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 Anasinae 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* (stemmer ducks) and *Athyria* (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
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). 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 extant 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-adsorption 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 μl proteinase K and 20 μl 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 (Thermo-Fisher) 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 (Dendrocycnis 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 (llumina 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 stellerti, in order to confirm relationships to extinct species recovered from analyses of matrix A. Note that the control region was

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1The 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 Porsazzi 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.
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 (Rosakovsky 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 Chenytes 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

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Table 1
Summary of mitogenome sequencing amount and coverage.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sequence length</th>
<th>Total reads in contig</th>
<th>Total bases</th>
<th>Avg. bp coverage</th>
<th>Min. bp coverage</th>
<th>Max bp coverage</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. labradorius (45S02)</td>
<td>16,647</td>
<td>2867</td>
<td>217,221</td>
<td>12.1</td>
<td>0</td>
<td>40</td>
</tr>
<tr>
<td>C. labradorius (45S03)</td>
<td>16,624</td>
<td>1,074,706</td>
<td>75,245,945</td>
<td>4631.4</td>
<td>26</td>
<td>11,988</td>
</tr>
<tr>
<td>M. f. deglandi</td>
<td>16,608</td>
<td>841,326</td>
<td>45,814,655</td>
<td>2819.8</td>
<td>12</td>
<td>8225</td>
</tr>
<tr>
<td>M. nigra</td>
<td>16,625</td>
<td>219,134</td>
<td>15,355,905</td>
<td>942.6</td>
<td>6</td>
<td>40</td>
</tr>
<tr>
<td>M. m. americana</td>
<td>16,613</td>
<td>439,024</td>
<td>30,748,205</td>
<td>1874.6</td>
<td>35</td>
<td>5080</td>
</tr>
<tr>
<td>M. serrator</td>
<td>16,632</td>
<td>575,166</td>
<td>841,326</td>
<td>15,355,905</td>
<td>942.6</td>
<td>40</td>
</tr>
</tbody>
</table>

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Fig. 1. Distribution maps for Chenytes sp. (A) and Campytorhynchus labradorius – Labrador Duck (B). Red circles demarcate localities of fossil recovery for Chenytes lawi and Chenytes 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.
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. labradorius

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 Chambytes lawii 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 (Lieveze, 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 (Zydalis & 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; Lieveze, 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 Chambytes 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 Chambytes, 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 Chambytes.

Steamer ducks (Tachyeres) are the only extant flightless diving anseriforms, and Chambytes lawi and Shirinianetta 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 Chambytes (Watanabe and Matsuoka, 2015), it could represent a third example of a derived Anatini lineage. Molecular systematics are required to support or refute this hypothesis. However, if S. hasegawai is indeed more closely related to Chambytes 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 \textit{Chenrytes} 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 \textit{Chenrytes} \textit{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 persist exclusively to wintering birds (see Fig. 1). Purposed eggs of the species were later shown through genetic analyses to be those of other ducks (Chilton and Sorensen, 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 \textit{C. lawi}, the Labrador Duck (\textit{Camptorhynchus labradorius}) does fall within the Mergini as previously argued. However, it is sister to Steller’s Eider, not a scoter of the genus \textit{Melanitta} as suggested by Livezey (1995). Similarities of the bill and plumage reflect this sister taxon relationship. Steller’s Eider, Long-tailed Duck (\textit{Clangula hyemalis}) and Harlequin Duck (\textit{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 \textit{Somateria} or scoters. Steller’s Eider also appears to have a lower dependence on bivalves and a greater dependence on gastropods than these larger convertivore 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, 1995).

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 Novaya 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 market 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 \textit{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)


References


