

A hybrid gadfly petrel suggests that soft-plumaged petrels (*Pterodroma mollis*) had colonised the Antipodes Islands by the 1920s

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Abstract A unique *Pterodroma* petrel shot at sea near the Antipodes Islands in 1926 has features intermediate between white-headed petrel (*Pterodroma lessonii*) and soft-plumaged petrel (*Pt. mollis*). Its mitochondrial DNA indicates that its mother was a *Pt. mollis* and we conclude that it is a hybrid. We theorise that *Pt. mollis* had begun colonising Antipodes Island by the 1920s and some pairing with the locally abundant congeneric *Pt. lessonii* occurred. Hybridisation in Procellariiformes is rare worldwide but several cases have now been reported from the New Zealand region.

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Keywords soft-plumaged petrel; *Pterodroma mollis*; mitochondrial DNA; hybrid; Antipodes Islands

INTRODUCTION

On 17 Feb 1926 an unusual male gadfly petrel (*Pterodroma* sp.) (American Museum of Natural History AMNH 211660) was collected at sea by the Whitney South Seas Expedition at 50° S 179° W, just east of the Antipodes Is (Bourne 1995). Although identified as a white-headed petrel (*Pterodroma lessonii*) on the expedition label, it was not among the skins of *Pt. lessonii*, mainly from the Whitney

Expedition, used in Murphy & Pennoyer's (1952) review paper on the larger gadfly petrels, because its small dimensions (Table 1) are not included in Murphy & Pennoyer's Table 2 data for *Pt. lessonii* males. Thus, there is a suggestion that those authors did not consider it to be *Pt. lessonii*, but no evidence was provided of what they thought it might be. Bourne (1995) examined this specimen in 1962 and noted that, although it was registered as a *Pt. lessonii*, its plumage more closely resembled the smaller soft-plumaged petrel (*Pt. mollis*). As both species breed on Antipodes I, he speculated that it may be: (1) a hybrid between *Pt. lessonii* and *Pt.*

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** Deceased

Fig. 1. Three views of a gadfly petrel (*Pterodroma* sp.) AMNH 211660 shot east of the Antipodes Is in Feb 1926. Photos by Matthew Shanley (AMNH).



mollis; (b) a pale variation or southern race of the Chatham Island taiko (*Pt. magentae*); or (c) a hybrid between *Pt. lessonii* and *Pt. magentae* (Bourne 1995). The Chatham Is archipelago is 700 km northeast of the Antipodes Is, so is well within the normal foraging range of gadfly petrels (e.g., Rayner *et al.* 2012). Another possibility briefly considered by Cooper & Tennyson (2008) is that AMNH 211660 is the recently extinct unnamed fossil Chatham Island "*Pterodroma* sp.1".

Since the 1970s regurgitated *Pterodroma* skulls were collected from subantarctic skua (*Catharacta antarctica lonnbergi*) food middens during several trips to the Antipodes Is as one means of identifying the distribution of petrels occurring there. Among the 457 skulls collected in 1978, MJI noted one *Pterodroma* skull (presumably Museum of New Zealand Te Papa Tongarewa NMNZ OR.29436) that he was unable to identify; this was reported as "*Pterodroma* sp." by Moors (1980). In 1994, among an additional collection of 339 skulls, MJI identified another similar skull (presumably NMNZ OR.29437). A further collection of 662 *Pterodroma* skulls by Jacinda Amey in Feb-Mar 1995 contained no such skulls. The 2 unusual skulls were well ossified (therefore fully grown) and considered to be

intermediate in size between those of *Pt. lessonii* and *Pt. mollis* but less robust than those of *Pt. magentae*, which has a deeper upper mandible.

In 1995 we borrowed the AMNH specimen to try and resolve its identity by re-examining its plumage and size, and examining its mitochondrial DNA in relation to known *Pterodroma* species. Additionally we reassessed the identity of unidentified *Pterodroma* skulls in case these had a bearing on the identity of the AMNH specimen.

METHODS

We recorded the plumage colours of AMNH 211660 and took measurements to compare it with similar species (see Table 1; Fig. 1). Measurements were taken using vernier calipers accurate to 0.1 mm, a ruler accurate to 1 mm and a Pesola scale accurate to 1 g. Our measurement techniques followed Marchant & Higgins (1990).

DNA from a feather removed from AMNH 211660 was extracted and part of the mitochondrial cytochrome-*b* gene was amplified using Polymerase Chain Reaction (PCR). DNA extraction and PCR set-up were carried out in the Allan Wilson Centre for Molecular Ecology and Evolution Ancient DNA

Table 1. Measurements (mm) of AMNH 211660 taken independently by AJDT, MJI and Bourne (1995), compared with those of *Pterodroma lessonii* and *Pt. mollis* from Antipodes I (1969, Warham & Bell 1979; Bourne *in* Bretagnolle 1995; 1995 live birds Nov, this study) and *Pt. magentae* from Chatham Is (Crockett 1994; GAT, *unpubl. data* for 1997-2011). The outer primary of AMNH 211660 was growing and may not have reached its full length (Bourne 1995) but it is near to its full length (authors, *pers. obs.*). For each species, measurements include mean \pm 1 SD, range (if available) and sample size (in parentheses).

Measure	AMNH 211660 (AJDT, MJI, Bourne)	Species						
		<i>Pt. lessonii</i> (1969)	<i>Pt. lessonii</i> (1995)	<i>Pt. mollis</i> (1969)	<i>Pt. mollis</i> (Bourne)	<i>Pt. mollis</i> (1995)	<i>Pt. magentae</i> (Crockett)	<i>Pt. magentae</i> (GAT)
Bill-length	30.9 30.8 31	36.7 \pm 1.2 (25)	37.2 \pm 1.9 35.2-39.8 (6)	28.7 \pm 0.9 (8)	27.9 \pm 0.9 (7)	28.6 \pm 0.9 26.4-30.0 (20)	33.0 \pm 1.3 30.3-35.1 (41)	33.1 \pm 1.1 30.9-35.1 (71)
Bill-depth	14.5 - -	-	17.4 \pm 0.8 16.4-18.3 (6)	-	-	12.8 \pm 0.7 11.7-14.0 (12)	15.5 \pm 0.9 13.1-17.4 (39)	15.8 \pm 0.7 14.5-17.5 (71)
Bill-width	13.1 - -	-	15.5 \pm 1.6 14.3-16.6 (2)	-	-	11.7 \pm 0.5 10.9-12.4 (8)	15.0 \pm 0.9 11.9-16.4 (40)	15.1 \pm 1.1 13.4-17.0 (8)
Wing-length	284 290 287+	302.6 \pm 5.7 (22)	304 \pm 0 (2)	255.8 \pm 3.9 (6)	256 \pm 5.3 (7)	254.5 \pm 2.8 250-263* (8)	302 \pm 7.1 284-316 (40)	304 \pm 6.1 285-315 (46)
Tail-length	126 125 127	130.6 \pm 5.5 (10)	130.0 \pm 3.0 128.1-133.4 (3)	114.9 \pm 4.0 (7)	113 \pm 5.1 (7)	111.3 \pm 3.2 106-116 (12)	129.1 \pm 4.1 116.5-139 (40)	126.9 \pm 4.2 116.8-132.4 (28)
Tarsus	40.5 41.9 42	44.0 \pm 1.5 (22)	46.8 \pm 0.7 45.7-47.4 (4)	33.9 \pm 0.7 (8)	35.9 \pm 0.9 (7)	36.1 \pm 0.9 34.0-37.3 (10)	41.3 \pm 1.6 38.0-45.0 (38)	41.6 \pm 1.5 39.5-43.4 (11)
Mid-toe	56.3 55.5 53	64.2 \pm 2.8 (16)	65.0 \pm 2.5 61.5-67.0 (4)	48.0 \pm 1.0 (8)	-	47.8 \pm 2.1 43.7-50.9 (10)	57.2 \pm 1.9 53.0-62.0 (41)	56.2 \pm 2.3 53.3-59.5 (11)
Weight (g)	- - -	574 \pm 34 (9)	612 \pm 21.5 583-634 (4)	276.2 \pm 27.1 (8)	-	298.4 \pm 22.9 279-347 (10)	459.4 \pm 30.6 415-560 (41)	477.8 \pm 36.5 390-585 (71)

* The outer primary of 3 of 6 *Pt. lessonii* and 15 of 23 *Pt. mollis* examined in 1995 were actively growing, so these measurements have not been included, except for one *Pt. mollis* whose wing length of 263 mm was longer than any other bird in our sample.

Laboratory at Massey University Albany, Auckland. DNA was extracted and amplified twice on separate occasions and sequenced in both directions using primers LCytB679 and HCytB780 (Lawrence *et al.* 2008a; methods as in Lawrence *et al.* 2009). We aligned the 102 base pair (bp) sequence (GenBank accession no. JX854039) with other *Pterodroma* cytochrome-*b* sequences available on GenBank. In addition, 3 of us (AJDT, GAT and MJI) participated in an expedition to the Antipodes Is in Oct-Nov 1995 which aimed, as one of its primary goals, to establish whether or not *Pt. magentae* occurred at this island group.

RESULTS

We agree with Bourne (1995; and his note on the specimen's label "tend towards mollis?"), that the plumage of AMNH 211660 is closer to *Pt. mollis* than to *Pt. lessonii* in that the dorsal surface of its head and neck are medium grey, not pale grey to whitish; and the outer tail feathers are grey on the outer webs, not white as in *Pt. lessonii* (Fig. 1). However the dark breast band is not complete, as in *Pt. lessonii*, whereas it usually is in *Pt. mollis*. *Pt. magentae* has a dark hood and is much darker dorsally than AMNH 211660 and there is little

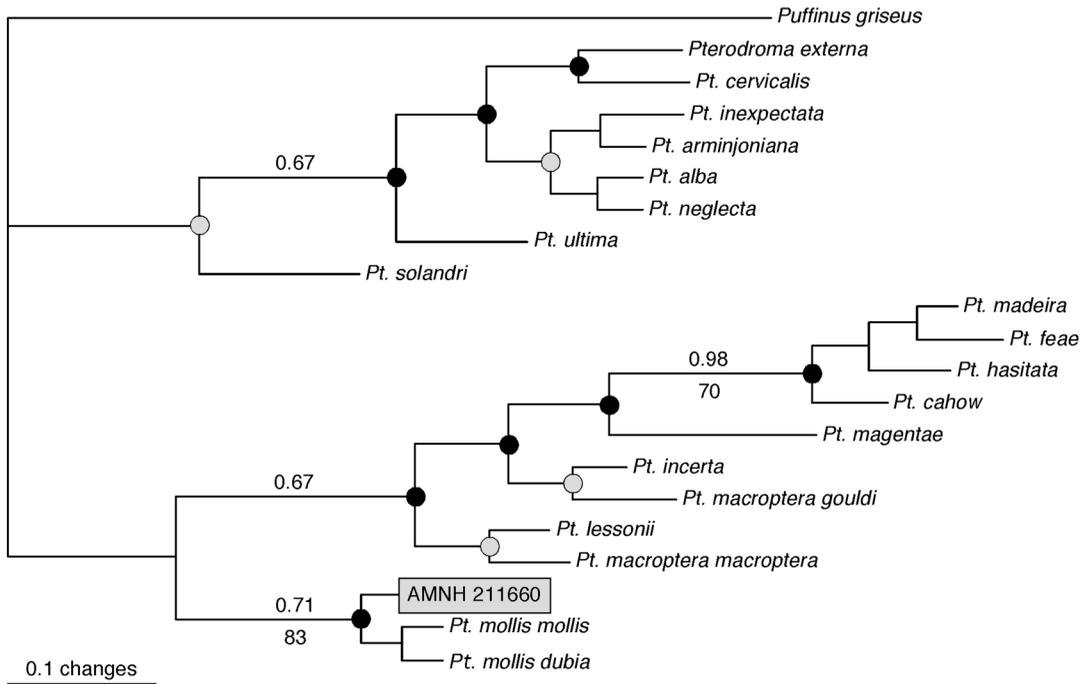


Fig. 2. Phylogenetic relationship of gadfly petrel (*Pterodroma* sp.) specimen AMNH 211660 (highlighted) to other *Pterodroma* petrels based on mitochondrial cytochrome-*b* sequence (102 bp). The Bayesian inference (BI) consensus tree (shown) was inferred with the HKY-I model of sequence evolution. Bayesian inference posterior probabilities of clades are presented above the branch; maximum likelihood (ML) bootstrap values are shown below the branch. Black circles indicate nodes that occurred in BI, ML and maximum parsimony trees; grey circles indicate nodes where only BI and ML trees concurred. Methods and GenBank accession numbers of sequences are in Lawrence *et al.* (2009).

plumage colour variation between individuals (authors, *pers. obs.*). The AMNH specimen had small gonads and its plumage was largely unworn, with some probable mixed older and newer body feathers. Therefore it was probably not a fledgling but may have been an immature bird.

In size the AMNH specimen is approximately intermediate between *Pt. lessonii* and *Pt. mollis* with none of its dimensions overlapping with samples of either species from Antipodes I, although its culmen and tarsus lengths are within the range of *Pt. mollis* from the Indian Ocean and its tail and tarsus are within the range of *Pt. lessonii* from some other breeding sites (Marchant & Higgins 1990; Table 1). All its measurements fall within the range of *Pt. magentae* (Table 1). As suggested previously (Cooper & Tennyson 2008), the extinct unnamed *Pterodroma* of the Chatham Is is too small to match AMNH 211660, whose tarsus length (40.5–42.0 mm, Table 1) falls outside the range of measurements for the extinct taxon (mean 37.4 mm, range 35.0–39.0 mm, $n = 23$). Thus, AMNH 211660 matches *Pt. magentae* in size but it is a much paler bird and has morphological characters intermediate between *Pt. mollis* and *Pt. lessonii*.

The DNA sequence of AMNH 211660 was identical to 8/9 *Pt. mollis* sequences (*Pt. mollis mollis* accession numbers HQ420380 to HQ420385, U74334, U74654; *Pt. mollis dubia* U74655), with only one nucleotide substitution between our sequence and HQ420384. We performed phylogenetic analyses of the 102 bp of cytochrome-*b* data, with Bayesian inference, maximum likelihood and maximum parsimony methods as in Lawrence *et al.* (2009). These analyses showed the sequence from the AMNH specimen grouping with *Pt. mollis* sequences with a Bayesian probability of 0.71 and maximum likelihood bootstrap value of 83% (Fig. 2). These results suggest that the AMNH specimen could be *Pt. mollis*, or a hybrid of such (as mitochondrial DNA is maternally inherited; Avise 2004).

During the 1995 expedition we did not detect any *Pt. magentae* during extensive night spotlighting for petrels. Skulls of 1,517 petrels, gathered from subantarctic skua middens, were examined but none was considered to be from *Pt. magentae*: 69.7% were from *Pt. lessonii* and 3.3% were from *Pt. mollis* (the remaining 27% of skulls were from other species that breed at the Antipodes Is). A selection of these *Pterodroma* skulls has been preserved (NMNZ

OR.27895, OR.28561). We concluded that the 2 skulls examined by MJI from the 1978 and 1994 Antipodes Is trips were simply small *Pt. lessonii* skulls but we cannot rule out that they were from hybrids.

DISCUSSION

Our morphological and genetic analyses did not indicate that AMNH 211660 has any relationship with *Pt. magentae* or the recently extinct Chatham Island *Pterodroma* species. Neither species has ever been reported at the Antipodes Is.

The plumage features of AMNH 211660 and our genetic results link the specimen with *Pt. mollis* but as the morphology of the specimen does not match any known species, we conclude that it is most likely to be a hybrid resulting from a pairing between a *Pt. lessonii* male and a *Pt. mollis* female. If *Pt. mollis* were prospecting in areas already occupied by *Pt. lessonii*, there would likely be instances of competition for burrows. As the breeding seasons of these 2 species coincide (Marchant & Higgins 1990), perhaps rare mixed pairs occurred.

A vagrant *Pt. mollis* pairing with a *Pt. magentae* on Chatham I could have produced AMNH 211600, but this theory seems much less likely. *Pt. mollis* is only a rare vagrant at the Chathams (Miskelly *et al.* 2006) and genetic profiling of the *Pt. magentae* population has shown no evidence of *Pt. mollis* genes in the extant *Pt. magentae* population (Lawrence *et al.* 2008b). However, a *Pt. mollis* giving aerial display calls was caught using spotlights on Chatham I on 11 Nov 2007 (GAT, *pers. obs.*). Therefore, there is a chance that a prospecting *Pt. mollis* might have paired with a *Pt. magentae* early in the 20th century when *Pt. magentae* were much more common than they are today (Crockett 1994). The possibility that the hybrid may have been reared at another *Pt. mollis* colony (*e.g.*, Crozet or Kerguelen Is in the Indian Ocean) seems highly unlikely as the bird was shot very close to the Antipodes Is.

Pt. lessonii is an abundant species at the Antipodes Is (with an estimated 100,000 - 300,000 breeding pairs), whereas *Pt. mollis* was first reported at this site only in 1969 - but their numbers have rapidly expanded since to 1,000 - 5,000 pairs by 1995 (Warham & Bell 1979; Tennyson *et al.* 2002). Along the shallow valley of the North Plains where *Pt. mollis* was first reported (but not confirmed breeding) in 1969 (Warham & Bell 1979), 50-100 pairs were estimated in 1978 (Imber 1983), whereas by 1995 numbers here had increased 10- to 15-fold and other concentrations were found around The Craters and on the south coast of Antipodes I. The relatively recent detection of *Pt. mollis* at the Antipodes Is and the species' subsequent expansion has been interpreted as indicating a colonisation event (Imber *et al.* 1998; Holdaway

et al. 2001). Our conclusion that AMNH 211660 is a hybrid *Pt. mollis* adds weight to this theory and suggests that the species had already colonised the Antipodes Is by the 1920s but that numbers were still small enough that some pairing with the locally abundant congeneric *Pt. lessonii* occurred. The recent discoveries of *Pt. mollis* nesting on Australia's Maatsuyker and Macquarie Is (Garnett *et al.* 2011) may be part of the same expansion of the species' breeding range.

Although hybrid Procellariiformes are extremely rare (Warham 1996: 495), several cases are known, including 4 examples from the New Zealand region: southern royal albatross (*Diomedea epomophora*) and northern royal albatross (*D. sanfordi*) (Croxall & Gales 1998); black-browed albatross (*Thalassarche melanophris*) and Campbell black-browed albatross (*Th. impavida*) (Moore *et al.* 1997, 2001); Salvin's albatross (*Th. salvini*) and Chatham Island albatross (*Th. eremita*) (Miskelly *et al.* 2006); Buller's shearwater (*Puffinus bulleri*) and sooty shearwater (*P. griseus*) (Holdaway *et al.* 2001; based on morphology and mitochondrial DNA, AJDT, *unpubl. data*).

Worldwide, the only well-proven case of *Pterodroma* hybridisation involves 3 species on Round I, Mauritius (Brown *et al.* 2010, 2011), although it has been suggested to occur at other sites (*e.g.*, Bourne 1975; Brooke & Rowe 1996). One such possibility involved the only record of a Cook's petrel (*Pt. cookii*) on Red Mercury I which was apparently paired with a Pycroft's petrel (*Pt. pycrofti*) in Oct 1998 but hybridisation was never confirmed (GAT, *unpubl. data*). The *Pt. cookii* was banded and found in the same burrow twice, one week apart; a *Pt. pycrofti* occupied this burrow also in Oct 1998 but the birds were never caught together. In Jan 2000, the *Pt. cookii* (now NMNZ OR.27679) was found recently dead in the same burrow after the site was flooded.

Lack of availability of conspecific mates is one of the primary reasons resulting in hybridisation in birds (McCarthy 2006: 32) and this would appear to explain most of the above examples where either birds are colonising a site or are out of their normal nesting range. *Pt. mollis* colonising the Antipodes I would also fit this pattern.

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