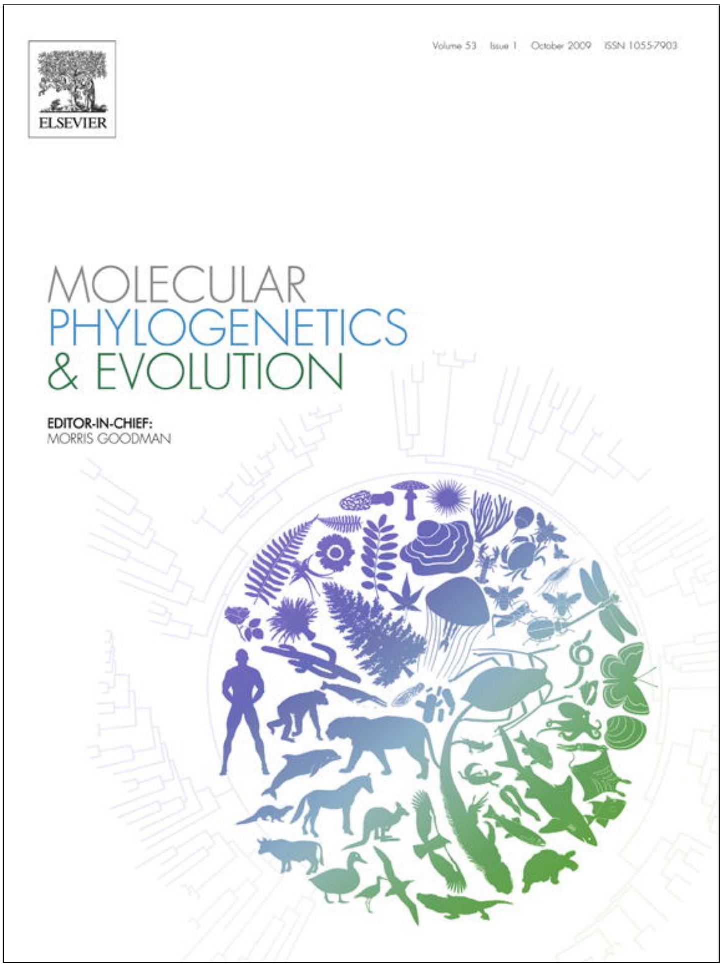
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The phylogenetic position of the Galápagos Cormorant

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ABSTRACT

The endangered Galápagos Cormorant, *Phalacrocorax harrisi*, is unique among the species of the Phalacrocoracidae in being flightless and sequentially polyandrous. It has had a vexed taxonomic history, variously being lumped with all the species in *Phalacrocorax*, being accorded its own genus, *Nannopterum*, or being included in *Leucocarbo* or *Compsohalieus*. Different authorities have similarly suggested a number of different species as being its closest relative. Here we use novel mitochondrial DNA sequence data to show that the Galápagos Cormorant is related to the sister pair of the mainland Americas, the Double-crested Cormorant, *P. auritus*, and the Neotropic Cormorant, *P. brasilianus*. This trio of species has high statistical support (Bayesian posterior probability of 1.00; NJ bootstrap 98%; MP bootstrap 91%). The Galápagos Cormorant is thus a relatively recent offshoot of the mainland form, which has subsequently evolved flightlessness. Until the phylogeny of the cormorants is more clearly resolved, we recommend the continued use of *Phalacrocorax* for all species.

1. Introduction

The Galápagos Cormorant, *Phalacrocorax harrisi*, is unique among the extant members of the Phalacrocoracidae in at least two ways. First, it is the only flightless species of this globally distributed group and the resultant adaptations mean it is arguably the most morphologically divergent cormorant species (Murphy, 1936; Livezey, 1992). Second, it is the only species to exhibit sequential polyandry, a breeding system in which the female mates serially with different males (and sex roles are partially reversed in courtship – females lead and are more active than males in courtship and compete aggressively for access to males; Valle, 1994). The male bird completes raising the young alone, while the female deserts to remate in an attempt to produce a subsequent brood (Tindle, 1984; Valle, 1993, 1994). Moreover, the species is of significant conservation concern, because of its limited geographical range (to just parts of the coasts of Isabela and Fernandina), small population size (estimated by Jiménez-Uzcátegui et al., 2006, at 1400 in 2006, having increased from ~700 since 1998; Travis et al., 2006) – an effective population size just above the minimum considered necessary to ensure long term persistence (Valle, 1995), and vulnerability to El Niño events (Valle and Coulter, 1987) and introduced predators (Valle, 1986). The Galápagos Cormorant appears on the IUCN's *Red List* and Birdlife International classifies the species as "Endangered".

Because of features like those described above, the phylogenetic position of the Galápagos Cormorant is of great interest. For instance, knowing how the species is related to other cormorants can provide information about the evolution of its mating behavior (see van Tets, 1965 and Kennedy et al., 1996 for examples involving other species). The Galápagos Cormorant's taxonomic history, however, shows little agreement about which species are its closest relatives, even when relatively modern phylogenetic techniques have been used.

For many years, the morphological changes arising from flightlessness led authorities (e.g., Murphy, 1936; Hellmayr and Conover, 1948) to classify the Galápagos Cormorant in its own genus, *Nannopterum*, and all other cormorant species in *Phalacrocorax*. Such an arrangement obscures phylogenetic relationships, but Murphy (1936) thought on morphological grounds that *Nannopterum* was closer to *Phalacrocorax brasilianus* (=*olivaceus*; Neotropic Cormorant), which occurs from the southern US to southern South America, than any other South American species.

In his behaviorally based taxonomy, however, van Tets (1976) separated the genus *Leucocarbo*, the "shags", from the true cormorants. He placed the Galápagos Cormorant in the nominate subgenus of *Leucocarbo*, the "king shags", which in his view were of Southern-Hemisphere origin. Siegel-Causey's (1988) classification subsequently split *Leucocarbo* into several genera, including *Compsohalieus*, the "marine cormorants". His cladistic analysis of osteological characters ostensibly unrelated to flightlessness placed the Galápagos Cormorant in *Compsohalieus*, sister to the pair of *C. fuscescens* (Black-faced Cormorant from southern Australia) and

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C. neglectus (Bank Cormorant from Namibia and western South Africa), and inside the branch leading to *C. penicillatus* (Brandt's Cormorant from the Pacific coast of North America) and that leading to the extinct *C. perspicillatus* (Pallas's Cormorant from the Commander Islands off Russia's Kamchatka Peninsula). All but the last of these species were included by van Tets (1976) in *Leucocarbo s. str.*, but he did not speculate about the relationships of the Galápagos Cormorant within the subgenus.

Kennedy et al. (2000) included just one of Siegel-Causey's *Compsohalieus* species in their mtDNA-based phylogeny and so could not confirm the position of the Galápagos Cormorant. But they noted that many of Siegel-Causey's clades did not match theirs and that these clades often implied some unexpected biogeographic relationships. Moreover, the one species they did sample, *C. penicillatus*, grouped closely with two species in Siegel-Causey's genus *Stictocarbo*, the "cliff shags", which he considered belonged in a different subfamily. This taxonomic disagreement extends to groupings throughout the family (reviewed in Johnsgard, 1993) and most recent classifications (e.g., Remsen et al., 2008) have avoided the issue by reverting to the single genus, *Phalacrocorax*, for all species including *P. harrisi*. Christidis and Boles (2008) show that a phylogenetically justifiable classification of the cormorants hinges, in part, on the relationships of the Galápagos Cormorant.

Here we use novel DNA-sequence data to place *P. harrisi* as sister to *P. auritus* (Double-crested Cormorant from North America) and *P. brasilianus*, thereby vindicating Murphy's (1936) intuition and moving us towards a natural taxonomy for all cormorants.

2. Materials and methods

We used sequences from 24 phalacrocoracids (out of up to 38 species; Johnsgard, 1993), and a gannet and booby as outgroups (see Table 1). Sequence from the Galápagos Cormorant (*P. harrisi*) was added to the data set used in Kennedy et al. (2001). Total genomic DNA was extracted from blood samples (preserved on filter paper) using the DNeasy Tissue Kit (Qiagen). Following extraction, the DNA was amplified for three mitochondrial genes, the 12S ribosomal RNA gene and the overlapping ATPase-8 and -6 genes, for three individuals. The polymerase chain reaction (PCR) was used to amplify these regions following the procedures described in Kennedy and Spencer (2004). Negative controls were included with each PCR. The PCR products were purified using the QIAquick Gel Extraction Kit (Qiagen) and then sequenced on an automated sequencer using the PCR primers for the ATPase genes and internal primers for 12S (see Kennedy and Spencer, 2004).

Sequences were aligned by eye following the procedure outlined in Kennedy et al. (2000). For 12S all gaps of more than one base were removed to avoid mistaken homology. The additional sequences have been submitted to GenBank (Accession Nos. GQ205456–GQ205457) and the data matrix and resultant phylogenetic tree to TreeBASE (www.treebase.org). Phylogenetic analyses were performed with MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) for Markov-chain Monte-Carlo Bayesian analysis and posterior probabilities, and PAUP* version 4b10 (Swofford, 2002) for maximum parsimony (MP) and Neighbor-joining (NJ) bootstrap searches (Felsenstein, 1985). We used the partition-homogeneity test (Swofford, 2002) to investigate whether the 12S and ATPase sequences contain similar signals and could thus be analyzed as a single data set. For visualization purposes the Red-footed Booby (*Sula sula*) and the Australasian Gannet (*Morus serrator*) were defined as outgroup taxa (see Kennedy et al., 2000).

The models of nucleotide substitution for the Bayesian analysis were selected using the Akaike Information Criterion of Modeltest 3.7 (Posada and Crandall, 1998). The models selected for each gene region were sub-models of GTR+I+G with more than two substitution types (K81uf+I+G for 12S and TrN+I+G for ATPase); thus, it was more appropriate to use 6, rather than 2, substitution types with each partition. Bayesian analysis was performed using MrBayes v3.1.2 with the following settings for each of the two partitions (i.e., 12S and the overlapping ATPase genes). The maximum likelihood model employed 6 substitution types ("nst = 6"). Rate variation across sites was modelled using a gamma distribution, with a proportion of the sites being invariant ("rates = invgamma"). The shape, proportion of invariable sites, state frequency and substitution rate parameters were estimated for each partition separately. The Markov-chain Monte-Carlo search was run twice with 4 chains for 5,000,000 generations, with trees being sampled every 100 generations. Convergence of the duplicate runs was assessed for the likelihood values in Tracer v1.4 (Rambaut and Drummond, 2007), and by plotting the average standard deviation of split frequencies. Following this assessment, the first 10,000 trees, i.e., 1,000,000 generations, were discarded as "burnin". Congruence with other measures of support was evaluated using NJ and MP bootstrap analyses. The NJ bootstrap analyses consisted of 10,000 replicates. The equally weighted MP bootstrap analyses consisted of 1000 replicates using a heuristic search (with 10 random addition sequence replicates and TBR branch-swapping).

3. Results

Our alignments resulted in a 383 bp fragment of 12S and an overlapping 758 bp fragment of ATPase-8 and -6. A partition-homogeneity test showed that there was no significant difference in the phylogenetic signals among these sequences (1000 replicates, $P = 0.315$) and hence they were subsequently analyzed as a single 1141 bp dataset. Of the 1141 characters, 762 were constant, 379 were variable and 242 of the variable characters were parsimony informative. The Bayesian phylogeny (see Fig. 1) is concordant with previous molecular phylogenies for the group (Kennedy et al., 2000, 2001). The Bayesian posterior probabilities show that the majority of the branches in the phylogeny are well supported. The positions of some taxa (and groups of taxa) remain somewhat ambiguous, however, with little support for the positions of *P. nigrogularis*, *P. aristotelis*, and the *P. penicillatus* + *P. pelagicus* + *P. urile* group. Relatively short internal branches like those leading to these taxa can be difficult to resolve with confidence (e.g., see Kennedy et al., 2005).

All our trees show the Galápagos Cormorant as sister to the Double-crested and Neotropic Cormorants with strong statistical support: a posterior probability from Bayesian MCMC searches of 1.0 and bootstrap percentages of 91% and 98% from equally weighted MP and NJ, respectively (Fig. 1).

4. Discussion

Our genetically based results (Fig. 1) unequivocally place the Galápagos Cormorant as sister to the mainland Americas' sister group of the Double-crested Cormorant and the Neotropic Cormorant. Such a relationship had been hinted at over 70 years ago, when Murphy (1936) argued that Galápagos Cormorant was related to species originating in the Northern Hemisphere, rather than being an offshoot of Southern-Hemisphere forms. Murphy specifically mentioned the Neotropic Cormorant as the closest relative found in South America, although he also thought it related to the Great Cormorant (*P. carbo*), which is almost cosmopolitan.

Our results are in stark contrast with those of van Tets (1976) and Siegel-Causey (1988). First, the Galápagos Cormorant is distant from the type species of *Compsohalieus*, Brandt's Cormorant (and so

Table 1
Species used in the analysis.

Species	Voucher information	Collection location
King Shag[a] *Phalacrocorax albiventer*	American Museum of Natural History[b]; Unvouchered sample	Chile and Argentina
European Shag *Phalacrocorax aristotelis*	Unvouchered DNA extracts	UK
Double-crested Cormorant *Phalacrocorax auritus*	Samples 166, 793, and 1285, Royal Ontario Museum	Canada
Guanay Shag *Phalacrocorax bougainvillii*	American Museum of Natural History[b]	Chile
Neotropic Cormorant *Phalacrocorax brasilianus*[c]	Samples 10220, 10371, and 10372, Museum of Natural Science at Louisiana State University	USA
Campbell Island Shag *Phalacrocorax campbelli*	Unvouchered samples	Campbell Island
Cape Shag *Phalacrocorax capensis*	Unvouchered samples	South Africa
Japanese Cormorant *Phalacrocorax capillatus*	Unvouchered DNA extract	Japan
Great (Black) Cormorant *Phalacrocorax carbo*	Samples 90–97 and 90–98, Auckland Institute and Museum; Sample 956, Museum of Victoria	Australia and New Zealand
Stewart Island Shag *Phalacrocorax chalconotus*	Unvouchered samples	New Zealand
Pitt Island Shag *Phalacrocorax featherstoni*	Unvouchered samples	Chatham Island
Red-legged Shag *Phalacrocorax gaimardi*	American Museum of Natural History[b]	Chile
Galápagos Cormorant *Phalacrocorax harrisi*	Unvouchered samples	Galápagos Islands
Rock Shag *Phalacrocorax magellanicus*	American Museum of Natural History[b]	Chile
Little Pied Cormorant *Phalacrocorax melanoleucos*	Samples 957 and 958, Museum of Victoria; Samples 1011 and 1013, Royal Ontario Museum; Sample 89–54, Auckland Institute and Museum	Australia and New Zealand
Socotra Shag *Phalacrocorax nigrogularis*	Unvouchered sample	Abu Dhabi
Chatham Island Shag *Phalacrocorax onslowi*	Unvouchered samples	Chatham Island
Pelagic Shag *Phalacrocorax pelagicus*	Sample 4708, Burke Museum; Samples 2518 and 2522, Royal Ontario Museum	Alaska
Brandt's Cormorant *Phalacrocorax penicillatus*	Samples 4926, 4927, and 4928, Burke Museum	USA
Spotted Shag *Phalacrocorax punctatus*	Sample 91–52, Auckland Institute and Museum; Unvouchered samples	New Zealand
Macquarie Island Shag *Phalacrocorax purpurascens*[d]	Unvouchered DNA extracts	Macquarie Island
Little Black Cormorant *Phalacrocorax sulcirostris*	Sample 90–80, Auckland Institute and Museum; Sample 959, Museum of Victoria; Unvouchered sample	Australia and New Zealand
Red-faced Shag *Phalacrocorax urile*	American Museum of Natural History[b]	Alaska
Pied Cormorant *Phalacrocorax varius*	Sample 42490, Museum of Victoria	Australia
Australasian Gannet *Morus serrator*	Unvouchered samples	New Zealand
Red-footed Booby *Sula sula*	Samples 15446 and 15447, Museum of Natural Science at Louisiana State University	Unknown

[a] Called the Imperial Shag by Kennedy et al. (2000). The samples were from South America where this taxon is sometimes included in the Imperial Shag, *P. atriceps* (see Devillers and Terschuren, 1978) or treated as a subspecies, *P. atriceps albiventer* (e.g., see del Hoyo et al., 1992).

[b] American Museum of Natural History samples were obtained prior to their having accession numbers and, thus, could be any one the samples from the AMNH collection (they have between four and 10 individuals of these species).

[c] As *H. olivaceus* (see Browning, 1989).

[d] Treated as subspecies of the Imperial Shag, *P. atriceps*, by Siegel-Causey (1988).

is not a member of *Compsohalieus*). Second, although Siegel-Causey classified both the Neotropic and Double-crested Cormorants in *Hypoleucos* (the mesocormorants), none of these species belong in that genus, as the type is *P. varius* (Pied Cormorant from New Zealand and Australia), which, according to our tree, is not related. Consequently, the Galápagos Cormorant cannot be a member of *Hypoleucos* either.

The close relationship between the Galápagos, Neotropic and Double-crested Cormorants means that the significant morphological and behavioral differences between the Galápagos Cormorant and other cormorants can now be examined in an appropriate comparative setting. For example, the osteological characters that underlie its superficial similarity with Brandt's Cormorant are likely to be parallel changes, possibly related to the large body size of both species: both species are the heaviest of their respective trios of closest relatives (Johnsgard, 1993). Siegel-Causey (1988) suggested that most of the convergences and reversals in his dataset are likely to be associated with adaptations for foraging and flight.

As with other many other members of the Galápagos fauna, the relationship we find suggests colonization from the mainland Americas (for a review of colonization and diversification of the Galápagos fauna see Parent et al., 2008). We can approximate the timing of the split between the Galápagos Cormorant and the mainland common ancestor of the Neotropic and Double-crested Cormorants. If we follow Kennedy et al. (2000) and use a rate of divergence of 0.2% per million years for transversions alone, we get an estimate of 1.97 million years ago (mya) for the split, whereas, if we follow Kennedy and Spencer (2004) and use an overall rate of 2% per million years, we get an estimate of 2.13 mya for the split. A divergence time of ~2 mya is concordant with the 2.3 mya estimate for the colonization of the antecedents of Darwin's finches (Sato et al., 2001). The ancestor of the Galápagos Penguin appears to have split from that of the Peruvian Penguin ~4 mya (Baker et al., 2006), whereas the forerunner of the Galápagos Hawk is estimated to have colonized the Galápagos within the last 300,000 years (Bollmer et al., 2006; Hull et al., 2008). Patterns of speciation (or lack thereof) in the Galápagos are thus taxon specific, and appear to reflect a combination of dispersal capability and habitat suitability (Parent et al., 2008).

Our ~2 mya estimate of divergence from the mainland Americas common ancestor raises interesting issues for the

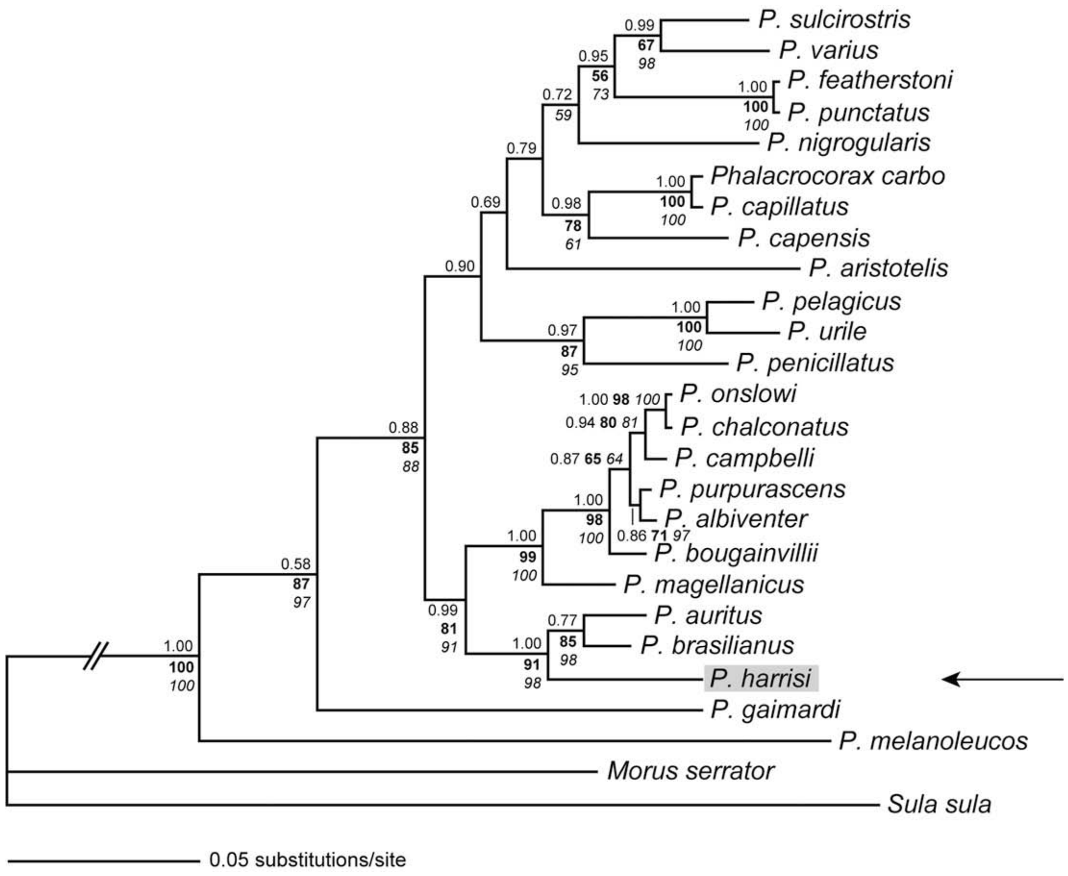

Fig. 1. The Bayesian phylogram. The numbers associated with the branches represent posterior probabilities from Bayesian MCMC searches, equally weighted MP bootstrap values (bold), and NJ bootstrap values (italic). The position of the Galápagos Cormorant (*P. harrisi*) is indicated by an arrow and shading.

distribution of the Galápagos Cormorant. Although the species is currently limited to parts of the coasts of Isabela and Fernandina, this distribution cannot have always been the case, as Isabela is thought to have arisen between 0.5 and 0.8 mya and Fernandina is thought to have surfaced less than 0.07 mya (Parent et al., 2008). If the ancestors of the Galápagos Cormorant colonized the Galápagos Islands approximately 2 mya, where were their flightless descendants prior to inhabiting Isabela and Fernandina?

A possible explanation may be found by investigating the suitable habitat that may be available to the Galápagos Cormorant as the different islands arise and change. Cormorants have high metabolic rates and do not store much of a fat reserve (Ainley, 1984). Consequently, they need to feed daily and cannot fast for long as several other seabirds can. Valle (1995) has suggested that such a physiological adaptation restricts the distribution of the Galápagos Cormorant to the upwelling zones associated with the Cromwell current on the west of the Galápagos archipelago where food is relatively abundant and reliable. Inferring their past distribution within the archipelago is difficult because geological processes such as those related to the dynamics of the Galápagos platform and island formation are likely to have had dramatic effects on the local marine currents and food supply for this species. Nevertheless, the western coast of Santa Cruz, which is estimated to have arisen up to 2.2 or 2.3 mya (Schmitz et al., 2007; Parent et al., 2008), may have been the species center of colonization and early evolution before the birds expanded to Santiago as this new island appeared (~1.4 mya, Parent et al., 2008) and from there to Isabela and Fernandina. The appearance of these two new islands and particularly the joining of the six interconnected volcanoes that made Isabela (Parent et al., 2008) are likely to have had profound consequences for local marine circulation. These changes may have rendered the foraging grounds around Santa Cruz and Santiago no longer suitable for the Galápagos Cormorant, thus restricting them to Isabela, and more recently also to Fernandina. Thus, the ancestral Galápagos Cormorant appears to have colonized the Galápagos archipelago, diverged from its continental progenitor, and subsequently relocated when necessary to obtain the best access (considering it became flightless) to its foraging habitat.

The improved resolution in our tree suggests that at some point, the genus *Phalacrocorax* as currently envisaged could be split into two or more monophyletic genera or subgenera. *Nannopterum* could be used for *P. harrisi*, *P. auritus* and *P. brasilianus*, for instance. At this point, however, we have yet to sample a number of important species, several branches are poorly resolved and we lack sequence of one or more nuclear genes that would confirm some of the apparently older divergences. Consequently, we recommend the continued usage of the single genus, *Phalacrocorax*, for all cormorant species until these matters are addressed.

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