

A NEW SPECIES OF SHEARWATER (*PUFFINUS*) RECORDED FROM MIDWAY ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

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Abstract. Small black-and-white shearwaters of the genus *Puffinus* are distributed globally, and their phylogenetic relationships are complex and uncertain. In 1963 a small shearwater collected at Midway Atoll in the North Pacific Ocean was identified as a Little Shearwater (*P. assimilis*), but several physical features suggest closer alliance with Audubon's Shearwater (*P. lherminieri*) and its relatives. Biometrics indicate that the taxon this specimen represents is smaller than any other known shearwater, and phylogenetic analyses indicate it is distinct, with a pair-wise sequence divergence of at least 3.8% from related taxa. We thus propose a new species based on the specimen: Bryan's Shearwater (*Puffinus bryani* *nom. nov.*). The breeding and nonbreeding ranges of Bryan's Shearwater are unknown, but a physical resemblance to the North Atlantic *boydi* (of controversial taxonomic status within *Puffinus*) suggests an affiliation with subtropical or tropical waters. Bryan's Shearwater is apparently rare and could be threatened by extinction; therefore, additional information is needed to increase our understanding of this taxon and its conservation requirements.

Key words: Bryan's Shearwater, *Puffinus bryani*, morphometrics, cytochrome b, phylogenetics, Procellariiformes.

Una Nueva Especie de *Puffinus* del Atolón Midway, Islas Hawaianas del Noroeste

Resumen. Las especies pequeñas blanco y negras del género *Puffinus* se distribuyen globalmente, y sus relaciones filogenéticas son complejas e inciertas. En 1963, un pequeño espécimen colectado en el Atolón Midway en el Océano Pacífico Norte fue identificado como *P. assimilis*, pero diversas características físicas sugieren una alianza más cercana con *P. lherminieri* y sus parientes. El espécimen es más pequeño que cualquier otro taxón conocido de *Puffinus*, y análisis de ADN indica que es diferente, con una divergencia en las secuencias de bases apareadas de al menos 3,8 % de todos los taxones relacionados. Por lo tanto, proponemos una nueva especie basada en el espécimen: *Puffinus bryani* *nom. nov.* Las áreas reproductivas y no reproductivas de *P. bryani* son desconocidas, pero una semejanza física con *boydi* del Atlántico Norte (de estatus taxonómico controversial dentro de *Puffinus*) sugiere una afiliación con aguas subtropicales o tropicales. *P. bryani* es aparentemente rara y podría encontrarse en riesgo de extinción; es por ello que es necesaria información adicional para incrementar nuestro entendimiento de este taxón y los requerimientos para su conservación.

INTRODUCTION

Small “black-and-white” shearwaters of the genus *Puffinus* breed on oceanic islands worldwide. Traditionally (e.g., Murphy 1927, Fleming and Serventy 1943, Murphy and Pennoyer 1952), these taxa were categorized into three groups of species: the larger-bodied Manx Shearwater (*P. puffinus*) group of the temperate zones, including at least eight currently recognized taxa, the smaller-bodied Little Shearwater (*P. assimilis*) group of the North Temperate and subantarctic zones, including at least six taxa, and the medium-sized and tropical to subtropical Audubon's Shearwater (*P. lherminieri*) group, including at least 11 taxa. The small shearwater breeding in the Cape Verde Islands (and formerly Bermuda) of the North Atlantic Ocean (*boydi*)

has variously been classified as either a subspecies of the Little Shearwater (e.g., Murphy 1924, Cramp and Simmons 1977, Carboneras 1992) or of Audubon's Shearwater (Murphy 1927, Jouanin and Mougis 1979, A.O.U. 1998).

Recent taxonomic treatments of these taxa, based on both phenotypic and molecular evidence (summarized by Bourne et al. 1988 and Austin et al. 2004), have recommended breaking the Manx group into two or three clades of six or seven species distributed around the world, the Little Shearwater group into North Atlantic (*baroli*) and subantarctic (*assimilis*) species, and the Audubon's group into tropical Atlantic (*lherminieri*), eastern Pacific (*subalaris*), and Pacific/Indian Ocean (*bailloni*) species. Many of these species would be monotypic, with the notable exceptions of

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bailloni (with up to eight subspecies) and *assimilis* (up to four subspecies). The placement of *boydi* remains controversial: Austin et al. (2004) considered it a subspecies of *Iherminieri* (in the Audubon's group), Sangster et al. (2005) considered it a subspecies of *baroli* (Macaronesian Shearwater) in the Little Shearwater (*assimilis*) group, and Olson (2010) regarded it as a separate species. Another uncertain taxon, *myrtae* of Rapa Island in the Cook Islands, South Pacific Ocean, has traditionally been placed with the Little Shearwater group (Bourne 1959) but appears to be allied genetically with Newell's Shearwater (*P. [auricularis] newelli*) of the traditional Manx Shearwater group (Austin et al. 2004).

On 18 February 1963, A. B. Amerson Jr. discovered and collected a small shearwater in a burrow within a Bonin Petrel (*Pterodroma hypoleuca*) colony on Sand Island, Midway Atoll, in the north-central Pacific Ocean (Clapp and Woodward 1968). The specimen, collected during the Pacific Ocean Biological Survey, was prepared as a round skin, identified as a male by examination of the gonads, deposited in the U.S. National Museum of Natural History (USNM), Washington, D.C., and given specimen number USNM 492974 (Fig. 1). Presumably because of the shearwater's small size, Clapp and Woodward identified it as a Little Shearwater and reported it as the first record of this species for the Hawaiian Islands and for the North Pacific Ocean. Alexander Wetmore compared the specimen with those at the American Museum of Natural History, New York, and suggested that it most closely matched the nominate subspecies of the southwestern Pacific Ocean, although he noted that it appeared to have more white

on the undertail coverts than is typical of that subspecies (Clapp and Woodward 1968). Clapp and Woodward thus identified the specimen as "Little Shearwater *Puffinus assimilis* (*assimilis*?)."

While attempting to confirm the subspecies of this specimen, Pyle noticed that it had a longer tail and, contrary to Wetmore's observation, blacker undertail coverts than typical of the Little Shearwater. These features are more characteristic of the Audubon's Shearwater group, but cursory measurements of the specimen indicated that it was smaller than any other shearwater in the Pacific. We thus performed additional mensural and molecular analyses to investigate the taxonomic placement of this specimen from Midway.

METHODS

MORPHOMETRICS

In addition to the specimen collected on Midway, we examined ten additional taxa, representing those of the traditional Manx, Little, and Audubon's shearwater groups to which the Midway specimen may belong. We measured and evaluated the plumage of 166 museum specimens and compiled data from an additional 703 individuals of 11 taxa from the literature (see Table 1 for measurement criteria and sources).

GENETICS

For genetic analysis, we sampled one toe pad from the Midway specimen and collected a tissue sample from one specimen of Newell's Shearwater. DNA was extracted via a standard



FIGURE 1. Lateral aspect of USNM 492974, collected 18 February 1963 on Sand Island, Midway Atoll.

TABLE 1. Measurements of small “black-and-white” shearwaters of the genus *Puffinus*^a.

Taxon (<i>n</i>) ^b	Culmen ^c	Tarsus ^d	Wing ^e	Tail ^f
<i>puffinus</i> (64)	34.8 (31–38)	45.2 (43–49)	236 (221–243)	73.9 (68–79)
<i>newelli</i> (44)	33.2 (30–36)	45.7 (43–48)	237 (223–250)	84.2 (80–89)
<i>auricularis</i> (35)	31.2 (29–35)	45.0 (43–48)	229 (220–238)	75.4 (65–79)
<i>lherminieri</i> (105)	29.5 (25–34)	39.7 (35–44)	206 (185–216)	85.2 (74–94)
<i>bailloni</i> (114) ^g	27.6 (23–30)	38.5 (35–41)	200 (188–212)	79.8 (73–84)
<i>bannermani</i> (9)	29.5 (28–31)	41.3 (40–42)	212.6 (206–219)	77.5 (74–81)
<i>subalaris</i> (100)	27.9 (24–30)	36.6 (33–38)	195 (187–205)	73.0 (66–77)
<i>assimilis</i> (296)	25.5 (22–29)	37.7 (35–43)	187 (175–197)	67.1 (61–73)
<i>myrtae</i> (1)	25	40	196	81
<i>baroli</i> (60)	25.4 (23–28)	36.7 (35–39)	180 (171–189)	72.1 (63–82)
<i>boydi</i> (40)	26.1 (23–29)	37.3 (35–39)	187 (178–193)	77.0 (71–84)
Midway specimen (1)	25.2	34.7	174	71

^aMean and range of the 95% confidence intervals of each taxon) as reported in the literature (Murphy 1927, Fleming and Serventy 1943, Murphy and Pennoyer 1952, Bourne 1959, King and Gould 1967, Cramp and Simmons 1977, Marchant and Higgins 1990) and from 166 specimens measured by Pyle (see acknowledgments for collections visited).

^bSpecies affiliations of many taxa within *Puffinus* uncertain (see text and Table 3).

^cExposed culmen, measured from base of forehead feathering to tip of bill.

^dMeasured transversely from the proximal tip of the lateral condyle to the last undivided scute at the distal end of the tibiotarsus.

^eMeasured from carpal joint to tip of longest primary with wing flattened. Wing-chord values reported in literature were increased by 3%, on the basis of differences between chord and flat measures in a sample of 30 specimens of various of these taxa obtained by Pyle.

^fMeasured from the insertion of the central rectrices to the tip of the longest rectrix.

^gIncludes the widespread Pacific taxa *polynesiae* and *dichrous* of traditional *lherminieri* and current *bailloni* groups. The restricted Pacific taxon *gunax* of the traditional *lherminieri* group is substantially larger; other Indian Ocean taxa of this group (*bailloni*, *temptator*, *atrodorsalis*, *colstoni*, *persicus*, and *nicolai*) are similar in size to *polynesiae* and *dichrous* (Murphy 1927).

phenol/chloroform procedure developed for and commonly used with ancient DNA (Fleischer et al. 2000). We amplified the entire mitochondrial cytochrome *b* gene by using an overlapping set of conserved primers developed in Primer 3 (Rozen and Skaletsky 2000) from shearwater and petrel sequences available on GenBank (see Table 2). Samples were not available for the nominate subspecies of Townsend’s Shearwater (*P. [auricularis] auricularis*) of the traditional *puffinus* group or of *bannermani* or *gunax* of (or closer to) the traditional *lherminieri* group (see Austin et al. 2004). We also amplified the previously published primer sets *cytb1*, *cytb2*, and *cytbWR* (Dumbacher et al. 2003), and these yielded identical sequences in the regions of overlap. Polymerase chain reaction and sequencing followed Welch et al. (2011), except that DNA was extracted and PCR was set up in a separate laboratory for ancient DNA, with strict protocols as well as extraction and negative controls to minimize and detect contamination. Additionally, we downloaded one representative sequence (>700 bp in length) from the GenBank database for all species of shearwaters available, as well as for the closely related genera *Procellaria*, *Bulweria*, and *Fulmarus*, which we used to root the tree (see Table 3). When multiple sequences were available for a taxon, we selected the

longest, except in cases where subspecific status was unclear. Sequences were aligned and visually inspected in Sequencher version 4.9 (Gene Codes Corporation).

Prior to constructing the phylogenetic trees, we translated the sequences in DAMBE version 5.1.2 (Xia and Xie 2002) and examined the dataset for indications of sequences of nuclear rather than mitochondrial origin (Sorenson and Quinn 1998). We evaluated the best-fit model of nucleotide substitution in jModelTest version 0.1.1 (Posada 2008) and, using the Akaike information criterion, selected the “general time reversible” model with rate variation modeled by a gamma distribution with four discrete rate categories (GTR + Γ). Trees were constructed under three separate optimality criteria: maximum parsimony, maximum likelihood, and Bayesian inference.

We ran maximum-parsimony analyses in PAUP* (Swofford 2002) by using a heuristic search with 100 replicates of random taxon addition sequences and the tree-bisection-reconnection (TBR) branch-swapping algorithm. A plot created in DAMBE (Xia and Xie 2002), of observed pair-wise transition and transversion substitutions against GTR-corrected distances, revealed a primarily linear relationship; therefore, for further analyses all sites and

TABLE 2. Conserved primer sequences developed for amplification of the mitochondrial cytochrome *b* gene in the family Procellariidae.

Primer	Sequence (5' to 3')
aCytbPro1F	CATCCTATCAACAYACAGACCAA
aCytbPro1R	CCGGTTAGRATYTGRTTA
aCytbPro2F	TCAAACATCTCYGCTGATG
aCytbPro2R	GAGGCTCCGTTTGCRGTG
aCytbPro3F	CACACATGCCGAAAYGTACA
aCytbPro3R	GCAGTTGCTATRAGRTRAG
aCytbPro4F	CAAAGAAACCTGAAAYACAGG
aCytbPro4R	CCCCCTCAGGCYCATTCTAC
aCytbPro5F	CAGCCATCCCYTAYATYG
aCytbPro5R	AATGGGATTTTRTCRCAGTTTG
aCytbPro6F	CACGAATCAGGYTCAAAYAA
aCytbPro6R	TGGTTTGATATGRGGDGGDG
aCytbPro7F	CCTACTAGGAGAYCCAGAAAAYTT
aCytbPro7R	GTTCGTTGTTTRGCYTTRTG
aCytbPro8F	AGCCCTAGCTGCHTCMGTA
aCytbPro8R	GTTGGCCGATGATGATRAAT
aCytbPro9F	TGAGTAGGCAGYCARCCAGT
aCytbPro9R	TTTGTTTACAAGACCAATGTTTT

TABLE 3. GTR-corrected genetic distances between the Midway specimen, small black-and-white shearwaters of the genus *Puffinus* (listed without species affiliation because of uncertain relationships; see text) and other shearwater and petrel taxa included in this study. Accession numbers for sequences retrieved from the GenBank database are given in parentheses.

Taxon	Genetic distance (%)	Source
<i>myrtae</i> (AY219939)	3.82	Austin et al. (2004)
<i>opisthomelas</i> (AF076087)	4.18	Nunn and Stanley (1998)
<i>newelli</i> (HQ589356)	4.19	This study
<i>temptator</i> (AY219980)	4.21	Austin et al. (2004)
<i>atrodorsalis</i> (AY219965)	4.22	Austin et al. (2004)
<i>bailloni</i> (AY219964)	4.22	Austin et al. (2004)
<i>puffinus</i> (U74355)	4.30	Nunn and Stanley (1998)
<i>dichrous</i> (AY219954)	4.37	Austin et al. (2004)
<i>yelkouan</i> (AY219973)	4.48	Austin et al. (2004)
<i>polynesiae</i> (AY219955)	4.50	Austin et al. (2004)
<i>lherminieri</i> (AF076085)	4.76	Nunn and Stanley (1998)
<i>loyemilleri</i> (AY219946)	4.78	Austin et al. (2004)
<i>baroli</i> (AY219936)	4.78	Austin et al. (2004)
<i>colstoni</i> (AY219962)	4.79	Austin et al. (2004)
<i>mauretanicus</i> (DQ230316)	4.91	Genovart et al. (2007)
<i>nicolae</i> (AY219960)	4.91	Austin et al. (2004)
<i>persicus</i> (AY219967)	4.93	Austin et al. (2004)
<i>boydi</i> (AY219937)	5.18	Austin et al. (2004)

(continued)

TABLE 3. Continued.

Taxon	Genetic distance (%)	Source
<i>aurakiensis</i> (AY219931)	5.36	Austin et al. (2004)
<i>elegans</i> (AY219933)	5.36	Austin et al. (2004)
<i>tunneyi</i> (AY219926)	5.78	Austin et al. (2004)
<i>assimilis</i> (AY219925)	5.95	Austin et al. (2004)
<i>huttoni</i> (AF076084)	6.14	Nunn and Stanley (1998)
<i>gavia</i> (AY219977)	6.19	Austin et al. (2004)
<i>subalaris</i> (AY219970)	8.00	Austin et al. (2004)
<i>Puffinus nativitatis</i> (AF076086)	8.82	Nunn and Stanley (1998)
<i>Puffinus pacificus</i> (AF076088)	9.58	Nunn and Stanley (1998)
<i>Calonectris diomedea</i> (AY139626)	9.81	Garcia-Moreno et al (2003)
<i>Puffinus creatopus</i> (AF076083)	9.88	Nunn and Stanley (1998)
<i>Puffinus gravis</i> (U74354)	9.89	Nunn and Stanley (1998)
<i>Puffinus bulleri</i> (AF076081)	10.06	Nunn and Stanley (1998)
<i>Puffinus tenuirostris</i> (U74352)	10.09	Nunn and Stanley (1998)
<i>Puffinus carneipes</i> (AF076082)	10.10	Nunn and Stanley (1998)
<i>Calonectris leucommelae</i> (AF076045)	10.23	Nunn and Stanley (1998)
<i>Puffinus griseus</i> (U74353)	11.24	Nunn and Stanley (1998)
<i>Procellaria cinerea</i> (AP009191)	12.15	Watanabe et al. (2006)
<i>Procellaria aequinoctialis</i> (U74350)	12.26	Nunn and Stanley (1998)
<i>Procellaria westlandica</i> (AF076078)	12.27	Nunn and Stanley (1998)
<i>Bulweria bulwerii</i> (U74351)	12.49	Nunn and Stanley (1998)
<i>Procellaria parkinsoni</i> (AF076077)	12.51	Nunn and Stanley (1998)
<i>Fulmarus glacialis</i> (U74348)	12.72	Nunn and Stanley (1998)

substitutions were weighted equally. Branch support was assessed through 1000 nonparametric bootstrap replicates. We ran maximum-likelihood analyses in Garli 0.96 (Zwickl 2006), using the GTR + Γ substitution model. To evaluate branch support, we ran 1000 nonparametric bootstrap replicates with a single replicate per tree search. Bootstrap consensus trees were created in PAUP*. We ran Bayesian-inference analyses in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003, Altekar et al. 2004), also using the GTR + Γ substitution model. Following the default heating scheme, we made a total of four independent runs for 10 million generations each with one cold and three heated

chains. Output was recorded every 1000 generations, with the first 10% discarded as burn-in. We assessed stationarity through plots of $-\ln L$ against generation in Tracer 1.4.1 (Drummond and Rambaut 2007) as well as examination of the effective sample sizes, which were >7000 for all parameters. We assessed convergence through comparison of multiple independent runs and, finally, calculated pair-wise GTR-corrected sequence divergence in PAUP*.

RESULTS

MORPHOMETRICS AND APPEARANCE

Measurements of the Midway specimen reveal that it is considerably smaller than all taxa of the Manx and Audubon's shearwater groups and that it does not accord well with any member of the Little Shearwater group (Table 1). It most closely matches *boydi* of the Atlantic Ocean, but three out of four of its measures fall below the 95% confidence intervals calculated from a sample of 40 specimens of *boydi* (Table 1). In small shearwaters, males average larger than females (Murphy 1927, Fleming and Serventy 1943), so it is likely that females of the Midway taxon are smaller than the single male available. Ten males of *boydi* (Yale Peabody Museum specimens on loan to USNM) measured by Pyle have a range in exposed culmen of 24.9–29.0 mm (vs. 25.2 in the Midway specimen), in tarsus of 35.6–37.7 (vs. 34.7), in wing length of 178–190 (vs. 174), and in tail length of 74–79 (vs. 71).

In plumage the Midway specimen is typical of the genus *Puffinus*, having slaty black upperparts and largely white underparts with dark feathering extending ventrally to the sides of breast and lower flanks (Fig. 1). The undertail coverts (Fig. 2) and inner webs of the primaries (Fig. 3) are largely blackish, more typical of the Audubon's Shearwater group, whereas the lores, auriculars, and superciliary region are white (Fig. 1), more typical of the Little Shearwater group. According to the specimen label, the legs were blue, typical of the Little Shearwater group. The secondaries and body feathers are worn to various degrees, consistent with the plumage of an adult (at least 2 years old) that had undergone a previous molt (Pyle 2008).

GENETICS

We obtained 1020 bp of mitochondrial cytochrome *b* sequence from the Midway specimen and the entire *cyt b* gene (1143 bp) from *newelli*. Sequences have been deposited in the GenBank database (accession numbers HQ589355 and HQ589356, respectively). All phylogenetic analyses included 36 taxa of shearwaters and 6 of petrels in the outgroup, with an average sequence length of 1047 bp and a total of 362 polymorphic sites. Of these, 18% occurred in the first codon position, 3% in the second position, and 79% in the third position. Ninety-three percent of the polymorphisms consisted of transitions, and 91% of the substitutions represented synonymous



FIGURE 2. Ventral region of USNM 492974, collected 18 February 1963 on Sand Island, Midway Atoll, showing longer tail and dark undertail coverts typical of the *Puffinus lherminieri* group.

changes. We detected no insertions, deletions, or stop codons. A comparison of the cytochrome *b* sequences of the Midway specimen and *P. newelli* with the complete sequence of *P. opisthomelas* revealed a similar pattern: 80% of substitutions occurred in the third codon position, 91% represented transitions, and 91% resulted in synonymous changes. Additionally, independent amplifications with different sets of primers resulted in identical sequences, consistent with a mitochondrial origin for the cytochrome *b* sequences.

Maximum parsimony, maximum likelihood, and Bayesian inference all produced congruent topologies. Maximum parsimony yielded 16 equally parsimonious trees of 1024 steps on the basis of 276 parsimony-informative sites (Rohlf's consistency index = 0.596). All maximum-likelihood tree-search replicates, and all four Bayesian-inference replicates, produced the same topology, which was also found by means of maximum parsimony. Bootstrap support for the maximum-parsimony and maximum-likelihood topologies was similar, although Bayesian posterior probabilities were somewhat higher for some branches (Fig. 4). The topology obtained matched that of Austin et al. (2004).

The Midway specimen was distinct from both a strongly supported clade containing the *P. lherminieri* and *P. assimilis* groups and a strongly supported clade containing *newelli* and *myrtae* (Fig. 4). The branch joining these clades with the Midway specimen and the Black-vented Shearwater



FIGURE 3. Underside of outer primary of USNM 492974, collected 18 February 1963 on Sand Island, Midway Atoll, showing darker inner web typical of the *Puffinus lherminieri* group.

(*P. opisthomelas* of the traditional *puffinus* group) received strong support from the Bayesian analysis, but the order of branching within clades remained unresolved. Additional taxa of the *P. lherminieri* and *P. assimilis* groups were basal. Pair-wise GTR-corrected sequence divergence indicates that the Midway specimen is distinct from all other taxa included in this study (Tables 3, 4). The shortest distance is that between the Midway specimen and *myrtae*, with a sequence divergence of 3.8% (Table 4). Pair-wise comparisons with all other taxa yielded divergences of 4.2% or greater, with divergence between the Midway specimen and *baroli* and *boydi* being 4.8% and 5.2%, respectively. Genetic distances between the Midway specimen and other small shearwaters (3.8–5.9%) are similar to or greater than distances between most other taxa of small shearwaters examined (0.4–4.8%, Table 4).

DISCUSSION

Despite the Midway specimen's originally being identified as a Little Shearwater (*P. assimilis*) by Clapp and Woodward (1968), its morphological features, such as its longer tail, dark undertail coverts, and dark undersides of the primaries make it unlikely to represent this subantarctic clade (cf. Olson 2010). On the other hand, its bluish legs and small measurements are uncharacteristic of the Audubon's Shearwater (*P. lherminieri*) group and all other taxa of small black-and-white shearwaters. The specimen is most similar to North Atlantic *boydi* in

appearance and biometrics; however, lengths of both its tarsus and wing are below the 95% confidence interval for *boydi* (both sexes), whereas culmen length is closer to the mean and tail length is at the lower limit. When the comparison is limited to males of *boydi*, measurements of the Midway specimen are smaller to an even greater degree. The specimen is of an adult according to feather-wear patterns, so the small measurements cannot be attributed to immaturity.

Only one specimen of the poorly known *myrtae* has been preserved (Bourne 1959), precluding comparison of the Midway bird with a range of measurements; however, given ranges found within the other taxa, the tarsus, wing, and tail of the Midway specimen are too short for *myrtae*, especially as the single specimen of *myrtae* is a female and the Midway specimen is a male. According to Bourne (1959), furthermore, *myrtae* has white undertail coverts and inner webs to the primaries, as well as white edging to upperpart feathers, unlike the Midway specimen.

The Midway specimen is also distinct genetically. The taxa *baroli*, *boydi*, and *assimilis* all fall within different, strongly supported clades, with sequence divergence between these and the Midway specimen being 4.8% or greater. The shortest pair-wise divergence (3.8%) is with *myrtae*, but this distance is still relatively large in comparison to those between similar species-level taxa. Additionally, with strong support, all three phylogenetic tree-construction methods group *myrtae* with *newelli* instead of with the Midway specimen. While the exact order of branching of some clades in the

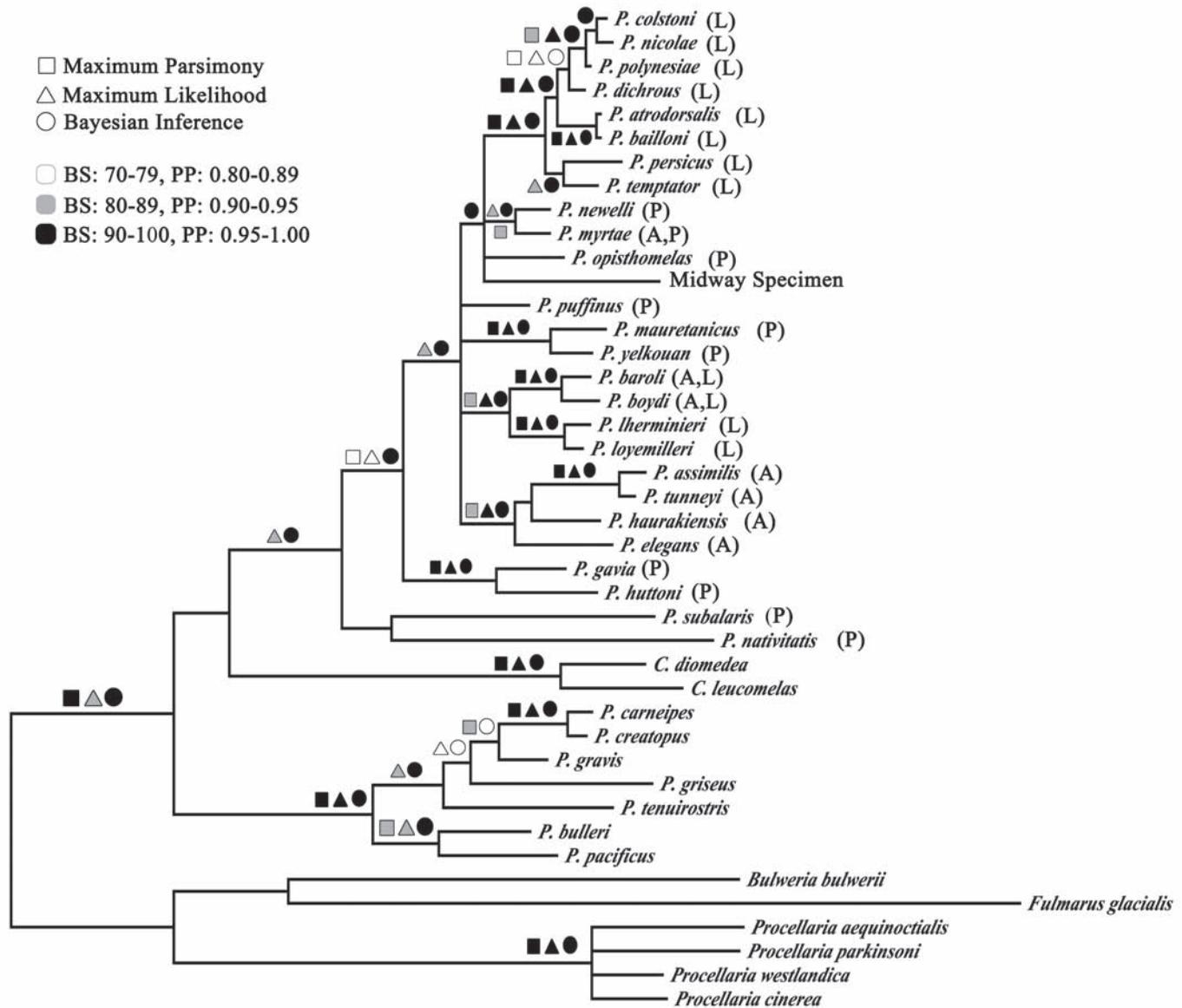


FIGURE 4. Bayesian 50% majority rule consensus tree for cytochrome *b* gene sequences from 36 shearwater taxa and 6 outgroups. Maximum likelihood and maximum parsimony analyses yielded the same topology as well. Letters in parentheses after taxon names indicate whether that taxon has previously been considered to belong to the traditional *puffinus* (P), *assimilis* (A), and/or *lherminieri* (L) groups. Support is indicated along branches and in the legend above: BS, bootstrap support for maximum parsimony and maximum likelihood; PP, posterior probability for Bayesian inference. See Table 3 for GenBank accession numbers.

tree is unresolved, it is clear that the Midway specimen does not group with any of the shearwater taxa examined.

Species-level sequence divergence between other shearwaters we examined ranges from 0.7% (e.g., between *Calonectris diomedea* and *C. leucomelas*) to about 12% (e.g., between *C. leucomelas* and *P. nativitatis*). In addition, distances between other species of small black-and-white shearwaters typically fell between 2.3 and 3.7% (Austin et al. 2004, Table 4);

for example, *puffinus* and nominate *assimilis* (3.3%), *puffinus* and *boydi* (3.5%), *puffinus* and *opisthomelas* (2.9%), nominate *assimilis* and *lherminieri* (2.6%), and *opisthomelas* and *newelli* (2.3%). Therefore, a genetic distance of greater than 3.8% from all other taxa investigated indicates that the Midway specimen has diverged to an extent comparable to or greater than other clearly recognizable shearwater species, and indeed to those among other procellariiform species in general (Austin

TABLE 4. Genetic distances (%) between the Midway specimen and selected closely related taxa of the traditional *puffinus* (P), *assimilis* (A), and *lherminieri* (L) groups of small black-and-white shearwaters, including those found in the Pacific Ocean. See Tables 2 and 3, Figure 4, and text for additional information on other taxa.

Taxon	Midway specimen	<i>puffinus</i>	<i>newelli</i>	<i>opisthomelas</i>	<i>myrtae</i>	<i>assimilis</i>	<i>boydi</i>	<i>baroli</i>	<i>lherminieri</i>	<i>polynesiae</i>
<i>puffinus</i> (P)	4.3									
<i>newelli</i> (P)	4.2	3.0								
<i>opisthomelas</i> (P)	4.2	2.9	2.3							
<i>myrtae</i> (A, P)	3.8	2.8	1.2	2.6						
<i>assimilis</i> (A)	5.9	3.9	4.8	4.8	4.2					
<i>boydi</i> (A, L)	5.2	3.5	3.7	3.5	3.6	4.7				
<i>baroli</i> (A, L)	4.8	3.6	3.8	3.5	3.6	4.7	1.1			
<i>lherminieri</i> (L)	4.8	3.6	3.7	4.3	2.9	5.0	2.7	2.5		
<i>polynesiae</i> (L)	4.5	3.2	2.5	2.7	2.4	4.9	4.0	4.0	3.3	
<i>dichrous</i> (L)	4.4	3.2	2.5	2.9	2.4	4.9	4.0	4.0	3.5	0.4

et al. 2004, Zino et al. 2008, Techow et al. 2009). Under the assumption of a substitution rate of 1.89% per million years for the Procellariiformes (Weir and Schluter 2008), it appears that the Midway taxon may have been separate from all other taxa included in this study for more than 2 million years.

Overall, knowledge of procellariid taxonomy is poor, stemming from insufficient material in museum collections, remote and unknown breeding localities, and frequent similarity in both size and plumage of distinct species. However, despite this poor knowledge of seabirds in general, genetic analyses have identified cryptic species among them (Hailer et al. 2010, Welch et al. 2011, Zino et al. 2008). Although a multigene dataset for the small species of *Puffinus* is unavailable for comparison with the Midway specimen, it has been argued that mitochondrial DNA often provides the earliest indication of divergence (Zink and Barrowclough 2008). Therefore, despite evidence from only a single specimen, it is likely that the Midway shearwater represents a genetically distinct lineage, and, given the lack of any closely related or morphologically similar taxa, we propose a new species based on the specimen:

***Puffinus bryani*, new species**

Bryan's Shearwater
(Tables 1–4, Figs. 1–3)

This published work, and the new species proposed here, have been registered in ZooBank, the proposed nomenclatural registry for zoology. Both the work and the nomenclatural act have been assigned ZooBank Life Science Identifiers (LSIDs), which can be associated with the registration information through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The ZooBank LSID for the new species is [urn:lsid:zoobank.org:pub:1233D7B7-0727-4540-99B3-67910BF7F1A8](http://zoobank.org/pub:1233D7B7-0727-4540-99B3-67910BF7F1A8); [urn:lsid:zoobank.org:act:BAF7217E-A360-42D5-941C-660F91FC94DA](http://zoobank.org/act:BAF7217E-A360-42D5-941C-660F91FC94DA), and the LSID for this published work is [urn:lsid:zoobank.org:pub:1233D7B7-0727-4540-99B3-67910BF7F1A8](http://zoobank.org/pub:1233D7B7-0727-4540-99B3-67910BF7F1A8).

Holotype. USNM 492974, male (testes 4 mm), from Sand Island, Midway Atoll, north-central Pacific Ocean (28° 05' 30"N, 177° 04' 33"W), collected by A. B. Amerson on 18 February 1963 (Figs. 1–3).

Paratypes. None available at this time.

Diagnosis. A shearwater typical of genus *Puffinus* in structure, size, plumage, and genetic relationships. In appearance, distinguishable from other members of the genus by the combination of small size, proportionally long tail, dark undertail coverts and under surfaces of the primaries, and bluish legs.

Description (Figs. 1–3). See Table 1 for lengths of exposed culmen, tarsus, wing, and tail. Additional measurements taken by Pyle: bill depth at base 7.9 mm, bill depth just distal to nostrils 6.5 mm, central claw chord (insertion point on dorsal side to tip) 8.1 mm.

Upperpart feathering uniformly slaty black, exposed feathers (including tertials and older body feathers) bleaching to brown; underparts white except for ventral extensions of slate-black coloration to sides of breast and lower flanks; undertail coverts largely blackish with 3- to 5-mm white tips on shorter lateral feathers; lores, auriculars, and superciliary region white, the demarcation with dark crown along anterior portion of eye. Undersides of outer primaries dark. From specimen label: “legs: blue, outer edge of tarsus black. feet: flesh underside web. bill: black, lateral plates blue-gray. iris: brown.”

Distribution. Breeding and nonbreeding distribution unknown; see Remarks, below.

Etymology. We name this species in honor of Edwin Horace Bryan, Jr., participant in the Whitney South Seas Expedition 1920–1923 and the Tanager Expedition to the Northwestern Hawaiian Islands 1923–1924; Curator of Collections at the Bishop Museum, Honolulu, 1919–1968; author of many publications on Hawaiian insects and birds, 1926–1958.

Similar species. Differs from all taxa of the traditional *puffinus* group (including the Pacific *opisthomelas*, *auricularis*, and *newelli*) by much smaller size and bluish leg color. From all subantarctic taxa of the *assimilis* group and *myrtae*

by shorter tarsus and wing, especially for a male, proportionally longer tail, and darker undertail coverts and undersides of the primaries. From all Pacific taxa of the traditional *lherminieri* group (including *subalaris*, *polynesiae*, *dichrous*, *gunax*, and *bannermani*) by much smaller size and bluish leg color. From Atlantic *baroli* by shorter tarsus, darker undertail coverts, and dark undersides of the primaries. Closest in measurements and appearance to Atlantic *boydi* but tarsus, wing, and tail shorter, especially for a male.

Genetically, *bryani* is not close to *boydi*, diverging in the sequence of cytochrome *b* 5.2% from it and to a similar degree from all members of the traditional *assimilis* group (except *myrtae*). Sequence divergence of $\geq 4.2\%$ from all members of traditional *lherminieri* group and $\geq 3.8\%$ from the *puffinus* group (now including *myrtae*). These divergence values are greater than those for most other small black-and-white species of *Puffinus*.

Remarks. Given the current complexity and uncertainty of the taxonomy of the small black-and-white shearwaters (Austin et al. 2004, Olson 2010), it is possible that *bryani* could represent a subspecies; however, with which species it could be included is unclear. It is doubtful that Bryan's Shearwater breeds regularly in the Northwestern Hawaiian Islands, given the thorough investigation of breeding seabirds on these islands during the Pacific Ocean Biological Survey (Clapp and Woodward 1968, Amerson 1971, Woodward 1972). The collected individual most likely was scouting the island from a breeding locality elsewhere in the Pacific. It is possible that Bryan's Shearwater breeds at similar latitudes to Midway in the northwestern Pacific Ocean, as do the Bonin Petrel and Tristram's Storm-Petrel (*Oceanodroma tristrami*), species that also breed in the Northwestern Hawaiian Islands. The only other small shearwater known to breed in the northwestern Pacific is the little-known *bannermani* of the Bonin Islands, which is much larger than Bryan's Shearwater (Table 1). Other Procellariiformes found in or flying over seabird colonies in the Northwestern Hawaiian Islands (see Pyle and Pyle 2009 for summaries) have included Jouanin's Petrel (*Bulweria fallax*) of the Indian Ocean (Clapp 1971, Seto et al. 1996), the Kermadec Petrel (*Pterodroma neglecta*) of the southern Pacific Ocean (Woodward 1972, Clapp 1974), Murphy's Petrel (*Pterodroma ultima*) of the south-central Pacific Ocean (Clapp and Woodward 1968, Clapp 1974), the Herald Petrel (*Pterodroma [arminjoniana] heraldica*) of the southwestern and south-central Pacific Ocean (Amerson 1971, Clapp 1974), and the Streaked Shearwater (*Calonectris leucomelas*) of the far western Pacific Ocean (Marks 1990). The diverse origins of species prospecting to the Northwestern Hawaiian Islands suggests that Bryan's Shearwater may breed anywhere in the Pacific or Indian oceans, perhaps even farther afield.

The phenotypic similarity of *bryani* to *boydi* suggests that *bryani* may occur in subtropical to temperate waters

similar to those around the Cape Verde Islands and Bermuda (at 14–32° N) where *boydi* breeds or has bred. Like *boydi*, *bryani* may disperse primarily to subtropical and tropical waters when not breeding, or it may occur along hydrographic fronts in a range of ocean temperatures (Olson 2010). Its smaller size than that of *boydi*, however, also suggests an association with colder water, like that of the subantarctic Little Shearwaters and North Atlantic *baroli*.

Given the lack of previous discovery, Bryan's Shearwater is undoubtedly uncommon to rare; we propose that it should be considered for lists of threatened or endangered species. A similar shearwater, likely of this species, was observed in a burrow at Midway Atoll during the winter of 1991–1992 (Pyle and Pyle 2009), suggesting the species' survival into at least the 1990s. We hope that ornithologists working in seabird colonies and at sea throughout the Pacific Ocean will discover additional Bryan's Shearwaters, revealing its breeding habits and conservation requirements.

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