Analysis of the taxonomy and nomenclature of the Procellariiformes based on complete nucleotide sequences of the mitochondrial cytochrome *b* gene

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Abstract. We used complete mitochondrial cytochrome *b* sequences, largely obtained from sequences deposited with GenBank, supplemented by published sequences, from most genera and most species among the Procellariiformes to infer their phylogeny and molecular taxonomy. We analysed both issues of higher-level relationships within the order, and questions of the correct classification of taxa at the levels of genus, subgenus, species and subspecies. Nucleotide sequence data of cytochrome *b* are insufficient to resolve all higher-relationship issues, which must await the analysis of additional mtDNA and nuclear sequence data, but they do suggest some striking new findings. Sequence and distance data allow us to make judgments about the boundaries between taxa at various levels that are less arbitrary in these matters than those based on morphological or phylogenetic data alone. Working within the multidimensional Biological Species Concept, we reject the recently proposed splits among albatross species, and lump *D. amsterdamensis* as a subspecies of *Diomedea exulans*. A strong relationship of the storm-petrels to the albatrosses is apparent. We subdivide the storm-petrels into two subfamilies, Hydrobatinae and Oceanitinae. Presently, *Oceanodroma* is paraphyletic, and is regrouped into four genera: *Hydrobates* (of which *Oceanodroma* becomes a junior synonym), *Cymochorea*, *Halocyptena*, and *Thalobata*. In the fulmar clade, *Macronectes halli* should be merged with *M. giganteus*. The shearwaters formerly assigned to *Puffinus* apparently cluster into two major clades at the generic level: *Puffinus* and *Ardenna*. *Puffinus creatopus* should become a subspecies of *P. carneipes*. *Lugensa* is a distinct genus, with its closest affinities to *Pachyptila*; and the evidence suggests reducing the prions to two species: *P. turtur* and *P. vittata*. However, the prion–*Lugensa* group remains *incertae sedis*. *Bulweria* groups with *Pseudobulweria* and *Procellaria*. Our data reveal that *Pterodroma* has internal structure at the subgeneric level; they establish the subgenera *Pterodroma*, *Hallstroma* and probably *Cookilaria*, but final analysis will require data from nearly all gadfly-petrel species. Amino acid distances are used to estimate times of divergence for the various branchings.

Introduction

A brief history of the classification of the Procellariiformes

The locus classicus of the 'standard' approach to the classification and nomenclature of the Procellariiformes can be found in Alexander *et al.* (1965). This paper, to which no less than 15 coauthors added their names, rejected the extreme 'splitting' approach of Mathews (1934) and the equally extreme 'lumping' approach of the same author (Mathews 1948). In the earlier paper, Mathews proposed 51 genera for 81 species; in the later paper, the number of genera was reduced to 12. Alexander *et al.* (1965) issued a strong plea for a more stable nomenclature, and complained that '... few of the major changes in the classification of the petrels proposed in recent years have been based on new research or

involve important reassessments of relationships' (Alexander *et al.* 1965: 402). They put forward an agreed statement to indicate the classification they preferred. We will discuss this, with brief comments on each of the families.

Diomedeidae

Alexander *et al.* (1965: 402–403) noted that the albatrosses could be divided into four groups: two large groups, one of medium-sized southern mollymawks, and one of North Pacific albatrosses; and two groups each consisting of two pairs: the great albatrosses and the sooty albatrosses. While noting that there were proposals to divide the mollymawks into two or three genera distinct from *Diomedea* Linnaeus,

1758, they concluded that '... since the mollymawks grade through the Black-browed Albatross *D. melanophris* and the north Pacific species into the great albatrosses, it seems doubtful whether any useful purpose would be served by the recognition of these additional genera' (1965: 403). Thus, only *Diomedea* and *Phoebetria* Reichenbach, 1852 were recognised for the albatrosses.

Procellariidae

Alexander *et al.* (1965: 403) endorsed the amalgamation of *Fulmarus* Stephens, 1826 with *Priocella* Hombron & Jacquinot, 1844, but recommended that genera seen as allied to the fulmars (*Macronectes* Richmond, 1905; *Thalassoica* Reichenbach, 1852; *Daption* Stephens, 1826; and *Pagodroma* Bonaparte, 1856) be retained as distinct. *Contra* Mathews (1948), they wished to retain *Bulweria* Bonaparte, 1842 as distinct from *Pterodroma* Bonaparte, 1856, thus avoiding the 'consequent vast name-changes'. They rejected Mathew's (1912) splitting of *Pachyptila* Illiger, 1811 into a number of genera, and retained *Halobaena* Bonaparte, 1856 as a genus close to *Pachyptila*. They deplored Mathew's (1948) amalgamation of *Procellaria* Linnaeus, 1758 with *Puffinus* Brisson, 1760, and recommended the retention of *Calonectris* Mathews & Iredale, 1915 as a distinct genus.

Hydrobatidae

The authors rejected Mathews' (1948) proposal to amalgamate most northern species in one genus, *Hydrobates* Boie, 1822, and most southern ones in *Oceanites* Keyserling & J. H. Blasius, 1840. They stated (1965: 404): '... current classifications appear to portray the nature of their relationships quite well, recognising a higher degree of differentiation in southern than in northern forms'. Thus they retain: *Oceanites*; *Garrodia* Forbes, 1881; *Pelagodroma* Reichenbach, 1852; *Fregetta* Bonaparte, 1855; *Nesofregetta* Mathews, 1912; *Hydrobates*; *Halocyptena* Coues, 1864; and *Oceanodroma* Reichenbach, 1852.

Pelecanoididae

These were seen as unproblematic, and the 15 authors unite in following Murphy's (1936) decision to combine all species in *Pelecanoides* Lacépède, 1799.

Alexander *et al.* (1965: 404) concluded by urging '... others to follow [their classification and nomenclature], and suggest that they should provide reasoned justification before they depart from it.'

The utilisation of genetic distances to define taxonomic rank

Classification of birds and other organisms is traditionally based on morphological characters, although data from acoustics, behaviour and distribution (if available) are also taken into account. Systematic classifications usually rely on similarity, such that taxa showing the least difference are considered to be closely related. Since morphological simi-

larity in two lineages of organisms can be due to adaptation to similar ecological constraints, adaptive characters can lead to incorrect taxonomic conclusions. The analysis of nuclear or mitochondrial marker genes has become a widely applied tool during the last 15 years in all fields of zoology, including ornithology, to reconstruct phylogenies and phylogeographic relationships (overviews in Avise 1994; Mindell 1997). Molecular data have the great advantage that convergence does not impair an analysis to the same degree as morphological data do. If taxa belong to the same species, their marker genes will be identical or almost identical, and intraspecific distances are significantly smaller than those between established species. Molecular data also provide an estimate for the time scale in which a particular evolutionary step has taken place ('molecular clock') and therefore allow both a phylogenetic and phylogeographic analysis of the unknown past of a group of organisms. Molecular data have therefore become an important tool for taxonomic and evolutionary studies.

It is our contention that the calibration of distances between taxa made possible by DNA sequencing of marker genes makes it possible to obtain more reliable decisions as to the boundaries between genera, subgenera, species and subspecies. We are aware that this is not a trivial matter. Issues of technique, and selection of genes arise. Nonetheless, by examining the distances between well recognised subspecies and species *within* a genus, or genera within a family, especially where there is independent evidence for that status, such as a broad area of interbreeding between subspecies, we can make soundly based decisions. A good example of using nucleotide distances to establish boundaries at the level of genera can be found in Nunn *et al.* (1996), which examined the phylogenetic relationships among members of the albatross family (Procellariiformes:Diomedeidae) and, *contra* the recommendations in Alexander *et al.* (1965), reallocated nine species formerly grouped in *Diomedea* Linnaeus, 1758. While the reassignment of genera was required in part by the paraphyly of *Diomedea*, the splitting of some genera was justified by the distances involved. For example, whereas the pairwise distances within *Thalassarche* range from 1.66% to 3.15%, within the more restricted *Diomedea* from 0.87% to 3.15%, and within *Phoebastria* from 1.75% to 4.72%, the distances between the members of the three different genera were much greater. Distances from *T. chlororhynchos* to the three members of *Diomedea* (in the narrower sense) range from 10.15% to 10.50%. Distances from *T. chlororhynchos* to the four members of *Phoebastria* range from 9.89% to 11.20%. However, it cannot be said that molecular data have solved the problem of establishing the boundaries between genera, subgenera, species and subspecies unambiguously.

A further issue is whether there exists a universal clock in relation to the molecular evolution. Avise and Walker (1998) used a 'conventional' mtDNA substitution rate of 2% per million years to date recent speciation events and to assess

the effects of events in the Pliocene and Pleistocene on genetic diversion of vertebrates. Avise and Johns (1999), furthermore, have proposed a standardised temporal scheme of biological classification for extant species. They propose a temporal-banding concept, which was applied to produce a time-standardised classification of organisms in terms of Genus, Tribe, Subfamily, Family, Superfamily, Suborder and Order. They argued that: 'The phylogenetic knowledge required for a time-standardized nomenclature arguably may emerge in the foreseeable future from vast increases in multilocus DNA sequence information'. We believe that their point is a valuable one, and provides a valuable goal. But we are not at that point yet.

Nunn and Stanley (1998: 1360) reported that 'rates of mitochondrial DNA evolution are slower for larger taxa', concluding that 'even lineage-specific molecular clocks may not be tenable if calibrations involve taxa with different metabolic rates'. They reported that fossil calibrations also showed that the largest procellariiform birds have the slowest rate of divergence '0.62% per Myr (0.88% using a Kimura-2 correction)'. The intermediate-sized Procellariidae appear to be evolving at an intermediate rate, '0.78% per Myr (0.90% using a Kimura-2 correction).' The smallest of the family, those in Oceanitinae show the fastest rate of evolution, '0.92% per Myr (1.29% using Kimura-2 correction)'. Nunn and Stanley also investigated factors in evolutionary rates other than body mass.

It appears that with nucleotide distances of up to 6–8%, the 2% per million years of Avise and Walker (1998) is a good approximation. But above that level multiple substitutions can occur over long divergence times. This fact may well undercut Nunn and Stanley's (1998) reliance on cytochrome *b* as a basis for estimating divergence times. Zuckerkandl and Pauling (1965) noticed that an almost linear relationship could be found between the degree of sequence divergence in proteins between pairs of organisms and their putative divergence times. This finding was the original basis for the 'molecular clock' hypothesis. But with the development of rapid DNA sequencing techniques, nucleotide sequences have been determined in recent years in preference to protein sequences. However, nucleotide sequences can easily be converted into amino acid sequences using the universal genetic code. Protein distances appear to be almost linear with time. Taking the divergence between Struthionidae (ostriches) and Rheidae (rheas) as a time marking, we can calibrate the protein clock, assuming that the taxa diverged ~90 million years ago, before the land masses had split (Hedges *et al.* 1996). This approach has been used to date the divergence of taxa among the Otitidae in Broders *et al.* (2003), who suggested a rate of ~0.1% per million years for non-synonymous amino acid substitutions and ~0.2% per million years for amino acid substitutions. Subsequently, the second author has reanalysed the calibration of the amino acid–based molecular clock. Through the

use of the splits between reptiles, birds and mammals and between birds and mammals as calibration points (Hedges *et al.* 1996), we have determined that ~0.1% is a better value for the rate of amino acid substitution per million years. We have used this approach to date the divergences between the various clades among the Procellariiformes. Fig. 1 displays a calibration of amino acid substitutions against time.

A split of amniotes (reptiles, birds, mammals) is assumed to have taken place ~335 million years ago; the split between bird and mammal lineages took place ~310 million years ago (Hedges *et al.* 1996).

The importance of different species concepts for taxonomic analysis

The interpretation of morphological and genetic data depends to some degree on which species concept is favoured by an author. For example, Robertson and Nunn (1998) published an important paper examining the phylogenetic relationships among members of the albatross family (Procellariiformes:Diomedeidae) on the basis of complete mitochondrial DNA cytochrome *b* sequences. This resulted in the splitting of the previously accepted 13 albatross species to form 24 species. Important in evaluating the proposed species splits is the fact that Robertson and Nunn (1998: 2–3) declared their acceptance of a version of the Phylogenetic Species Concept (PSC), the hallmark of which is the application of the label 'species' to the terminal taxa of the evolutionary tree.

There are, of course, several versions of the PSC. As J. H. Haffer (in del Hoyo *et al.* 1997: 15) pointed out, at least two versions of the PSC, including that of Hennig (1966),
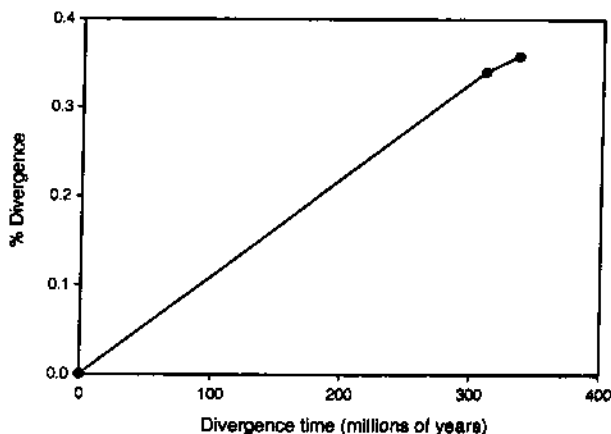
Fig. 1. Calibration of amino acid distances of the cytochrome *b* gene with divergence time. A split of amniotes (reptiles, birds, mammals) is assumed to have taken place ~335 million years ago; the split between bird and mammal lineages 310 million years ago (Hedges *et al.* 1996). The following sequences were selected as references: Reptiles; *Lacerta vivipara* (U69834); mammals, *Microtus oeconomus* (AY220044); *Elephas maximus* (AB002412); birds, several members of Ratitidae, Procellariiformes and Otitidae.

and the so-called 'monophyly version, PSC2', accept the possibility of subspecies within species. The third version, PSC1 (Cracraft 1983; Zink and McKitrick 1995; Zink 1996, 1997), assigns species status to any population that is morphologically diagnosable, and thus elevates most subspecies to species rank. It is this narrow species concept that Robertson and Nunn (1998) embrace.

Haffer (1997: 15–16) emphasised some strongly subjective aspects of PSC1: 'The term 'phylogenetic species' subsumes taxa of conspicuously varying biological differentiation from those at early stages of speciation to taxa that have already reached phylogenetic independence. Another problem under PSC1 is that the number of species taxa recognised is a matter of the resolving power of the analytical tools available ...; therefore species limits are highly subjective. Numerous small populations or even groups of individuals may be 'diagnosable' with improved laboratory techniques and would thus qualify as species'.

The PSC has arisen largely in opposition to the Biological Species Concept (BSC), the central concept of which is 'Species are groups of interbreeding natural populations that are reproductively isolated from other such groups' (Mayr 1996: 263). The application of the emphasis on interbreeding can be most easily studied with sympatric populations, the so-called Non-Dimensional BSC. But questions arise in relation to allopatric populations. This led to the Multidimensional BSC (Mayr 1996), according to which species are often composed of local or temporarily circumscribed populations that differ slightly from each other. Such populations, when they are considered to be conspecific, are combined into a *polytypic species*. Mayr (1996: 272) recognised: 'The major species problem in species level taxonomy is to decide which local populations to combine into polytypic species. Since this decision is based on inference, it is always somewhat uncertain'.

We suspect that the main factor driving the splitting of albatross species in Robertson and Nunn (1998) was the fact that conservation legislation in many countries considers only species as worthy of protection, and not subspecies. We sympathise with this strategy. Conservation legislation is flawed. The entities that become extinct are often genetic lineages (or populations) rather than species, except, of course, where a species consists of a single population. And we endorse the proposal of Schodde and Mason (1999) for the use of a distinct term, 'ultrataxon', to refer to monophyletic species plus the subspecies of polytypic species. But we agree with Schodde and Mason (1999) that the inadequacy of conservation legislation is not an adequate reason to change one's considered scientific position in relation to the question of species.

For the purposes of this paper, we wish to highlight one issue: the Multidimensional BSC's need to rely on inference in deciding on the status of allopatric taxa. We quoted Mayr (1996) before as saying: 'Since this decision is based on

inference, it is always somewhat uncertain'. Zink (1997: 101) stated: 'Many problems with using the BSC are familiar ..., such as the need to speculate whether allopatric populations are reproductively isolated'. Particularly for anyone interested in the application of DNA sequencing data of marker genes to issues of avian classification, a problem arises from the 'narrow' PSC's decision to apply the term 'species' to all terminal taxa. Suppose a pairwise distance of 0.5% nucleotide substitutions in a relevant gene is found between two taxa A and B, and also between two closely related taxa C and D, as compared with one of 5.0% or of 10.0% in the same gene between either of A and B and either of C and D. The position of the 'narrow' PSC is that as long as A, B, C and D are terminal taxa, they are all equally to be considered as 'species'. This is difficult to accept. As we shall see in considering distance data below, the picture that emerges there supports the Multidimensional BSC's view of polytypic species including evolutionarily younger subspecies. In this communication, we follow the Multidimensional BSC in maintaining the subspecies level to denominate young evolutionary lines, when they are allopatric and do not differ substantially in morphological or ecological terms.

Methods

Nunn and Stanley (1998) carried out an analysis based on complete mtDNA cytochrome *b* sequences of a much larger set of the Procellariiformes. They used these data essentially to address the question of the relation of body size to the rate of cytochrome *b* evolution. They did not, however, investigate the taxonomic implications of their sequences. We downloaded their sequences from GenBank, with a view to applying their data to that taxonomy. Their sequence numbers are given in Table 1.

We also added a number of sequences for members of the order produced by Heidrich *et al.* (1998, 2000), and also deposited in GenBank. Details of the generation of mtDNA cytochrome *b* sequences (PCR conditions, DNA sequencing) can be found in the corresponding studies.

Uncorrected 'p' distance data, obtained from these sequences, are placed below the diagonal in the distance matrices. Using MEGA (Kumar *et al.* 2001), we converted the nucleotide sequences into amino acid sequences; protein distances were calculated with a poisson correction. Since any change at the amino acid level demands a non-synonymous substitution, such changes are quite rare. For this reason, as noted above, amino acid distances provide a better guide to divergence time over longer periods than nucleotide data. Amino acid distances are placed above the diagonal in the tables that follow.

We generated six phylogenetic trees from the nucleotide dataset. Fig. 2 shows a bootstrap cladogram (1000 replicates) reconstructed with the Neighbourhood Joining (NJ) method using Jukes Cantor as a distance algorithm. Other distance algorithms, such as Kimura-2, produced identical trees. Bootstrap values at or above 80% are given above or below the relevant branch lengths. Fig. 3 provides a Maximum Likelihood (ML) tree. ML has proven to be most powerful and is now widely applied (Huelsenbeck and Crandall 1997). In addition, we generated four Maximum Parsimony (MP) trees that attempt to correct, to some extent, for differential rates of evolution among different codon positions and transitions/transversions. Since mtDNA changes at a faster rate than nuclear DNA in genes (Meyer 1994), this makes

mitochondrial marker genes so useful for the analysis of closely related taxa. But that same faster rate means that beyond a time-scale of ~19–20 million years, multiple substitutions in uncorrected data reduce the usefulness of mtDNA because of homoplasy.

Accordingly, we generated four weighted MP trees, with a view to clarifying deeper branching patterns within the phylogenetic tree. We used the following weightings in connection with MP analysis: (a) omitting third codon positions altogether; (b) downweighting third positions to 0.2, while weighting first and second positions at 1.0; (c) weighting transversions (that is, cases where a purine (adenine or guanine) is substituted by a pyrimidine (cytosine or thymine) or *vice versa*) ten times more than transitions (where a purine is replaced by the other purine, or a pyrimidine by the other pyrimidine base); and (d) weighting transversions three times more than transitions. Of the four weighted trees, we place particular emphasis on (d), for the reason, as will become clear below, that in several cases it most accurately

Table 1. GenBank accession numbers using the data of Nunn and Stanley (1998) and Heidrich *et al.* (1998, 2000)

Cytochrome *b* sequences were obtained from GenBank (http://www.ncbi.nlm.nih.gov/). Note: The size of the distance matrices, occupying 22 A4 pages in the case of both the nucleotide and amino acid tables, made it impossible to publish them with this paper. The full distance matrices are available from the first author at jpenhall@bigpond.net.au

Genus	GenBank accession number
Albatrosses	
Diomedea	U48946–48; AF076047–50
Thalassarche	U48944–45; U48953–55; AF76091–094
Phoebastria	U48949–52
Phoebetria	U48942–43
Storm-Petrels	
Oceanodroma	AF076063–67
Hydrobates	AF076059
Halocyptena	AF076058
Garrodia	AF076056
Pelagodroma	AF076072
Fregetta	AF076053–54
Fulmars	
Macronectes	AF076060–61
Fulmarus	U74348; AF076055
Thalassoica	AF076095
Pagodroma	AF076071
Daption	AF076046
Shearwaters	
Calonectris	U74356; AF076045
Puffinus	U74352–55; AF076080–88
Lugensa	U74357
Prions	
Halobaena	AF076057
Pachyptila	U74349; AF076068–70
Procellaria	
Bulweria	U74351
Pseudobulweria	U70482–83 (partial cds only; not included in matrix)
Procellaria	U74350; U48940; AF076077–78
Gadfly Petrels	
Pterodroma	U74331–47
Diving-Petrels	
Pelecanoides	AF076073–76

represents the differences between within-group and between-group distance means in the matrix.

Broughton *et al.* (2000) have argued against down-weighting transitions relative to transversions on the basis of the common-sense assumption that transitions should exhibit relatively more homoplasy, and that they should therefore be less reliable phylogenetic characters. They found that although homoplasy was greater for transitions, the absolute number of consistent transitions greatly exceeded the number of consistent transversions. Consequently transitions tended to provide '... substantially more useful phylogenetic information than transversions' (2000: 617) with the result that down-weighting transitions may be unwarranted in many cases. They observed (2000: 617) that: '... a range of transition:transversion weighting schemes applied to various mitochondrial genes and genomic partitions rarely provided improvement in phylogenetic estimates relative to equal weighting, and in some cases weighting transitions more heavily than transversions was more effective'. This perhaps explains why maximum likelihood trees (as in Fig. 3) have been found to be generally the most reliable kind of tree. Certainly, it was true in our case that Fig. 4, which was judged to be better than the other weighted trees on independent grounds, closely matched the maximum-likelihood Fig. 3. It was also true that weighting transversions three times more than transitions produced a much more plausible tree than that produced by weighting transversions ten times more than transitions.

In this paper, because of space limitations, we reproduce only (d) as Fig. 4. The second author will be happy to provide the other three trees on request.

Results and Discussion

We have assembled a dataset containing all published cytochrome *b* sequences of Procellariiformes and used NJ (Fig. 2), ML (Fig. 3) and weighted MP (Fig. 4) to infer the underlying phylogeny. We will discuss groups in order from top to bottom of the ML Tree (Fig. 3).

Albatrosses

The bootstrap figures in relation to the Diomedeidae in Fig. 2 provide 100% support for all four branches of the family in relation to the genera *Diomedea*, *Phoebastria*, *Thalassarche* and *Phoebetria*, supporting the reclassification of *Diomedea* proposed by Nunn *et al.* (1996).

In Robertson and Nunn (1998), as noted above, the question of the classification of albatrosses was carried further with the raising of what had previously been considered subspecies to species status. The following splits were proposed or supported:

- *Diomedea sanfordi* Murphy, 1917 (Northern Royal Albatross) from *Diomedea epomophora* Lesson, 1825 (Southern Royal Albatross);
- *Diomedea gibsoni* Robertson & Warham, 1992 (Gibson's Albatross), *Diomedea antipodensis* Robertson & Warham, 1992 (Antipodean Albatross) and *Diomedea chionoptera* Salvin, 1896 (Snowy Albatross) from *D. exulans* Linnaeus, 1758 (Wandering Albatross);
- *Thalassarche carteri* (Rothschild, 1903) (Indian Yellow-nosed Albatross) from *Thalassarche chlororhynchos* (J. F. Gmelin, 1789) (Atlantic Yellow-nosed Albatross);
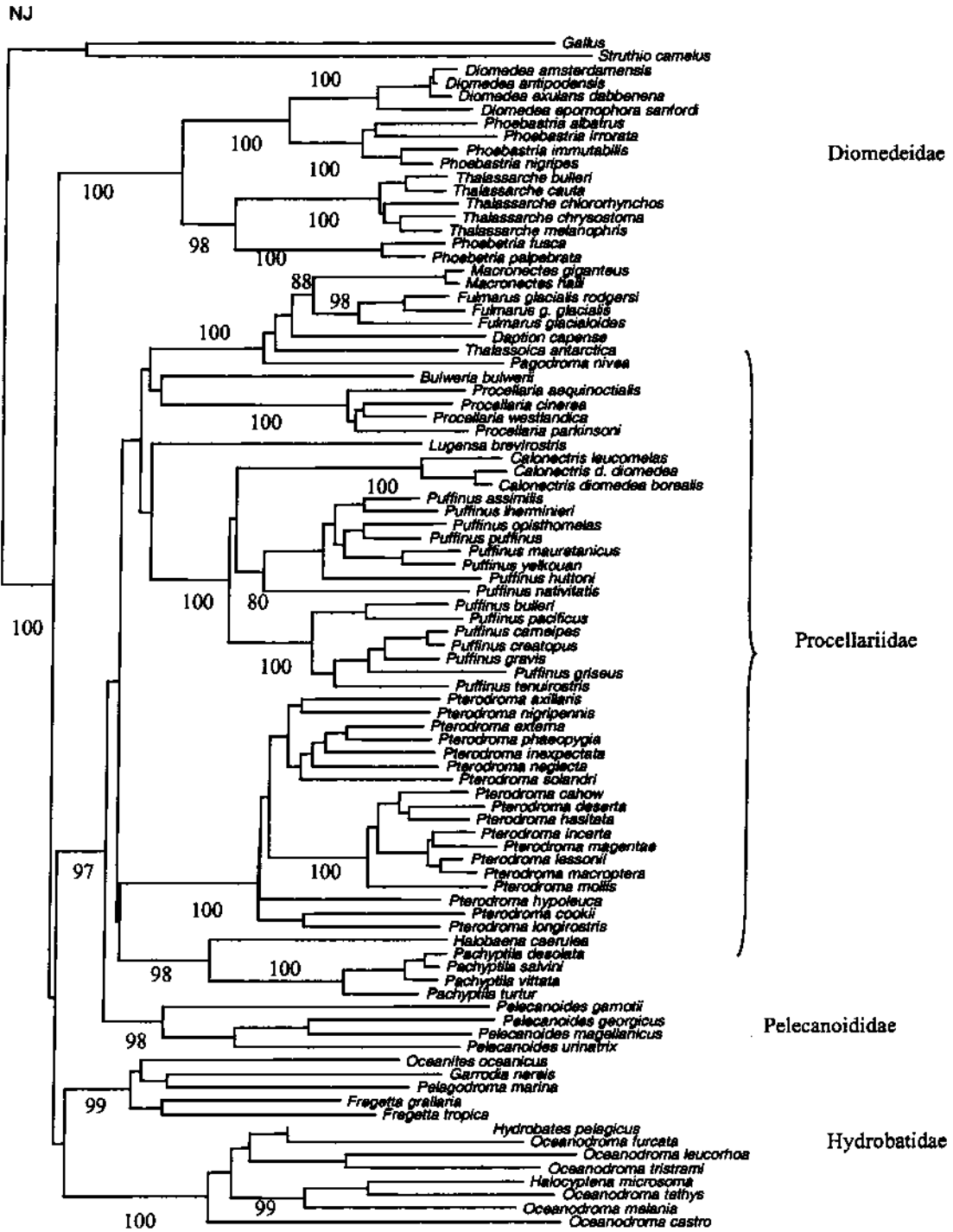
Fig. 2. Molecular phylogeny of the Procellariiformes: bootstrap cladogram (1000 replicates) reconstructed with the Neighbourhood Joining (NJ) method using Jukes–Cantor as a distance algorithm.
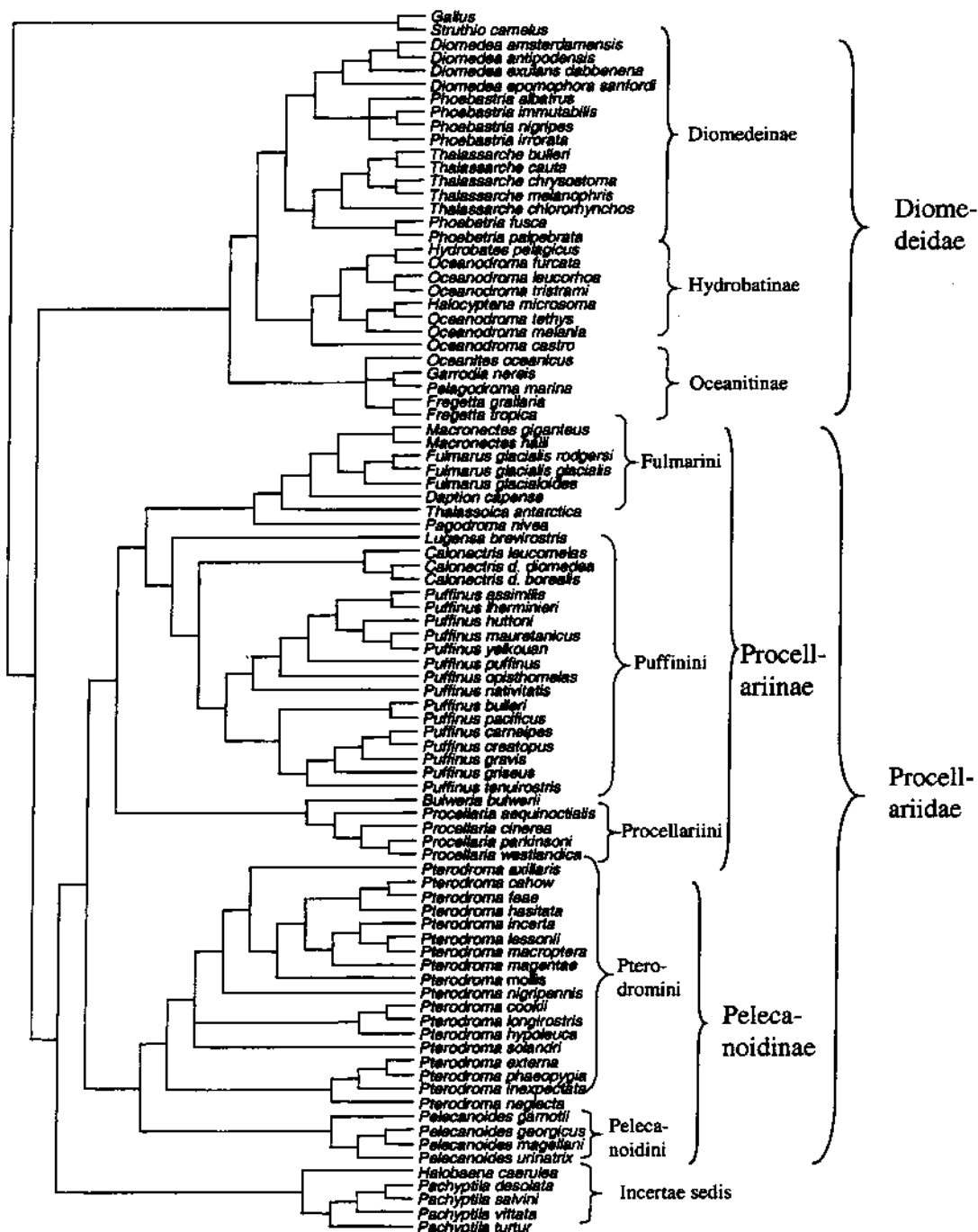
Strict

Fig. 3. Maximum Likelihood tree. Likelihood settings are in accordance with the HKY85 model; starting branch lengths were obtained using least-squares method with JC distances. Best tree: −ln(L) = 20908.97; A = 0.282; C = 0.334; G = 0 = 0.125; T = 0.259.

Strict

Gallus
Struthio camelus
Bulweria bulwerii
Procellaria aequinoctialis
Procellaria cinerea
Procellaria parkinsoni
Procellaria westlandica
Halobaena caerulea
Pachyptila desolata
Pachyptila salvini
Pachyptila vittata
Pachyptila turtur
Lugensa brevirostris
Calonectris leucomelas
Calonectris diomedea diomedea
Calonectris diomedea borealis
Puffinus assimilis
Puffinus lherminieri
Puffinus opisthomelas
Puffinus puffinus
Puffinus mauretanicus
Puffinus yelkouan
Puffinus huttoni
Puffinus nativitatis
Puffinus bulleri
Puffinus pacificus
Puffinus carneipes
Puffinus creatopus
Puffinus gravis
Puffinus griseus
Puffinus tenuirostris
Pterodroma axillaris
Pterodroma nigripennis
Pterodroma externa
Pterodroma phaeopygia
Pterodroma inexpectata
Pterodroma neglecta
Pterodroma solandri
Pterodroma cookii
Pterodroma longirostris
Pterodroma hypoleuca
Pterodroma cahow
Pterodroma feae
Pterodroma hasitata
Pterodroma incerta
Pterodroma lessonii
Pterodroma macroptera
Pterodroma magentae
Pterodroma mollis mollis
Macronectes giganteus
Macronectes halli
Fulmarus glacialis rodgersi
Fulmarus g. glacialis
Fulmarus glacialoides
Thalassoica antarctica
Pagodroma nivea
Daption capense
Pelecanoides garnoti
Pelecanoides georgicus
Pelecanoides magellanicus
Pelecanoides urinatrix
Diomedea amsterdamensis
Diomedea exulans antipodensis
Diomedea exulans dabbenena
Diomedea epomophora sanfordi
Phoebastria albatrus
Phoebastria immutabilis
Phoebastria nigripes
Phoebastria irrorata
Thalassarche bulleri bulleri
Thalassarche cauta cauta
Thalassarche chrysostoma
Thalassarche melanophris
Thalassarche chlororhynchos
Phoebetria fusca
Phoebetria palpebrata
Oceanites oceanicus
Garrodia nereis
Pelagodroma marina
Fregetta grallaria
Fregetta tropica
Hydrobates pelagicus
Oceanodroma furcata
Halocyptena microsoma
Oceanodroma tethys
Oceanodroma melania
Oceanodroma leucorhoa
Oceanodroma tristrami
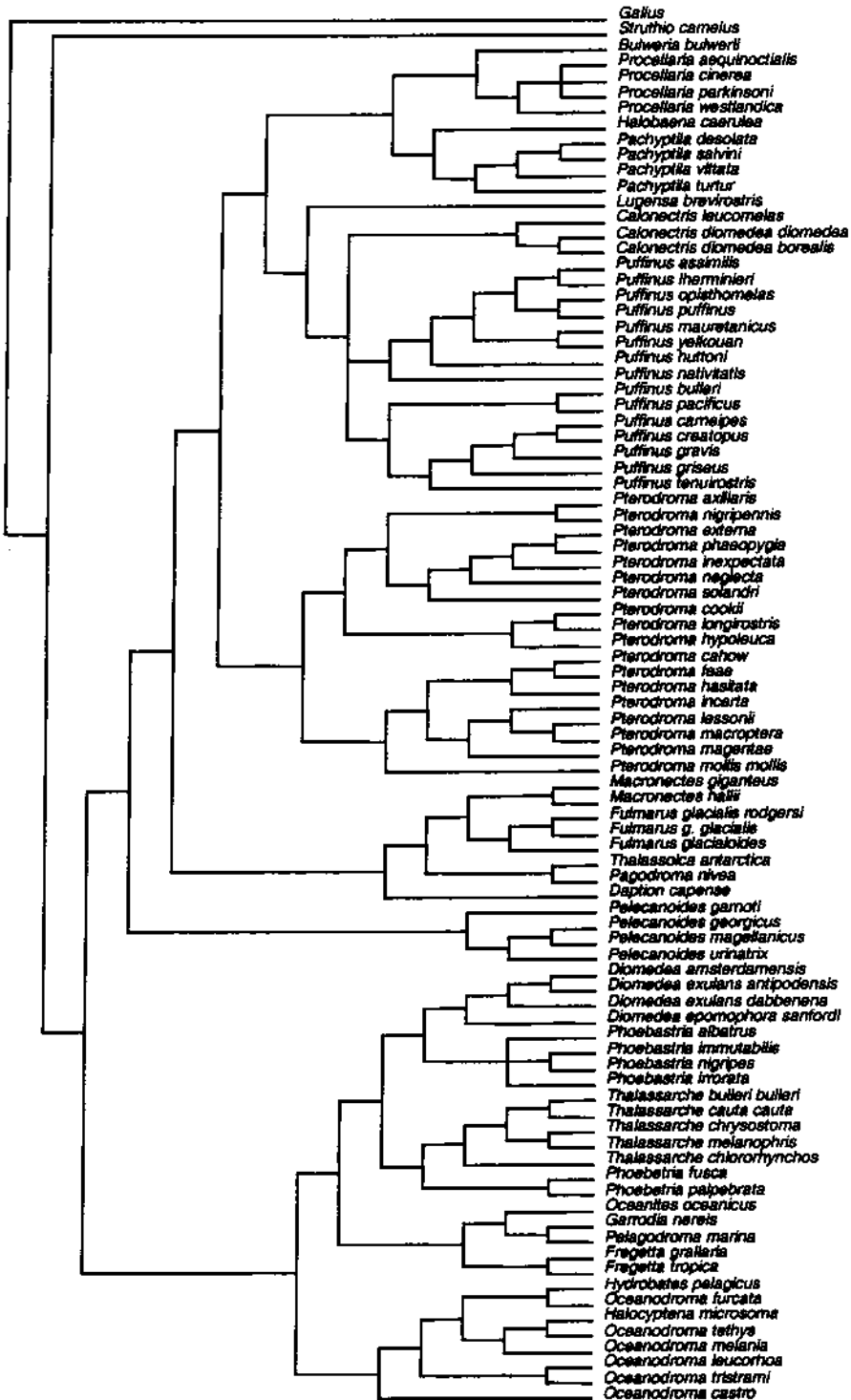*Oceanodroma castro*

Fig. 4. Maximum Parsimony tree, with transversions weighted three times more than transitions. In all, 611 characters are constant, 50 parsimony uninformative, and 482 parsimony informative. Branch-swapping algorithm for heuristic search: tree-bisection-reconnection. Tree length 3734 steps; CI = 0.227; RI = 0.639; RC = 0.145; HI = 0.773; G-fit: -202, 2.

- *Thalassarche impavida* Mathews, 1912 (Campbell Albatross) from *Thalassarche melanophris* (Temminck, 1828) (Black-browed Albatross);
- *Thalassarche* sp. nov. (not *platei*) (Pacific Albatross) from *Thalassarche bulleri* (Rothschild, 1893) (Buller's Albatross); and
- *Thalassarche steadi* Falla, 1933 (White-capped Albatross), *Thalassarche salvini* (Rothschild, 1893) (Salvin's Albatross), and *Thalassarche eremita* Murphy, 1930 (Chatham Albatross) from *Thalassarche cauta* (Gould, 1841) (Shy Albatross).

T. platei had been proposed for the split *Thalassarche* taxon known as 'Pacific Albatross'. However, Robertson and Nunn (1998: 18) stated that *platei* 'should be reduced to a synonym, being just a juvenile plumage phase of *T. bulleri*'.

Robertson and Nunn's (1998) use of *D. exulans* beside *D. chionoptera* makes it clear that they, like Marchant and Higgins (1990: 265), are identifying Linnaeus's *exulans* with the Tristan da Cunha population named *Diomedea dabbenena* by Mathews (1929). We agree with Bourne (1989: 112, Table 4) in naming the taxon on Tristan-Gough *dabbenena* and in designating the larger, more southern forms traditionally named *chionoptera* as *exulans*, as was done by Nunn and Stanley (1998).

Robertson and Nunn (1998) did not publish or otherwise provide an input matrix containing the distance data for the proposed new albatross species, an omission that left supporters of the Multidimensional BSC uncertain as to whether the proposed splits were valid within that framework. They did state (Robertson and Nunn 1998: 14): 'Idiosyncratically among birds, the level of mitochondrial DNA sequence divergence between albatross taxa is relatively small compared to their diagnosable morphological and ecological character differences. Reassuringly, traditional taxonomic and novel phylogenetic methods are largely supportive of each other'. This is not enough to resolve the problem of the status of the proposed splits, given that pairwise distances among traditionally recognised species within *Thalassarche* range from 1.66% to 3.15%. We also regret the practice in recent years of publishing only trees but not the distance matrices on which the trees are based. Tree-generating packages often generate cladograms with similar terminal branches for taxa differing by less than 1% and those differing by, say, 5%.

We provide a distance matrix for albatrosses as Table 2. In the text that follows, nucleotide distances are given, with amino acid distances following in parentheses. Considering the distances in Table 2, those between the species that were split by Robertson and Nunn (1998) are much smaller than those between previously recognised 'good' species of albatross. For example, within the *D. exulans* complex, the distance between Robertson and Nunn's *D. chionoptera* [= nominate *exulans*] and *D. antipodensis* is 0.52% (0.00%); in the case of their *D. exulans* [= *dabbenena*], 0.87%

(0.00%); and in the case of *D. gibsoni*, 0.52% (0.00%). *D. gibsoni* shows a percentage difference of 0.00% (0.00%) from *D. antipodensis* and 0.70% (0.00%) from *D. dabbenena*. Compare these nucleotide distances, all of less than 1.0%, with the distances of 3.2–3.6% between *D. e. epomophora* and *D. e. sanfordi* from all of the taxa in the *exulans* complex. We conclude that *gibsoni, antipodensis* and *dabbenena* are better recognised as subspecies of *D. exulans* than as good species in their own right. We note that both *antipodensis* and *gibsoni* were described as subspecies of *D. exulans* in their original description by Robertson and Warham (1992: 74, 76).

Somewhat surprising is the distance evidence relating to *D. amsterdamensis*, which has generally been treated as a good species since its description by Roux *et al.* (1983), although Bourne (1989: 112,table 4) treated it as a subspecies of *D. exulans*. The fact that it is only 0.52% (0.00%) distant from *antipodensis, gibsoni* and *exulans*, and only 0.87% (0.00%) removed from *dabbenena* strongly suggests that it belongs among the subspecies of *exulans*.

Given that the pairwise difference between *D. epomophora* and *D. sanfordi* is 0.0009% (0.00%), it is difficult to claim that they are distinct species. Identical cytochrome *b* sequences are not unusual in the case of subspecies. Although clear differences in appearance mean that there must be differences elsewhere in their genomes, the near-identity of the cytochrome *b* sequences of *D. epomophora* and *D. sanfordi* suggests that they must have diverged very recently in evolutionary terms, and that *sanfordi* is better retained as a subspecies of *epomophora*.

Among the Yellow-nosed Albatross taxa, the distance of 0.35% (0.00%) between *T. carteri* [was *D. bassi* Mathews, 1912] and *T. chlororhynchos* strongly suggests that *carteri* should also be treated as a subspecies of *T. chlororhynchos*. While slightly larger, the distance of 0.79% (0.26%) between *T. impavida* and *T. melanophris*, as opposed to distances between *melanophris* and other traditionally recognised species of *Thalassarche* of 1.92% (0.53%) in the case of *chrysostoma*, 2.80% (0.79%) in the case of *cauta*, 2.80% (0.53%) in the case of *chlororhynchos*, and 3.15% (1.32%) with *bulleri*, also suggests that *impavida* is better treated as a subspecies of *T. melanophris*.

Burg and Croxall (2001) have reported sequence divergence distances of '0.55–7.20%' in 73 Black-browed Albatrosses and '2.10–3.90%' in 50 Grey-headed Albatrosses. Their table 3 (2001: 2654) showed statistically significant percentage differences of 0.7408 between *impavida* of Campbell Island and specimens of *melanophris* from Kerguelen. But these sequence divergence distances are based on incomplete sequences of 219 bp from the mtDNA control region (domain I) (2001: 2650) and thus are not comparable with the complete sequences for cytochrome *b* mtDNA on which the percentage distance data considered in this paper are based. Note that the control region evolves

4–10 times faster than protein-coding genes (Mindell 1997). What Burg and Croxall's data do is confirm that *impavida* is distinct from nominate *melanophris*.

In the case of the *T. cauta* complex, Table 2 shows 1.05% (0.26%) between *cauta* and *eremita*, 0.96% (0.26%) between *cauta* and *salvini*, and 0.26% (0.00%) between *eremita* and

salvini. Although *salvini* and *eremita* have clearly diverged further from the ancestor they share with *cauta* than in the other cases considered above, the distance of 0.26% between them strongly suggests that *eremita* and *salvini* are better treated as conspecific; and, since even 1.05% is well below the difference found between traditional species within

Table 2. Pairwise distance matrix for Albatrosses

Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	1	2	3	4	5	6	7	8	9	10	11
[1] *Diomedea exulans amsterdamensis*		0.0000	0.0132	0.0000	0.0132	0.0000	0.0000	0.0213	0.0213	0.0375	0.0186
[2] *Diomedea exulans antipodensis*	0.0052		0.0132	0.0000	0.0132	0.0000	0.0000	0.0213	0.0213	0.0375	0.0186
[3] *Diomedea epomophora sanfordi*	0.0359	0.0341		0.0132	0.0000	0.0132	0.0132	0.0294	0.0240	0.0348	0.0267
[4] *Diomedea exulans dabbenena*	0.0087	0.0070	0.0315		0.0132	0.0000	0.0000	0.0213	0.0213	0.0375	0.0186
[5] *D. epomophora epomophora*	0.0350	0.0332	0.0009	0.0306		0.0132	0.0132	0.0294	0.0240	0.0348	0.0267
[6] *Diomedea exulans gibsoni*	0.0052	0.0000	0.0341	0.0070	0.0332		0.0000	0.0213	0.0213	0.0375	0.0186
[7] *Diomedea exulans exulans*	0.0052	0.0052	0.0359	0.0087	0.0350	0.0052		0.0213	0.0213	0.0375	0.0186
[8] *Phoebastria albatrus*	0.0674	0.0639	0.0700	0.0639	0.0709	0.0639	0.0621		0.0106	0.0267	0.0079
[9] *Phoebastria immutabilis*	0.0674	0.0656	0.0665	0.0674	0.0674	0.0656	0.0639	0.0367		0.0267	0.0079
[10] *Phoebastria irrorata*	0.0717	0.0691	0.0682	0.0709	0.0691	0.0691	0.0691	0.0437	0.0472		0.0240
[11] *Phoebastria nigripes*	0.0621	0.0604	0.0665	0.0621	0.0674	0.0604	0.0586	0.0350	0.0175	0.0437	
[12] *Thalassarche bulleri bulleri*	0.1015	0.0997	0.1006	0.1024	0.1015	0.0997	0.1015	0.1102	0.1041	0.1094	0.0980
[13] *Thalassarche cauta cauta*	0.0971	0.0954	0.0989	0.0980	0.0997	0.0954	0.0971	0.1059	0.1032	0.1085	0.0954
[14] *T. chlororhynchos chlororhynchos*	0.1006	0.0989	0.1050	0.1015	0.1059	0.0989	0.1006	0.1111	0.1094	0.1120	0.0989
[15] *Thalassarche chrysostoma*	0.1015	0.0997	0.1024	0.1032	0.1032	0.0997	0.0997	0.1085	0.1032	0.1094	0.0945
[16] *T. melanophris melanophris*	0.0997	0.0980	0.1024	0.0997	0.1032	0.0980	0.0997	0.1085	0.1050	0.1102	0.0962
[17] *T. chlororhynchos carteri*	0.0989	0.0971	0.1050	0.0997	0.1059	0.0971	0.0989	0.1129	0.1129	0.1137	0.1024
[18] *Thalassarche cauta eremita*	0.0997	0.0980	0.0997	0.1006	0.1006	0.0980	0.0997	0.1067	0.1059	0.1111	0.0997
[19] *Thalassarche cauta salvini*	0.0989	0.0971	0.0989	0.0997	0.0997	0.0971	0.0989	0.1059	0.1050	0.1102	0.0989
[20] *T. melanophris impavida*	0.1024	0.1006	0.1032	0.1024	0.1041	0.1006	0.1024	0.1111	0.1076	0.1076	0.0989
[21] *Phoebetria fusca* .	0.0971	0.0971	0.0980	0.0962	0.0989	0.0971	0.0936	0.1015	0.0989	0.1076	0.0927
[22] *Phoebetria palpebrata*	0.0884	0.0884	0.0971	0.0875	0.0962	0.0884	0.0866	0.0997	0.0962	0.1041	0.0910

Note: [7] *Diomedea exulans exulans* = *Diomedea chionoptera* AF076048

	12	13	14	15	16	17	18	19	20	21	22
[1] *Diomedea exulans amsterdamensis*	0.0430	0.0403	0.0430	0.0430	0.0430	0.0430	0.0403	0.0403	0.0458	0.0267	0.0267
[2] *Diomedea exulans antipodensis*	0.0430	0.0403	0.0430	0.0430	0.0430	0.0430	0.0403	0.0403	0.0458	0.0267	0.0267
[3] *Diomedea epomophora sanfordi*	0.0485	0.0458	0.0485	0.0485	0.0541	0.0485	0.0458	0.0458	0.0513	0.0348	0.0348
[4] *Diomedea exulans dabbenena*	0.0430	0.0403	0.0430	0.0430	0.0430	0.0430	0.0403	0.0403	0.0458	0.0267	0.0267
[5] *D. epomophora epomophora*	0.0485	0.0458	0.0485	0.0485	0.0541	0.0485	0.0458	0.0458	0.0513	0.0348	0.0348
[6] *Diomedea exulans gibsoni*	0.0430	0.0403	0.0430	0.0430	0.0430	0.0430	0.0403	0.0403	0.0458	0.0267	0.0267
[7] *Diomedea exulans exulans*	0.0430	0.0403	0.0430	0.0430	0.0430	0.0430	0.0403	0.0403	0.0458	0.0267	0.0267
[8] *Phoebastria albatrus*	0.0485	0.0513	0.0541	0.0541	0.0541	0.0541	0.0513	0.0513	0.0568	0.0375	0.0375
[9] *Phoebastria immutabilis*	0.0485	0.0513	0.0541	0.0541	0.0541	0.0541	0.0513	0.0513	0.0568	0.0375	0.0375
[10] *Phoebastria irrorata*	0.0541	0.0568	0.0596	0.0596	0.0652	0.0596	0.0568	0.0568	0.0624	0.0485	0.0485
[11] *Phoebastria nigripes*	0.0403	0.0430	0.0458	0.0458	0.0458	0.0458	0.0430	0.0430	0.0485	0.0294	0.0294
[12] *Thalassarche bulleri bulleri*		0.0053	0.0079	0.0079	0.0132	0.0079	0.0079	0.0079	0.0106	0.0240	0.0240
[13] *Thalassarche cauta cauta*	0.0166		0.0026	0.0026	0.0079	0.0026	0.0026	0.0026	0.0053	0.0213	0.0213
[14] *T. chlororhynchos chlororhynchos*	0.0297	0.0271		0.0000	0.0053	0.0000	0.0053	0.0053	0.0026	0.0240	0.0240
[15] *Thalassarche chrysostoma*	0.0262	0.0236	0.0262		0.0053	0.0000	0.0053	0.0053	0.0026	0.0240	0.0240
[16] *T. melanophris melanophris*	0.0315	0.0280	0.0280	0.0192		0.0053	0.0106	0.0106	0.0026	0.0294	0.0294
[17] *T. chlororhynchos carteri*	0.0332	0.0289	0.0035	0.0297	0.0315		0.0053	0.0053	0.0026	0.0240	0.0240
[18] *Thalassarche cauta eremita*	0.0201	0.0105	0.0289	0.0236	0.0271	0.0306		0.0000	0.0079	0.0213	0.0213
[19] *Thalassarche cauta salvini*	0.0192	0.0096	0.0280	0.0227	0.0262	0.0297	0.0026		0.0079	0.0213	0.0213
[20] *T. melanophris impavida*	0.0289	0.0271	0.0271	0.0201	0.0079	0.0306	0.0280	0.0271		0.0267	0.0267
[21] *Phoebetria fusca*	0.0770	0.0761	0.0814	0.0787	0.0805	0.0831	0.0831	0.0805	0.0849		0.0053
[22] *Phoebetria palpebrata*	0.0770	0.0770	0.0779	0.0770	0.0770	0.0796	0.0805	0.0796	0.0814	0.0210	

Thalassarche (1.66–3.15%), it seems more appropriate to consider both *salvini* and *eremita* as conspecific with *cauta*.

Translating the amino acid percentage into divergence times, and using the bifurcations in Figs 3 and 4, our data suggest that the earliest split among the albatross taxa was between the ancestors of the *Diomedea–Phoebastria* clade and the *Thalassarche–Phoebetria* clade, which occurred ≈44.4 million years ago. The split between *Diomedea* and *Phoebastria* occurred ≈25.8 million years ago. *D. exulans* and *D. epomophora* diverged ≈13.2 million years ago. From the 0.00% amino acid distance score among the subspecies of *exulans*, they must have diverged less than a million years ago, as must also be the case for *D. epomophora epomophora* and *D. e. sanfordi*. Within the *Phoebastria* clade, the divergence between *P. irrorata* of the Atlantic Ocean from the Pacific Ocean taxa dates back ≈25.8 million years, in other words, at about the same time as the divergence of *Diomedea* from *Phoebastria*. In the Pacific, *P. albatrus* diverged from *P. immutabilis* ≈10.6 million years ago, and *P. immutabilis* and *P. nigripes* diverged ≈7.9 million years ago.

The divergence between *Thalassarche* and *Phoebetria* dates back to ≈24 million years ago. The two *Phoebetria* albatrosses diverged ≈5.3 million years ago. The oldest divergence within *Thalassarche* was between *T. chlororhynchos* and the remainder ≈8.0 million years ago. The split between the *melanophris–chrysostoma* clade and the *bulleri–cauta* clade occurred soon after, ≈7.9 million years ago, while *melanophris* and *chrysostoma* diverged ≈4.0 million years ago and *bulleri* and *cauta*, ≈7.0 million years ago. *Thalassarche melanophris melanophris* and *T. m. impavida* appear to have diverged ≈2.6 million years ago, and the Atlantic *T. chlororhynchos chlororhynchos* and Indian Ocean *T. c. carteri* less than 1 million years ago.

To conclude our discussion of the albatrosses, we recommend the following taxonomy:

- *Diomedea exulans* Linnaeus, 1758 (Wandering Albatross):
    D. exulans exulans,
    D. exulans amsterdamensis Roux *et al.*, 1983,
    D. exulans gibsoni Robertson & Warham, 1992,
    D. exulans antipodensis Robertson & Warham, 1992, and
    D. exulans dabbenena Mathews, 1929;
- *Diomedea epomophora* Lesson, 1825 (Royal Albatross):
    D. epomophora epomophora, and
    D. epomophora sanfordi Murphy, 1917;
- *Phoebastria irrorata* (Salvin, 1883) (Waved Albatross);
- *Phoebastria albatrus* (Pallas, 1769) (Short-tailed Albatross);
- *Phoebastria immutabilis* (Rothschild, 1893) (Laysan Albatross);
- *Phoebastria nigripes* (Audubon, 1839) (Black-footed Albatross);
- *Thalassarche bulleri* (Rothschild, 1893) (Buller's Albatross):

    T. bulleri bulleri, and
    T. bulleri subsp. nov. (was *platei*);
- *Thalassarche cauta* (Gould, 1841) Shy Albatross:
    T. cauta cauta,
    T. cauta steadi Falla, 1933,
    T. cauta salvini (Rothschild, 1893), and
    T. cauta eremita Murphy, 1930;
- *Thalassarche chrysostoma* (J. R. Forster, 1785) (Grey-headed Albatross);
- *Thalassarche melanophris* (Temminck, 1828) (Black-browed Albatross):
    T. m. melanophris, and
    T. m. impavida Mathews, 1912;
- *Thalassarche chlororhynchos* (J. F. Gmelin, 1789) (Yellow-nosed Albatross):
    T. chlororhynchos chlororhynchos, and
    T. chlororhynchos carteri (Rothschild, 1903);
- *Phoebetria fusca* (Hilsenberg, 1822) (Sooty Albatross); and
- *Phoebetria palpebrata* (J. R. Forster, 1785) (Light-mantled Sooty-Albatross).

Storm-petrels

ML (Fig. 3) and MP (Fig. 4) agree in placing the storm-petrels as a sister-clade of the albatrosses. Further, although they do not cluster as a strict sister group in Fig. 2, the storm-petrels are the closest neighbour of albatrosses in the NJ tree. So the net effect of all three diagrams is to suggest that the link between the albatrosses and storm-petrels is stronger than has been assumed. The length of the branches is meaningful only in Figs 2 and 3, the NJ and ML trees; Fig. 4, as a strict MP consensus tree, is a cladogram, so there is no meaning in the length of its branches. That said, there is a striking contrast between the shallowness of the basal branches in Fig. 2, which suggests that the basal relationships shown herein are not reliable, and the depth of the branches in Fig. 3. It is usual for ML trees to have longer branches than NJ trees because NJ uses only more-or-less simple distances for tree building, whereas ML takes multiple substitutions and the frequency of bases into account. That is one reason, why, as noted before, ML is generally judged as a more reliable tree-building method.

The strong suggestion of all three trees that the storm-petrels are the closest relatives of the albatrosses is contrary to all major recent treatments. Sibley and Monroe (1990: xii) divide a family Procellariidae into subfamilies Procellariinae (Petrels, Shearwaters, Diving-Petrels), Diomedeinae (Albatrosses), and Hydrobatinae (Storm-Petrels). Marchant and Higgins (1990: 264) analyse the Procellariiformes into four families: Diomedeidae, or large to huge aerial albatrosses; Procellariidae, or medium-sized, mainly aerial but sometimes aquatic, petrels, shearwaters and prions; Hydrobatidae, or small to tiny, aerial storm-petrels; and Pelecanoididae, or small aquatic diving-petrels. Fig. 3 places the Hydrobatinae

as a sister clade of the albatrosses, with the Oceanitinae as a sister-clade to the resulting node; Fig. 4 reverses the links, with Oceanitinae a sister-clade to the albatrosses, and Hydrobatinae a sister-clade to the resulting node. It is also notable that the higher branches relating to the storm-petrels in Fig. 3 are relatively shallow, suggesting that they are less reliable. Given this disagreement, the most conservative course is to treat both the Hydrobatinae and Oceanitinae as subfamilies, along with Diomedeinae, of the family Diomedeidae. As this study is based on a single mitochondrial gene, we do not have sufficient evidence to propose that this should replace the standard analysis of Diomedeidae and Hydrobatidae as distinct families, but if an investigation is made into nuclear DNA of the Procellariiformes it would be worth testing this hypothesis further.

All trees support the split between the southern (Oceanitinae: genera *Oceanites, Garrodia, Pelagodroma, Fregetta*) and northern (Hydrobatinae: genera *Oceanodroma, Hydrobates, Halocyptena*) storm-petrels supported by Carboneras (in del Hoyo *et al.* 1992: 258), with bootstrap support in Fig. 2 for the node containing the southern clade of 99% and for the node containing the northern clade of 100%. All of the trees further indicate problems within the classification of the storm-petrels, in that, in all trees, *Oceanodroma* is paraphyletic. In all three trees, *Oceanodroma* occurs in four distinct groups:

• *O. furcata* (J. F. Gmelin, 1789) (Fork-tailed Storm-Petrel) groups with *Hydrobates pelagicus* (Linnaeus, 1758) (European Storm-Petrel);
• *O. leucorhoa* (Vieillot, 1818) (Leach's Storm-Petrel) groups with *O. tristrami* Salvin, 1896 (Tristram's Storm-Petrel);
• *Halocyptena microsoma* Coues, 1864 (Least Storm-Petrel) groups with *O. tethys* (Bonaparte, 1852) (Wedge-rumped Storm-Petrel); these, in turn, form a sister-clade with *O. melania* (Bonaparte, 1854) (Black Storm-Petrel); and

• *O. castro* (Harcourt, 1851) (Band-rumped Storm-Petrel) forms a sister clade with all other members of the Hydrobatinae.

In structural terms, we appear to have two choices here: either to split the genus *Oceanodroma* or to lump all storm-petrels in this clade into a single genus, which, in terms of priority, would be *Hydrobates* Boie, 1822, which predates both *Oceanodroma* Reichenbach, 1852, and *Halocyptena* Coues, 1864. This possibility was also recognised by Wolters (1975–82: 35).

Important in making judgments about genera within the storm-petrels are the genetic distances in the distance matrix, presented in Table 3. The Oceanitinae includes *Oceanites* Keyserling & J. H. Blasius, 1840; *Garrodia* Forbes, 1881; *Pelagodroma* Reichenbach, 1852; and *Fregetta* Bonaparte, 1855. *Oceanites* is 10.76% (5.41%) from *Garrodia*, 9.36% (3.21%) from *Pelagodroma*, and 9.27% (3.21%) from *Fregetta grallaria*, with a mean of 9.9% for all the distances between each of the four genera, and a standard deviation of 0.6. These distances are consistent with recognising four distinct genera. Between the congeneric *Fregetta grallaria* and *F. tropica*, we find a lower distance of 7.44% (1.59%). We have no data for the monotypic genus *Nesofregetta* Mathews, 1912, and accordingly let that genus stand as part of the Oceanitinae.

The amino acid distances within the Oceanitinae clade indicate that the earliest divergence was *Oceanites* from *Garrodia* ≈54.1 million years ago, followed by the divergence of *Pelagodroma* from *Garrodia* ≈45.8 million years ago. *Fregetta* diverged from the *Oceanites–Garrodia–Pelagodroma* clade ≈37.6 million years ago.

Within the Hydrobatinae clade, *Hydrobates pelagicus* is 8.22% (1.59%) from *Oceanodroma furcata*, but distances to the clade containing *Halocyptena microsoma*, *Oceanodroma tethys* and *O. melania* range from 10.06% (1.59%) to 11.37% (1.86%), and distances to the clade containing *O. leucorhoa* and *O. tristrami* are, respectively, 10.67% (4.30%) and

Table 3.   Pairwise distance matrix for Storm-petrels
Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	78	79	80	81	82	83	84	85	86	87	88	89	90
[78] *Oceanites oceanicus*		0.0541	0.0321	0.0321	0.0348	0.0709	0.0737	0.0781	0.0681	0.0794	0.0681	0.0709	0.0937
[79] *Garrodia nereis*	0.1076		0.0458	0.0430	0.0403	0.0880	0.0880	0.1034	0.0908	0.0966	0.0966	0.0908	0.1024
[80] *Pelagodroma marina*	0.0936	0.0962		0.0348	0.0403	0.0794	0.0822	0.0907	0.0765	0.0880	0.0822	0.0851	0.1024
[81] *Fregetta grallaria*	0.0927	0.0989	0.0884		0.0159	0.0652	0.0709	0.0781	0.0681	0.0737	0.0765	0.0765	0.0822
[82] *Fregetta tropica*	0.0892	0.1015	0.1076	0.0744		0.0709	0.0765	0.0844	0.0681	0.0765	0.0851	0.0794	0.0880
[83] *Hydrobates pelagicus*	0.1277	0.1409	0.1330	0.1269	0.1312		0.0159	0.0383	0.0159	0.0430	0.0375	0.0186	0.0321
[84] *Halocyptena microsoma*	0.1409	0.1505	0.1435	0.1286	0.1382	0.1006		0.0443	0.0159	0.0403	0.0294	0.0079	0.0294
[85] *Thalobata castro*	0.1538	0.1615	0.1635	0.1462	0.1490	0.1212	0.1163		0.0413	0.0657	0.0565	0.0413	0.0565
[86] *Hydrobates furcatus*	0.1330	0.1435	0.1356	0.1321	0.1339	0.0822	0.0971	0.1173		0.0267	0.0348	0.0186	0.0267
[87] *Cymochorea leucorhoa*	0.1382	0.1531	0.1479	0.1260	0.1356	0.1067	0.1085	0.1240	0.0989		0.0485	0.0458	0.0458
[88] *Halocyptena melania*	0.1295	0.1505	0.1417	0.1295	0.1347	0.1085	0.0796	0.1346	0.1076	0.1129		0.0267	0.0541
[89] *Halocyptena tethys*	0.1417	0.1496	0.1479	0.1304	0.1356	0.1137	0.0656	0.1192	0.1067	0.1155	0.0892		0.0348
[90] *Cymochorea tristrami*	0.1487	0.1531	0.1566	0.1339	0.1365	0.1050	0.1094	0.1221	0.1076	0.0805	0.1199	0.1155	

10.50% (3.21%), and to the monophyletic *O. castro*, 12.12% (3.83%). *Halocyptena microsoma* is 6.56% (0.79%) from *O. tethys* and 7.96% (2.94%) from *O. melania*, but 10.85% (4.03%) to *O. leucorhoa*, and 10.94% (2.94%) to *O. tristrami*. *O. leucorhoa* is 8.05% (4.58%) from *O. tristrami*, but 12.40% (6.57%) from *O. castro*.

The picture that emerges from the Hydrobatinae clade is consistent with what we saw within the Oceanitinae clade. In terms of the four terminal clades within that clade, the highest separation *within* a terminal clade is 8.2%. The smallest distance *between* the terminal clades is 10.1%, with a mean distance between all taxa in different terminal nodes of 12.0% and a standard deviation of 1.3. We suggest that the logical conclusion is to postulate four distinct genera corresponding to the four terminal clades within the Hydrobatinae. Thus we propose:

- *Hydrobates pelagicus* (European Storm-Petrel), and
- *Hydrobates furcatus* (Fork-tailed Storm-Petrel).

Since the type of *Oceanodroma* Reichenbach, 1852, *Procellaria furcata* J. F. Gmelin, 1789, is congeneric in this arrangement with the type of *Hydrobates* Boie, 1822, this makes *Oceanodroma* a junior subjective synonym of *Hydrobates*.

The earliest available name for the *leucorhoa–tristrami* group is *Cymochorea* Coues, 1864, with *Procellaria leucorhoa* Vieillot, 1818 as its type. Also assigned to this genus will be *monorhis* (Swinhoe, 1867) (Swinhoe's Storm-Petrel), which Sibley and Monroe (1990: 330) group in the *leucorhoa* superspecies; they further state that *monorhis* 'may be conspecific with *leucorhoa*'. Sibley and Monroe (1990) assigned *tristrami* to the *markhami* superspecies, again with the comment: 'May be conspecific with *markhami*'. On this basis, *markhami* will also be assigned to *Cymochroa*. This gives:

- *Cymochorea leucorhoa* (Leach's Storm-Petrel),
- *Cymochorea monorhis* (Swinhoe's Storm-Petrel),
- *Cymochorea tristrami* (Tristram's Storm-Petrel), and
- *Cymochorea markhami* (Markham's Storm-Petrel).

For the *microsoma–tethys–melania* group, the earliest available name is *Halocyptena* Coues, 1864, with *Halocyptena microsoma* Coues, 1864, as its type. *Loomelania* Mathews, 1933, with *Procellaria melania* Bonaparte, 1854, as its type, is a junior subjective synonym of *Halocyptena*. Here we also tentatively include *matsudairae* Kuroda, 1922 (Matsudaira's Storm-Petrel), on the basis that Sibley and Monroe (1990: 330) place *matsudairae* in the *melania* superspecies, and of which they state: 'May be conspecific with *O. melania*'. Thus we have:

- *Halocyptena microsoma* (Least Storm-Petrel),
- *Halocyptena tethys* (Wedge-rumped Storm-Petrel),
- *Halocyptena melania* (Black Storm-Petrel), and
- *Halocyptena matsudairae* (Matsudaira's Storm Petrel).

Finally, we need a name for the monotypic genus containing *castro*. The only available name is *Thalobata* Mathews,

1943, which has *Thalassidroma castro* Harcourt, 1851, as its type. Thus we have:

- *Thalobata castro* (Band-rumped Storm-Petrel).

We lack data from *O. homochroa* (Coues, 1864) (Ashy Storm-Petrel), of the coast of California and the Pacific coast of Mexico, and *O. hornbyi* (G. R. Gray, 1854) (Ringed Storm-Petrel), of the Pacific coast of South America from Peru to Chile. All recent species sequences have placed these two species between *O. matsudairae* and *O. furcata* (see Jouanin and Mougin, in Mayr and Cottrell 1979: 117; Sibley and Monroe 1990: 330; and Carboneras, in del Hoyo *et al.* 1992: 271). The last-named source also says of *O. homochroa*, though without any further explanation, 'May form superspecies with *O. monorhis* and *O.leucorhoa*'. If this suggestion is correct, we would have *Cymochroa homochroa* and perhaps also *Cymochroa hornbyi*.

Distances within storm-petrels are astonishingly large, indicating that these taxa are phylogenetically rather old. The amino acid data suggest that the divergence between the Hydrobatinae and the Diomedeinae appears to date from 87.9 million years ago. Within the Hydrobatinae, the oldest divergence appears to involve *Thalobata castro*, which split from *Cymochorea leucorhoa* ≈65.7 million years ago. *Hydrobates* and *Cymochorea* diverged ≈37.6 million years ago, while *Halocyptena* diverged from *Hydrobates* ≈15.9 million years ago. *Hydrobates pelagicus* and *H. furcatus* also diverged ≈15.9 million years ago. Within *Halocyptena*, Fig. 3 suggests that *melania* split off first, with the splitting of *microsoma* and *tethys* occurring later. Consistent with this, the amino acid data indicate that *microsoma* and *tethys* diverged ≈7.9 million years ago, while the divergence between *melania* and the ancestor of the other two taxa occurred ≈28.05 million years ago. However, the amino acid data suggest that the divergence between *Cymochorea leucorhoa* and *C. tristrami* is more ancient, at ≈45.8 million years ago.

Procellariidae

As Imber (1985: 199) observed: 'Relationships between the genera of the Procellariidae have always been difficult to resolve'. Kuroda (1954, 1955) amalgamated the gadfly petrels with fulmars (*Halobaena*), prions (*Pachyptila*) and *Bulweria* in the subfamily Fulmarinae; the shearwaters and allies were placed in the subfamily Puffininae. If we look at the higher relationships within our figures, all trees confirm the monophyly of a procellariid clade including fulmars, shearwaters and true petrels and, in Figs 2 and 3, the diving-petrels (*Pelecanoides*). Note that the node that has 97% bootstrap support in Fig. 2 is that which unites the diving-petrels with the taxa conventionally allocated to the Procellariidae.

As we observed above in discussing the taxonomy of the Diomedeidae, the basal branches of Fig. 2 are quite shallow, which suggests that the relationships indicated by Fig. 2 are relatively unreliable. But as with the Diomedeidae, we have

much deeper branches in Fig. 3, and, ignoring for the moment the prion clade, which, as we shall explain below, remains *incertae sedis* within the Procellariidae, what is suggested in Fig. 3 is a fundamental division of the Procellariiformes into just two families: Diomedeidae (discussed above) and Procellariidae, the latter with two major divisions at subfamily level: Puffininae and Pelecanoidinae. The Puffininae include three tribes: Fulmarini, Puffinini and Procellariini. The Pelecanoidinae include two tribes: Pterodromini and Pelecanoidini. We realise that this is a radically different analysis of the higher relationships within the Procellariiformes, and the relevant branches in Fig. 3 are unfortunately shallow, and hence less reliable. As we said in relation to the Diomedeidae above, we accept that this analysis will require further support from the analysis of nuclear genes for full acceptance. But we remind readers that the inclusion of *Pelecanoides* within the procellariid clade has bootstrap support of 97% in Fig. 2.

One major clade contains the Fulmarini, including the genera *Macronectes*, *Fulmarus*, *Thalassoica*, *Pagodroma* and *Daption* (100% bootstrap support for the node containing *Macronectes* through *Thalassoica*, 88% support for the branch uniting *Macronectes* and *Fulmarus*, and 100% support for the branch containing all *Fulmarus*). There is strong support for the following:

* *Procellaria* (bootstrap 100%), and its union with *Buweria*, which occurs in all trees, and in our account comprises the Procellariinii;
* *Calonectris* (bootstrap 100%) and the smaller shearwaters (*Puffinus assimilis* to *P. nativitatis*) (bootstrap 80%) and the larger shearwaters (*Puffinus bulleri* to *P. tenuirostris* (bootstrap 100%) and the union of these three clades (bootstrap 100%), in our account, with *Lugensa*, comprising the Puffininii; and
* *Pterodroma* (100% bootstrap support), in our account comprising the Pterodromini.

The Fulmars: Fulmarini

Our analysis confirms that *Thalassoica*, *Pagodroma* and *Daption* cluster with *Fulmarus* and *Macronectes* as a distinct group (100% bootstrap support), rather than being part of an undifferentiated Procellariidae, grouped with *Pterodroma* and all the shearwaters and *Procellaria*, as in Jouanin and Mougin in Mayr and Cottrell (1979: 58–101). Table 4 shows nucleotide distances from *Macronectes giganteus* of between 5.51% (1.06%) and 5.94% (1.16%) to the three *Fulmarus* taxa, of 7.09% (1.59%) to *Thalassoica*, of 6.91% (1.59%) to *Daption*, and 8.40% (1.86%) to *Pagodroma*, consistent with distinct genera in these cases. However, the distance between *M. giganteus* and *M. halli* is only 0.61% (0.26%). Since we allocated subspecies status to taxa within the albatrosses whose percentage distances were below 1%, it would seem consistent on the basis of cytochrome *b* distances to treat *halli* as a subspecies of *M. giganteus*.

The decision to recognise *M. giganteus* and *M. halli* as sibling species was originally taken by Bourne and Warham (1966), who attempted to sort out a mass of variational data. They emphasised the presence of two forms occurring on Macquarie Island, with little, if any interbreeding. Under the Multidimensional BSC, such evidence from breeding is less straightforward. The two species breed at different times on Macquarie Island: *M. giganteus* having laying dates from 27 September to 19 October (Marchant and Higgins 1990: 363), and *M. halli* having laying dates from 11 August to 6 September (Marchant and Higgins 1990: 374). Thus their apparent failure to interbreed is not quite as straightforward as if they bred at the same time without interbreeding.

There is evidence relevant to the *Macronectes* taxa beyond Macquarie Island. For example, the breeding birds of Gough Island and the Falkland Islands are of uncertain systematic status: 'Although birds on Gough I. are morphologically like *M. giganteus*, their breeding schedule [is] much earlier than all other populations of *giganteus* and similar to many populations of *halli*. Bourne and Warham (1966) regarded these birds as *M. halli*. The Falkland Is population shares similar intermediate characters with Gough I. birds ...' (Marchant and Higgins 1990: 367). Hunter (1983: 314) reported pairings between *giganteus* and *halli* on Bird Island, South Georgia, with the percentage of hybrid pairs reaching 2.46% of all pairs checked in 1979–80. He stated: 'It is certain, however, that the interspecific pairs at Bird Island are fully capable of producing and raising off-spring'

Table 4.   Pairwise distance matrix for Fulmarini
Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	23	24	25	26	27	28	29	30
[23] *Macronectes giganteus giganteus*		0.0026	0.0106	0.0116	0.0053	0.0159	0.0159	0.0186
[24] *Macronectes giganteus hallii*	0.0061		0.0079	0.0087	0.0026	0.0132	0.0132	0.0159
[25] *Fulmarus glacialis rodgersi*	0.0551	0.0542		0.0116	0.0053	0.0159	0.0159	0.0186
[26] *Fulmarus glacialis glacialis*	0.0594	0.0584	0.0192		0.0058	0.0087	0.0174	0.0174
[27] *Fulmarus glacialoides*	0.0586	0.0560	0.0376	0.0441		0.0106	0.0106	0.0132
[28] *Thalassoica antarctica*	0.0709	0.0700	0.0700	0.0738	0.0717		0.0186	0.0132
[29] *Daption capense*	0.0691	0.0665	0.0682	0.0718	0.0717	0.0735		0.0240
[30] *Pagodroma nivea*	0.0840	0.0814	0.0857	0.0833	0.0805	0.0779	0.0919	

(1983: 313), and further suggested that indeterminate females found mating with male *M. giganteus* are also hybrids, and 'clearly fertile and capable of rearing a chick'. Hunter concludes: 'Apart from the small numbers of birds available at such times, there does not appear presently to be any obvious selection against interspecific matings and one would predict a gradual increase in the incidence of hybridization at Bird Island' (1983: 314). Even within approaches that rely primarily on data regarding interbreeding, the data from breeding sites other than Macquarie Island might give one pause in claiming that the two forms are specifically distinct. It is also notable that Shaughnessy (1970), after analysing the serum proteins of *giganteus* and *halli*, found no differences between the two taxa.

The present situation suggests that the common ancestor split into two populations: one nesting on more northern islands, with an earlier breeding period; and one nesting on more southern islands with a later breeding period. The difference in breeding period, under the Multidimensional BSC, would not of itself be sufficient to establish different species, as staggered breeding periods from north to south are not uncommon within seabird species breeding on several islands; but together with morphological differences, notably bill-tip colour and plumage differences, it would suggest subspecies status. At some later point both populations colonised certain islands, including Macquarie. It would seem ill-advised to claim that the co-occurrence of the two taxa with different breeding periods on Macquarie immediately establishes species status under the BSC. As species develop over time, presumably we would need a considerable period without genetic flow between the two taxa for them to attain species rank. But the percentage distance of 0.61% between *giganteus* and *halli* suggests that they are young evolutionary lines; given the amino acid distance of 0.26%, the divergence rate of ≈0.1% per million years for amino acid suggests that these two taxa diverged ≈2.6 million years ago. The confirmed interbreeding of the two taxa on other islands is exactly what we would expect of subspecies. We conclude that *halli* and *giganteus* are better assigned subspecies status under the Multidimensional BSC. Thus we recommend the restoration of:

> *Macronectes giganteus giganteus* and
> *Macronectes giganteus halli.*

The amino acid distances suggest that within the Fulmarini clade, *Daption* diverged earliest, ≈26.2 million years ago. *Thalassoica* and *Pagodroma* diverged from the rest of the clade ≈15.9 million years ago, with *Thalassoica* and *Pagodroma* diverging from each other ≈13.2 million years ago. The *Fulmarus–Macronectes* divergence dates from ≈7.8 million years ago, and the divergence between *Fulmarus glacialis glacialis* and *F. glacialoides* occurred ≈5.8 million years ago. Within the genus *Fulmarus*, *F. glacialis rodgersi* is, as expected, closer to *F. glacialis glacialis* 1.92% (1.16%) than it is to *F. glacialoides* 3.76%

(0.53%). *F. glacialis glacialis* is still further from *F. glacialoides* 4.41% (0.58%). This is an instance unique in the dataset when the amino acid distances contradict the nucleotide distances, and since a small sequencing error may confound the amino acid distances, we suspect that such an error may have confounded the data here. Further analysis of the Fulmarini is required.

Shearwaters: Puffinini

The pairwise distance matrix for Puffinini is presented in Table 5.

Moving downward in the ML tree in Fig. 3, we come to the shearwaters. The node containing all the shearwaters (*Calonectris* plus *Puffinus*) in Fig. 2 has 100% bootstrap support. The congruence of the trees supports the monophyly of *Calonectris*, and the *Calonectris* node in Fig. 2 also has 100% bootstrap support. We commented above on the distances between *Calonectris* and *Puffinus*, which range from a minimum of 7.38% (1.45%) between *C. diomedea borealis* and *P. assimilis* to a maximum of 10.25% (1.74%) between *C. d. diomedea* and *P. griseus*, distances consistent with the distinct generic status of *Calonectris*. Within *Calonectris*, the Mediterranean and the Atlantic lineages differ morphologically and genetically, but distances are rather small, suggesting that *C. d. diomedea* and *C. d. borealis* should be treated as subspecies.

The situation within traditional *Puffinus* is more complex, since all trees indicate that it represents a paraphyletic group. All trees include *Calonectris* either as a sister-node to part of *Puffinus* (Fig. 2), or as a sister node to two distinct *Puffinus* nodes (Figs 3, 4). There is also strong bootstrap support in Fig. 2 for two distinct *Puffinus* clades: 80% for the smaller shearwaters (*P. assimilis* to *P. nativitatis*) and 100% for the larger shearwaters (*P. bulleri* to *P. tenuirostris*).

The mean for the within-group distances for the second group, the smaller shearwaters (*P. assimilis* to *P. nativitatis*) was 4.99, with a standard deviation of 1.73; the mean for the within-group distances for the third group, the larger shearwaters (*P. bulleri* to *P. tenuirostris*) was 4.34, with a standard deviation of 1.37; and the mean for the between-groups distances (that is, the distances between each member of the second group and each member of the third group) was 8.5% with a standard deviation of 0.7. This clearly suggests the need to recognise two genera.

Wolters (1975–82) recognised two genera within the group of larger shearwaters (although *griseus* and *tenuirostris* remained in *Puffinus*): *Ardenna* Reichenbach, 1853, to which he assigned *gravis* and *carneipes*, with *creatopus* as a subspecies; and *Thyellodroma* Stejneger, 1888, to which he assigned *pacificus* and *bulleri* (1975–82: 36). The last two species form a well resolved clade in all trees. Since within the Fulmar clade we found distances between distinct genera of 5.51–5.94% from *Macronectes giganteus* to the three *Fulmarus* taxa, of 7.09% from *Macronectes giganteus* to

Table 5.   Pairwise distance matrix for Puffinini

Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	31	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77
[31] *Lagensa brevirostris*		0.0430	0.0382	0.0382	0.0430	0.0458	0.0430	0.0485	0.0485	0.0485	0.0458	0.0430	0.0430	0.0403	0.0458	0.0458	0.0485	0.0472	0.0472
[60] *Calonectris leucomelas*	0.1094		0.0058	0.0058	0.0106	0.0079	0.0053	0.0106	0.0106	0.0106	0.0159	0.0053	0.0106	0.0132	0.0079	0.0079	0.0106	0.0145	0.0116
[61] *Calonectris diomedea diomedea*	0.1082	0.0326		0.0000	0.0145	0.0145	0.0174	0.0174	0.0174	0.0174	0.0116	0.0145	0.0116	0.0174	0.0145	0.0079	0.0174	0.0204	0.0116
[62] *Calonectris diomedea borealis*	0.1044	0.0307	0.0096		0.0145	0.0116	0.0174	0.0174	0.0174	0.0174	0.0116	0.0145	0.0116	0.0174	0.0145	0.0079	0.0174	0.0204	0.0174
[63] *Puffinus assimilis*	0.0989	0.0814	0.0776	0.0738		0.0026	0.0079	0.0079	0.0079	0.0132	0.0106	0.0026	0.0079	0.0053	0.0053	0.0000	0.0079	0.0058	0.0174
[64] *Ardenna bulleri*	0.1050	0.0875	0.0862	0.0852	0.0805		0.0053	0.0053	0.0053	0.0106	0.0106	0.0053	0.0079	0.0079	0.0026	0.0026	0.0053	0.0058	0.0174
[65] *Ardenna carneipes carneipes*	0.1067	0.0962	0.0948	0.0939	0.0866	0.0525		0.0053	0.0053	0.0053	0.0106	0.0106	0.0053	0.0079	0.0053	0.0079	0.0053	0.0087	0.0058
[66] *Ardenna carneipes creatopus*	0.1050	0.0962	0.0967	0.0958	0.0831	0.0525	0.0070		0.0000	0.0053	0.0106	0.0106	0.0053	0.0079	0.0079	0.0079	0.0053	0.0087	0.0058
[67] *Ardenna gravis*	0.1015	0.0901	0.0910	0.0920	0.0831	0.0446	0.0236	0.0219		0.0053	0.0106	0.0106	0.0053	0.0132	0.0079	0.0079	0.0106	0.0145	0.0087
[68] *Ardenna griseus*	0.1190	0.0980	0.1025	0.1034	0.0910	0.0595	0.0411	0.0394	0.0420		0.0106	0.0106	0.0106	0.0132	0.0079	0.0079	0.0132	0.0145	0.0087
[69] *Puffinus huttoni*	0.1102	0.0945	0.0939	0.0900	0.0534	0.0831	0.0945	0.0892	0.0849	0.0945		0.0159	0.0159	0.0106	0.0132	0.0079	0.0106	0.0204	0.0145
[70] *Puffinus lherminieri*	0.1085	0.0840	0.0814	0.0776	0.0254	0.0849	0.0901	0.0857	0.0875	0.0954	0.0577		0.0106	0.0106	0.0053	0.0079	0.0106	0.0116	0.0204
[71] *Puffinus nativitatis*	0.1120	0.0989	0.0967	0.0891	0.0787	0.0866	0.0901	0.0901	0.0875	0.1041	0.0770	0.0726		0.0132	0.0132	0.0079	0.0106	0.0058	0.0087
[72] *Puffinus opisthomelas*	0.1050	0.0884	0.0833	0.0795	0.0367	0.0761	0.0849	0.0849	0.0796	0.0945	0.0534	0.0411	0.0709		0.0079	0.0079	0.0132	0.0087	0.0087
[73] *Ardenna pacifica*	0.1102	0.0927	0.0900	0.0910	0.0761	0.0350	0.0542	0.0542	0.0481	0.0612	0.0840	0.0770	0.0892	0.0752		0.0106	0.0106	0.0087	0.0087
[74] *Puffinus puffinus*	0.1094	0.0840	0.0824	0.0795	0.0315	0.0709	0.0805	0.0770	0.0752	0.0831	0.0464	0.0341	0.0691	0.0280	0.0700		0.0053	0.0087	0.0087
[75] *Ardenna tenuirostris*	0.1076	0.0866	0.0948	0.0958	0.0831	0.0551	0.0464	0.0481	0.0402	0.0551	0.0945	0.0884	0.0901	0.0849	0.0612	0.0735		0.0079	0.0058
[76] *Puffinus mauretanicus*	0.1140	0.0900	0.0929	0.0891	0.0460	0.0824	0.0920	0.0900	0.0872	0.0929	0.0546	0.0489	0.0785	0.0469	0.0833	0.0364	0.0910		0.0145
[77] *Puffinus yelkouan*	0.1130	0.0881	0.0910	0.0872	0.0412	0.0872	0.0891	0.0852	0.0843	0.0891	0.0498	0.0421	0.0795	0.0441	0.0862	0.0316	0.0833	0.0220	

Thalassoica, of 6.91% from *Macronectes giganteus* to *Daption*, and 8.40% from *Macronectes giganteus* to *Pagodroma*, the contrast between the within-group (4.99% and 4.34%) and between-group (8.5%) figures indicate the need to recognise two genera. *Puffinus* Brisson, 1760, with *Procellaria puffinus* Brünnich, 1764, as its type, remains the genus for the smaller shearwaters (*P. assimilis* to *P. nativitatis*). The earliest available generic name applying to the larger shearwaters (*P. bulleri* to *P. tenuirostris*) appears to be:

Ardenna Reichenbach, '1853', *Avium systema naturale* (1852), p. iv. Type, by original designation, *Procellaria major* Faber, 1822 = *Puffinus gravis* O'Reilly, 1818.

The distinctness of the *pacificus–bulleri* clade, commented on above, justifies the recognition of *Thyellodroma* Stejneger, 1888, as a subgenus. The mean within-group distance of 4.3% within the *Ardenna* clade also draws attention to the distances of only 0.70% (0.00%) between *creatopus* Coues, 1864, and *carneipes* Gould, 1844 (Flesh-footed Shearwater). The next lowest distance within the whole *Ardenna* clade is 2.2% (0.53%) between *creatopus* and *gravis*. Sibley and Monroe (1990: 325) stated under *Puffinus creatopus* 'May be conspecific with *P. carneipes*' and Carboneras (in del Hoyo *et al.* 1992: 253) stated under *P. creatopus* that it 'may be merely pale phase [of *P. carneipes*] at end of W–E cline'. One is justified in returning *creatopus* Coues, 1864, to the status of a subspecies of *carneipes* Gould, 1844. The distances of 2.2% between *creatopus* and *gravis*, and 2.4% between *carneipes* and *gravis* confirm the existence of a superspecies relationship between *A. gravis* and the lumped *A. carneipes*, as proposed by Sibley and Monroe (1990: 325).

Within the *Puffinus* clade, the group of Manx shearwaters had been split on the basis of morphological, geographic and genetic evidence into *P. p. puffinus* Brünnich, 1764 (Manx Shearwater), inhabiting Atlantic islands, *P. yelkouan* (Acerbi, 1827) (Mediterranean Shearwater), and *P. mauretanicus* Lowe, 1921 (Balearic Shearwater), living in the Eastern or Western Mediterranean (Heidrich *et al.* 1998, 2000).

Figs 2–4 agree in placing *Lugensa brevirostris* (Lesson, 1831) (Kerguelen Petrel) as a sister clade to a clade containing all the shearwaters. This species has usually been assigned either to *Pterodroma* Bonaparte, 1856 (e.g. Jouanin and Mougin, in Mayr and Cottrell 1979: 72) or to *Lugensa* Mathews, 1942 (Sibley and Monroe 1990: 321). Imber (1985: 215), relying on morphology and data from the taxonomy of feather-lice, stated that '... Kerguelen Petrels are thus

more closely related to fulmars than previous taxonomy has shown. Their relationship to gadfly petrels is less clear ... Like *Pagodroma*, *Lugensa* seems to be a very specialised fulmar'. Marchant and Higgins (1990: 355),[1] with *Pterodroma (Lugensa) brevirostris*, treat *Lugensa* as a subgenus of *Pterodroma*, and thus group this species with the gadfly petrels (*Pterodroma*), although they also note that the species '... has distinctly big eyes like *Pagodroma* ...'. In the distance matrix, the percentage distances between *Lugensa* and all members of *Pterodroma* have a mean of 12.0 with a standard deviation of 0.7. The mean of distances between *Lugensa* and *Calonectris* is 10.9 with a standard deviation of 0.1, while the mean for *Lugensa* and *Puffinus* (in the broader sense, that is, including *Ardenna*) is 10.8 with a standard deviation of 0.5. So, on average, *Lugensa* is closer to the shearwaters than it is to *Pterodroma*. This supports the grouping of *Lugensa* with *Calonectris*, *Puffinus* and *Ardenna* in the Puffinini, whose closest relatives are *Procellaria*, *Bulweria* and *Pseudobulweria* in the Procellariini, with the more distant relationship with the gadfly petrels being captured by the sister relationship in Figs 3 and 4 of the Procellariini with the Pterodromini to form together the Procellariidae.

The amino acid data suggest that *Lugensa* diverged from *Calonectris* ≈39.8 million years ago. *Calonectris* diverged from the other shearwater clades from ≈13.8 million years ago. *Puffinus* and *Ardenna* appear to have diverged ≈10.4 million years ago.

Thus within the Puffinini, we propose:

- *Lugensa brevirostris* (Lesson, 1830) (Kerguelen Petrel);
- *Calonectris leucomelas* (Temminck, 1835) (Streaked Shearwater);
- *Calonectris diomedea* (Scopoli, 1769) (Cory's Shearwater):
  - *C. diomedea diomedea*,
  - *C. diomedea borealis* (Cory, 1881), and
  - *C. diomedea edwardsii* (Oustalet, 1883);
- *Ardenna (Ardenna) carneipes* (Gould, 1844) (Flesh-footed Shearwater):
  - *A. (Ardenna) carneipes creatopus* (Coues 1864), and
  - *A. (Ardenna) carneipes carneipes*;
- *Ardenna (Ardenna) gravis* (O'Reilly, 1818) (Greater Shearwater);
- *Ardenna (Ardenna) grisea* (J. F. Gmelin, 1789) (Sooty Shearwater);
- *Ardenna (Ardenna) tenuirostris* (Temminck, 1835) (Short-tailed Shearwater);

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[1]Olson (2000) argued that the type designated by Mathews for *Lugensa*, namely *Procellaria lugens* Kuhl, 1820, is unidentifiable, and proposed a new name, *Aphrodroma*, with *Oestrelata kidderi* Coues, 1875, as its type, because of doubts in relation to the putative holotype of *P. brevirostris* Lesson, 1831, both as to whether it is the type of Lesson's name, and also whether it is indeed a specimen of the Kerguelen Petrel. If either of these should be resolved in the negative, the correct Latin name would become *Aphrodroma kidderi* (Coues, 1875). However, Bourne (2001: 216) pointed out that Mathews specifically stated that he wished to bestow the generic name *Lugensa* on the species 'formerly known as *Pterodroma brevirostris*' (1942: 305) and that thus *Lugensa* should stand. Bourne also argued that 'while Kuhl may have included '*Procellaria lugens* Banks' in the synonymy of his equally mistaken '*Proc. grisea* L.', it seems likely that he was actually referring to one or both of the two early specimens of the Kerguelen Petrel that had not yet been safely lodged in national museums'.

- *Ardenna (Thyellodroma) pacifica* (J. F. Gmelin, 1789) (Wedge-tailed Shearwater);
- *Ardenna (Thyellodroma) bulleri* (Salvin, 1888) (Buller's Shearwater);
- *Puffinus nativitatis* Streets, 1877 (Christmas Shearwater);
- *Puffinus puffinus* (Brünnich, 1764) (Manx shearwater);
- *Puffinus yelkouan* (Acerbi, 1827) (Mediterranean Shearwater);
- *Puffinus mauretanicus* Lowe, 1921 (Balearic Shearwater);
- *Puffinus persicus* Hume, 1873 (Persian Shearwater);
- *Puffinus huttoni* Mathews, 1912 (Hutton's Shearwater);
- *Puffinus opisthomelas* Coues, 1864 (Black-vented Shearwater);
- *Puffinus newelli* Henshaw, 1900 (Newell's Shearwater);
- *Puffinus auricularis* Townsend, 1890 (Townsend's Shearwater);
- *Puffinus gavia* (J. R. Forster, 1844) (Fluttering Shearwater);
- *Puffinus assimilis* Gould, 1838 (Little Shearwater);
- *Puffinus lherminieri* Lesson, 1839 (Audubon's Shearwater);
- *Puffinus bannermani* Mathews & Iredale, 1915 (Bannerman's Shearwater); and
- *Puffinus heinrothi* Reichenow, 1919 (Heinroth's Shearwater).

Prions

The pairwise distance matrix for Prions is presented in Table 6.

The next clade in Fig. 3 contains prions, *Pachyptila*, and *Halobaena*. All trees, without exception, place *Halobaena* as a sister clade to a clade containing all of *Pachyptila*, with Fig. 2 showing bootstrap support of 98% for the node uniting *Halobaena* with *Pachyptila*. Distances between the two genera range from 8.3% to 9.0% (amino acid distances from 2.40% to 2.94%, indicating divergence ≈24–29.4 million years ago). The association of *Halobaena* with *Pachyptila* confirms the view expressed by Imber (1985: 218): 'In consideration of the combined evidence of anatomy ..., plumage ..., calls ..., breeding distribution ..., and their feather lice ..., the close affinity between Blue Prions and prions seems proven'. Our distances clearly support the recognition of *Halobaena* as a distinct genus, although its closest affinities

are with *Pachyptila*, and not, *contra* Marchant and Higgins (1990: 355), with the gadfly-petrels, *Pterodroma*. Unfortunately, the *Pachyptila–Halobaena* clade occupies a different position in every single tree. In this case, the clade remains *incertae sedis* within the Procellariidae.

The taxonomy of the prions has long been a vexed question, thanks in no small part to the changeable analyses of G. M. Mathews. A full history of the controversy before 1980 can be found in Cox (1980), and a summary can also be found in Bretagnolle *et al.* (1990: 305). These two papers are the most detailed recent studies of the prions and reach radically different conclusions. Recent authorities (e.g. Harper 1980; Sibley and Monroe 1990: 324; Marchant and Higgins 1990: 515–554) have generally recognised six species:

- *Pachyptila vittata* (J. R. Forster, 1777) (Broad-billed Prion);
- *Pachyptila salvini* (Mathews, 1912) (Salvin's (or Medium-billed) Prion);
- *Pachyptila desolata* (J. F. Gmelin, 1789) (Antarctic Prion);
- *Pachyptila belcheri* (Mathews, 1912) (Slender-billed Prion);
- *Pachyptila turtur* (Kuhl, 1820) (Fairy Prion); and
- *Pachyptila crassirostris* (Mathews, 1912) (Fulmar Prion).

Cox (1980: 91) rightly rejected the suggestion of classification of the group in terms of three genera or subgenera, as proposed by Mathews (1934); our distance data certainly do not support any proposals at generic or subgeneric levels within *Pachyptila*. Cox (1980: 119–120) proposed to analyse the prions into two groups on essentially morphological grounds: one polytypic species, the Fairy Prions, consisting of *P. turtur* (and including *P. t. crassirostris* as a subspecies); and the Whale-Birds, consisting of one monotypic species, *P. belcheri*; and one polytypic species, *P. vittata*, including as subspecies *P. v. desolata* and *P. v. salvini*. We note that Cox (1980: 119) stated under *P. belcheri*: 'N.B. Interbreeds with [*P. vittata*] where both occupy the same islands'. The essence of Cox's view of the *desolata–salvini–vittata* complex is: 'Southern *desolata* and northern *vittata* are in all probability conspecific and evidently *salvini* is an intermediate form of hybrid origin'. Cox (1980: 91) stated that although in the South Atlantic and New Zealand, there are no intermediates between *desolata* and *vittata*, 'in the southern Indian Ocean

Table 6.   Pairwise distance matrix for Prions
Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	50	51	52	53	54
[50] *Halobaena caerulea*		0.0294	0.0267	0.0240	0.0294
[51] *Pachyptila vitatta desolata*	0.0866		0.0026	0.0079	0.0000
[52] *Pachyptila vitatta salvini*	0.0901	0.0070		0.0106	0.0026
[53] *Pachyptila turtur*	0.0831	0.0350	0.0385		0.0079
[54] *Pachyptila vitatta vittata*	0.0884	0.0122	0.0157	0.0315	

region, their differences are less pronounced and intergrade through *salvini* populations'.

Bretagnolle *et al.* (1990) studied the morphometrics, breeding biology, genetics and calls of *P. desolata*, *P. salvini*, *P. belcheri* and *P. turtur* in the southern Indian Ocean, and called for the recognition at species level of each of the four study taxa. On *desolata–belcheri*, they stated (1990: 312): 'The differences in morphology [although they note, p. 312, that 'some overlap occurred'], ecology and behaviour lead us to conclude that *desolata* and *belcheri* are closely related but distinct taxa, which should be ranked at the species level because reproductive isolation is achieved on Kerguelen'. On *vittata–salvini*, they concluded that '... *vittata* and *salvini* constitute separate populations that exploit different ecological niches and should be ranked at the species level' (Bretagnolle *et al.* 1990: 13). On *desolata–salvini*, they stated (Bretagnolle *et al.* 1990: 313) that the calls of the two taxa are different and that 'Together with the differences in the phenology, morphology ... and genetics, we conclude that these taxa definitely constitute two distinct species'.

Pachyptila turtur and *P. crassirostris* were not studied by Bretagnolle *et al.* (1990). Cox (1980: 119) lumped these two into *P. turtur*, whereas Marchant and Higgins (1990: 541–554) treated the two as distinct species. Cox was clearly relying on morphology, and stated (1980: 91): 'Characters described as differentiating *turtur* and *crassirostris* intergrade through many island populations north–south and west–east. However, the sharp boundary between each form in the Chatham Is. allows their recognition as subspecies, although elsewhere delimitations are arbitrary'. We have no DNA data from *crassirostris*. But in the context of what follows, we believe that Cox was correct and that *crassirostris* is probably a young evolutionary split from *turtur*, and not yet fully differentiated throughout its range.

Turning to the *belcheri–desolata–salvin–vittata* complex, we find that both Cox (1980) and Bretagnolle *et al.* (1990) agree in recognising *P. belcheri* as specifically distinct from the other three, although Cox stated (1980: 91): 'they have a zone of overlap and hybridization in the subantarctic Indian Ocean'. Bretagnolle *et al.* (1990: 312), however, denied that there was any evidence of hybridisation. All recent authorities recognise *P. belcheri* as specifically distinct from the *desolata–salvini–vittata* group, but we will argue below that the little data that are available suggest that *belcheri* is a subspecies of *P. vittata*.

Bretagnolle *et al.* (1990) reach different conclusions. On the relationship between *vittata* and *salvini*, they concluded (1990: 313): '... *vittata* and *salvini* constitute separate populations that exploit different ecological niches and should be ranked at the species level'. Marchant and Higgins (1990: 521–526) also view *salvini* as a species distinct from *vittata*, although they commented: '... the Broad-billed Prion *P. vittata* appears to intergrade with Salvin's Prion *P. salvini* through *macgillvrayi* of Ile St Paul; so they may be better treated as subspecies of the same species'. On the *desolata–salvini* relationship, Bretagnolle *et al.* (1990: 313) stated: '... the two taxa had different calls ... Together with the differences in their phenology, morphology ... and genetics, we conclude that these taxa definitely constitute two distinct species'.

Consideration of the information about breeding, and particularly egg-laying dates, in Marchant and Higgins (1990) suggests that while some species may be sympatric, perhaps without interbreeding in geographical terms, they are not sympatric in temporal terms, which we suggest is equally important for sea-birds. For example, Marchant and Higgins (1990: 538) describe the breeding of *P. belcheri*, which breeds mainly on the Falklands and Kerguelen, as 'Not well known. Studied only in Falkland Is outside our limits'. Egg-laying dates are given as 'Laying in middle two weeks of Nov.' (Marchant and Higgins 1990: 538). The breeding of *P. desolata*, whose main breeding areas are the South Orkney Islands, South Georgia, Kerguelen and Macquarie Island, is also described by Marchant and Higgins (1990: 531) as 'Not well known. Only comprehensive study at Signy I.'. Laying is said to occur 'with first eggs in first week, and last in last week of Dec. Variations in different parts of range or caused by weather not known' (Marchant and Higgins 1990: 531). Thus the situation on Kerguelen appears to recall that of the Giant Petrels on Macquarie.

The cytochrome *b* evidence suggests conclusions very different from those of Bretagnolle *et al.* (1990). Our distance data within *Pachyptila* show *P. turtur* differing from *P. desolata* by 3.50% (0.79%), from *P. salvini* by 3.85% (1.06%), and from *P. vittata* by 3.15% (0.79%). Thus the other taxa and *P. turtur* diverged from ≈7–10.6 million years ago. In contrast, the distance from *P. desolata* to *P. salvini* is only 0.70% (0.26%), and to *P. vittata* 1.22% (0.00%), and from *P. salvini* to *P. vittata* 1.57% (0.26%). These distances suggest that *desolata*, *salvini* and *vittata* should be considered as subspecies of a single species, *P. vittata* (J. R. Forster, 1777). The amino acid distances indicate that *P. desolata* and *P. vittata* diverged from each other less than ≈1 million years ago, and that *P. salvini* diverged from *P. vittata* ≈2.6 million years ago.

Bretagnolle *et al.* (1990: 310) cited unpublished electrophoretic data from Viot in support of their claims. Such data are not, of course, directly comparable with genetic distance data. But we might expect proportional correspondence between the two sets of data. Viot's electrophoretic data show a distance between *desolata* and *belcheri* of 0.051 as compared with 0.067 between *desolata* and *salvini* (Bretagnolle *et al.* 1990: 310). Since our data indicate a distance of 0.70% between *desolata* and *salvini*, Viot's data imply that the distance between *desolata* and *belcheri* would be proportionately less than 0.70%. Accordingly, we suggest lumping *belcheri* into *vittata*.

Thus, within *Pachyptila*, our evidence justifies the recognition of only two species, with additional subspecies following the account in Marchant and Higgins (1990: 515–554):

- *Pachyptila vittata* (J. R. Forster, 1777) (Broad-billed Prion) with five subspecies:
  P. vittata vittata,
  P. vittata salvini (Mathews, 1912),
  P. vittata macgillivrayi (Mathews, 1912),
  P. vittata desolata (J. F. Gmelin, 1789), and
  P. vittata belcheri (Mathews, 1912);
- *P. turtur* (Kuhl, 1820) (Fairy Prion), with four subspecies:
  P. turtur turtur,
  P. turtur subantarctica Oliver, 1955,
  P. turtur crassirostris (Mathews, 1912), and
  P. turtur eatoni (Mathews, 1912).

Bulweria, Pseudobulweria and Procellaria: Procellariini

The pairwise distance matrix for Procellariini is presented in Table 7. The next clade in Fig. 3 includes *Bulweria bulwerii* (Jardine & Selby, 1828) (Bulwer's Petrel) and four species of *Procellaria*. Marchant and Higgins placed *Bulweria* within the group of gadfly-petrels *Pterodroma*, and stated (1990: 355): '*Bulweria* has some structural resemblance to shearwaters. At present it is difficult to determine their precise relationships'. In this respect, they follow Olson (1975), who examined, and rejected, many of the possible anatomical features used to characterise *Bulweria*. Olson (1975: 112) concluded: '... the other alleged differences between [*Pterodroma* and *Bulweria*] are not substantiated and there seems little doubt that that they are very closely related. It is perhaps more reasonable that the comparatively slight differences between the two taxa should be recognised at the subgeneric rather than the generic level'.

Figs 2–4 all group *Bulweria* as a sister-clade to *Procellaria*, at distances of 0.91% (3.21%) to 1.03% (3.21%). That is, *Bulweria* diverged from *Procellaria* ≈32.1 million years ago. The within-group means between the four *Procellaria* species is 3.9%, with the smallest distance, 2.97% (0.53%), between *Procellaria cinerea* J. F. Gmelin, 1789 (Grey Petrel) and *P. westlandica* Falla, 1946 (Westland Petrel). The distances suggest that *P. cinerea* is closer to both *P. parkinsoni* 4.11% (1.32%) and *P. westlandica* 2.97% (0.53%) than is *P. aequatorialis* (4.72% (0.79%) and 4.11% (0.53%), respec-

tively). However, the amino acid data suggest that *parkinsoni* and *cinerea* diverged ≈13.2 million years ago, and *aequatorialis* and *parkinsoni* ≈7.9 million years ago. For *Pseudobulweria* only two cytochrome *b* sequences of 500 bp lengths are deposited in GenBank. A preliminary MP analysis suggests that *Bulweria/Procellaria* and *Pseudobulweria* share a common ancestry, but that *Pseudobulweria* forms a distinct group within that clade, and that the affinities of that genus lie with *Bulweria* and *Procellaria* rather than *Pterodroma*.

Pterodroma Petrels: Pterodromini

The pairwise distance matrix for Pterodromini is presented in Table 8. The next clade in Fig. 3 contains the whole of the genus *Pterodroma*. All trees confirm the monophyly of the genus *Pterodroma* (100% bootstrap support). It should be noted that the name used by Nunn and Stanley in their GenBank submission for *Pterodroma feae* (Salvadori, 1899) is *Pterodroma deserta*, based on *Pterodroma mollis deserta* Mathews, 1934, a junior synonym of *feae*, although *P. feae* was used in their 1998 publication. Until Bonaparte (1856a), gadfly petrels were placed in *Procellaria*; Bonaparte applied the name *Pterodroma* to the all-dark petrels, *Aestrelata* to some larger species with white bellies, and, in (Bonaparte 1856b), *Cookilaria* for smaller species that are white below.

We saw above with the traditional genus *Puffinus* how percentage distances can be used to evaluate possible groupings: not only through the trees, but also by contrasting mean within-group distances with mean between-group distances. We used comparisons of within-group and between-group means, as exemplified above in relation to both the storm-petrels and shearwaters, to test various possible groupings with *Pterodroma*. We could not arrive at a clear solution, and suspect that a final solution to the structure within *Pterodroma* will require DNA from almost all species. We are also confident that the internal structure will be at the level of subgenera. This is in contrast to the situation with the former *Puffinus*, where the between-group means were almost twice the value of the within-group means, and where the between-group means approximated the distances between genera nearby in the tree. So we offer the following tentative analysis of subgenera:

- *Pterodroma* Bonaparte, 1856, including at least *P. cahow* (Nichols & Mowbray, 1916) (Bermuda Petrel); *P. feae* (Salvadori, 1899) (Fea's Petrel); *P. hasitata* (Kuhl ex

Table 7. Pairwise distance matrix for Procellariini

Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	55	56	57	58	59
[55] *Procellaria aequinoctialis*		0.0106	0.0079	0.0053	0.0321
[56] *Procellaria cinerea*	0.0394		0.0132	0.0053	0.0321
[57] *Procellaria parkinsoni*	0.0472	0.0411		0.0132	0.0294
[58] *Procellaria westlandica*	0.0411	0.0297	0.0359		0.0321
[59] *Bulweria bulwerii*	0.1032	0.1015	0.1032	0.0910	

Forster, 1820) (Black-capped Petrel); *P. incerta* (Schlegel, 1863) (Atlantic Petrel); *P. lessonii* (Garnot, 1826) (White-headed Petrel); *P. macroptera* (A. Smith, 1840) (Great-winged Petrel); *P. magentae* (Giglioli & Salvadori, 1869) (Magenta Petrel); and *P. mollis* (Gould, 1844) (Soft-plumaged Petrel). [This group has within-group mean of 3.39% with a standard deviation of 0.86. It is interesting that *P. feae* (and *P. madeira* Mathews, 1934 (Madeira Petrel), not present in our sample) have been grouped with *P. mollis* (as in Sibley and Monroe 1990: 323). However, Fig. 3 and the nucleotide and amino acid distances all confirm that the affinities of *P. feae* lie with *P. cahow* rather than with *P. mollis: feae* is 2.9% (0.00%; in other words, a very young species) from *cahow*, but 4.55% (0.79%, or divergence 7.9 million years ago) from *mollis*.]

- *Hallstroma* Mathews & Hallstrom, 1943, with *Procellaria neglecta* Schlegel, 1863 as its type. This includes at least: *P. externa* (Salvin, 1875) (Juan Fernandez Petrel); *P. phaeopygia* (Salvin, 1876) (Galapagos Petrel); *P. sandwichensis* (Ridgway, 1884) (Hawaiian Petrel); *P. inexpectata* (J. R. Forster 1844) (Mottled Petrel); and *P. neglecta* (Schlegel, 1863) (Kermadec Petrel). [The within-group mean for this group is 4.23% with a standard deviation of 0.71. We also note that Nunn and Zino, the authors of the sequence for *P. phaeopygia* in GenBank include a note: 'identification of *phaeopygia* race not established: *phaeopygia/sandwichensis*'. Given their closeness, we can safely assume both taxa would be assigned in this subgenus.]
- ?*Proaestrelata* Imber, 1985 with *Oestrelata axillaris* Salvin, 1893, as its type, perhaps containing at least *P. axillaris* (Chatham Islands Petrel) and *P. nigripennis*

(Rothschild, 1893) (Black-winged Petrel); but not (*contra* Imber 1985: 219) *inexpectata* or *hypoleuca*. [This is the least certain grouping. *P. axillaris* forms a sister-clade in Fig. 3 to the whole of the subgenus *Pterodroma* node, while *P. nigripennis* forms a sister-clade to the *axillaris–Pterodroma* node. The two taxa differ by 5.8% (though the amino acid data indicates they diverged 6.6 million years ago), and it is possible that the addition of other species might lead to the reallocation of *nigripennis*.]
- *Cookilaria* Bonaparte, 1856, with *Procellaria cookii* G. R. Gray, 1843, as its type, including at least *P. longirostris* (Stejneger, 1893) (Stejneger's Petrel); *P. cookii* (Cook's Petrel); and *P. hypoleuca* (Salvin, 1888) (Bonin Petrel). [This group is well supported on a very deep branch in Fig. 3. The mean within-group distance is 6.73%, while the amino acid data indicate that *P. cookii* and *P. longirostris* diverged from the each other ≈24 million years ago, and *P. cookii* and *P. hypoleuca* diverged 18.6 million years ago.]

Diving Petrels: Pelecanoidini

The pairwise distance matrix for Pelecanoidini is presented in Table 9. The final clade to be discussed, the bottom clade in Fig. 3, contains the diving-petrels, members of the genus *Pelecanoides*. This genus is monophyletic in all Figs (98% bootstrap support). The percentage distances between members of *Pelecanoides* and all other taxa are very high, ranging from a maximum of 16.01% (7.37%) between *P. georgicus* Murphy & Harper, 1916 (South Georgia Diving-Petrel) and *Diomedea exulans amsterdamensis*, to a minimum of 11.55% (10.83%) between *P. garnotii* (Lesson, 1828) (Peruvian Diving-Petrel) and *Pterodroma nigripennis*. The within-group mean for *Pelecanoides* is 10.0%. The

Table 8. Pairwise distance matrix for Pterodromini
Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with Poisson correction above the diagonal 381 sites

	32	33	34	35	36	37	38	39	40	41	42	43	44	45
[32] *Pterodroma axillaris*		0.0159	0.0106	0.0159	0.0053	0.0213	0.0132	0.0186	0.0026	0.0159	0.0186	0.0213	0.0213	0.0132
[33] *Pterodroma cahow*	0.0744		0.0213	0.0000	0.0106	0.0053	0.0186	0.0079	0.0132	0.0106	0.0240	0.0106	0.0106	0.0079
[34] *Pterodroma cookii*	0.0709	0.0910		0.0213	0.0159	0.0267	0.0186	0.0240	0.0132	0.0213	0.0240	0.0267	0.0267	0.0186
[35] *Pterodroma feae*	0.0709	0.0289	0.0875		0.0106	0.0053	0.0186	0.0079	0.0132	0.0106	0.0240	0.0106	0.0106	0.0079
[36] *Pterodroma externa*	0.0595	0.0691	0.0674	0.0709		0.0159	0.0079	0.0132	0.0026	0.0159	0.0186	0.0159	0.0159	0.0079
[37] *Pterodroma hasitata*	0.0717	0.0297	0.0866	0.0271	0.0700		0.0240	0.0132	0.0186	0.0159	0.0294	0.0159	0.0106	0.0132
[38] *Pterodroma hypoleuca*	0.0691	0.0744	0.0691	0.0831	0.0665	0.0822		0.0186	0.0106	0.0213	0.0240	0.0186	0.0213	0.0106
[39] *Pterodroma incerta*	0.0691	0.0420	0.0822	0.0411	0.0726	0.0376	0.0796		0.0159	0.0026	0.0186	0.0026	0.0026	0.0106
[40] *Pterodroma inexpectata*	0.0630	0.0814	0.0682	0.0831	0.0402	0.0840	0.0674	0.0761		0.0132	0.0213	0.0186	0.0186	0.0106
[41] *Pterodroma lessonii*	0.0639	0.0402	0.0822	0.0359	0.0744	0.0341	0.0761	0.0192	0.0761		0.0213	0.0053	0.0053	0.0132
[42] *Pterodroma longirostris*	0.0665	0.0787	0.0577	0.0761	0.0647	0.0717	0.0752	0.0726	0.0717	0.0735		0.0213	0.0213	0.0267
[43] *Pterodroma macroptera*	0.0674	0.0394	0.0840	0.0350	0.0709	0.0315	0.0796	0.0201	0.0779	0.0114	0.0726		0.0053	0.0132
[44] *Pterodroma magentae*	0.0709	0.0420	0.0892	0.0376	0.0726	0.0306	0.0849	0.0210	0.0831	0.0192	0.0787	0.0219		0.0132
[45] *Pterodroma mollis*	0.0691	0.0481	0.0857	0.0455	0.0726	0.0437	0.0761	0.0420	0.0796	0.0411	0.0761	0.0420	0.0411	
[46] *Pterodroma neglecta*	0.0569	0.0787	0.0787	0.0822	0.0394	0.0796	0.0709	0.0752	0.0516	0.0752	0.0709	0.0752	0.0805	0.0752
[47] *Pterodroma nigripennis*	0.0516	0.0717	0.0700	0.0717	0.0621	0.0744	0.0639	0.0752	0.0604	0.0717	0.0752	0.0717	0.0770	0.0665
[48] *Pterodroma phaeopygia*	0.0630	0.0726	0.0717	0.0761	0.0315	0.0735	0.0682	0.0717	0.0429	0.0726	0.0682	0.0744	0.0761	0.0726
[49] *Pterodroma solandri*	0.0560	0.0761	0.0630	0.0744	0.0560	0.0770	0.0639	0.0726	0.0586	0.0726	0.0682	0.0779	0.0726	0.0752

Table 9.   Pairwise distance matrix for Pelecanoidini
Uncorrected 'p' distances (nucleotides) below the diagonal 1143 sites; amino acid distances with
Poisson correction above the diagonal 381 sites

	91	92	93	94
[91] *Pelecanoides garnotii*		0.0513	0.0485	0.0375
[92] *Pelecanoides georgicus*	0.1199		0.0186	0.0267
[93] *Pelecanoides magellani*	0.1251	0.0674		0.0240
[94] *Pelecanoides urinatrix*	0.1102	0.0892	0.0884	

amino acid data indicate that *P. garnotii* diverged from the remaining taxa ≈45.8 million years ago, the next divergence was *P. urinatrix* ≈25.4 million years ago, and the final divergence between *P. georgicus* and *P. magellani* ≈18.6 million years ago.

Acknowledgments

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