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CYTOCHROME-*B* EVIDENCE FOR VALIDITY AND PHYLOGENETIC RELATIONSHIPS OF *PSEUDOBULWERIA* AND *BULWERIA* (PROCELLARIIDAE)

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ABSTRACT.—Although the genus *Pseudobulweria* was described in 1936 for the Fiji Petrel (*Ps. macgillivrayi*), its validity, phylogenetic relationships, and the number of constituent taxa it contains remain controversial. We tried to clarify these issues with 496 bp sequences from the mitochondrial cytochrome-*b* gene of 12 taxa representing three putative subspecies of *Pseudobulweria*, seven species in six other genera of the Procellariidae (fulmars, petrels, and shearwaters), and one species each from the Hydrobatidae (storm-petrels) and Pelecanoididae (diving-petrels). We also include published sequences for two other petrels (*Procellaria cinerea* and *Macronectes giganteus*) and use *Diomedea exulans* and *Pelecanus erythrorhynchos* as outgroups. Based on the pronounced sequence divergence (5 to 5.5%) and separate phylogenetic history from other genera that have been thought to be closely related to or have been synonymized with *Pseudobulweria*, we conclude that the genus is valid, and that the Mascarene Petrel (*Pseudobulweria aterrima*) and the Tahiti Petrel (*Ps. rostrata*) are distinct species. In trees constructed with maximum parsimony and maximum likelihood, *Pseudobulweria* is the sister taxon to *Puffinus* and *Calonectris*, and these genera in turn are most closely related to *Bulweria* (and *Procellaria* in the maximum-parsimony tree). *Pseudobulweria* is not closely related to *Pterodroma* in either tree. Because *Ps. r. trouessarti* from New Caledonia, and *Ps. r. rostrata* from Polynesia differ by only 0.6%, these taxa do not deserve species status and should be regarded as valid subspecies. *Received 7 October 1996, accepted 23 July 1997.*

THE GENUS *PSEUDOBULWERIA*, first proposed by Mathews in 1936 for the Fiji Petrel (*Ps. macgillivrayi*), remains one of the least-known genera of petrels (Warham 1996, Attié et al. 1997). Although it has been synonymized with *Pterodroma* (e.g. Jouanin and Mougin 1979, Warham 1990, Del Hoyo et al. 1992), some systematists have reinstated it as a separate genus (Imber 1985, Warham 1996), either close to *Pterodroma* (Sibley and Monroe 1990) or to *Bulweria* and *Procellaria* (Imber 1985). In his reappraisal of the petrels, Imber (1985) also included in *Pseudobulweria* the Mascarene Petrel (*Ps. aterrima*), the Tahiti Petrel (*Ps. rostrata*), and a fossil taxon (*Ps. rupinarum*). Beck's Petrel (*Ps. rostrata becki*) is known from only two specimens and may be extinct. Similarly, *Ps. macgillivrayi* is known from only two specimens (Watling and Lewanavanua 1985), *Ps. aterrima* is known from seven specimens and is on the verge of extinction (Attié et al. 1997), and *Ps. rupinarum* already is extinct (Olson 1975). Therefore, systematic studies on this group have relied nearly exclusively on *Ps. r. rostrata* and on morphological attributes assessed from museum specimens (e.g. Jouanin 1970, 1987; De Naurois and Erard 1979; Imber 1985).

Using available data as well as new information provided by DNA sequencing, we examined: (1) the validity of the taxon *aterrima* compared with *rostrata*, because these two taxa have been suggested to be conspecific (e.g. Jouanin 1970); (2) the validity of the genus *Pseudobulweria*; and (3) the phylogenetic positions of *Pseudobulweria* and *Bulweria* within the family Procellariidae. For this latter aspect, we paid particular attention to *Bulweria*, which has been claimed to be close to (Kuroda 1954) or synonymous with *Pterodroma* (Olson 1975), and together with *Pseudobulweria* is thought to be ancient (Bourne 1975; Imber 1985; Warham 1990, 1996). We used the mtDNA sequence (496 bp

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segment) at the cytochrome-*b* locus because this segment has proved valuable for phylogenetic analysis at the species, generic, and familial levels in birds (e.g. Lanyon 1994, Baker et al. 1995, Helbig et al. 1995, Arctander et al. 1996, Friesen et al. 1996, Krajewski and King 1996).

Material and Methods

Species and sampling techniques.—We obtained samples from seven procellariid genera as well as one species of storm-petrel and one species of diving-petrel: Tahiti Petrel (*Ps. r. trouessarti*; New Caledonia, blood sample and *Ps. r. rostrata*; Gambier Is., blood), Mascarene Petrel (Réunion I., tissue), Barau's Petrel (*Pterodroma baraui*; Réunion I., tissue), Black-winged Petrel (*Pt. nigripennis*; New Caledonia, blood), Bulwer's Petrel (*Bulweria bulwerii*; Canary Is., blood), Cory's Shearwater (*Calonectris diomedea*; Malta, blood), Wedge-tailed Shearwater (*Puffinus pacificus*; New Caledonia, blood), Northern Fulmar (*Fulmarus glacialis*; Brittany, tissue), Snow Petrel (*Pagodroma nivea*; Adélie Land, Antarctica, blood), Leach's Storm-Petrel (*Oceanodroma leucorhoa*; French Guyana, tissue), and Common Diving-Petrel (*Pelecanoides urinatrix*; New Zealand, tissue). We also used published sequences from *Procellaria cinerea* and *Macronectes giganteus* (Nunn et al. 1996), making available data from 9 of the 13 genera in this family (sensu Warham 1996). *Diomedea exulans* (Nunn et al. 1996) and *Pelecanus erythrorhynchos* (Avise et al. 1994) were used as outgroup taxa. Blood samples (ca. 1 mL) were taken from the tarsus for the larger species and from the wing for the smaller species and preserved in a buffered solution of 4M guanidine-thiocyanate (see Laulier et al. 1995). Tissue samples (liver) were taken from specimens frozen at −18°C. One specimen was sampled for each species.

DNA extraction and PCR amplification.—A small amount of tissue or blood (ca. 0.1 g) was powdered in liquid nitrogen and suspended within CTAB buffer containing proteinase K (Doyle and Doyle 1987, Winnepenninckx et al. 1993). Digestion was at 60°C for 1 h, and protein isolation was carried out with chloroform-isoamyl alcohol. In addition, 0.5 units of RNAase were added to the second aqueous phase and incubated at 37°C for 30 min to remove RNA. Total genomic DNA was precipitated with isopropanol. DNA concentration and quality were evaluated with a spectrophotometer. Extracted DNA was amplified with the following two primers, whose numbers correspond to the location of the 3′ end of the primer respectively in the full sequence of human mtDNA (Anderson et al. 1981, in bold) and chicken mtDNA (Desjardins and Morais 1990): **L14841**/L14990 (5′-CATCCAACATCTCTGCTTGATGAAA-3′) defined by Kocher et al. (1989), and **H15338**/H15487 (5′-GATCCTGTTTCGTGGAGGAAGGT-3′). These primers amplify a DNA segment of 496 bases. PCR was performed in a 50-μL volume using ca. 0.3 μg of template DNA and 50 picomoles of each of the primers. The PCR mix (final concentrations) contained 20 mM Tris-HCL, pH 8.55, 16 mM $(NH_4)2SO_4$, 2.5 mM $MgCl_2$, 150 μg/mL BSA, 330 μM dNTP, and 0.3 μL (1.5 units) of Goldstar *Taq* DNA polymerase (Eurogenetec). The PCR profile for amplifications was 35 cycles of 60 s at 93°C, 40 s at 50°C, and 40 s at 72°C. PCR products were opened under a specially designed hood and checked by electrophoresis in 1% agarose-BET and TBE buffer (Sambrook et al. 1989) with the molecular weight marker VI (Boehringer). PCR products were cloned using the PCRscript TM SK(+) cloning kit (Stratagene) according to recommended specifications. A classical white/blue selection (Sambrook et al. 1989) was used for screening recombinant clones. Four white colonies per cloning were grown overnight in L-broth at 37°C, the phagemidic DNA extracted (Sambrook et al. 1989), and the insert was checked by digestion of the recombinant phagemidic DNA with BssHII. Sequencing on microtiter plates was performed with the T7 sequencing kit (Pharmacia), using the method of terminator dideoxynucleotides (Sanger et al. 1977). Two colonies per cloning were sequenced with external vector primers KS and T3 to check for artifacts introduced by cloning of PCR products. Differences between clones occurred in only two samples (both one-transition difference in the 496 bp), and a third colony was sequenced to confirm the correct sequence.

Data analysis.—Sequences were read and entered twice using the computer package MUST (Philippe 1993) and were easily aligned because no insertions or deletions were found. Relative transitional saturation was examined by plotting transitional against transversional pairwise raw differences. Maximum-likelihood (ML) analyses (Felsenstein 1981) were performed with program FastDNAml (Olsen et al. 1994). The options F (empirical frequencies) and G (global rearrangements) were used, and 10 random-input order of species were done for each model to minimize input-order bias. We used three models differing in the number of categories of substitution rates (CSR). In 1-CSR, the three codon positions had equal substitution rates; in the 2-CSR model, first and second codon positions had equal rates whereas the third differed; and in the 3-CSR model, each codon position had a different rate of substitution. Two sets of relative codon-position evolutionary rates (1st:2nd for the 2-CSR model, and 1st:2nd:3rd for the 3-CSR model) were used: 1:5 and 1:10, and 2:1:5 and 2:1:10, respectively. Three transition-transversion ratios (TS:TV) were used and thus defined *a priori* in the likelihood computations: 2:1, 5:1, and 10:1. The best likelihood values were obtained for 2-CSR and 3-CSR models with TS:TV=5:1, and with evolution-

ary category rates being respectively 1:10 or 2:1:10. These parameters produced two trees that differed in the position of *Procellaria cinerea*, with either a basal position to the clade *Pterodroma-Fulmarus-Pagodroma-Macronectes* (Model 2-CSR), or an inner position in this clade, as sister-group of fulmarines (Model 3-CSR). However, because three short branches did not significantly differ from zero, these two trees effectively gave the same topology, and thus we have presented only this tree beyond.

We also performed maximum-parsimony (MP) analyses with PAUP 3.1.1 (Swofford 1991) with unordered characters. Branch and bound searches were performed with the complete data set of 14 taxa. Weights were given to the transversions via a step matrix. The two optimizations used, Accelerated Transformation (ACCTRAN) and Decelerated Transformation (DELTRAN), yielded similar topological results. Likelihoods of the MP trees were calculated and compared with those of ML trees. Bootstrapping (Felsenstein 1985) was performed using FastDNAml and PAUP. For the MP trees, heuristic searches were used for 100 and 1,000 iterations. *Pelecanus erythrorhynchos* was used as an outgroup in all analyses.

RESULTS

Sequence variation.—Sequences were deposited in GenBank under accession numbers U70482 to U70493. Within the 14 species analyzed, 174 sites (35% of the 496 sites) were found to be variable, and 126 (25.4%) were phylogenetically informative, i.e. were present in two or more states in more than one species. Of the 174 variables sites, 32 (18%) were at the first position of the codon, seven (4%) at the second, and the remaining 135 (75.6%) at the third position, representing at each position 19.4, 4, and 81%, respectively, of all such sites. These are similar proportions to those found for albatrosses (Nunn et al. 1996) and are typical proportions in cytochrome-*b* gene of vertebrates (see Cicero and Johnson 1995, Arctander et al. 1996).

Sequence divergence.—Among taxa within the same genus, uncorrected sequence divergences ranged from 0.6% between the two subspecies of the Tahiti Petrel to 7.1% between the two species of *Pterodroma* (Table 1), values that are within the range found for other nonpasserine genera (Cicero and Johnson 1995, Helbig et al. 1995, Nunn et al. 1996). The sequence of the Mascarene Petrel differed from that of the two subspecies of the Tahiti Petrel by an average of 5.3%, typical of levels of divergence among

TABLE 1. Pairwise comparisons of the partial cytochrome-*b* sequence data (496 nucleotides); % global substitutions are below the diagonal, and % transversions in the variable sites are above the diagonal.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 *Pelecanus erythrorhynchos*	—	35.1	48.7	36.2	46.1	39.1	27.5	26.7	29.2	33.8	35.0	37.1	37.3	35.6	33.9	33.3
2 *Diomedea exulans*	15.1	—	37.3	34.3	34.8	34.8	27.6	33.8	36.4	28.8	36.7	32.9	34.9	33.9	35.4	34.8
3 *Oceanodroma leucorhoa*	15.3	15.1	—	32.6	39.0	39.0	31.8	31.4	31.0	28.4	39.5	36.6	35.3	38.9	42.0	41.4
4 *Pelecanoides urinatrix*	13.9	14.1	17.3	—	29.0	29.5	22.1	20.6	17.4	22.4	23.7	25.4	28.6	24.1	26.3	25.8
5 *Pterodroma nigripennis*	12.7	13.9	16.5	13.9	—	5.7	21.1	18.0	21.5	21.3	23.3	25.4	24.6	25.9	26.3	25.0
6 *Pt. baraui*	13.9	13.9	15.5	12.3	7.1	—	23.2	15.2	19.7	22.5	21.4	21.2	21.9	22.6	26.5	25.0
7 *Procellaria cinerea*	16.1	15.3	17.1	13.7	14.3	11.3	—	10.9	13.0	17.0	9.4	10.6	9.2	9.2	9.8	9.4
8 *Pagodroma nivea*	15.1	13.7	17.3	12.7	12.3	11.9	11.1	—	7.4	22.5	8.8	10.8	10.1	9.1	9.8	10.0
9 *Fulmarus glacialis*	14.5	13.3	16.9	13.9	13.1	12.3	10.9	8.1	—	13.5	12.5	12.7	13.5	11.3	12.5	12.3
10 *Macronectes giganteus*	14.3	13.3	16.3	11.7	12.3	9.9	11.9	9.7	7.5	—	17.0	18.0	16.7	14.8	18.9	18.5
11 *Bulweria bulwerii*	12.1	12.1	14.3	11.9	12.1	11.3	10.7	11.5	9.7	10.7	—	12.5	9.8	8.7	7.1	6.9
12 *Calonectris diomedea*	12.5	14.7	16.5	12.7	12.7	13.3	13.3	13.1	12.7	12.3	9.7	—	11.4	13.1	13.2	12.9
13 *Puffinus pacificus*	11.9	13.3	17.1	11.3	13.1	12.9	13.6	12.9	11.9	12.1	10.3	9.1	—	9.6	12.0	11.7
14 *Pseudobulweria aterrima*	11.9	13.1	14.5	11.7	10.9	10.7	10.9	11.1	10.7	12.3	9.3	9.3	10.7	—	11.9	10.6
15 *Ps. rostrata trouessarti*	11.9	13.1	13.9	11.5	11.5	9.9	12.3	12.3	11.3	10.7	8.5	10.7	10.3	5.0	—	0.0
16 *Ps. rostrata rostrata*	12.1	13.3	14.1	11.7	12.1	10.5	12.9	12.1	11.5	10.9	8.7	10.9	10.5	5.6	0.6	—

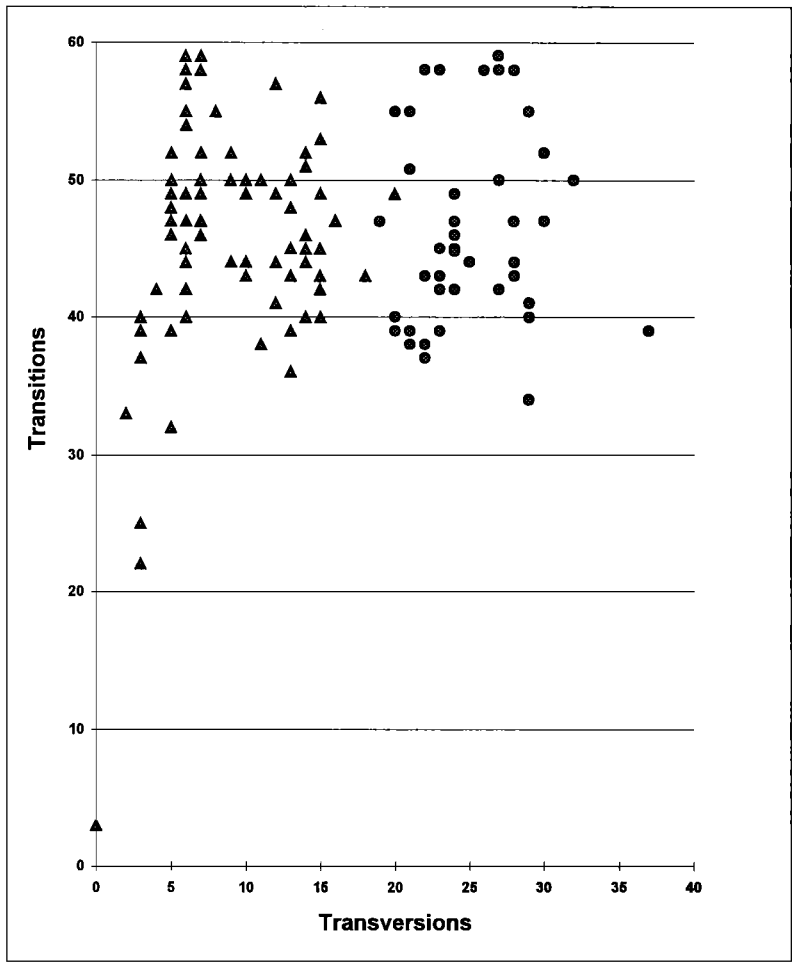

FIG. 1. Pairwise plots of transitions versus transversions (between Procellariidae, triangle; between the Procellariidae and other Procellariiformes or *Pelecanus*, circle).

congeneric species of birds. Among genera within the family Procellariidae, sequence divergences ranged from 8.1 to 14.3% (Table 1). Divergence between the Procellariidae sequenced in this study and other published sequences of procellariiforms ranged from 11.5 to 17.3%. Lastly, among the 14 taxa studied, the proportions of transversional substitutions in pairwise comparisons among taxa were highly variable, ranging from 0 to 0.49.

Saturation effects.—Relative saturation of transitions appeared fairly rapid (Fig. 1), which indicated that using transitions and transversions with equal weight for phylogenetic analysis was not acceptable. The very beginning of the curve, corresponding to the most closely related taxa, indicated that TS:TV ratio was near 10:1 (Fig. 1; see also Austin 1996, Nunn et al. 1996), whereas the unweighted MP analysis indicated that the relative frequencies of TS:TV was 5:1. Therefore, we used both of these ratios for subsequent construction of MP trees.

Phylogenetic position of Pseudobulweria *and* Bulweria.—Although the topologies of the ML and MP trees (Figs. 2 and 3) differ somewhat in their placement of genera, in both trees *Pseudobulweria* is the sister group to *Puffinus* and *Calonectris*, and these genera in turn are most closely related to *Bulweria* (and *Procellaria* in the MP tree). *Pseudobulweria* is not closely related to *Pterodroma* in either tree. Bootstrap support is strong only for the monophyly of *Pseudobulweria* on the one hand and for the monophyly of

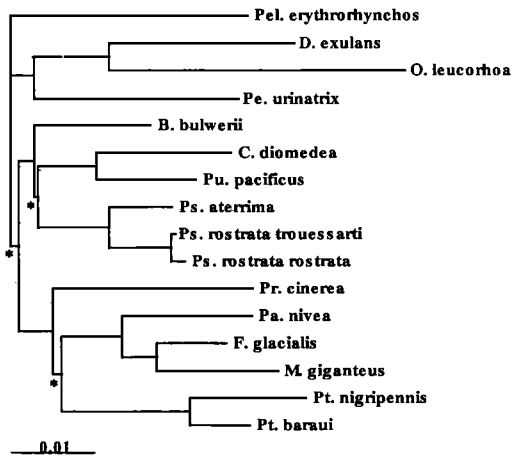

FIG. 2. Maximum-likelihood tree based on 496 bp of cytochrome-*b* DNA sequences with transition/transversion ratio (TS:TV = 5:1) and two categories of substitution rates (1:10; see Methods). The branches marked with a star are not significantly positive. Data for *Pelecanus erythrorhynchos* are from Avise et al. (1994); data for *Diomedea exulans, Macronectes giganteus,* and *Procellaria cinerea* are from Nunn et al. (1996).

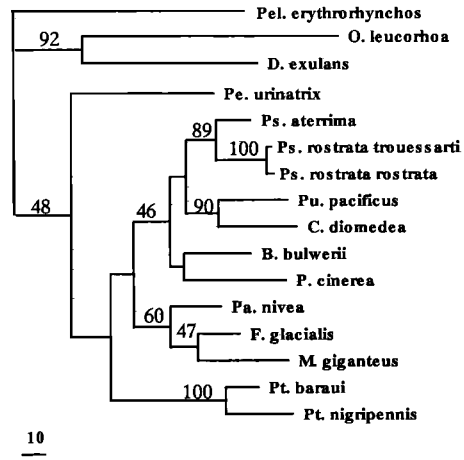

FIG. 3. Single most-parsimonious tree obtained using a TV:TS = 5:1 weighting scheme with bootstrap proportions (percentages) shown to the left of internal branches. The same topology was found with the 10:1 weighting scheme (see text for method and parameters). Bootstrap proportions are given only when >40%. Similar values were obtained with maximum-likelihood analysis.

Pterodroma on the other. Weaker support for other nodes is a common result when short cytochrome-*b* sequences are analyzed at this phylogenetic level (e.g. Wink 1995).

DISCUSSION

Validity and phylogenetic position of Bulweria *and* Pseudobulweria.—The genus *Pseudobulweria* has long been thought to be closely related to, or even included within, *Pterodroma.* Our genetic analyses do not support this belief; *Pseudobulweria* and *Pterodroma* are not members of the same clade within the Procellariidae (Figs. 2 and 3), and they are quite divergent. The same conclusion applies to *Bulweria.* Therefore, we conclude that *Pseudobulweria,* as suggested by Mathews (1936), is a valid genus, consisting of four to five species. Imber (1985) reached the same conclusion based on nongenetic evidence, and he further suggested that *Pseudobulweria* was linked to *Procellaria* and *Bulweria,* and more distantly, to *Puffinus.* In the ML tree (Fig. 2), *Pseudobulweria* and *Bulweria* were linked to *Puffinus* (and *Calonectris*) but apparently not to *Procellaria,* although the phylogenetic positions of *Bulweria* and *Procellaria* within the clade remain imprecise due to low bootstrap values and/or sequences that are too short.

Subspecies of Pseudobulweria rostrata.—Three subspecies of the Tahiti Petrel currently are recognized: *rostrata, trouessarti,* and *becki* (Jouanin and Mougin 1979, Warham 1990). However, the validity of the first two subspecies is controversial (Murphy and Pennoyer 1952, De Naurois and Erard 1979), as is the taxonomic status of *becki,* which may require full species status (e.g. King 1978, Collar and Andrew 1988, Sibley and Monroe 1990), although all recent systematic studies of the Procellariiformes regard it as a subspecies (Jouanin and Mougin 1979, Imber 1985, Warham 1990). This latter taxon could not be included in our analysis because breeding colonies are undiscovered, but the other two subspecies were considered. Moreover, we sampled birds from the two geographic extremes: (1) New Caledonia, the westernmost breeding location of the species; and (2) the Gambier Islands, a newly discovered breeding site for this species (2,000 km east of its previous known range; Bretagnolle and Thibault unpubl. data). Our DNA sequence data show that populations from New Caledonia and Gambier are closely linked, differing by only three transitions and leading to the smallest percentage of difference among the

taxa we analyzed (0.6 %). This is at the lower end of sequence divergence found at the subspecific level among birds in general (see Helbig et al. 1995), and petrels in particular (e.g. Randi et al. 1989; Wink et al. 1993a, b), although Brooke and Rowe (1996) recently split a species of petrel with only 1% difference.

According to our molecular evidence, *trouessarti* from New Caledonia and *rostrata* from Polynesia do not deserve species status, and they should be regarded as valid subspecies. This conclusion is supported both by morphometrics and vocalizations (De Naurois and Erard 1979, Bretagnolle unpubl. data), although data on *rostrata* from Vanuatu and Fiji currently are lacking, and these birds may prove to be intermediate between the two forms.

Taxonomic status of Mascarene and Tahiti petrels.—Using external morphology, Jouanin (1970) suggested that the Mascarene and Tahiti petrels might be conspecific (along with *becki*). Our results from mtDNA show that the difference between the two petrels (5 to 5.5% sequence divergence; Table 1) involves 3 transversions and 20 to 22 transitions. This is clearly outside the range found between subspecies in birds, but within the range of divergence for congeneric species (Helbig et al. 1995). Bootstrap values also were high, and therefore it can be concluded that *Ps. aterrima* and *Ps. rostrata* are indeed valid congeneric species. Although nothing is known about the breeding ecology of *Ps. aterrima* (Attié et al. 1997), studies of external morphology have convincingly reached the same conclusion of species status (see Imber 1985).

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