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EVOLUTIONARY RELATIONSHIPS AMONG EXTANT ALBATROSSES (PROCELLARIIFORMES: DIOMEDEIDAE) ESTABLISHED FROM COMPLETE CYTOCHROME-*B* GENE SEQUENCES

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ABSTRACT.—Complete mitochondrial cytochrome-*b* gene sequences (1,143 bp) were determined from the 14 extant species in the Diomedeidae (albatrosses and mollymawks) and in two outgroup species from the Procellariidae (petrels and shearwaters). Phylogenetic analysis using maximum parsimony and maximum likelihood methods identified a single best-supported hypothesis of evolutionary relationships within the Diomedeidae, namely that two lineages arose early in the evolution of the Diomedeidae. A further bifurcation in each of these lineages resulted in four monophyletic groups of albatrosses: (1) southern mollymawks, (2) sooty albatrosses, (3) North Pacific albatrosses, and (4) "great" albatrosses. Monophyly of the southern mollymawks (*Diomedea bulleri, D. cauta, D. chlororhynchos, D. chrysostoma,* and *D. melanophris*) and sooty albatrosses (*Phoebetria fusca* and *P. palpebrata*) indicates that *Diomedea* is paraphyletic. Resurrection of two genera, dropped historically in taxonomy of the Diomedeidae, results in a total of four genera. Calibrations based on the fossil record indicate that cytochrome-*b* evolutionary rates in albatrosses are slow compared with those of most mammals. *Received 21 August 1995, accepted 10 May 1996.*

THE ALBATROSSES AND MOLLYMAWKS (Family Diomedeidae) are the most familiar and best studied group of procellariiform (or tube-nosed) seabirds due largely to their highly philopatric nature and diurnal attendance at breeding localities, where their surface nests are easily monitored (Warham 1990). The 13 traditionally accepted species of albatrosses are widely distributed throughout the southern oceans, the North Pacific Ocean, and, in a single case, the tropical Pacific Ocean (Harris 1973, Harrison 1983, Marchant and Higgins 1990). Fossil evidence of albatross species present in the North Atlantic Ocean (Lydekker 1891a,b; Wetmore 1943), which are most similar to the extant *Diomedea albatrus* of the North Pacific Ocean, indicates that the Diomedeidae once were truly cosmopolitan in oceanic distribution.

The discovery of a small population of an undescribed "great" albatross on Amsterdam Island in the Indian Ocean (*D. amsterdamensis;* Roux et al. 1983) brought the total number of species to 14 (Sibley and Monroe 1990). Much controversy exists regarding the exact taxonomic status of *D. amsterdamensis.* In particular, its relationship to subspecific taxa of *D. exulans,* which breed on low-latitude islands in the southern Pacific and Atlantic Oceans, is not well understood (Bourne 1989, Robertson and Warham 1992). An affinity among these taxa seems likely because, to differing degrees, they share the retention of dark juvenal or immature plumage as reproducing adults (plumage paedomorphosis). In contrast, populations of the larger-sized *D. exulans,* which occur on subantarctic islands at higher latitudes, have a white plumage as breeding adults. Additional genetic analysis of individuals from all populations of *exulans* will help resolve the much-debated tax-

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TABLE 1. The introduction and principal changes to described genera within the Diomedeidae.

Authority	Genera and changes
Linnaeus (1758)	*Diomedea* gen. nov.
Reichenbach (1852)	*Thalassarche* gen. nov.; *Phoebastria* gen. nov.; and *Phoebetria* gen. nov.
Coues (1866)	Subsumed *Thalassarche* and *Phoebastria* into *Diomedea*
Baird et al. (1884)	*Thalassageron* gen. nov.
Mathews (1912)	Resurrected *Thalassarche*; *Diomedella* gen. nov.; *Nealbatrus* gen. nov.
Murphy (1917)	*Rhothonia* subgen. nov.
Mathews (1934)	Resurrected *Phoebastria*
Mathews and Hallstrom (1943)	Subsumed *Rhothonia* into *Diomedea*; transferred taxon from *Phoebastria* to *Julietata* gen. nov.
Mathews (1948)	Subsumed all albatrosses into *Diomedea*
Boetticher (1949) *in* Jouanin and Mougin (1979)	*Galapagornis* gen. nov.; *Laysanornis* gen. nov.; *Penthirenia* gen. nov.
Alexander et al. (1965)	Standardized use of *Diomedea* and *Phoebetria*

onomy of the *amsterdamensis-exulans* complex (G. Nunn unpubl. data).

Based on elements of biogeographic distribution, a simple allometric relationship of wing and tail length, and characters of the divided plates making up the rhamphotheca of the bill, the 14 albatross species fall into four natural groups: (1) the southern mollymawks, (2) the North Pacific albatrosses, (3) the "great" albatrosses, and (4) the sooty albatrosses (Warham 1990). On the basis of complete adult fuliginous plumage coloration, longer wedge-shaped tail, cuneate body form, and presence of a colored fleshy sulcus separating the ramicorns of the lower mandible (a morphological feature found in other procellariiforms), a traditional hypothesis of relationships within the Diomedeidae recognizes a simple demarcation of two genera: the "primitive" sooty albatross genus *Phoebetria* and a more comprehensive genus *Diomedea* that envelopes the North Pacific albatrosses, the "great" albatrosses, and the southern mollymawks (Coues 1866, Peters 1931, Murphy 1936, Alexander et al. 1965, Jouanin and Mougin 1979, Warham 1990). Consideration of other morphological features historically have led to the splitting of current members of *Diomedea* into additional generic groups (see Table 1), although none has gained common acceptance. Indeed, Mathews (1948) went on to produce an entirely lumped albatross genus *Diomedea* comprised of all known species, including *Phoebetria*.

In view of both the traditional hypothesis of albatross relationships based on a small number of morphological features in this conservative group, and the confusing taxonomy within the comprehensive genus *Diomedea*, we used mitochondrial DNA sequences to investigate higher-level phylogenetic relationships among the 14 extant species of Diomedeidae. The choice of the mitochondrial cytochrome-*b* (cyt-*b*) gene as an evolutionary marker for our study was based on several factors. First, the complete gene sequence, as well as flanking regions, are well characterized in birds (Desjardins and Morais 1990, Helm-Bychowski and Cracraft 1993, Kornegay et al. 1993, Nunn and Cracraft 1996) and other vertebrate groups (Jermiin et al. 1994), enabling the design of oligonucleotide primers that amplify by polymerase chain reaction (PCR) in a broad phylogenetic range of birds. Second, the fast evolutionary rate of change in cyt-*b* has proven most suitable for studying recently divergent groups (Meyer 1994) and in birds has successfully resolved relationships from the species level (Richman and Price 1992, E. Smith et al. 1992, Blechschmidt et al. 1993) to generic and familial levels (Krajewski and Fetzner 1994, Lanyon and Hall 1994, Murray et al. 1994). Third, cyt-*b* is one of the larger protein-coding genes in the avian mitochondrial genome (Desjardins and Morais 1990), and, so far, presents no problem of alignment among birds. Finally, the expanding use of cyt-*b* gene sequences as a source of qualitative data for studies of avian systematics ensures that in the near future a dense sampling of diverse taxa will be available, leading to a common improvement of phylogeny-building within birds.

Our genetic study explored several basic questions concerning the patterns and rates of evolution among extant albatross species: (1) Is the traditional classification congruent with a molecular phylogeny, i.e. is *Phoebetria* a sister-group to the remaining Diomedeidae, as tenuously surmised by a handful of "primitive"

characters (see Murphy 1936) that are shared with other petrels? (2) Does the molecular evidence offer any support for morphologically defined groups previously delimited within *Diomedea* (Coues 1866)? (3) What absolute evolutionary rate calibration is suggested for cyt-*b* in the Diomedeidae, and how does this compare with other estimates of the molecular clock for this gene (Irwin et al. 1991, Martin et al. 1992)?

METHODS

Study organisms.—Samples of fresh blood or liver tissue were collected from the extant species of albatrosses and two species of the Procellariidae. Most blood samples were collected from chicks or incubating adults at nesting colonies to ensure known breeding provenance, although samples were taken from adult birds at sea for three of the species. All tissue samples were stored in 100% ethanol in the field and transported without freezing. The binomen, or current trinomen where appropriate, and collection locality of each taxon in this study are listed in the Appendix. Based on simple morphological comparisons (Murphy 1936), our two outgroup species from the Procellariidae (Southern Giant Petrel [*Macronectes giganteus*] and Gray Petrel [*Procellaria cinerea*]) represent members of the most likely sister group to the Diomedeidae.

DNA isolation.—We extracted DNA suitable for enzymatic amplification by boiling a minute piece of tissue (<5 μg) or suspended blood (5 μL) for 15 min in 500 μL of a 5% w/v Chelex-bead suspension (Singer-Sam et al. 1989, Walsh et al. 1991). After brief vortexing to break up the tissue, the beads were pulse-centrifuged for a few seconds, and 300 μL of the supernatant were removed as a source of template DNA.

Mitochondrial cytochrome-b gene isolation and sequencing.—The cyt-*b* gene and short flanking regions were amplified and isolated as a single fragment using the PCR primers L14863 5'-TTTGCCCTATCTATCCTCAT-3' situated at the end of ND5 (numbered following the chicken mitochondrial genome [Desjardins and Morais 1990]) and designed from a consensus of Procellariidae and Diomedeidae partial ND5 sequences (unpubl. data), and H15915 in tRNA-threonine (Edwards and Wilson 1990). The human mitochondrial genome (Anderson et al. 1981) numbered primer H15915 is equivalent to chicken mitochondrial number H16065 (Desjardins and Morais 1990). Of several experimental temperature-cycling parameters tried we found that a four-step cycle most efficiently and reliably amplified this approximately 1.2-kilobase fragment in a Peltier-effect thermocycler (MJ Research): viz. 1 min at 94°C, 1 min at 40°C, 1 min at 60°C, and 3 min at 72°C, for 35 cycles. Amplifications were performed in 50-μL reaction volumes containing 67 mM Tris-HCl (pH 8.8); 6.7 mM $MgCl_2$; 16.6 mM $(NH_4)2SO_4$; 10 mM β-mercaptoethanol; 1 mM each of dGTP, dATP, dTTP, and dCTP; 1 M of each primer; 10–1,000 ng of complete genomic DNA; and 2.5 units of *Taq* polymerase (*Thermus aquaticus* DNA polymerase, Perkin-Elmer-Cetus). The dsDNA products were visualized in a 2% NuSieve low-melting point agarose gel (FMC Bioproducts) containing 2 $pg \cdot ml^{-1}$ ethidium-bromide (Maniatis et al. 1982). The dsDNA product was cut directly from the gel and resuspended in 300 μL water by heating to 73°C for 15 min.

Further primer pairs were used to amplify double-stranded DNA subfragments from the isolated cyt-*b* gene (i.e. L14863/H15104, L14863/H15298, L14990/H15298, L15236/H15505, L15311/H15710, L15656/H16065); for original primer descriptions see Helm-Bychowski and Cracraft (1993) and references therein. A large degree of fragment overlap, as well as the sequencing of both DNA strands, ensured accurate data collection. An air thermocycler (Idaho Technologies) was used to perform 10-μL amplifications of dsDNA in glass microcapillary tubes using standard buffers described elsewhere (Wittwer et al. 1989, Wittwer 1992). All subfragments were amplified with conditions: 1 sec at 94°C, 0 sec at 48°C (i.e. a drop to 48°C without pause before climbing to extension temperature), 10 sec at 72°C, and 35 cycles at slope 9 (machine-specific fastest temperature ramping rate available). Subfragments were visualized, isolated, and resuspended as described above. Concurrent negative and positive controls were performed for each experiment.

Single-stranded DNA for direct sequencing was generated using 1:100 dilutions of one primer in 50-μL amplification reactions together with 1 μL of the resuspended subfragment of dsDNA (Gyllensten and Erlich 1988). Amplification reagents were the same as described above for initial gene isolation and were performed in a Peltier-effect thermocycler with conditions: 1 min at 94°C, 1 min at 52°C, 2 min at 72°C, and 35 cycles. Products were concentrated and desalted by spin-dialysis (Millipore 30,000 NMWL) before sequencing by the Sanger termination-dideoxy method (Sanger et al. 1977) using Sequenase® 2.0 (U.S. Biochemical). Sequencing products were subjected to denaturing gel electrophoresis followed by autoradiography.

Corrected distance computation.–We computed codon third-position corrected distances for comparison with previously estimated values (Irwin et al. 1991, Thomas and Martin 1993). Corrected distances were made using DNADIST from the Phylip 3.5 set of programs (Felsenstein 1993), set to the ML substitution model (Felsenstein 1981) with a 10:1 explicit transition bias (a conservative estimate for birds [Kocher et al. 1989]) and empirical nucleotide frequencies of the total analyzed gene sequences used in the distance computation.

Phylogenetic analysis.—Phylogenetic relationships were estimated using maximum parsimony and max-

imum likelihood methods with bootstrapping to assess support for internal branches (Felsenstein 1985, Hillis and Bull 1993). The two methods have "basic equiprobable" (i.e. symmetrical) assumptions of the evolutionary process (i.e. cladistic parsimony [Farris 1983]) versus a suite of *a priori* assumptions implicit in a model of the evolutionary process at the DNA level (Felsenstein 1981). Parameterization of a model of evolution at the DNA level may be considered an appropriate approach in phylogeny building given mounting evidence for a high transition bias in the avian mtDNA mutational spectrum (Kocher et al. 1989, Edwards and Wilson 1990, E. Smith et al. 1992, Nunn and Cracraft 1996) and a general appreciation of the effects of base-compositional bias upon character-state change, i.e. character-state bias (Collins et al. 1995).

Maximum parsimony analyses and bootstrapping (100 replicates) were accomplished with PAUP 3.1.1 (Swofford 1993). Ten replicate heuristic searches were performed with random addition of taxa to minimize input order bias. Branch-swapping was made by the tree bisection-reconnection (TBR) algorithm. Contemporaneous changes were favored (i.e. parallelisms over reversals) by using delayed transformation (DELTRAN) optimization. These analyses included all characters and substitutions equally weighted.

Maximum likelihood analyses and bootstrapping (100 replicates) were performed with the program fastDNAml 1.1.1 (Felsenstein 1981, Olsen et al. 1994). Heuristic searches were repeated with random addition of taxa. Overall empirical base frequencies of the cyt-*b* gene sequences in this study, relative codon position evolutionary rates of 5:1:20 (1st:2nd:3rd), and a 10:1 transition (Ti) to transversion (Tv) substitution bias, were defined *a priori* as parameters of the nucleotide substitution model in the likelihood computations.

Following phylogenetic analysis, we performed a parsimony-based "winning-sites" test (Templeton 1983) to compare possible alternate arrangements among the major groups established within the Diomedeidae. Assuming a data set is potentially uninformative, a winning-sites test can be used to compare character support among any number of opposing phylogenetic hypotheses (i.e. topologies) with an expectation of stochastically equal support for each. When a comparison of character support for any two particular topologies departs from equality, a binomial test determines if one is significantly better-supported than the other, and is therefore more likely to be the correct topological arrangement (Templeton 1983, Prager and Wilson 1988). This test is a conservative indicator of significance levels for tree support (Felsenstein 1988). Based on the constrained topological outcome of the winning-sites test, we explored the range of rooted hypotheses for the Diomedeidae by creating the five possible rooted arrangements including all 16 taxa. The most-parsimonious topologies were determined by searching for rearrangements within constrained groups using MacClade 3.1 (Maddison and Maddison 1993). The resultant topologies were then compared using parsimony as well as maximum likelihood methods (Kishino and Hasegawa 1989).

Results

Alignment of cyt-*b* sequences (1,143 bp) of the 14 albatross species and two members of the Procellariidae shows no nucleotide insertions or deletions among sequences (data available from Genbank, inclusive accession numbers U48940 to U48955). For a variety of reasons we consider the cyt-*b* gene sequences reported to be solely mitochondrial in origin. The entire cyt-*b* gene and flanking regions initially were isolated as a single, contiguous fragment. This procedure minimizes the potential amplification of smaller fragments that are more likely to be translocated into the nuclear genome (Quinn 1992, M. Smith et al. 1992, Kornegay et al. 1993). The gene sequences can be fully translated using the chicken mitochondrial code (Desjardins and Morais 1990) without nonsense or intervening stop codons. Finally, the alignment revealed neither a particular overabundance of first and second codon position changes, nor a shift in the typical avian mtDNA transition bias, phenomena known to occur in mtDNA sequences translocated to the nuclear genome (Arctander 1995).

There are 333 variable nucleotide positions among the 16 gene sequences (29.1% of the total cyt-*b* gene sequence). Variable nucleotides predominantly were at codon third positions (260 sites, 78.1%), followed by first positions (63 sites, 18.9%), and then second positions (10 sites, 3.0%). The distribution of variable sites reflects the majority of substitutions occurring at synonymous sites (codon third positions and leucine codon first positions).

Patterns of pairwise sequence divergence and saturation.—Uncorrected pairwise percentage difference (Table 2) between albatross species ranged from 0.87% (*D. amsterdamensis* vs. *D. exulans*) to 11.20% (*D. irrorata* vs. *D. chlororhynchos*), i.e. the largest difference occurs within *Diomedea*. Differences across the deepest node, i.e. from members of the Diomedeidae to the Procellariidae, ranged from 12.60% (both *Phoebetria* species vs. *Macronectes giganteus*) to 15.84% (*D. epomophora* and *D. irrorata* vs. *Procellaria cinerea*), potentially indicating some rate variability

TABLE 2. Pairwise percentage differences in cytochrome-*b* gene sequences among Diomedeidae and Procellariidae. Uncorrected all codon positions (above the diagonal), and corrected third positions (below the diagonal).

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 *D. chlororhynchos*	—	2.97	2.62	2.80	2.71	10.15	10.06	10.50	10.94	9.89	11.20	11.11	7.79	8.14	13.30	14.26
2 *D. bulleri*	8.57	—	2.62	3.15	1.66	10.24	10.15	10.06	10.41	9.80	10.94	11.02	7.70	7.70	14.00	14.44
3 *D. chrysostoma*	7.87	7.67	—	1.92	2.36	10.32	10.15	10.24	10.32	9.45	10.94	10.85	7.70	7.87	13.74	14.70
4 *D. melanophris*	8.06	9.25	5.14	—	2.80	9.97	9.97	10.24	10.50	9.62	11.02	10.85	7.70	8.05	13.74	14.09
5 *D. cauta*	8.22	4.83	7.32	8.48	—	9.80	9.71	9.89	10.32	9.54	10.85	10.59	7.70	7.61	13.82	14.26
6 *D. exulans*	43.74	45.76	47.05	45.96	42.11	—	0.87	3.15	6.74	6.21	7.09	6.39	8.75	9.62	14.09	14.79
7 *D. amsterdamensis*	42.50	44.41	45.51	46.19	40.90	2.85	—	3.59	6.74	6.21	7.17	6.74	8.84	9.71	14.00	14.87
8 *D. epomophora*	43.94	41.63	43.30	43.83	40.35	9.18	10.95	—	6.65	6.65	6.82	7.00	9.71	9.80	14.87	15.84
9 *D. immutabilis*	42.18	40.76	38.92	42.59	39.12	25.47	25.29	22.93	—	1.75	4.72	3.67	9.62	9.89	14.35	15.40
10 *D. nigripes*	37.71	39.49	35.86	39.20	36.52	24.11	23.94	23.74	4.28	—	4.37	3.50	9.10	9.27	14.35	14.61
11 *D. irrorata*	40.87	41.33	40.76	42.17	39.75	23.59	24.09	21.20	13.23	12.23	—	4.37	10.41	10.76	15.05	15.84
12 *D. albatrus*	40.67	42.78	40.56	42.66	38.45	22.17	24.05	22.85	10.86	10.62	11.98	—	9.97	10.15	14.26	15.49
13 *P. palpebrata*	28.16	27.74	28.62	28.63	28.91	38.96	39.60	42.91	38.85	38.61	40.64	39.11	—	2.10	12.60	13.47
14 *P. fusca*	29.59	27.31	28.98	30.15	27.75	45.73	46.43	42.48	40.16	39.01	42.17	39.28	6.22	—	12.60	13.82
15 *M. giganteus*	101.37	112.48	115.23	113.08	113.46	126.05	123.11	130.73	116.27	118.62	112.10	98.97	99.63	94.77	—	11.37
16 *Pr. cinerea*	114.30	122.07	123.53	122.16	117.55	138.13	138.40	138.94	124.42	118.09	120.90	115.34	115.94	115.91	49.56	—

among the albatross lineages ($\bar{x}$ = 14.31 ± SD of 0.81%, n = 28). The two procellariids (*Macronectes* vs. *Procellaria*) differed by 11.37%, which was comparable to the largest difference found within the Diomedeidae.

Within the Diomedeidae, corrected codon third-position distances ranged from 2.85% (*D. exulans* vs. *D. amsterdamensis*) to 47.05% (*D. exulans* vs. *D. chrysostoma*), again emphasizing that the largest differences are within the traditional genus *Diomedea* (Table 2). From Diomedeidae to the Procellariidae, this computed value increased substantially to a mean value of 117.91% (n = 28, SD = 11.64) and identified the outgroup comparisons at codon third positions highly affected by multiple substitutions, i.e. within a zone of saturation.

Pairwise empirical numbers of substitutions between the procellariiform cyt-*b* sequences partitioned into transitions (Ti) and transversions (Tv) revealed a consistent bias in favor of Ti changes (Table 3, Fig. 1). However, computation of the ratio of Ti to Tv substitutions identified a large range of variation in the relative contribution of each substitution class to these comparisons. Ratios of Ti:Tv ranged from a low of 2.1:1 between distantly related taxa (both *Phoebetria* species vs. *Macronectes giganteus*), to a difference composed entirely of Ti substitutions (31:0) between closely related taxa (*D. chlororhynchos* vs. *D. cauta*). A comparison of all nucleotide positions showed that the growth of Ti differences between diverging taxa departs from linearity at approximately 11% uncorrected total pairwise difference (Fig. 1A). The cluster of points greater than 11% comprised all pairwise comparisons of Procellariidae to Diomedeidae and indicated deeper comparisons have progressed into a zone of saturation.

Dependent upon codon position, however, there is a differing pattern of divergence in the cyt-*b* gene sequences. The growth of Ti substitutions at codon first positions increases linearly between all taxa in this study (Fig. 1B) without evidence of a drop or plateau in divergence occurring as more remote comparisons are made. Codon second positions warrant no special attention because they do not contribute significantly to overall differences. In contrast to codon first positions, the codon third position Ti divergence increases linearly to a limit of approximately 25% total difference (Fig. 1C) and then plateaus into the zone of saturation. The plateau effect is most pronounced at third po-

TABLE 3. Pairwise substitutional differences in cytochrome-*b* genes among Diomedeidae and Procellariidae. Transitions (Ti) above the diagonal, and transversions (Tv) below the diagonal.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 *D. chlororhynchos*	—	31	27	27	31	99	96	106	113	102	115	117	83	87	105	116
2 *D. bulleri*	3	—	24	28	16	97	94	98	104	98	109	113	79	79	112	115
3 *D. chrysostoma*	3	6	—	18	24	98	94	100	103	94	109	11	79	81	109	120
4 *D. melanophris*	5	8	4	—	27	92	90	98	103	94	108	109	77	81	109	111
5 *D. cauta*	0	3	3	5	—	95	92	99	106	98	111	111	82	81	111	116
6 *D. exulans*	17	20	20	22	17	—	8	33	66	61	69	64	85	95	111	119
7 *D. amsterdamensis*	19	22	22	24	19	2	—	36	64	59	68	66	84	94	110	120
8 *D. epomophora*	14	17	17	19	14	3	5	—	68	69	69	74	98	100	121	132
9 *D. immutabilis*	12	15	15	17	12	11	13	8	—	19	49	40	100	103	117	129
10 *D. nigripes*	11	14	14	16	11	10	12	7	1	—	46	39	95	97	118	121
11 *D. irrorata*	13	16	16	18	13	12	14	9	5	4	—	47	108	112	124	135
12 *D. albatrus*	10	13	13	15	10	9	11	6	2	1	3	—	106	108	118	132
13 *P. palpebrata*	6	9	9	11	6	15	17	12	10	9	11	8	—	22	97	107
14 *P. fusca*	6	9	9	11	6	15	17	12	10	9	11	8	2	—	97	111
15 *M. giganteus*	47	48	48	48	47	50	50	49	47	46	48	45	47	47	—	104
16 *Pr. cinerea*	47	50	48	50	47	50	50	49	47	46	46	45	47	47	26	—

sitions because of the preponderance of synonymous changes that can occur at these sites. In view of the overall pattern of divergence among these sequences, we believe that third-position comparisons to the outgroup Procellariidae will almost certainly exhibit some effect of site saturation. Among the Diomedeidae, however, comparisons should be largely unaffected by saturation at any given site.

Base compositional bias.—The pattern of compositional bias (Prager and Wilson 1988) at each codon position in procellariiform cyt-*b* (Table 4) is almost identical to that found in mammals (Irwin et al. 1991) and other birds (Kornegay et al. 1993, Nunn and Cracraft 1996). First positions are little-biased ($C = 0.088$), being G-poor ($\bar{x} = 21.1 \pm 1.15\%$) and slightly C-rich ($\bar{x} = 30.5 \pm 0.64\%$). Second positions are more biased than first ($C = 0.219$), again G-poor ($\bar{x} = 12.9 \pm 0.00\%$) but T-rich ($\bar{x} = 39.6 \pm 0.17\%$). The highest compositional bias is found at third positions ($C = 0.428$), which have very low G ($\bar{x} = 3.8 \pm 0.77\%$) and low T ($\bar{x} = 14.1 \pm 1.41\%$) content, and are rich in A ($\bar{x} = 37.4 \pm 1.13\%$) and C ($\bar{x} = 44.7 \pm 1.65\%$). The overall GC content of each sequence ($\bar{x} = 0.468 \pm 0.009$, range 0.450 [*Procellaria cinerea*] to 0.485 [*Diomedea irrorata*]) falls within the range of other known bird cyt-*b* genes and averages slightly higher than available passerine sequences and lower than the Muscovy Duck (*Cairina moschata*) and most phasianids (summarized in Jermiin et al. [1994]).

Cytochrome-b protein sequence variation.—There was a low number of amino-acid replacements among the translated cyt-*b* protein sequences (following chicken codon usage [Desjardins and Morais 1990]). In total, 46 (12.1%) of the 380 amino acid sites were variable among the 16 translated sequences. Variable residues largely were confined to the transmembrane regions of the molecule. A majority of amino acid replacements involved exchanges between hydrophobic residues—a replacement pattern similar to that found in mammals and other organisms (Irwin et al. 1991, Degli Esposti et al. 1993).

Phylogenetic analysis.—An identical branching topology was best supported by both maximum parsimony (single most-parsimonious tree L = 574 steps, CI [excluding uninformative characters] = 0.591) and maximum likelihood (LnL = −4103.65) analyses (phylogeny shown in Fig. 2). Further parsimony analyses including a greater number of outgroup taxa from the Procellariidae, Hydrobatidae, and Pelecanoididae (a total of 85 taxa) resulted in no change in root location or branching pattern within the Diomedeidae (data not shown). The "phylogenetic tree" indicated an initial bifurcation in the Diomedeidae. The main lineages each subdivided once more, resulting in four phylogenetic groups: (1) southern mollymawks, (2) sooty albatrosses, (3) "great" albatrosses, and (4) North Pacific albatrosses. The full description for this tree is: ((((*Diomedea chlororhynchos*, ((*D. bulleri*, *D. cauta*), (*D. chrysostoma*, *D. melanophris*, (*Phoebetria palpebrata*, *P. fusca*)), ((*D. epomophora*, (*D. amsterdamensis*, *D. exulans*)), ((*D. immutabilis*, *D. nigripes*), (*D. irrorata*, *D. albatrus*)))), (*Macronectes giganteus*, *Procellaria cinerea*)).

Maximum parsimony (MP) and maximum

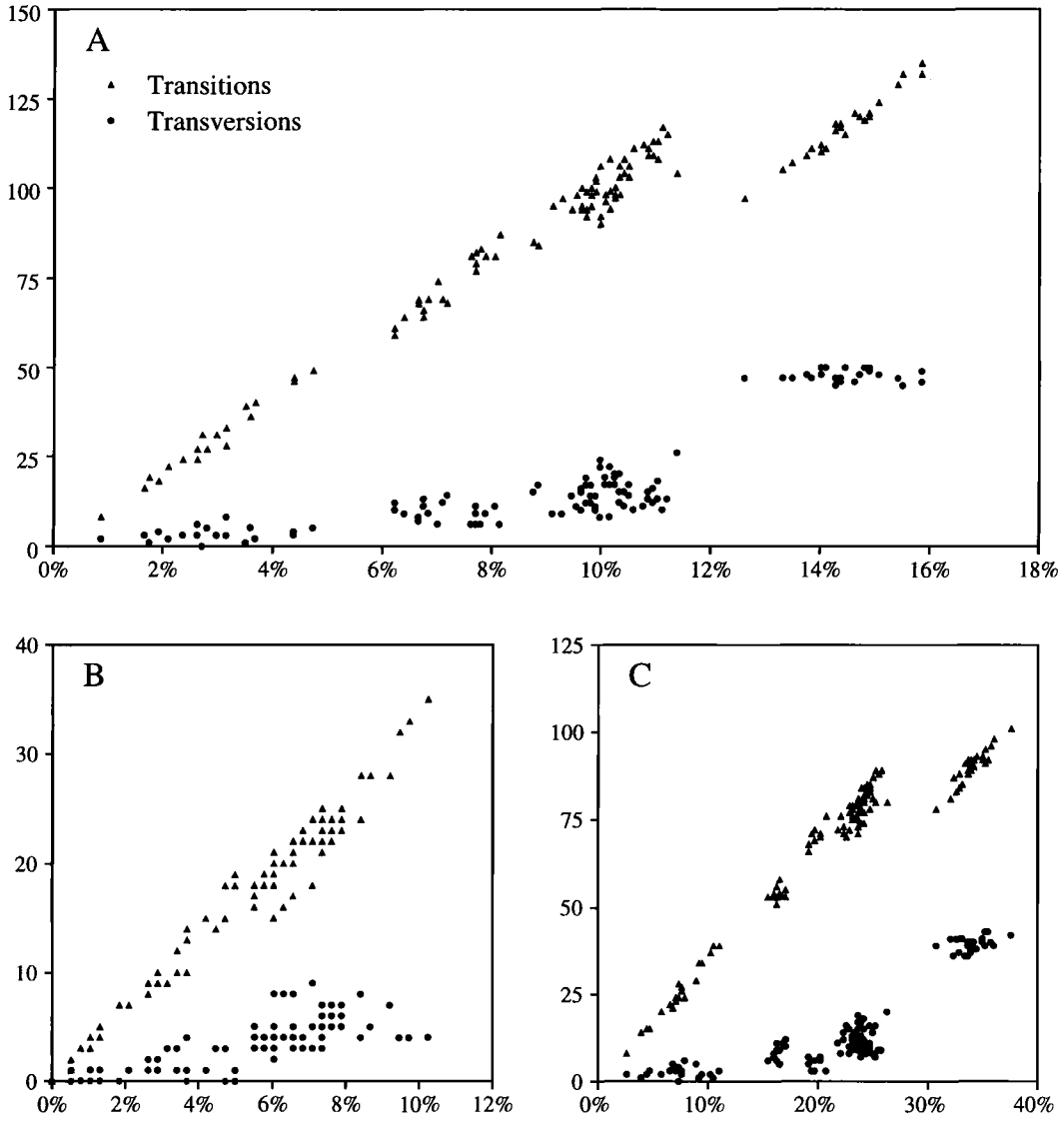


FIG. 1. Empirical numbers of transition (Ti) and transversion (Tv) substitutions (on y axis) plotted against total uncorrected pairwise percentage difference (on x axis) for (A) all codon positions (i.e. 1,143 sites), (B) codon first positions (i.e. 381 sites), and (C) codon third positions (i.e. 381 sites).

likelihood (ML) bootstrap analyses identified broadly concordant levels of support for branches within the phylogeny. Bootstrap support for the first lineage, comprised of southern mollymawks and sooty albatrosses, was relatively low (79% MP, 52% ML) compared with values for other deep branches. Complete bootstrap support (i.e. from all replicates) was found for monophyly of the second lineage, containing "great" and North Pacific albatrosses (100% MP, 100% ML). In addition, the four monophyletic groups within the Diomedeidae all were highly supported: southern mollymawks (100% MP, 100% ML; five taxa), sooty albatrosses (100% MP, 100% ML; two taxa), great albatrosses (100% MP, 100% ML; three taxa), and North Pacific albatrosses (99% MP, 99% ML; four taxa).

Further branching events within the three groups with more than two members (i.e. excluding sooty albatrosses) were robustly supported. Within southern mollymawks, the paraphyletic branching of *D. chlororhynchos* was

TABLE 4. Nucleotide composition, bias by codon position, and the overall GC content of cytochrome-*b* genes of Diomedeidae and Procellariidae.

Species	First				Second				Third				Overall GC content
	G	A	T	C	G	A	T	C	G	A	T	C	
1 *D. chlororhynchos*	19.9	27.0	22.3	30.7	12.9	20.7	39.6	26.8	4.2	37.0	14.4	44.4	46.4
2 *D. bulleri*	19.7	27.0	22.0	31.2	12.9	20.7	39.6	26.8	4.5	36.2	13.6	45.7	47.0
3 *D. chrysostoma*	19.9	27.0	22.0	31.0	12.9	20.7	39.6	26.8	4.2	36.7	14.2	44.9	46.7
4 *D. melanophris*	19.7	27.3	22.0	31.0	12.9	20.5	39.6	27.0	3.7	36.5	13.4	46.5	47.0
5 *D. cauta*	19.9	27.0	22.0	31.0	12.9	20.7	39.6	26.8	3.7	37.5	13.9	44.9	46.5
6 *D. exulans*	21.8	25.2	22.6	30.4	12.9	20.7	39.6	26.8	2.9	38.6	13.1	45.4	46.8
7 *D. amsterdamensis*	21.8	25.2	22.6	30.4	12.9	20.7	39.6	26.8	3.4	38.1	13.1	45.4	47.0
8 *D. epomophora*	22.3	24.7	22.3	30.7	12.9	20.7	39.6	26.8	3.1	38.6	12.6	45.7	47.3
9 *D. immutabilis*	21.8	25.5	22.0	30.7	12.9	20.7	39.6	26.8	4.2	36.7	13.1	45.9	47.5
10 *D. nigripes*	21.8	25.5	22.0	30.7	12.9	20.7	39.4	27.0	3.1	38.1	13.4	45.4	47.1
11 *D. irrorata*	23.1	24.7	22.0	30.2	12.9	20.7	39.4	27.0	5.5	35.2	12.9	46.5	48.5
12 *D. albatrus*	22.3	24.9	22.3	30.4	12.9	20.7	39.4	27.0	5.0	36.0	14.7	44.4	47.5
13 *P. palpebrata*	19.9	27.3	21.8	31.0	12.9	20.7	39.4	27.0	3.1	38.8	15.5	42.5	45.6
14 *P. fusca*	20.5	26.8	21.8	31.0	12.9	20.7	39.4	27.0	3.1	38.8	17.1	40.9	45.3
15 *M. giganteus*	21.3	26.2	22.8	29.7	12.9	20.5	39.9	26.8	4.2	37.0	13.6	45.1	46.8
16 *Pr. cinerea*	22.3	25.5	23.6	28.6	12.9	20.7	39.9	26.5	2.9	38.3	17.3	41.5	45.0
Mean	21.1	26.0	22.3	30.5	12.9	20.7	39.6	26.9	3.8	37.4	14.1	44.7	46.8
SD	1.15	1.00	0.46	0.64	0.00	0.09	0.17	0.16	0.77	1.13	1.41	1.65	0.01
Bias[a] *C*		0.088				0.219				0.428			

[a] Base compositional bias calculated as $C = \frac{3}{3} \sum_{i=1}^{4} |c_i - 0.25|$, where C is the compositional bias and c_i is the frequency of the *i*th nucleotide.

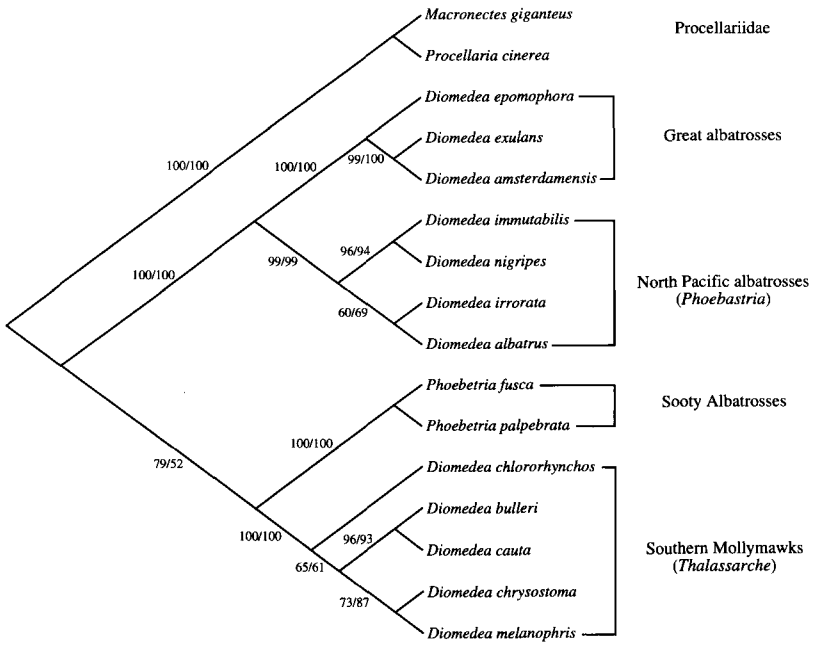
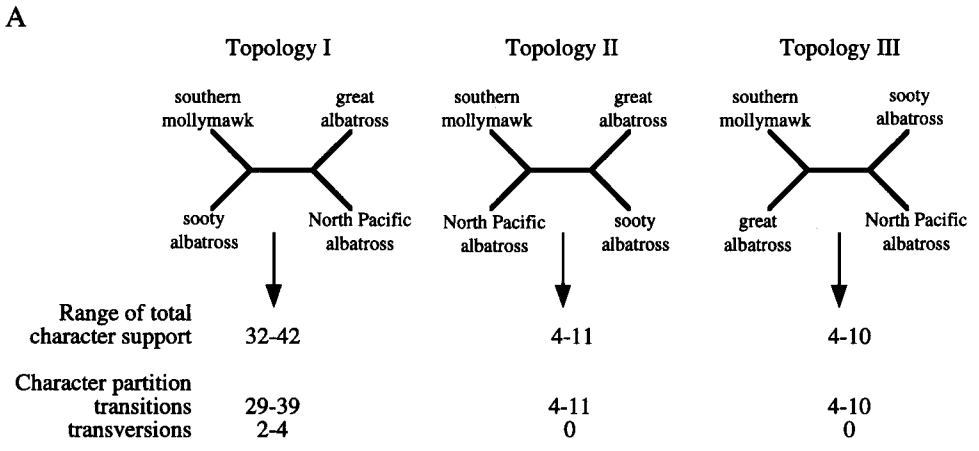


FIG. 2. Phylogenetic relationships among the Diomedeidae based on maximum parsimony (MP) and maximum likelihood (ML) analyses of cytochrome-*b* gene sequences (rooted to the outgroup Procellariidae). Identical branching patterns were determined by both analyses (most parsimonious tree L = 574, CI [excluding uninformative characters] = 0.591; maximum likelihood tree LnL = −4103.65). Percentage bootstrap support found in phylogenetic analyses are shown to the left of internal branches (MP/ML).

marginally supported (65% MP, 61% ML) as occurring before the origin of the remaining four species in this group. Among the remaining four taxa, a sister-taxa relationship of *D. bulleri* and *D. cauta* was highly supported (96% MP, 93% ML), and *D. chrysostoma* and *D. melanophris* also formed sister taxa supported by relatively high bootstrap values (73% MP, 87% ML). Inspection of replicates revealed minor support for the branching of *D. chlororhynchos* between the two species-pairs described above, i.e. resolution at the base of the three lineages (*chlororhynchos, cauta/bulleri, chrysostoma/melanophris*) could be considered problematic based on the current data set. Similarly, among the North Pacific albatrosses most replicates supported monophyly of *D. irrorata* and *D. albatrus* (60% MP, 69% ML), although the remaining replicates supported a paraphyletic branching order for these taxa (*D. irrorata* basal) before the well-supported monophyletic apical origin of *D. immutabilis* and *D. nigripes* (96% MP, 94% ML).

To further assess the higher-level relationships determined from our phylogenetic tree we tested character support for an unrooted network of one taxon sampled from each of the four high bootstrap-supported groups shown in Figure 2. Assuming monophyly of the four groups and including all 14 albatross sequences, 120 possible combinations of taxa exist for this test. We extracted from the data set and tested separately each possible combination of four taxa. Character support was assessed for the three topological arrangements possible among each four-taxon combination (i.e. we computed 360 separate values; results summarized in Fig. 3A). For all 120 combinations of taxa, a monophyletic origin of sooty albatrosses and southern mollymawks (i.e. Topology I; Fig. 3A) was best supported in comparison to the two alternative arrangements (i.e. Topologies II and III; Fig. 3A). Four combinations of sampled taxa tied equally highest support with a ratio of 42 characters (38 or 39 transitions and 3 or 4 transversions) supporting the Topology I arrangement to 7 characters (only transitions) supporting a best alternative arrangement (three combinations for Topology II and one combination for Topology III). The character support for these four identical higher-level topologies when compared with the nearest scoring alternative topology (i.e. 42:7) was highly significant ($P <$



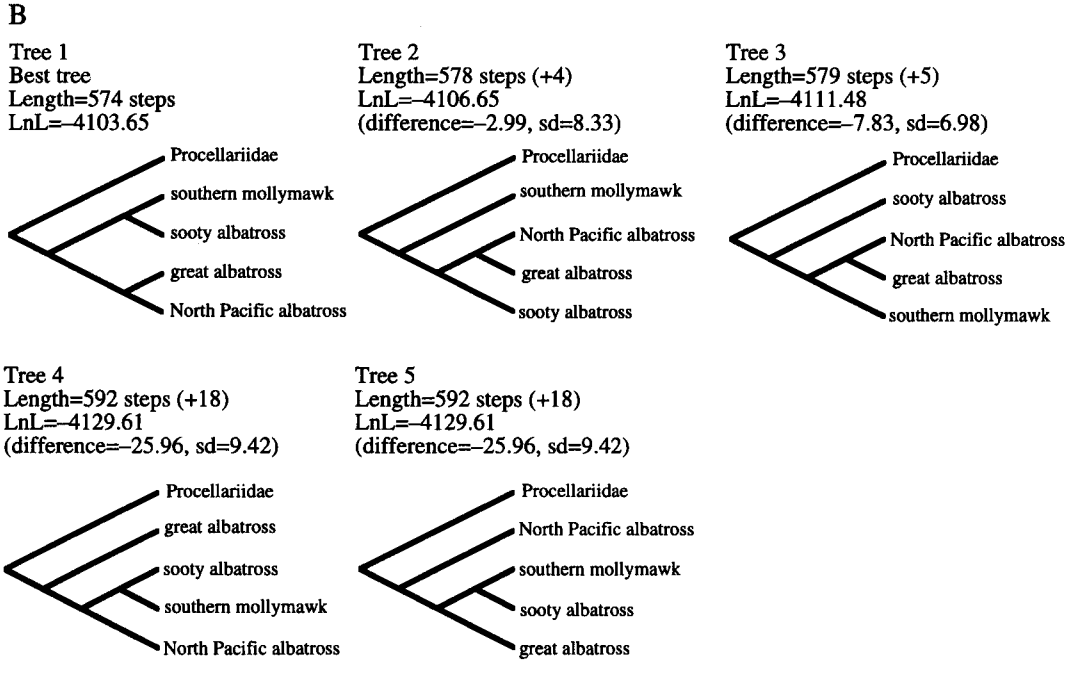


Fig. 3. (A) Four-taxon test of character support for the internal branch of topological arrangements among sampled taxa of the higher-level groups and (B) the five possible rooted arrangements of Fig. 3A. Topology I. Most-parsimonious trees include all 16 taxa and were determined based on the higher-level group constraints shown (i.e. rearrangements were allowed only within these groups). Exact tree descriptions are: Tree 1, best tree as described in Results; Tree 2, (((((*Diomedea epomophora*, (*D. amsterdamensis, D. exulans*)), (((*D. immutabilis, D. nigripes*), *D. albatrus*), *D. irrorata*)), (*Phoebetria palpebrata, P. fusca*)), (*D. chlororhynchos*, ((*D. bulleri, D. cauta*), (*D. chrysostoma, D. melanophris*)))), (*Macronectes giganteus, Procellaria cinerea*)); Tree 3, ((((*D. chlororhynchos*, ((*D. bulleri, D. cauta*), (*D. chrysostoma, D. melanophris*, ((*D. epomophora*, (*D. amsterdamensis, D. exulans*)), (((*D. immutabilis, D. nigripes*), *D. albatrus*), *D. irrorata*))), (*P. palpebrata, P. fusca*)), (*Macronectes giganteus, Procellaria cinerea*)); Tree 4, (((((*P. palpebrata, P. fusca*), (*D. chlororhynchos*, ((*D. bulleri, D. cauta*), (*D. chrysostoma, D. melanophris*)))), ((*D. immutabilis, D. nigripes*), (*D. albatrus, D. irrorata*))), (*D. epomophora*, (*D. amsterdamensis, D. exulans*))), (*Macronectes giganteus, Procellaria cinerea*)); and Tree 5, (((((*P. palpebrata, P. fusca*), (*D. chlororhynchos*, ((*D. bulleri, D. cauta*), (*D. chrysostoma, D. melanophris*)))), (*D. epomophora*, (*D. amsterdamensis, D. exulans*))), ((*D. immutabilis, D. nigripes*), (*D. albatrus, D. irrorata*))), (*Macronectes giganteus, Procellaria cinerea*)).

0.001) based on a binomial test (Templeton 1983). The four-taxon higher-level topology was congruent in branching pattern with the phylogenetic tree derived from analyses of the complete data set.

We estimated the root location to Topology I by creating complete 16-taxa trees constrained to this topology. A branch to the Procellariidae outgroup was attached to the five possible branch positions of Topology I and parsimony and likelihood support computed for the different higher-level group arrangements (Fig. 3B). As expected, our phylogenetic tree (Tree 1; L = 574 steps) is the most parsimonious and most likely rooted hypothesis of relationships among these birds (Fig. 3B). Based on a parsimony criterion, the four alternative trees (i.e. Tree 2 to Tree 5) are rejected as hypotheses of relationships because they are less parsimonious (L = 578–592 steps). Of the four rejected trees, numbers 4 and 5 are 18 steps longer (L = 592 steps) and also are significantly rejected based on log-likelihood comparisons (i.e. the log-likelihood difference is outside a 95% confidence interval compared with the maximum likelihood tree [Kishino and Hasegawa 1989]). Although rejected by a parsimony criterion, the two remaining trees (2 and 3), at four steps longer (L = 578), are not significantly rejected based on log-likelihood differences. We note, however, that the inclusion of many invariant sites—in the case of mtDNA primarily the first and second codon positions—creates a considerable inflation of the estimate of likelihood variance. This inflation in turn affects the potential rejection of alternative hypotheses by unrealistically widening the confidence interval based on the computed standard error (e.g. see the discussion of codon first and second position characters grouped together as "class-2 sites" by Hasegawa and Kishino [1989]). Interestingly, however, Tree 2, which postulates southern mollymawks as the sister-group to remaining albatrosses, is more likely (LnL = −4105.15) than Tree 3, which postulates the sooty albatrosses as the sister-group (LnL = −4111.48). Further tree-searching determined the existence of an additional 10 trees (not including Tree 1, the most parsimonious tree) that were more parsimonious than Tree 2 and Tree 3 (i.e. in the range L = 575,577 steps; LnL = −4104.81, −4116.65). These 10 trees were congruent with the phylogenetic tree in terms of their higher-level branching pattern (i.e. a topology of Tree 1 but with trivial apical rearrangements occurring within the higher-level groups).

Discussion

Genera of albatrosses.—The status and number of genera in the Diomedeidae (Table 1) have varied widely since the formal description of the first known taxon *Diomedea exulans* (Linnaeus 1758). Nearly a century elapsed before Reichenbach (1852) introduced three additional genera (i.e. *Phoebetria, Phoebastria,* and *Thalassarche*), assigning a member of *Diomedea* into each of the four. In a taxonomic synopsis of the petrels that followed Reichenbach's work, Coues (1866) presented unique morphological characters that established monophyly of known species of Diomedeidae among the procellariiforms. Further, he (1866:187–188) developed a hierarchically defined classification based on the presence or absence of well-described morphological characters among albatrosses. Although Coues presented evidence for "morphological-groups" within *Diomedea,* he did not name them formally at that time. In fact, Coues arbitrarily rejected two of Reichenbach's genera (*Phoebastria* and *Thalassarche*) and adopted a more conservative arrangement, admitting only *Diomedea* (southern mollymawks, North Pacific albatrosses, and "great" albatrosses) and *Phoebetria* (for the single sooty albatross known at that time; see Table 1).

The discovery of new albatross taxa, particularly from the southern oceans and the Australia/New Zealand region, led to an increased interest in the taxonomy of the group, and several genera either were reintroduced or created (see Table 1). Generic-level revisions finally culminated in Mathews' (1934) treatment of the family Diomedeidae, which admitted all eight genera that had been described previously (Table 1). Subsequently, however, Mathews and Hallstrom (1943) subsumed the monotypic genus *Rhothonia* back into *Diomedea,* reuniting the morphologically similar "great" albatrosses. In addition, Mathews and Hallstrom elected a new monotypic genus *Julietata* for the unique equatorial species *Phoebastria irrorata* based on morphological differences from other North Pacific albatrosses (*albatrus, immutabilis, nigripes*), which again resulted in a total of eight genera for the 18 known taxa. Shortly thereafter, in a wave of lumping by avian taxonomists (including G. M. Mathews), the "generically oversplit" taxono-

mies of Diomedeidae (Mathews 1934, Mathews and Hallstrom 1943) were abandoned in favor of a single, all-encompassing genus *Diomedea* (Mathews 1948).

In response to the chaotic and in many cases confusing changes that Mathews' introduced into the ornithological literature (e.g. see Murphy 1945, Serventy 1950), a standardization of procellariiform taxonomy arose (Alexander et al. 1965). The taxonomic revision of Alexander et al. (1965) essentially was an "agreed statement" among a committee of leading seabird taxonomists to reject the plethora of superfluous naming in the "Mathews" classifications in favor of prior taxonomic treatments of the order Procellariiformes (e.g. Alexander 1928, Peters 1931, Murphy 1936). Although Mathews' work certainly suffered from nomenclatural zealousness, numerous higher-level procellariiform groups were returned to less-sophisticated taxonomic treatments despite being founded on well-defined morphological features. In the process of circumventing Mathews' "inconsistent new classifications," Alexander et al. (1965) returned the genera of albatrosses to the earlier classification that essentially had been devised by Coues (1866) and in which Reichenbach's genera *Thalassarche* and *Phoebastria* had been subsumed into *Diomedea*. Since the revision by Alexander et al. (1965), little research has occurred on albatross evolutionary relationships, and the generic designations advocated have persisted in the literature (e.g. Jouanin and Mougin 1979, Sibley and Monroe 1990). Suggestions for defining "subgeneric" groups within the comprehensive genus *Diomedea* have resurfaced, however (e.g. Wolters 1975, Warham 1990).

A phylogenetic classification of the Diomedeidae.—Our results from phylogenetic analysis of cyt-*b* gene sequences revealed very clear evidence of four higher-level species-groups in the Diomedeidae (see Fig. 2). These phylogenetic species-groups are congruent with some traditional morphologically defined groups of albatrosses (i.e. current or discarded genera, or unnamed morphological groups). However, the traditional taxonomic framework for albatross relationships, i.e. sooty albatrosses *Phoebetria* versus all other *Diomedea* (e.g. Coues 1866, Murphy 1936, Alexander et al. 1965) is not supported based on most-parsimonious rooting of the arrangement among the well supported higher-level groups (see Fig. 2). Our cyt-*b* phylogenetic hypothesis supports the notion of an early basal dichotomy among members of the Diomedeidae. This initial dichotomy led to a lineage limited in distribution to the southern oceans comprised of two groups, southern mollymawks and sooty albatrosses, versus a more geographically widespread lineage also with two groups, the North Pacific albatrosses and the "great" albatrosses from the southern oceans. The molecular phylogeny provides for the first time evidence of monophyly of sooty albatrosses and southern mollymawks and indicates that the traditional genus *Diomedea* is paraphyletic. The current taxonomy of albatrosses, traceable to Coues (1866), provides an illustrative avian example of an "either-or" type of classification. Historically, the genus *Diomedea* received all albatross taxa that were not *Phoebetria*, regardless of the clear morphological affinities that united groups within *Diomedea*. Indeed, Coues presented the morphological evidence for these groups but refrained from providing formal names. Unfortunately, the later and more sophisticated taxonomies of albatrosses that recognized these affinities and provided named groups (e.g. Mathews 1934, Mathews and Hallstrom 1943) were rejected during the taxonomic "cleansing" of the Procellariiformes (Alexander et al. 1965).

It is interesting to note that the molecular phylogeny is concordant with monophyly of Coues' morphologically defined groups within the paraphyletic traditional genus *Diomedea*. Based on discrete characters of the bill and simple diagnostic allometric measurements, Coues proposed two natural groups within the *Diomedea* (i.e. with the prior exclusion of *Phoebetria*). Coues' "Genus I. *Diomedea*: Group A" (i.e. *D. exulans, D. albatrus, D. irrorata* [the first description of a partial cranium of this species and correctly assigned to the group], and *D. nigripes*) is concordant with a primary lineage in our phylogeny. This group, some of which were later transferred to the resurrected genus *Phoebastria* (*albatrus, immutabilis, nigripes,* and *irrorata*; Mathews 1934), contains the largest albatrosses and can be characterized by features including a relatively short tail, laterally broadened bill (particularly a wide boss-like broadening of the culminicorn posterior of the nostrils), as well as large, wide nostrils. The later division of taxa to *Phoebastria* also is congruent with the cyt-*b* phylogeny. Coues' second major group "Genus *Diomedea*: Group B" (i.e. *D. melanophris, D. cauta,*

TABLE 5. A phylogenetic classification of the Diomedeidae.

Family Diomedeidae	
Genus *Thalassarche*	
Species	*T. chlororhynchos*
	T. bulleri
	T. cauta
	T. chrysostoma
	T. melanophris
Genus *Phoebetria*	
Species	*P. palpebrata*
	P. fusca
Genus *Diomedea*	
Species	*D. exulans*
	D. amsterdamensis
	D. epomophora
Genus *Phoebastria*	
Species	*P. immutabilis*
	P. nigripes
	P. irrorata
	P. albatrus

D. chlororhynchos, and *D. chrysostoma*) is the second clade within the other primary cyt-*b* lineage. This group is now more commonly known as the southern mollymawks (including *D. bulleri*, discovered after this date) and can be characterized in comparison with Group A by a laterally compressed and much weaker bill with narrow culminicorn, and a relatively longer and slightly rounded tail. Interestingly, *Phoebetria* shares some of these morphological features with the southern mollymawks (*Thalassarche*), providing useful corroborative evidence for their monophyly. For example, even Coues (1866) remarked on the unclear distinction in bill morphology between *Thalassarche* and *Phoebetria*, pointing out similar general features such as extreme overall lateral compression and the acute narrowing of the culminicorn posterior to the nostrils. Indeed, Coues considered the bill of *Phoebetria* "hardly separable" from that of some members of *Diomedea* (i.e. *Thalassarche*) but eventually relied upon additional "features radically distinct from. . .those presented by *Diomedea* proper" to distinguish at a generic level the single known species of sooty albatross (*Phoebetria fuliginosa* [*palpebrata*]) established at that time. It seems clear that the supposedly primitive morphological features that Coues used to define Reichenbach's genus *Phoebetria* (i.e. complete fuliginous plumage, presence of a sulcus in the lower mandible, and acuminate elongation of the rectrices) are in fact plesiomorphic in origin, as they can be found in various combinations in several other petrel lineages.

The evolutionary relationships among albatrosses inferred from their traditional taxonomy presents a subjective hypothesis of groupings. We therefore recommend a formal revision of the taxonomy of Diomedeidae to achieve a classification congruent with the new phylogenetic hypothesis of relationships. Our revision constitutes four genera of coordinate phylogenetic rank, each equivalent to one of the higher-level phylogenetic groups, and eliminates paraphyly of the traditional genus *Diomedea*. We resurrect two previously described genera: (1) *Thalassarche* Reichenbach 1852 (type species *melanophris* Temminck 1828), by original designation, to include the southern mollymawks; and (2) *Phoebastria* Reichenbach 1852 (type species *brachyura* Temminck 1829 [synonym *albatrus* Pallas 1769]), by original designation, to include the North Pacific albatrosses. These genera have historical precedence over later synonyms (see Table 1). Thus, a total of seven traditional species-level taxa are transferred from the genus *Diomedea* to the resurrected genera. This classification leaves the "great" albatrosses as the sole members of the genus *Diomedea* Linnaeus 1758 and retains the genus *Phoebetria* Reichenbach 1852 for the sooty albatrosses. The adoption of phylogenetically defined higher-level species-groups refines the nomenclature of the Diomedeidae and establishes four comparable biological units within the family. The recommended traditional species-level taxa within the genera are given in Table 5.

Albatross nest building.—The evolution of behavioral and life-history (BLH) characters in birds has been shown to map closely to phylogenetic relationships (Prum 1990, Winkler and Sheldon 1993, Paterson et al. 1995). Members of Diomedeidae possess a diversity of stereotyped courtship and specialized nest-building behaviors that are well described (e.g. Marchant and Higgins 1990). The inspection of a complex nest-building character among the albatrosses in our study provides a valuable example of the benefits gained from a comparative phylogenetic approach to analysis of BLH characters (Brooks and McLennan 1991). Within the Diomedeidae, only sooty albatrosses and southern mollymawks build a tall pedestal-shaped nest made primarily from earth but with occasional rock and plant material included. Birds return each breeding season to the previous year's pedestal-nest, which is both repaired and increased in size, and from which both members of the

pair perform elaborate courtship and territorial displays. This contrasts with the low nest mounds of gathered vegetation of the "great" albatrosses and the scantily lined nest scrapes of North Pacific albatrosses, which in both cases are rebuilt each breeding season (Warham 1990).

Given that no other petrel builds a nest pedestal, the traditional taxonomic arrangement of albatrosses would lead us to expect either that an ancestor of all albatrosses built a pedestal nest and subsequently was lost from a lineage within the genus *Diomedea*, or that both *Phoebetria* and a lineage within *Diomedea* independently gained the pedestal nest-building behavior from an ancestor that did not build a pedestal nest. However, it seems more likely that the complex and stereotyped nest-building behavior arose only once. Our cyt-*b* phylogeny resolves a single, i.e. monophyletic, origin of this behavioral character in an ancestor of *Phoebetria* and *Thalassarche* that has persisted throughout this major albatross lineage. Similar to some BLH characters analyzed by Paterson et al. (1995), it appears that building a pedestal nest has remained stable over a considerable evolutionary period. It is likely that the evolution of a laterally compressed bill morphology also arose in the ancestor of *Thalassarche* and *Phoebetria*. The bill morphology is of particular importance because nest building is accomplished by a lateral plastering action of the bill while the bird rotates on top of the pedestal nest (G. Nunn pers. obs.). Further comparative analyses of other such characters among albatrosses may provide valuable insight into the patterns of evolution of complex BLH characters in seabirds (e.g. see Paterson et al. 1995).

Calibration of evolutionary rate.—Considerable evidence suggests that molecular evolutionary rates vary among taxonomic lineages (Britten 1986, Li et al. 1987). In particular, the assumption of a molecular clock is unlikely to extend throughout a phylogeny whose members exhibit diverse reproductive or metabolic rates, the latter being inversely correlated with body size (Martin et al. 1992, Martin and Palumbi 1993). Within the Diomedeidae, however, both basal metabolic rate (Adams and Brown 1984) and age at first breeding (Jouventin and Weimerskirch 1988) vary by much less than an order of magnitude, and evolutionary-rate calibrations among the now well-established phylogenetic lineages are possible.

Fossil remains of seabirds, mostly from the Northern Hemisphere (Warheit 1992), indicate the existence of a diverse albatross fauna during the late Tertiary period. A stratigraphically dated fossil from California suggests the presence of an albatross that shared affinities with *D. albatrus* (= *Phoebastria*) in the North Pacific Ocean as early as the mid-Miocene, approximately 15 million years before present (MYBP; Miller 1962). Relatively few procellariiforms have been discovered from Tertiary deposits bordering the southern oceans (Olson 1985a,b), in contrast to the abundance of Northern Hemisphere fossils. However, the discovery of a cranial fragment of a southern mollymawk of surprisingly modern appearance in Australia indicates the presence of a member of the genus *Thalassarche* at the Miocene-Pliocene boundary about 10 MYBP (Wilkinson 1969).

Previous assessment of corrected mitochondrial cyt-*b* codon third-position divergence in homeotherms suggested an evolutionary rate of approximately 10% per million years in a number of mammalian lineages (Irwin et al. 1991); this value has been corroborated by further studies of ground squirrels (Thomas and Martin 1993). On the basis of the fossil evidence outlined above, we were able to calibrate cyt-*b* third-position rate estimates for the phylogenetically defined higher-level groups *Phoebastria* and *Thalassarche*, given well-supported relationships to their respective sister groups, i.e. *Diomedea* and *Phoebetria*. The corrected third-position pairwise divergence between members of (1) *Phoebastria* and *Diomedea* ($\bar{x} = 23.62 \pm 1.21\%$, $n = 12$) and (2) *Thalassarche* and *Phoebetria* ($\bar{x} = 28.58 \pm 0.88\%$, $n = 10$) leads to rate calibrations of 1.58% and 2.86% per million years, respectively. These independently derived estimates are not perfectly concordant with one another but are lower than estimates derived in mammals (Irwin et al. 1991). The inclusion of a wider array of mammalian lineages suggests that rates may be substantially slower in those of larger body size (i.e. lower basal metabolic rate) such as the baleen whales (Martin and Palumbi 1993). Low metabolic and reproductive rates of albatrosses may be causal factors explaining the low cyt-*b* rate calibrations, but these observations are not idiosyncratic. Rates of mtDNA evolution established from the split between the anseriform genera *Anser* and *Branta* (Shields and Wilson 1987) suggest that, in comparison with their body size, geese have a slower mtDNA substitution rate than other homeo-

therms (Martin and Palumbi 1993). Similarly, comparative restriction fragment analyses of mtDNA evolutionary rates among a selection of passerine and nonpasserine groups also support a rate slow-down in comparison with nonavian vertebrate groups (Kessler and Avise 1985). The surprisingly low cyt-*b* calibrations obtained here support the hypothesis that avian mitochondrial genomic evolutionary rates are considerably slower in birds than in mammals.

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APPENDIX. Individual taxa sequenced (with binomen or current trinomen for traditional polytypic species) and their collection localities and dates. Taxonomic scheme of genera follows our suggested phylogenetic classification of higher-level groups in Diomedeidae.

Taxon	Collection locality and date
Diomedeidae	
Thalassarche (southern mollymawks)	
Thalassarche chlororhynchos chlororhynchos (Yellow-nosed Mollymawk)	Gough Island, Atlantic Ocean; October 1990.
Thalassarche bulleri bulleri (Buller's Mollymawk)	Snares Islands, New Zealand; March 1993.
Thalassarche chrysostoma (Gray-headed Mollymawk)	Marion Island, Indian Ocean; April 1993.
Thalassarche melanophris melanophris (Black-browed Mollymawk)	Near Cape Town, South Africa; April 1992.
Thalassarche cauta cauta (Shy Mollymawk)	Pedra Branca, Tasmania; August 1992.
Phoebetria (sooty albatrosses)	
Phoebetria palpebrata (Light-mantled Sooty Albatross)	Marion Island, Indian Ocean; April 1993.
Phoebetria fusca (Dark-mantled Sooty Albatross)	Marion Island, Indian Ocean; April 1993.
Diomedea "great" albatrosses)	
Diomedea exulans dabbenena (Wandering Albatross)	Gough Island, Atlantic Ocean; October 1990.
Diomedea amsterdamensis (Amsterdam Albatross)	Ile Amsterdam, Indian Ocean; July 1993.
Diomedea epomophora sanfordi (Royal Albatross)	Forty-fours, Chatham Islands, New Zealand; March 1992.
Phoebastria (North Pacific albatrosses)	
Phoebastria immutabilis (Laysan Albatross)	North Pacific Ocean (40°06'N, 161°30'E); August 1991.
Phoebastria nigripes (Black-footed Albatross)	North Pacific Ocean (Washington State, USA); 1988.
Phoebastria irrorata (Waved Albatross)	Isla Española, Galapagos Islands; October 1993.
Phoebastria albatrus (Short-tailed Albatross)	Torishima, Japan; April 1993.
Procellariidae	
Macronectes giganteus (Southern Giant Petrel)	Marion Island, Indian Ocean; October 1990.
Procellaria cinerea (Gray Petrel)	Gough Island, Atlantic Ocean; October 1990.