A new species of extinct *Pterodroma* petrel (Procellariiformes: Procellariidae) from the Chatham Islands, New Zealand

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Summary.—A new species of extinct gadfly petrel (Procellariidae, *Pterodroma*) is described from the Chatham Islands, New Zealand. Its remains have been recovered in Holocene fossil deposits on Chatham, Pitt and Mangere Islands. Its extinction, possibly as late as the 19th century, was a result of human colonisation of the island group. The new species was identified by a combination of morphological and molecular evidence. A complete humerus was selected as the holotype by soaking DNA from the fossil bone, leaving its morphology intact.

Cooper & Tennyson (2008) suggested that an undescribed extinct Holocene species of gadfly petrel (*Pterodroma* sp., Procellariiformes, Procellariidae) occurred on the Chatham Islands (44°S, 176°W), New Zealand. They used max. post-cranial bone lengths to identify isolated elements that probably belonged to an undescribed species, which they referred to as '*Pterodroma* sp. 1'. In size, this taxon fell between the range of the known *Pterodroma* species that breed on the Chatham Islands today: it was smaller than Magenta Petrel *P. magentae* (Giglioli & Salvadori, 1869) and larger than Chatham Petrel *P. axillaris* (Salvin, 1893) and Black-winged Petrel *P. nigripennis* (Rothschild, 1891). However, they were unable to assign with absolute certainty any bone to *Pterodroma* sp. 1 because many species in the diverse large genus *Pterodroma* have morphologically very similar skeletons, and the quality of the available specimens was too poor (i.e. they were incomplete, and/or were represented almost entirely by isolated elements only) and no cranial material was available to enable full comparisons.

The existence of an extinct, possibly undescribed, medium-sized *Pterodroma* petrel at the Chatham Islands has previously been suggested by several authors (e.g. Bourne 1967, Tennyson & Millener 1994, Holdaway *et al*. 2001). Also, possible relationships between this extinct taxon and Murphy's Petrel *P. ultima* Murphy, 1949 (see Bourne 1967) or Mottled Petrel *P. inexpectata* (J. R. Forster, 1844) (see Millener 1999, Worthy & Holdaway 2002) have been proposed. In size, however, this taxon is closer to Soft-plumaged Petrel *P. mollis* (Gould, 1844) (Cooper & Tennyson 2008).

We used molecular techniques to clarify the identity of this Chatham Island bird, whose bones were considered by Cooper & Tennyson (2008) to be an undescribed species. In addition, we present an extraction technique to isolate DNA from bones, which not only reduces physical damage to a minimum but, also, permitted us to identify a suitable specimen as the holotype of the new species described herein.

Methods

Specimens examined and used for DNA extraction are all deposited in the collection of the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (Te Papa) (NMNZ).

The sequence and nomenclature of taxa follow Dickinson & Remsen (2013), with the exception of Kerguelen Petrel *Lugensa brevirostris* (Lesson, 1833) and White-naped Petrel *P. cervicalis* (Salvin, 1891), whose nomenclature follows Gill *et al*. (2010).

All DNA extractions and polymerase chain reaction (PCR) set-ups were performed in a dedicated ancient DNA (aDNA) laboratory physically isolated from where modern DNA and PCR products were handled. Potential contamination was monitored by the use of negative extraction and PCR controls.

Approximately 5 mm from the broken ends of three humeri (NMNZ S.27584.1, S.37589.1, S.37589.2 examined by Cooper & Tennyson (2008) and considered by them to belong to species *Pterodroma* sp. 1) were removed using a Dremel grinder with a new Dremel wheel used for each bone. Each sample was powdered by grinding in a sterilised mortar and pestle. Bone powder was then decalcified and a phenol-chloroform extraction performed (Shepherd & Lambert 2008).

Additionally, an alternative method using a Qiagen DNeasy Blood and Tissue kit was used for DNA extraction from eight relatively undamaged humeri (NMNZ S.29601.1, S.30019, S.30985.1, S.31531.1, S.31633, S.32287, S.35342.1, S.37622.1) considered by Cooper & Tennyson (2008) to belong to the same taxon. With this method, we aimed to extract aDNA without damaging the gross morphology of the bones. The method is modified from extraction methods for powdered bone described by Rohland & Hofreiter (2007a,b) but uses a commercial kit and is much quicker. The distal end of each bone was soaked in 2 ml of 0.5M EDTA, 40 μl SDS and 30 μl 50 mg/ml proteinase-K for six hours. The first five humeri that we soaked were heated to 55°C with a heating block but this caused a small amount of surface bone to dissolve. For the subsequent three bones we reduced the temperature to 45°C and were able to eliminate almost any morphological damage. This solution was then added to 2 ml AL Buffer (Qiagen) and incubated for ten minutes, 2 ml of 100% EtOH was added and the resulting solution centrifuged through a Qiagen DNeasy column. The extraction was completed by washing with the kit's buffers, following the manufacturer's instructions, and eluting in a final volume of 50 μl of Buffer AE. Following the extraction, the bones were soaked in distilled water for eight hours, then allowed to dry at room temperature.

The collection locations, collection dates, collectors and former identities of the sampled bones are shown in Table 1. Humeri were selected for sampling because they are relatively large bones and were the most common of the elements preserved of the putative new taxon (Cooper & Tennyson 2008).

We used multiple Soft-plumaged Petrel samples for our comparisons because of the similarity in size between this species and '*Pterodroma* sp. 1' (Cooper & Tennyson 2008). DNA from footpads of four Soft-plumaged Petrel study skin specimens (NMNZ OR.22888 Macquarie Island, OR.23060 Kerguelen Island, OR.25195 New Zealand beach, OR.26227 Antipodes Island) was extracted using a Qiagen DNeasy Blood and Tissue kit, following the manufacturer's instructions.

For PCR amplification of DNA extracted from the broken bones, we targeted short overlapping fragments of two mitochondrial DNA loci. Although it would be ideal to analyse sequences from multiple independent nuclear loci, rather than relying on a single locus, such data are presently not available for the majority of petrels. Primer pairs from Patel *et al*. (2010) were used to amplify fragments of the cytochrome *c* oxidase (CO1) locus from *Pterodroma* sp. 1 and Soft-plumaged Petrel. Fragments of cytochrome *b* were amplified for *Pterodroma* sp. 1 using the primers from Brace *et al*. (2014).

For PCR amplification of the soaked bones, novel primers (shortPBF: TCGCCCTACACTTCCTCCTA and shortPBR: GATTTTGTCGCAGTTTGATACGA) were

TABLE 1
Sampled *Pterodroma* bones from the Chatham Islands, including collection locations, collection dates, collectors, and former identities. The former identities were mostly by P. R. Millener, but bones collected by R. Richards & AJDT were identified by AJDT. All were subsequently re-identified as '*Pterodroma* sp. 1' by Cooper & Tennyson (2008).

NMNZ reg. no.	Locality	Date and collector	Original identifications
S.27584.1	Pitt I.	1947, C. Jefferson	'*Pterodroma*' and '*Pterodroma* cf. *inexpectata*'
S.29601.1	Okawa dunes, Chatham I.	21 Feb 1991, P. R. Millener	'*Pterodroma*' and '*Pterodroma* > *inexpectata*'
S.30019	Long Beach, Chatham I.	2 Mar 1991, P. R. Millener	'*Pterodroma* ?'
S.30985.1	Maunganui Beach, Chatham I.	2 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.31531.1	North Head, Pitt I.	8 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.31633	Te Ana a Moe, Chatham I.	10 Feb 1992, P. R. Millener	'*Pterodroma* cf. *inexpectata*'
S.32287	Long Beach, Chatham I.	16 Feb 1991, P. R. Millener & N. Hyde	'*Pterodroma inexpectata*'
S.35342.1	Waipawa Mouth, Pitt I.	27 Feb 1992, R. Richards	'*Pterodroma* cf. *inexpectata*'
S.37589.1	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'
S.37589.2	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'
S.37622.1	North Head, Pitt I.	6 Dec 1997, AJDT	'*Pterodroma* > *inexpectata*'

designed to target a short region of cytochrome *b* containing two substitutions unique to *Pterodroma* sp. 1.

PCR amplification was performed in 10 ul volumes containing 1× PCR buffer, 200 μM of each dNTP, 0.5 U of Taq DNA polymerase (Roche), 0.3 M of BSA and 0.5 μM of each primer. For all amplifications, the thermo-cycling conditions involved an initial denaturation of two minutes at 94°C, followed by 35 cycles of 94°C for 30 seconds, 50°C for 40 seconds and 72°C for one minute, followed by a final extension of ten minutes at 72°C.

PCR products were purified by digestion with one U shrimp alkaline phosphatase (SAP, USB Corp., Cleveland, USA) and five U exonuclease I (Exo I, USB Corp., Cleveland, USA) at 37°C for 30 minutes, followed by inactivation of the enzymes at 80°C for 15 minutes. DNA sequencing was performed by capillary separation at the Massey Genome Service, Palmerston North, New Zealand.

Sequences were edited in Sequencer 5.2.3 (Gene Codes Corporation). We aligned sequences from publicly available *Pterodroma* taxa (Table 2) to our own data. No indels were present in either CO1 or cytochrome *b* and sequences were aligned by eye.

Phylogenetic analyses were conducted with PAUP for maximum parsimony (MP), the PhyML v3.0 web server (http://www.atgc-montpellier.fr/phyml/, Guindon *et al*. 2010) with maximum likelihood (ML) and MrBayes v3.2.1 (Huelsenbeck & Ronquist 2001) for Bayesian analyses (BA). The short sequences obtained from the soaked bones (NMNZ S.30019 and S.35342.1) were not included in phylogenetic analyses. Analyses were performed with alignment gaps treated as missing data and Buller's Shearwater *Ardenna bulleri* (Salvin, 1888) was selected as the outgroup.

For the MP analyses a heuristic tree search was used, with 100 random addition sequence replicates and tree bisection-reconnection (TBR) branch swapping. Branch support was assessed with 1,000 pseudo-replicates. For the ML analyses the best-fit models of sequence evolution were determined for each locus using the Akaike information criterion in jModelTest v0.1.1 (Posada 2008). PhyML was run with subtree pruning-regrafting and nearest-neighbour-interchange branch swapping with ten random addition

TABLE 2

Details of DNA sequences used for this study. Corrected genetic distances (%) between Imber's Petrel *Pterodroma imberi* sp. nov., and other petrel taxa are shown for CO1 and cytochrome *b*. Taxa not referred to elsewhere in the text are as follows: Stejneger's Petrel *P. longirostris* (Stejneger, 1893), Cook's Petrel *P. cookii* (G. R. Gray, 1843), Providence Petrel *P. solandri* (Gould, 1844), Kermadec Petrel *P. n. neglecta* (Schlegel, 1863), Herald Petrel *P. a. arminjoniana* (Giglioli & Salvadori, 1869), Juan Fernández Petrel *P. externa* (Salvin, 1875), Mascarene Petrel *Pseudobulweria aterrima* (Bonaparte, 1857).

Taxon	Voucher (NMNZ)	CO1 GenBank number	CO1 genetic distance	Cytochrome *b* GenBank number	Cyt *b* genetic distance
P. imberi	S.37589.1	KT001455		KT027379	
P. imberi	S.37589.2	KT001456		-	
P. imberi	S.30019	KT001457		KT027380	
Lugensa brevirostris		AY158678	12.39	-	-
P. longirostris		JQ176028	8.45	-	-
P. cookii		GQ387307	8.45	U74345	11.27
P. nigripennis		-	-	PNU74343	8.28
P. axillaris		-	-	PAU74342	8.75
P. ultima		JF522137	10.09	JF522109	10.42
P. solandri		-	-	PSU74347	9.52
P. n. neglecta		JF522135	8.14	GQ328987	10.48
P. a. arminjoniana		-	-	GQ328979	11.07
P. alba		JQ176021	8.70	EU979352	-
P. inexpectata		-	-	PIU74346	10.78
P. sandwichensis		-	-	JF264907	-
P. cervicalis		KT001458	8.95	EU979353	-
P. externa		JQ176023	8.67	PEU74339	10.77
P. mollis	OR.22888	KT001459	2.65	-	-
P. mollis	OR.26227	KT001460	2.65	-	-
P. mollis		-	-	HQ420380	4.68
P. mollis		-	-	HQ420384	4.45
P. mollis		-	-	HQ420385	4.93
P. cahow		JQ176022	4.42	U74331	4.45
P. h. hasitata		JQ176025	4.16	U74332	4.43
P. f. feae		JX674085	3.90	FJ196356	5.25
P. f. deserta		JX674148	3.92	U74333	5.74
P. madeira		JX674273	4.67	FJ196363	4.94
P. magentae		-	-	PMU74338	4.69
P. lessonii		-	-	PLU74337	4.71
P. macroptera gouldi		E188462	4.15	EU979357	4.28
Ardenna bulleri		AB443940	15.48	AF076081	12.83
Pseudobulweria aterrima		JF522121	15.00	-	-

trees and ML-optimised equilibrium frequencies. ML branch support was assessed with 500 pseudo-replicates.

For BA, two concurrent analyses were run, each with four Markov chains of five million generations and sampling every 1,000 generations. The analyses used default priors with nst = 6 and rates = invgamma. Tracer v.1.5 (Rambaut & Drummond 2009) was used to assess stationarity, with the first 25% of samples discarded as 'burn-in' for both the combined and individual locus datasets.

Corrected pairwise distances were calculated for each locus in PAUP 4.0a136 (Swofford 2002) based on the models of nucleotide substitution selected in jModelTest. For cytochrome *b*, Phoenix Petrel *P. alba* (J. F. Gmelin, 1789), Hawaiian Petrel *P. sandwichensis* (Ridgway, 1884) and White-naped Petrel were excluded from this calculation owing to the short sequences we obtained from GenBank for these taxa. Only unambiguous nucleotides present in the entire alignments were used to calculate the distances (complete deletion), following the recommendation of Fregin *et al*. (2012).

The divergence time of *Pterodroma* sp. 1 was determined from the cytochrome *b* sequence data using BEAST 2.1.3 (Bouckaert *et al*. 2014) as described in Welch *et al*. (2014), except that priors were set to uniform. TreeAnnotator 2.1.2 was used to summarise the trees produced by BEAST and FigTree 1.4.2 (Rambaut 2012) was used to visualise the maximum clade credibility tree.

Results

For the CO1 locus, we successfully amplified and sequenced 511 bp of DNA from two fossil humeri (NMNZ S. 35789.1, S. 35789.2), 145 bp from one soaked fossil humerus (NMNZ S.30019) and 648 bp from two of the Soft-plumaged Petrel skin specimens (NMNZ OR.22888, OR.26227). For cytochrome *b* we obtained 450 bp from fossil humerus NMNZ S.35789.1 and 76 bp from fossil humeri NMNZ S.30019 and S.35342.1. No gaps or unexpected stop codons were detected and most of the variation occurred in the third codon position, suggesting that these sequences are of mitochondrial, rather than nuclear, origin.

The CO1 sequences obtained from all bones considered to be *Pterodroma* sp. 1 were identical to each other but differed from those of all other known taxa. The smallest observed corrected distance between *Pterodroma* sp. 1 and any other taxon at the CO1 locus was 2.65% to Soft-plumaged Petrel (Table 2). The cytochrome *b* sequences from *Pterodroma* sp. 1 were also identical to each other and differed from all other available sequences, with the smallest pairwise distance being 4.28% to Great-winged Petrel *P. macroptera gouldi* (Hutton, 1869) (Table 2). Genetic distances of *c*.1% for pairwise cytochrome *b* and CO1 sequences divergences are considered within the normal range for well-accepted species of petrel (Jesus *et al*. 2009, Pyle *et al*. 2011, Welch *et al*. 2014), so genetically *Pterodroma* sp. 1 is well differentiated from other known taxa. Both phylogenetic analyses indicate that *Pterodroma* sp. 1 belongs within a clade of *Pterodroma* including Soft-plumaged Petrel, Bermuda Petrel *P. cahow* (Nichols & Mowbray, 1916), Black-capped Petrel *P. h. hasitata* (Kuhl, 1820), Fea's Petrel *P. feae* (Salvadori, 1899), Madeira Petrel *P. madeira* Mathews, 1934, Magenta Petrel, Atlantic Petrel *P. incerta* (Schlegel, 1863), White-headed Petrel *P. lessonii* (Garnot, 1826) and Great-winged Petrel (Figs. 1–2). However the closest relative of *Pterodroma* sp. 1 is unclear, with it being recovered as sister to Soft-plumaged Petrel in the CO1 phylogeny (Fig. 1) but sister to a clade including Bermuda Petrel, Black-capped Petrel, Fea's Petrel, Madeira Petrel, Magenta Petrel, Atlantic Petrel, White-headed Petrel and Great-winged Petrel in the cytochrome *b* phylogeny (Fig. 2). Both relationships received only low to moderate support, so while Soft-plumaged Petrel is a fairly close relative of *Pterodroma* sp. 1, both Murphy's Petrel and Mottled Petrel—with which it was linked by Bourne (1967), Millener (1999) and Worthy & Holdaway (2002), but see Cooper & Tennyson (2008)—are more distantly related.

The divergence time estimate calculated from the strict molecular clock cytochrome *b* tree BEAST analysis indicates that *Pterodroma* sp. 1 diverged from its closest relatives around 1.37 million years ago (MYA) (95% highest posterior density 1.07–1.68 MYA; see Fig. 3). Using the same technique, the other two Chatham Island endemic *Pterodroma* species

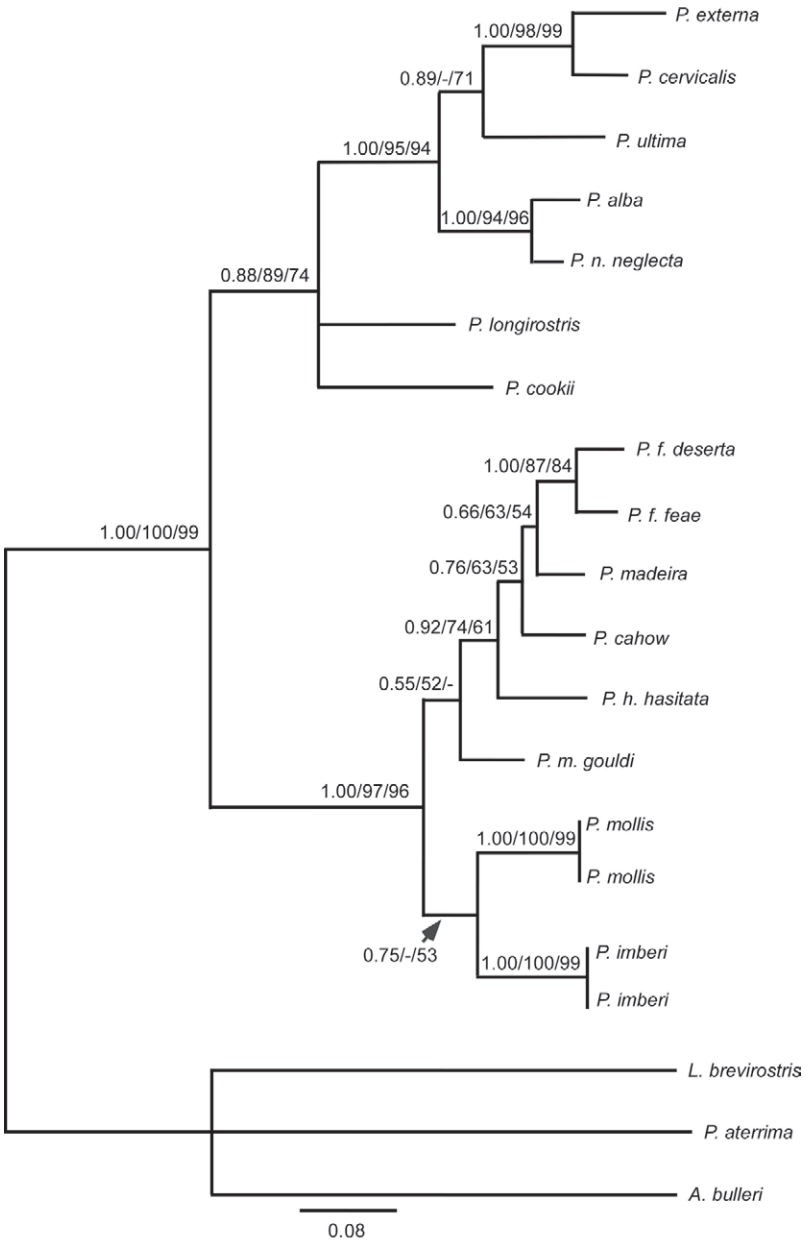

Figure 1. Bayesian consensus phylogenies constructed from CO1 sequences. Support values for nodes are as follows: Bayesian posterior probability/ maximum-parsimony bootstrap /maximum likelihood bootstrap.

diverged from their nearest relatives 1.98 MYA (*P. axillaris* from *P. nigripennis*) and 0.56 MYA (*P. magentae* from *P. macroptera gouldi*).

The combination of this genetic distinctiveness, with the previously reported morphological differences (Cooper & Tennyson 2008), strongly indicate that these bones represent an undescribed species.

NMNZ S.35342.1 was selected as a holotype because it was the best-preserved bone that yielded DNA.

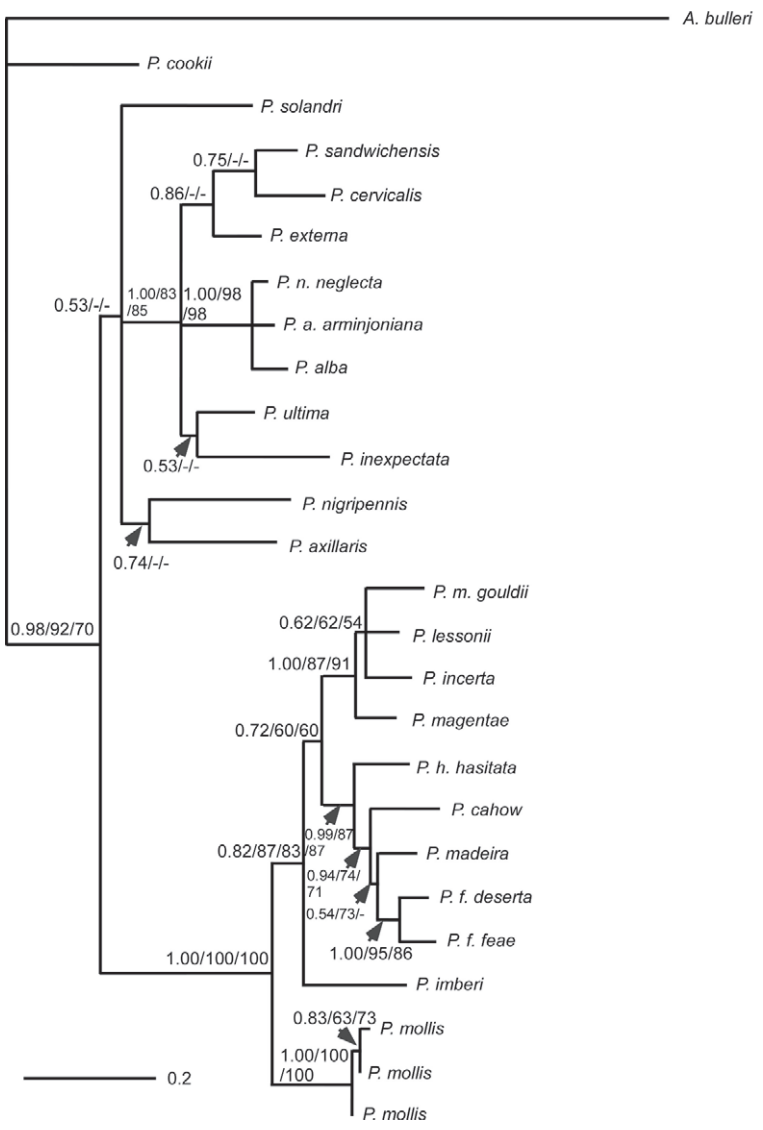

Figure 2. Bayesian consensus phylogenies constructed from cytochrome *b* sequences. Support values for nodes are as follows: Bayesian posterior probability/ maximum-parsimony bootstrap /maximum likelihood bootstrap.

Systematics

Order Procellariiformes

Family Procellariidae Leach, 1820

Genus *Pterodroma* Bonaparte, 1856

Species *Pterodroma imberi* sp. nov.

Etymology.—The species epithet is a noun in the genitive case honouring Dr Michael J. Imber (1940–2011) who had a passionate interest in the conservation, ecology and taxonomy of *Pterodroma* petrels and who undertook extensive research on the Chatham Islands.

Holotype.—Complete left humerus (NMNZ S.35342.1) collected on 27 Feb 1992 at the Waipawa Stream mouth, Pitt Island, Chatham Islands (map grid reference NZMS 260 Chatham Islands sheet 2 739160), by Rhys Richards, Holocene age. See Fig. 4.

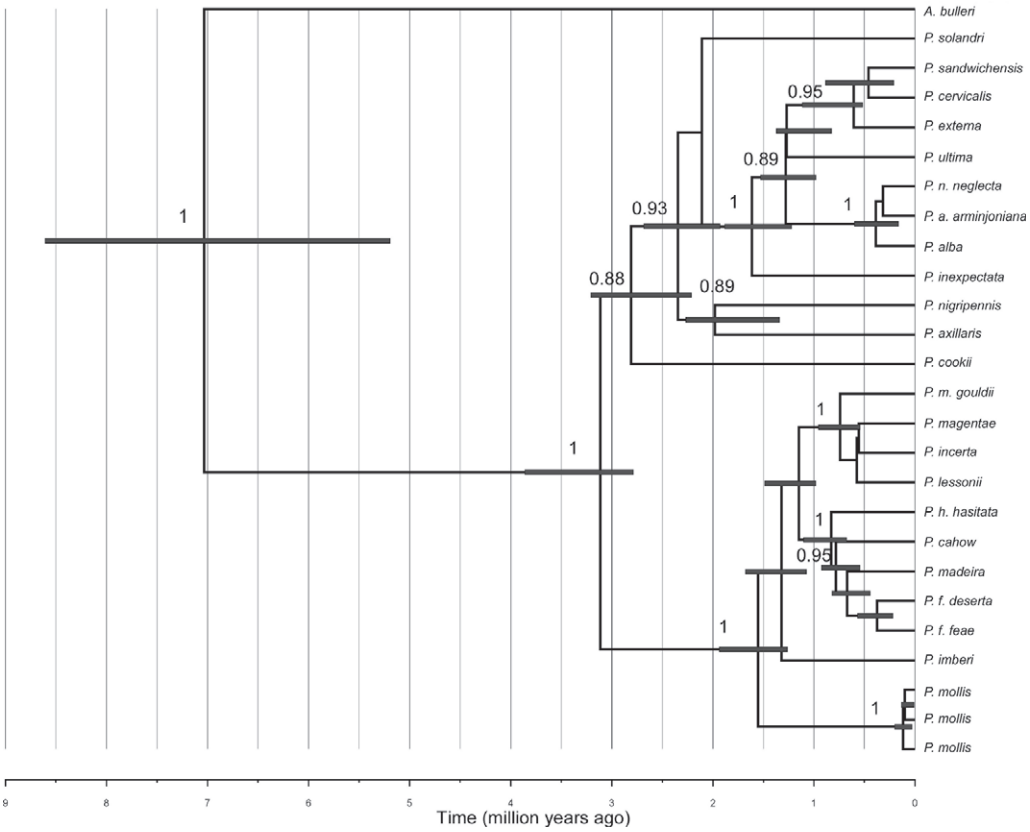

Figure 3. Maximum clade credibility tree from the BEAST analysis of *Pterodroma* cytochrome *b* sequences. Nodes are posterior mean ages (MYA), with node bars representing the 95% HPD intervals.

Measurements of holotype.—Max. total length 86.3 mm, max. proximal width *c*.20.7 mm, max. distal width (including the processus supracondylaris dorsalis) 13.4 mm, mid-shaft width 5.6 × 3.9 mm.

Paratypes.—All other humeri that have been successfully sequenced for DNA: NMNZ S.30019, NMNZ S. 35789.1, NMNZ S. 35789.2; the collection details for these specimens are presented in Table 1.

Distribution of species.—Extinct. Formerly common and widespread on Chatham, Pitt and Mangere Islands, Chatham Islands, New Zealand (Cooper & Tennyson 2008).

Suggested vernacular English name.—Imber's Petrel.

Diagnosis.—A medium-sized *Pterodroma* species with a median humerus length of 86 mm (averaging slightly larger than that of Mottled Petrel and Soft-plumaged Petrel: Cooper & Tennyson 2008). Other elements that probably belong to Imber's Petrel suggest that the other main limb bones were also slightly larger than those of Mottled Petrel and Soft-plumaged Petrel but that the tibiotarsus was proportionately longer in Imber's Petrel (Cooper & Tennyson 2008). The skeletal proportions of Imber's Petrel appear to differ from all other *Pterodroma* species occurring in the New Zealand region (Cooper & Tennyson 2008).

Extant *Pterodroma* taxa from outside the New Zealand region and similar in size to Imber's Petrel do exist (e.g. Phoenix Petrel, Fea's Petrel *P. f. feae*, Fea's Petrel *P. f. deserta* Mathews, 1934, and Madeira Petrel; see Brooke 2004) but none are genetically close relatives.

Figure 4. Holotype left humerus of *Pterodroma imberi* sp. nov., NMNZ S.35342.1. © Te Papa. 4A. caudal view. 4B. cranial view.

There are three described extinct *Pterodroma* species but none is closely related to *P. imberi*. *P. rupinarum* Olson, 1975, from the Pleistocene (and younger) of St. Helena, in the South Atlantic Ocean, is a similar-sized bird (Olson 1975) but is placed within a clade of petrels distributed in the North Atlantic, and most closely related to Fea's Petrel based on cytochrome *b* sequences (Welch *et al*. 2014). *P. kurodai* Harrison & Walker, 1978, from the Pleistocene of Aldabra Atoll, Indian Ocean, is notably smaller than Imber's Petrel (Harrison & Walker 1978), and *P. jugabilis* Olson & James, 1991, from the Holocene of Hawaii is even smaller (Olson & James 1991).

Discussion

The genus *Pterodroma* is diverse with a high number of taxa endemic to islands and several taxa threatened with extinction (Brooke 2004). The Chatham Islands have two surviving but endangered endemic species, Magenta Petrel and Chatham Petrel; the remains of both have been found alongside those of Imber's Petrel in fossil dune sites. Imber's Petrel was intermediate in size between these two species and presumably filled a separate ecological niche. The 20th century colonisation of the New Zealand subantarctic region by the similarly sized Soft-plumaged Petrel (Tennyson *et al*. 2013) may be related to an ecological niche becoming available in the region as the result of the extinction of Imber's Petrel. There is evidence that Imber's Petrel may have survived into the late 19th century (Tennyson & Millener 1994) but there are no known records of it alive.

The extinction of Imber's Petrel was undoubtedly a result of human colonisation of the Chatham Islands, beginning *c*.400–700 years ago (Wood *et al*. 2014). Human hunting, combined with the impacts of other introduced mammals, are the probable causes of its extinction. Likely key predators on Chatham Island were Pacific Rats *Rattus exulans*, Ship Rats *R. rattus*, Norway Rats *R. norvegicus* and feral cats *Felis catus*. Cats are present on Pitt

Island but rats have never established there. Human hunting may have contributed to its decline on Mangere Island but cats are the likely cause of its final demise (Tennyson & Millener 1994).

The estimated divergence times of the three endemic Chatham Island *Pterodroma* species from their nearest relatives, based on the cytochrome *b* gene tree, range from 1.98 MYA to 0.56 MYA. These dates are what might be expected for endemic birds on an archipelago that has been emergent for only *c*.2.5 million years (Campbell 2008).

The formal description of Imber's Petrel adds yet another extinct bird, and the first *Pterodroma* species, to the list of human-caused extinctions in the New Zealand archipelago (Holdaway *et al*. 2001, Boessenkool *et al*. 2009, Williams *et al*. 2014, Wood *et al*. 2014).

While DNA has been soaked from modern bones (e.g. Asher & Hofreiter 2006) and teeth (Rohland *et al*. 2004) previously, the soaking extraction method presented here provides a non-destructive technique for obtaining DNA from Holocene fossils. Our trials with multiple fossil bones from different species (LDS & AJDT unpubl. data) have shown that our soaking method is less successful at yielding DNA than the method of removal and digestion of bone fragments. However, it is a useful technique for extracting DNA from particularly valuable specimens, such as types or those of rare species, as it minimises overall morphological damage. When applying this method to other taxa, it is likely that the soaking time will need to be varied according to the size of the bones. Contamination may also be more likely with this method because the outer surface of the bone is not removed prior to DNA extraction. We suggest following the recommendations made by Gilbert *et al*. (2005) in assessing whether results obtained through soaking are likely to be genuine or contamination.

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