAACAGCACCCCGCTAGCAAGACAGGTCAAGGTATAGCTCATGGGACGGA
R.B. Merganser            ........................A.............AT.....................CT.........
*Dresden.3597-1           ........................A.............AT..
*Dresden.3597-2           ........................A.............AT.....................CT.........
*Dresden.3597-3           ........................A.............AT.....................CT.........
Bufflehead                ........................A.............AT.....................C......G....
Common Eider              ............C.........G..........T.......A.....................C......G....
King Eider                ............C.........G..........T.......A.....................C......G....
Spectacled Eider          ............C.........G..........T.......A.....................C......G....
Mallard                   ............G.........G..................AT.....................CT.........
Spot-billed Duck          ............G.........G..................AT.....................CT.........
Pacific Black Duck        ............G.........G..................AT.....................CT.........
*Tring.1962.1.559         ............G.........G..................AT.....................CT.........
*Scotland                 ............G.........G..................AT.....................CT.........
*domestic duck            ............G.........G..................AT.....................CT.........

*Labrador Duck         AGAAATGGGCTACATTCCCTATGCATAGGGTA-ACACGGAAAGAAGCATGAAACTGCTTCTGG
R.B. Merganser            ......................C.......C.-.............................AG
*Dresden.3597-1
*Dresden.3597-2           ......................C.......C.-.............................AG
*Dresden.3597-3           ......................C.......C.-.............................AG
Bufflehead                ......................T.......C.TG..........G.............C....G
Common Eider              ......................C..G.....C.-.............................AG
King Eider                ......................C........C.-.............................AG
Spectacled Eider          ......................C........C.-.............................AG
Mallard                   ..............................C.-.............T...............AG
Spot-billed Duck          ..............................C.-.............T...............AG
Pacific Black Duck        ..............................C.-.............T...............AG
*Tring.1962.1.559         ..............................C.-.............T...............AG
*Scotland                 ..............................C.-.............T...............AG
*domestic duck            ..............................C.-.............T...............AG
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FIG. 1. Alignment of ND2 and 12S sequences for Labrador Duck, the eggs examined in the present study, and other waterfowl species. Sequences from eggs are indicated by an asterisk. Sequence positions identical to Labrador Duck are indicated by a dot. The 12S sequence for Tring 1901.11.15.266 was consistent with that for the Common Eider in having a G at position 100 (indicated in bold) but is not shown, because a contaminating sequence (perhaps a Common Eider nuclear copy or numt; see Sorenson and Quinn 1998) precluded unambiguous determination of the complete sequence (see text).

The six eggs in Dresden were produced by one or more Red-breasted Mergansers. The dimensions of these eggs are within the published range of sizes for Red-breasted Merganser eggs (mean ± SD, 63.4 ± 2.5 mm × 44.6 ± 1.0 mm) and are consistent in color (Titman 1999). No collection details were available for these specimens, and so we cannot speculate as to why they were mistakenly identified as Labrador Duck eggs. The two species are not similar in appearance, but the current breeding distribution of the Red-breasted Merganser encompasses the entire supposed breeding distribution of the Labrador Duck (Chilton 1997, Titman 1999).

Tring egg 1901.11.15.266 was apparently produced by a Common Eider. The egg is smaller than the published range of sizes for Common Eider eggs (78.4 ± 3.16 mm × 52.8 ± 1.10 mm to 75.5 ± 3.29 mm × 49.2 ± 1.05 mm), but eggs in this species vary considerably in size (Goudie et al. 2000). This Tring egg is consistent with those of Common Eiders in

both color and texture (Goudie et al. 2000). The circumpolar breeding distribution of the Common Eider (Goudie et al. 2000) includes both of the possible collection sites of this egg (see above). In the letter to Oates (see above), Tristram described how he showed a drawing of a Labrador Duck to the egg's collector Henry Piers, who mistakenly identified it as the drake of the layer of the egg. Given the circumstances of the egg's collection and the general similarities of male Common Eiders and Labrador Ducks, the error is understandable.

Tring egg 1962.1.559 was most likely produced by a Mallard or a domestic duck. The egg is within the published range of sizes for Mallard eggs (52.5–64 mm × 38.5–45 mm; Drilling et al. 2002). Its color is consistent with some Mallard eggs (M. Walters pers. comm.). Like the other Tring egg, the egg in the private collection in Scotland was produced by a Mallard or a domestic duck. Its size and color are consistent with Mallard eggs (Drilling et al. 2002).

There is a reasonable explanation for why Tring egg 1962.1.559 and the Scottish egg, both products of Mallards or their relatives, were identified as Labrador Duck eggs. In the 19th century, the name "Labrador Duck" was often used to describe a breed of domestic duck now more commonly known as the "Black East Indies" (e.g., Darwin 1890). Most breeds of domestic duck, including the Black East Indies, were derived from Mallards (Drilling et al. 2002). The techniques used here are unable to resolve a difference between the wild Mallard ancestor and derived domestic breeds.

Museum specimens are a source of material for studies involving analysis of protein allozymes and DNA (Cooper 1994, Christidis and Norman 2003, Payne and Sorenson 2003). To the best of our knowledge, this is the first time that DNA analysis has been applied to material taken from old avian eggshells to identify the species of bird that produced them. The technique may have considerable value in confirming the identity of eggs in old collections. In retrospect, however, our study would have been stronger had each sample been divided and processed in two independent laboratories. Depending on the age of specimens involved and the question(s) of interest, this approach should be considered for future studies. Likewise, a better choice for a positive control for our study would have been material from positively identified eggs of similar vintage.

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