Ibis (2008), doi: 10.1111/j.1474-919x.2007.00794.x

The separation of *Pterodroma madeira* (Zino's Petrel) from *Pterodroma feae* (Fea's Petrel) (Aves: Procellariidae)

FRANCIS ZINO,[1]* RUTH BROWN[2] & MANUEL BISCOITO[3]
[1]*Freira Conservation Project, Av. do Infante, 26, 9000-015 Funchal, Portugal*
[2]*Institute of Zoology, Nuffield Building, Zoological Society of London, London NW1 4RY, UK*
[3]*Museu Municipal do Funchal (História Natural), Rua da Mouraria, 31, 9004-546 Funchal, Portugal*

The taxonomic status of petrels from the North East Atlantic has long been a matter of debate. Breeding colonies of petrels occurring on the islands of Madeira, Bugio and Cape Verde were originally thought to be outlying populations of the polytypic species *Pterodroma mollis*. Subsequent taxonomic treatments have varied considerably in their classification of birds from these islands. The petrel populations on Madeira and Bugio represent some of Europe's rarest breeding birds and their exact species designation, and hence relation to conservation mandates, is a question of considerable importance. In this study we use molecular techniques alongside more traditional taxonomic characters to confirm the existence of two species of the genus *Pterodroma* in the Archipelago of Madeira. We also discuss identification of these species in the field and the implications for their conservation management.

Keywords: cytochrome-*b*, Madeira, phylogeny, *Pterodroma*, seabirds, taxonomy.

In the North East Atlantic Ocean, petrels of the genus *Pterodroma* (Procellariidae) are known to breed at the Madeiran Archipelago (*c.* 650 km west of Morocco) and also *c.* 1900 km further south at the Cape Verde Islands. Two separate populations are found in the Madeiran Archipelago, one occupying the mountainous regions of Madeira and the other about 40 km away on Bugio, one of the offshore islands known as the Desertas (Bugio, Deserta Grande and Ilheu Chão) (Fig. 1). Since their discovery, the taxonomy of petrels from these islands has been the cause of much debate.

In 1903, four petrel specimens were collected from the mountains above Santo António, Madeira, by the Rev. Ernesto Schmitz. These he identified as *Oestrelata feae*, a species described 4 years earlier based on a specimen collected at the Cape Verde Islands (Salvadori 1899, Bourne 1983, Zino & Zino 1986). During the 1890s, Schmitz had also handled several specimens from the Desertas, which he referred to as *Oestrelata* (= *Pterodroma*) *mollis*, a Southern Ocean species described in 1844. In 1934, Mathews conducted a review of the systematics of Procellariiformes, in which he synonymized the races from the North East Atlantic with *P. mollis* (Mathews 1934a, 1934b). *P. mollis* has a wide distribution throughout the Antarctic, Indian and Atlantic oceans, with variation in morphometrics, coloration and breeding behaviour occurring across its range (Bretagnolle 1995). In his notice on *P. mollis*, Mathews (1934a) assigned the three North East Atlantic birds the rank of subspecies, considering the population from Madeira as *P. mollis madeira*, the population from Bugio as *P. mollis deserta* and the population from Cape Verde as *P. mollis feae*. Since then most authors have found *deserta* inseparable from *feae* (Bourne 1957, Jouanin *et al.* 1969, Cramp & Simmons 1977, Jouanin & Mougin 1979).

In 1957, W.R.P Bourne noted that there were differences in the size, breeding season and habitat of the petrels from Madeira and Bugio. Madeiran birds are conspicuously smaller and breed throughout May and June in the cool, moist, heavily vegetated regions of the island at an altitude of around 1600 m. The larger Bugio birds breed in July and August on a bare and arid plateau at around 375 m, a habitat similar to that preferred by Cape Verde petrels. Bourne (1983) proposed the splitting of the North East Atlantic petrels from the *P. mollis* complex and suggested

*Corresponding author.
Email: fzino@mail.telepac.pt

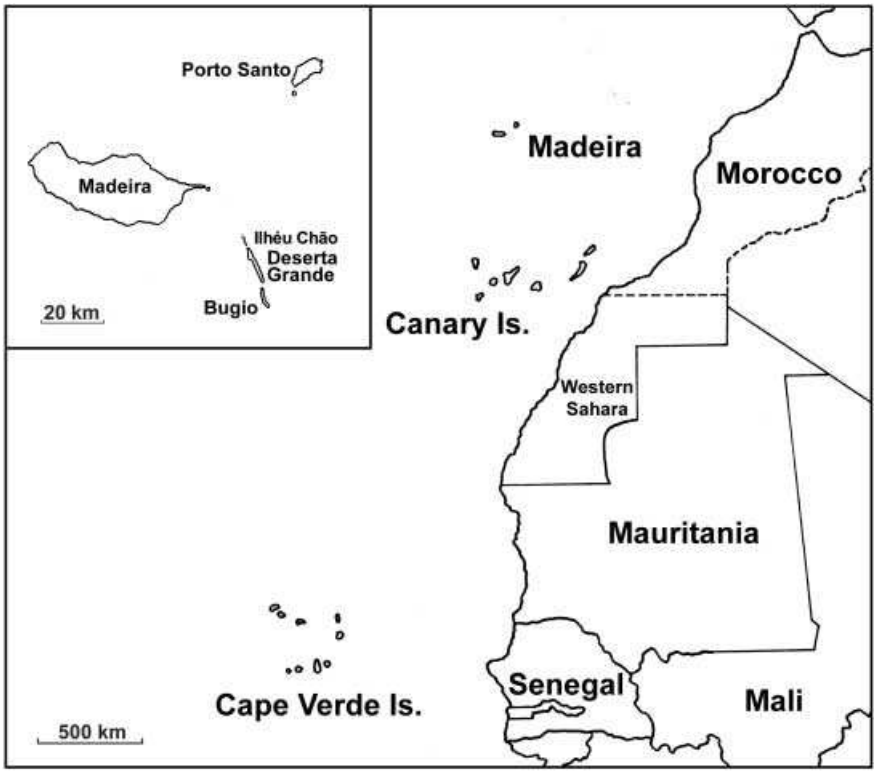

Figure 1. Islands of the North East Atlantic.

species-level distinction for the birds of Madeira (*P. madeira*) and those of Bugio/Cape Verde (*P. feae*).

In their comprehensive review of Madeiran *Pterodroma*, Zino and Zino (1986) confirmed the differences in size and breeding biology of these two petrel populations. Madeiran birds weigh an average of 53% less than those of Bugio and are consistently smaller across a number of standard morphometric measurements. However, the authors also note that the calls of petrels from Madeira and Bugio are indistinguishable from one another and that there is no plumage feature that can be consistently used to identify either bird.

Bretagnolle (1995) conducted a survey of the systematics of the entire *P. mollis* complex, using analysis of calls as well as morphometrics and coloration. Bretagnolle placed particular emphasis on calls as a distinguishing feature of petrel species as pair formation occurs at night and therefore calls seem to have a direct role in species recognition. In his analysis, Bretagnolle found that birds from Madeira and Bugio could not be completely distinguished based on their vocalizations (73–80% of calls were correctly assigned to their island of origin using discriminant analysis). He concluded that *P. mollis* should be split into two distinct species, *P. mollis* in the South Atlantic and *P. feae* in the North Atlantic, with subspecies *feae*, *madeira* and *deserta* retained for Cape Verde, Madeira and Bugio, respectively. Bretagnolle (1995) did acknowledge the morphological differences between the birds of Bugio and Madeira, but concluded that 'the similarity of their calls suggests that there is no behavioural isolation between these two populations.'

Deciding the exact species designation of Madeiran petrels is more than simply an exercise in taxonomic pedantry. By the mid-1960s petrels on Madeira were believed to be extinct, but extensive searching led to the discovery of a small number of active nest-sites in 1969. Monitoring of these sites during the 1980s revealed that no chicks were fledging due to heavy predation of eggs and chicks by rats. At that time the breeding population was estimated at fewer than 30 pairs, making *P. madeira* (Zino's Petrel or Freira) the most endangered seabird species in Europe, with little chance of survival (Zino & Zino 1986). In 1986 the Freira Conservation Project was launched with the objective of reversing the decline of *P. madeira*. However, the question of whether or not Zino's Petrel was a unique endemic species remained. Confirmation of this would no doubt lend weight to the conservation

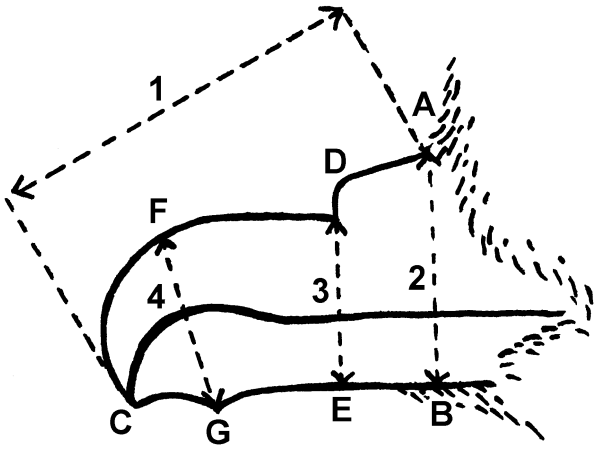

Figure 2. Bill measurements used (from Zino & Zino 1986).

Table 1. Morphometric measurements (mm) of *P. madeira* and *P. feae*. Bill heights follow Zino and Zino (1986).

	P. madeira	*n*	*P. feae*	*n*
Total length	331.5 ± 7.2	66	361.5 ± 8.2	338
Wing length	251.1 ± 4.8	70	271.0 ± 5.9	337
Tail length	109.0 ± 3.2	66	110.7 ± 3.8	334
Tarsus	34.3 ± 1.3	62	38.0 ± 1.6	185
Middle toe	38.8 ± 1.6	66	44.3 ± 2.2	188
Bill length	25.8 ± 0.9	71	29.7 ± 1.1	258
Bill height AB	11.3 ± 0.5	71	14.7 ± 0.7	306
Bill height FG	9.6 ± 0.4	71	12.5 ± 0.5	306
Bill height DE	8.0 ± 0.4	71	10.4 ± 0.6	256

efforts on Madeira, and in this study we use molecular techniques to help resolve the taxonomic confusion surrounding the petrels of Madeira.

The identification of petrels as originating from Madeira or Bugio is extremely difficult both in flight and in the hand (Steele 2006). However, morphometric measurements, particularly of the bill, provide a method for distinguishing between the two. In this study we use multivariate analysis to demonstrate the subtle morphological differences between the populations on these two islands.

MATERIAL AND METHODS

Morphological analysis

A total of 71 adult petrels were examined between 1986 and 2006 in the central mountain massif of Madeira and a further 338 were examined between 1985 and 2004 on Bugio, Desertas Islands. Whenever possible, the following measurements were taken: wing length, total length, tail length, tarsus length, middle toe length, bill length and bill height at three positions (Table 1, Fig. 2). Relative lengths of primary feathers of the left wing were also recorded in eight adult specimens of each species (Appendix 1). A principal components analysis (PCA) was carried out using the nine morphometric measurements listed above. Only birds for which all measurements had been recorded were included in the analysis (Madeira, n = 58; Bugio, n = 175).

DNA analysis

Samples of fresh blood were collected from 15 petrels on Madeira and 11 petrels on Bugio between September 2003 and September 2005. Blood was stored in 90% ethanol at ambient temperature for transportation to the laboratory, whereupon it was stored at –20 °C. DNA was isolated from approximately 5 mg of coagulated blood using the Promega Wizard 96 Genomic DNA Purification System. Final elution was in 500 µL ddH_2O and eluted template DNA was stored at –20 °C.

Mitochondrial cytochrome-*b* gene isolation and sequencing

An 830-bp section of the cytochrome-*b* (cyt-*b*) gene was amplified as a single fragment using the PCR primers L15236/H16065 (Helm-Bychowski & Cracraft 1993). Amplifications were performed in a 30-µL reaction mix containing *c*. 10 ng genomic DNA; 1× PCR buffer; 2.5 mM $MgCl_2$; 125 µM each of dGTP, dATP, dTTP and dCTP; 3.75 µM of each primer and 3 units of *Taq* DNA polymerase (Invitrogen). Thermal cycling was performed in a GeneAmp PCR System 9700 (Applied Biosystems) and consisted of 1 min at 95 °C then 35 cycles of 1 min at 94 °C, 1 min at 40 °C, 1 min at 60 °C and 3 min at 72 °C with a final cycle of 5 min at 72 °C. PCR products were visualized in 2% agarose gel containing 0.3 µg/mL ethidium bromide. Due to multiple bands appearing in the PCR product, fragments of length 830 bp were cut directly from the gel and purified using a QIAquick Gel Extraction Kit (Qiagen). This purified product was then used for direct sequencing using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and 0.16 µM of the original PCR primers. Sequences were visualized on an ABI Prism 3100 Genetic Analyser. This protocol produced poor quality sequence data, but we were able to use the sequence obtained to design the following primers

in order to facilitate the amplification and sequencing of cyt-*b* in the study taxa: L15281, 5′-CCCTTATGGCAACTGCCTTCGTAGG-3′; L15653, 5′-CAGAAAACTTTACTCCAGCA-3′; H15535, 5′-TAGGGGTGGAATGGGATTTTGTCGCAGTT-3′.

Subsequent amplifications of cyt-*b* were performed using primers L15281/H16065, producing a fragment of around 780 bp in length. The reaction mix was the same as above and PCR cycling conditions were 1 min at 95 °C followed by 35 cycles of 1 min at 94 °C, 1 min at 45 °C and 3 min at 72 °C with a final cycle of 5 min at 72 °C. PCR products were visualized as above and cyt-*b* fragments were again purified from agarose gel and were sequenced using primers L15281, L15653, H15535 and H16065. This produced four fragments of sequence, which were aligned and edited using Sequencher 4.1 (Applied Biosystems) and Bioedit 7.0.5 (Hall 1999).

Phylogenetic analysis

Phylogenetic relationships were estimated using PAUP 4.0b10 (Altivec). Both maximum-parsimony and maximum-likelihood methods were used with bootstrapping to assess support for internal branches. Maximum-parsimony analysis involved multiple replicate heuristic searches with random addition of taxa to minimize the effect of input order bias. Branch swapping was carried out using the tree bisection–reconnection (TBR) algorithm and all characters were weighted equally. Bootstrapping was performed using 1000 replicates. Maximum-likelihood analysis also involved multiple heuristic searches with random addition of taxa. The model of nucleotide evolution used was the HKY85 model (Hasegawa *et al.* 1985) with a Gamma distribution (shape parameter = 0.0147). The model was chosen as having the best fit to the data using Modeltest 3.7 (Posada & Crandall, 1998). A number of additional species were also included in the phylogenetic analysis, using cyt-*b* sequences obtained from Genbank. These species and their Genbank accession numbers are as follows: *P. cahow* (U74331), *P. incerta* (U74332), *P. hasitata* (U74335), *P. macroptera* (U74336), *P. lessonii* (U74337), *P. magentae* (U74338) and *P. mollis mollis* (U74334).

RESULTS

Morphology

PCA of the nine morphometric measurements produced complete separation of birds from Madeira and Bugio along PC1 (Fig. 3), which accounts for 74% of the variance within the sample. A pattern of striations can be seen along PC2, with points forming three rough bands in the two species (although the effect is more pronounced in *P. feae*). Exploration of the raw data reveals that this pattern is caused by the tail length measurements. Tail length is a continuous variable but appears to have a tri-modal distribution in this case, which may be a reflection of sex or age classes within these species. However, too few data are currently available to provide any robust explanation. Differences between the two species were also found in the relative primary lengths (Appendix 1). The tips of the wings in *P. madeira* are rounder than in *P. feae*. In the former, either the 9th or 10th primary may be the longest and in some birds the two feathers are equal in length, whilst in the latter the 10th primary is always the longest.

Molecular analysis

A fragment of the cyt-*b* gene spanning 774 bp was sequenced from all samples. The gene sequences can be fully translated using the vertebrate mitochondrial code (Stothard 2000) and do not contain nonsense or stop codons. For the 26 *Pterodroma* samples sequenced, there were 20 nucleotide positions where a base substitution occurred. Two variable sites were located at the first codon position, one was at the second codon position (resulting in an amino acid replacement Ile↔Thr) and 17 were at the third

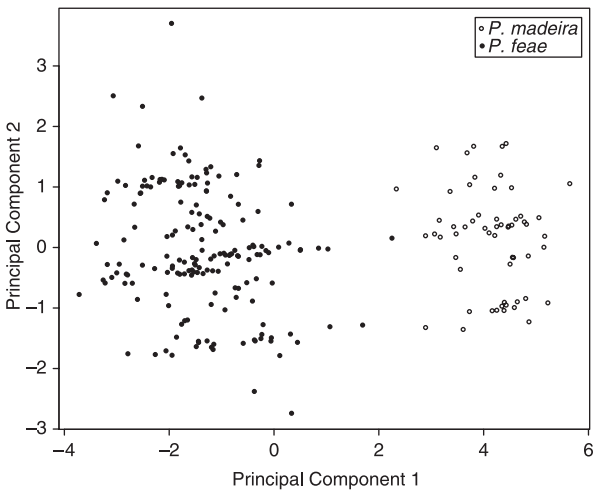

Figure 3. Principal Component Analysis of morphometric measurements in *P. madeira* and *P. feae*, showing a complete separation of the two species.

codon position. The ratio of transitions to transversions was 19 : 1.

Sequencing of the *Pterodroma* samples recovered five haplotypes. Of these, two were found within the Bugio population (designated B1 and B2) and three were found within the Madeira population (designated M1, M2 and M3). Cyt-*b* sequence data are also available on Genbank for one *Pterodroma* from Bugio (accession no. U74333). This sequence proved to be identical to haplotype B1. Haplotypes from the two islands are mutually exclusive and differ from one another at 17 nucleotide positions (2.2% of the total sequence). The two Bugio haplotypes differ from one another at one nucleotide position (0.13%) and the three Madeira haplotypes differ from one another at two nucleotide positions (0.26%). Complete sequence data are available on Genbank (accession numbers EF537882–EF537886).

A number of other *Pterodroma* species were included in the analysis in order to illustrate the taxonomic position of the Madeira/Bugio populations within a larger scheme of Atlantic and Southern Ocean taxa. *P. cahow* and *P. hasitata* are considered to be closely allied with the petrels of the North East Atlantic based on morphology, breeding behaviour and, more recently, molecular studies (Nunn & Stanley 1998, Brooke 2004). *P. mollis mollis* was chosen as the outgroup. Four other petrel species – *P. incerta*, *P. macroptera*, *P. lessonii* and *P. magentae* – were also included in the analysis. Molecular studies have placed these four taxa, which are variously distributed across the Southern Ocean, as the sister group to the North Atlantic clade (Nunn & Stanley 1998).

Phylogenetic analysis of these data using maximum parsimony and maximum likelihood produced one tree in each case, with identical topologies. The maximum-parsimony tree is shown in Figure 4.

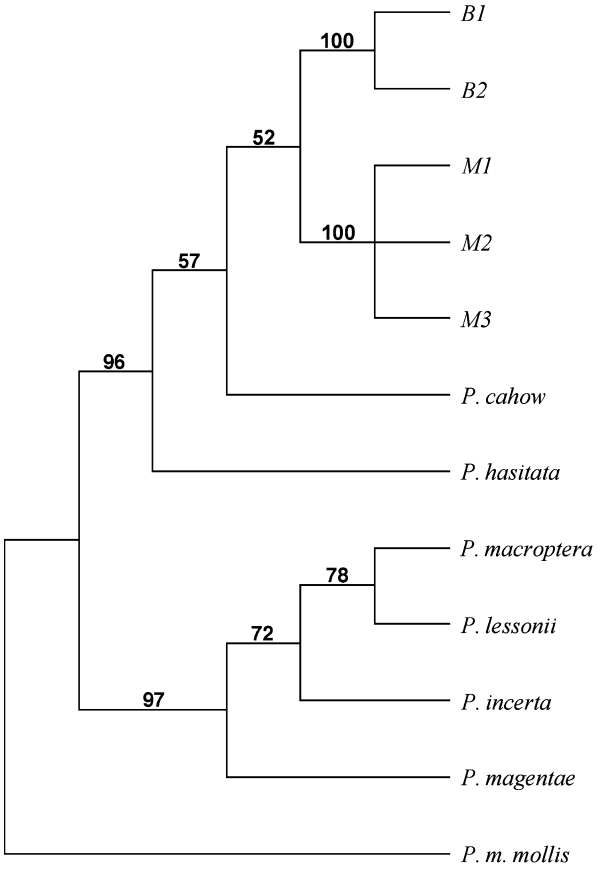

Figure 4. Phylogenetic relationships between *Pterodroma* from Madeira (M1–M3) and Bugio (B1, B2), determined using maximum parsimony. Bootstrap values (1000 replicates) are shown.

DISCUSSION

It is our opinion that the petrel populations of Madeira and Bugio should be regarded as separate species – *Pterodroma madeira* (Zino's Petrel) and *Pterodroma feae* (Fea's Petrel) – corroborating the suggestions of previous authors (Bourne 1983, Imber 1985, Zino & Zino 1986). The morphological analyses of the two populations, based on the largest sampling to date, fully support this separation. Of all the measurements taken, bill measurements were the most reliable for distinguishing the two species, with *P. feae* having a much more robust bill structure than *P. madeira* (Fig. 5). The structure of the bill allows four clearly defined measurements and is independent of the bird's nutritional status, permitting accurate measurements to be taken in the difficult conditions in which these birds are usually studied – at night and during adverse weather conditions. However, morphometrics alone may be insufficient evidence to merit a species-level classification. The Galapagos Petrel *P. phaeopygia* shows significant differences in body size among populations from different islands (Brooke 2004), although Friesen *et al.* (2006) discovered a very low level of sequence divergence in the mitochondrial ATPase gene across all islands. Similarly, the Tahiti Petrel *Pseudobulweria rostrata* displays significant differences in the bill measurements of its two subspecies *trouessarti* and *rostrata* (Brooke 2004). Therefore, a genetic characterization of the petrels from Madeira and Bugio was also undertaken.

The cyt-*b* data from *Pterodroma* populations on Madeira and Bugio support the case for a species-level

Figure 5. Heads of *Pterodroma madeira* (left) and *P. feae* (right), showing bill differences.

split of these two taxa. No haplotypes are shared between the two populations, indicating reproductive isolation. The approximately 2% difference between mtDNA haplotypes from the two islands is an order of magnitude larger than within-island differences (0.13 and 0.26%). In comparison, the haplotypes of *P. macroptera* and *P. lessonii*, for which a species-level classification is undisputed, differ by only 1% over the same section of the cyt-*b* gene.

The decision to split a population into two species is dependent on the particular species concept adopted by the observer. Strict adherence to the Biological Species Concept (BSC) (Mayr 1942), where any indication of gene flow between two populations will preclude species-level distinction, tends to uncover fewer species than the Phylogenetic Species Concept (PSC) (Cracraft 1983), where gene flow is permitted as long as some character discontinuity between populations is evident. These two concepts are not mutually exclusive, but simply focus on different stages of the speciation process – the slow divergence of one species into two. The PSC relies on diagnosable characters as criteria for the separation of species. We are confident that the molecular and morphological data presented here, along with observations on breeding season and habitat preference (Bourne 1983, Zino & Zino 1986), satisfy these criteria and indicate that the petrel populations of Bugio and Madeira should be treated as separate species under the PSC.

The BSC demands complete reproductive isolation as the grounds for separating species; however, this is impossible to deduce for allopatric populations. The petrels of Madeira and Bugio undoubtedly come into contact at sea and might be regarded as sympatric given that they breed within a single small archipelago. Nevertheless, their breeding colonies remain separated, as do their breeding seasons, and no bird ringed on Madeira has ever been re-captured on Bugio, or vice versa, over a 20-year period (F. Zino unpubl. data). Therefore, within the archipelago itself we assume the populations to be allopatric, and no direct evidence of reproductive isolation can be obtained. However, the reciprocal monophyly of cyt-*b* haplotypes from the two islands supports the idea that these two populations are not interbreeding. The Madeiran population forms a monophyletic clade with 100% bootstrap support, as does the population from Bugio. Nevertheless, one must be cautious when drawing conclusions based on data from a single gene. As mtDNA is maternally inherited, the same pattern could be produced if there was unequal dispersal between the sexes; for example, if females did not disperse from their natal breeding site but males were moving between the two islands. However, this scenario seems unlikely given that all birds appear to remain faithful to the island where they were ringed. Further evidence of reproductive isolation between the two islands could potentially be gained by looking at nuclear markers such as microsatellites, although polymorphic microsatellite loci are not yet described for these species.

Phylogenetic analysis of the Madeira/Bugio birds and other Atlantic/Southern Ocean species reveals a well-supported monophyletic origin for the North Atlantic *Pterodroma* clade. *Pterodroma cahow* (the Bermuda Petrel) shows the closest affinity to the Madeira/Bugio clade, followed by *Pterodroma hasitata* (the Black-capped Petrel). Both of these conclusions have been suggested by previous authors (Bretagnolle 1995, Nunn & Stanley 1998, Penhallurick & Wink 2004).

The fact that the two populations maintain reproductive isolation despite their close proximity, similar appearance and similar calls is intriguing. Bourne (1983) speculates that the Madeiran archipelago may have been colonized twice by gadfly petrels. *P. madeira* may have evolved there when the climate was cooler and wetter during the Pleistocene. Then, as the climate became warmer and drier in recent times, *P. madeira* retreated to higher ground whilst Bugio was colonized by birds migrating from the arid environment of Cape Verde. This scenario is

compatible with the data presented here. Nunn and Stanley (1998) used fossil data to calibrate the rate of molecular evolution in a number of Procellariiform groups and arrived at a figure of 0.78% Ma^{-1} (0.9% using a K-2 correction) for medium-sized *Pterodroma* spp. This estimate suggests divergence of the two species at around 2.5 million years ago (Madeira and Bugio Islands were formed by volcanic activity some 4–5 million years ago; Schwartz *et al.* 2005), placing the split between the Madeira and Bugio populations in the late Pliocene. Assuming Bugio was then colonized from the south during climatic change in the Pleistocene, temporal variation in breeding could have maintained a reproductive barrier between the two island populations. Philopatry to natal breeding sites may also act as a mechanism of isolation between petrel populations and promote speciation in this group.

This route of radiation of petrels in the North Atlantic is, of course, highly speculative. Data from the petrels of the Cape Verde Islands would be necessary before firmer conclusions could be reached. Although a few specimens of *P. feae* from the Cape Verde Islands have been measured, the sample was not large enough for inclusion in this paper. It is, however, interesting to note that the population of *P. feae* in Cape Verde does not share the same breeding season as the population from Bugio (Bannerman & Bannerman 1968), thus suggesting a degree of isolation. The few Cape Verde birds handled would suggest significant biometric differences from the Bugio population. A morphological and genetic characterization of the Cape Verde birds should be undertaken.

The separation of Zino's and Fea's Petrels in flight has been much debated amongst experienced ornithologists and birdwatchers (Fisher 1989, Gantlett 1995, Tove 1997, 2001, Steele 2006). From the biometrics analysed, the bill is by far the easiest form of differentiating the two species, but for an observer in the field this is difficult. Using digital photography and image analysis, Tove (2001) demonstrated that there are differences in the shape of the wings of these species. The relative primary lengths measured (Appendix 1) confirm this, the tip of the wing of *P. madeira* being rounder, but such technology is available to few people. Wing feather pattern in the sample studied showed a large individual variation with very similar patterns in both species (Fig. 6). Steele (2006) discusses the problem at length and is in agreement that it is still nearly impossible to differentiate between *P. madeira* and *P. feae* in flight.

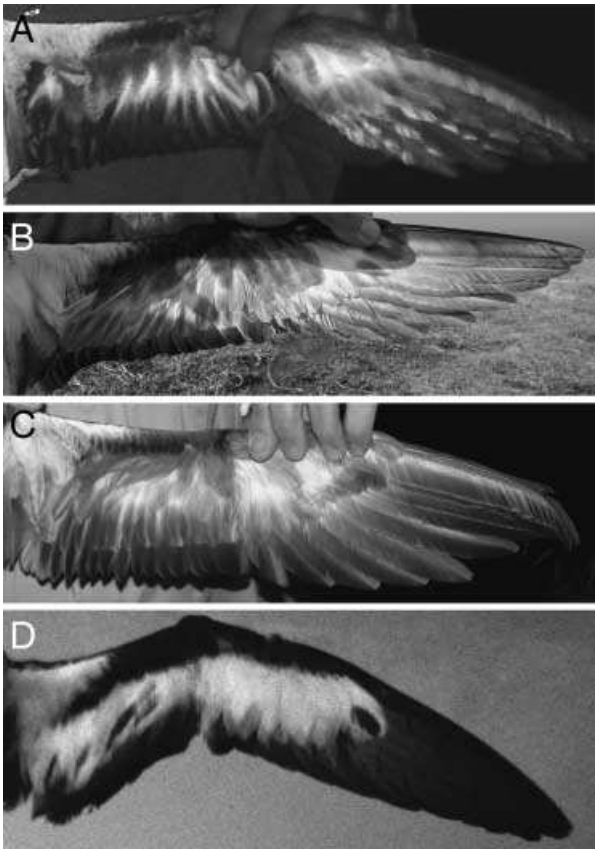

Figure 6. Underwings of *Pterodroma feae* from Cape Verde (A) and Bugio (B) and *P. madeira* (C), showing similar feather patterns. *P. cahow* (D) from Bermuda, showing the distinctive 'thumb print'.

As a direct result of ongoing predator control measures initiated by the Freira Conservation Project, the productivity of *P. madeira* has risen (though with some fluctuations) since 1987 (Zino *et al.* 2001). In 2005, with an estimated population of 65–80 pairs, *P. madeira* was down-listed from Critically Endangered to Endangered in the IUCN Red List of Endangered Species (Birdlife International 2006). The breeding sites on Madeira have been designated a Special Protected Area under the European Union's Wild Bird Directive, an action which has not only provided protection for the petrels but also for many other Madeiran endemics including plants, insects, molluscs, a lizard and a bat (Zino *et al.* 2001). The future of Zino's Petrel, and other endemic species on Madeira, depends on the continuation of such projects. It is our hope that by removing any trace of doubt about the unique status of this petrel species, we will help to guarantee the future of this important conservation initiative.

We have counted on the help of many individuals over the years, without whom it would have been difficult to gather the information obtained. Of these, our particular thanks go to Edward (Ted) Gerrard, Miguel Moreira, Henrique Costa Neves, Elizabeth Zino, Alexander Zino, Francesca Zino, João de Gouveia, Adam Blandy, João Borges, Amílcar Vasconcelos, Rui Dantas and Donato Caires. Thanks also to Jacob González-Solis for providing a photograph of *P. feae* from Cape Verde. We are deeply indebted to the Portuguese Air Force, British Navy and French Navy for the transport to Bugio in their helicopters, the Portuguese Navy for several sea transports and the staff of the Madeira Natural Park, notably Dr. Paulo Oliveira and his team of climbers, for the invaluable help provided in the field with Zino's Petrel. We are also indebted to Richard Nichols and Bill Jordan for assistance with the analysis, and to Christian Jouanin and W. (Bill) Bourne for critical reading of the manuscript and useful suggestions.

REFERENCES

Bannerman, D.A. & Bannerman, W.M. 1968. *History of the Birds of the Cape Verde Islands. Birds of the Atlantic Islands*, Vol. IV. Edinburgh: Oliver and Boyd.

Birdlife International 2006. Species factsheet: *Pterodroma madeira*. Downloaded from http://www.birdlife.org.

Bourne, W.R.P. 1957. Additional notes on the birds of the Cape Verde Islands. *Ibis* **99**: 182–190.

Bourne, W.R.P. 1983. The Soft-plumaged Petrel, the Gon-gon and the Freira, *Pterodroma mollis, P. feae* and *P. madeira*. *Bull. Brit. Orn. Club* **103**: 52–58.

Bretagnolle, V. 1995. Systematics of the Soft-plumaged Petrel *Pterodroma mollis* (Procellariidae): new insight from the study of vocalizations. *Ibis* **137**: 207–218.

Brooke, M. 2004. *Albatrosses and Petrels Across the World*. Oxford: Oxford University Press.

Cracraft, J. 1983. Species concepts and speciation analysis. *Curr. Ornithol.* **1**: 159–187.

Cramp, S. & Simmons, K.E.L. (eds) 1977. *The Birds of the Western Palearctic*, Vol. 1. Oxford: Oxford University Press.

Fisher, D. 1989. Pterodroma petrels in Madeira. *Birding World* **2**: 283–287.

Friesen, V.L., González, J.A. & Cruz-Delgado, F. 2006. Population genetic structure and conservation of the Galapagos petrel (*Pterodroma phaeopygia*). *Conserv. Genet.* **7**: 105–115.

Gantlett, S. 1995. Identification forum: field separation of Fea's, Zino's and Soft-plumaged Petrels. *Birding World* **8**: 256–260.

Hall, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* **41**: 95–98.

Hasegawa, M., Kishino, H & Yano, T-A. 1985. Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. *J. Mol. Evol.* **22**: 160–174.

Helm-Bychowski, K. & Cracraft, J. 1993. Recovering phylogenetic signal from DNA sequences: relationships within the Corvine Assemblage (Class Aves) as inferred from complete sequences of the mitochondrial DNA cytochrome-b gene. *Mol. Biol. Evol.* **10**: 1196–1214.

Imber, M.J. 1985. Origins, phylogeny and taxonomy of the gadfly petrels *Pterodroma* spp. *Ibis* **127**: 197–229.

Jouanin, C. & Mougin, J.-L. 1979. Order Procellariiformes. In Mayr, E. & Coterell, G.W. (eds) *Peters' Check-list of Birds of the World*, Vol. 1, 2nd edn: 48–121. Cambridge, MA: Harvard University Press.

Jouanin, C., Roux, F. & Zino, A.P. 1969. Visites aux lieux de nidification de *Pterodroma mollis* 'deserta'. *Oiseau Rev. Fr. Ornithol.* **39**: 161–175.

Mathews, G.M. 1934a. Remarks on the races of *Pterodroma mollis*. *Bull. Brit. Orn. Club* **54**: 161, 178–179.

Mathews, G.M. 1934b. A check-list of the order Procellariiformes. *Novit.Zool.* **39**: 151–206.

Mayr, E. 1942. *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. New York: Columbia University Press.

Nunn, G.B. & Stanley, S.E. 1998. Body size effects and rates of cytochrome b evolution in tube-nosed seabirds. *Mol. Biol. Evol.* **15**: 1360–1371.

Penhallurick, J. & Wink, M. 2004. Analysis of the taxonomy and nomenclature of the Procellariiformes based on complete nucleotide sequences of the mitochondrial cytochrome b gene. *Emu* **104**: 125–147.

Posada, D. & Crandall, K.A. 1998. Modeltest: testing the model of DNA substitution. *Bioinformatics* **14**: 817–818.

Salvadori, T. 1899. Collezioni ornitologische fatte nelle isole del Capo Verde de Leonardo Fea. *Ann. Mus. Civ. Genova* series ii **20**: 3–32 (in Bourne 1983).

Schwartz, S., Klugel, A., van den Bogaard, P. & Geldmacher, J. 2005. Internal structure and evolution of a volcanic rift system in the eastern North Atlantic: the Desertas rift zone, Madeira archipelago. *J. Volcan. Geother. Res.* **141**: 123–155.

Steele, J. 2006. From the Rarities Committee's files: do we know what British 'soft-plumaged petrels' are? *Br. Birds* **99**: 404–419.

Stothard, P. 2000. The Sequence Manipulation Suite: JavaScript programs for analyzing and formatting protein and DNA sequences. *Biotechniques* **28**: 1102–1104.

Tove, M.H. 1997. Fea's Petrel in North America. *Birding* **29**: 206–315.

Tove, M. 2001. Verification of suspected field identification differences in Fea's and Zino's Petrels. *Birding World* **14**: 283–289.

Zino, A. & Zino, F. 1986. Contribution to the study of the petrels of the genus *Pterodroma* in the archipelago of Madeira. *Bol. Mus. Municipal Funchal* **38**: 141–165.

Zino, F., Oliveira, P., King, S., Buckle, A., Biscoito, M., Costa Neves, H. & Vasconcelos, A. 2001. Conservation of Zino's petrel *Pterodroma madeira* in the archipelago of Madeira. *Oryx* **35**: 128–136.

Received 14 January 2007;
revision accepted 2 November 2007.

Appendix 1 Relative primary lengths (mm) of eight *P. madeira* and eight *P. feae* . TL = total length of wing.

Feather										
P10	P9	P8	P7	P6	P5	P4	P3	P2	P1	TL
Pterodroma madeira										
Longest	–5	–12	–20	–17	–18	–28	–23	–24	–23	*
Equal	Equal	–11	–16	–19	–21	–21	–25	–25	–17	*
Longest	–2	–7	–20	–20	–25	–23	–24	–22	–17	249
Longest	–2	–7	–20	–20	–25	–23	–24	–22	–17	260
Equal	Equal	–10	–15	–20	–20	–15	–20	–20	–15	251
–3	Longest	–10	–15	–20	–20	–20	–20	–15	–10	250
Longest	–1	–10	–30	–20	–20	–20	–17	–15	–10	257
–2	Longest	–8	–14	–20	–20	–20	–20	–20	–15	245
Pterodroma feae										
Longest	–1	–14	–20	–22	–20	–30	–28	–25	–18	270
Longest	–3	–12	–20	–22	–25	–25	–30	–25	–20	275
Longest	–4	–12	–18	–22	–30	–30	–25	–25	–20	272
Longest	–3	–11	–25	–25	–30	–30	–25	–25	–17	274
Longest	–4	–11	–20	–25	–30	–30	–25	–25	–20	270
Longest	–5	–12	–18	–25	–28	–30	–30	–20	–15	275
Longest	–4	–12	–20	–20	–30	–25	–22	–25	–17	265
Longest	–4	–15	–25	–25	–25	–29	–25	–20	–15	255