A New Species of Bush-warbler from Bougainville Island and a Monophyletic Origin for Southwest Pacific Cettia

Authors: Lecroy, Mary, and Barker, F. Keith

Source: American Museum Novitates, 2006(3511) : 1-20

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2006)3511[1:ANSOBF]2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3511, 20 pp., 8 figures, 5 tables March 16, 2006

A New Species of Bush-Warbler from Bougainville Island and a Monophyletic Origin for Southwest Pacific *Cettia*

MARY LECROY[1,3] AND F. KEITH BARKER[1,2]

ABSTRACT

We describe a new species of *Cettia* from the Crown Prince Range, Bougainville Island, North Solomons Province, Papua New Guinea. By combining morphometric and molecular phylogenetic techniques, we attempt to broaden our understanding of evolutionary processes within the genus *Cettia* in the southwest Pacific. The new species proves to be distinct with respect to several morphological characteristics that are most probably related to a more terrestrial lifestyle than that of its congeners. Molecular data agree with morphological data in establishing that these birds are at least as distinct from the other island forms of *Cettia* as those forms are from each other, far exceeding intraspecific variation. These data and the restricted distribution of the population on Bougainville strongly support recognition of a new species. The application of molecular phylogenetic techniques also supports the idea that the new species and other island forms of *Cettia* confined to mountains on southwest Pacific islands are derived from a single common ancestor rather than being independently derived from one or more mainland forms. In addition, the relatively recent discovery of two new species of *Cettia* suggests that additional forms await discovery in other poorly known areas of the southwest Pacific. Our results point to the need for further molecular studies and for additional field research into the distribution and ecology of forest songbirds on islands.

INTRODUCTION

The island archipelagoes of the southwest Pacific offer an unparalleled opportunity for the study of biogeography, adaptation, and speciation (MacArthur and Wilson, 1967; Mayr and Diamond, 2001). The proximity of many of these islands to much larger landmasses not only has the potential to generate patterns far more complex than those observed in isolated archipelagoes (e.g., Hawaii; Paxinos et al., 2002, and Lovette et al., 2002), but also may offer insights not available in such settings (e.g., Cockburn, 2003). However, until recently, understanding of many evolutionary questions pertinent to this region has

[1]Department of Ornithology, American Museum of Natural History (lecroy@amnh.org).
[2]Bell Museum of Natural History, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108 (barke042@umn.edu).
[3]Author for correspondence.

 ISSN 0003-0082

been limited to traditional taxonomies based almost entirely on external morphology. The application of molecular phylogenetic techniques (Slikas et al., 2000; Zerega et al., 2004; Filardi and Moyle, 2005; Filardi and Smith, 2005; and Jansa et al., in press) is now providing a means of presenting explicit phylogenetic hypotheses as an aid to addressing these evolutionary questions. By combining these techniques in the description of the new species given below, we attempt to further our understanding of evolution within the genus *Cettia* in the southwest Pacific.

The genus *Cettia*, as currently delineated (Dickinson, 2003), includes 14 species distributed from Europe (*C. cetti*) through Southeast Asia and the southwest Pacific (*C. ruficapilla* in Fiji). Currently, four species are known from the southwest Pacific: *C. seebohmi* from Luzon in the Philippines, *C. annae* from Palau in the Caroline Islands, *C. parens* from the island of Makira (= San Cristobal) in the Solomon Islands, and *C. ruficapilla* from Fiji. It has been argued that these island forms are a natural group, based on morphological traits and vocalizations (Orenstein and Pratt, 1983), and that they were derived from an ancestor that was widespread through the southwest Pacific. More recently, a new species (*C. carolinae*) was described from Tanimbar, in the Moluccas (Rozendaal, 1987). Its describer thought it allied to the Pacific species group, rather than the geographically closer *C. vulcania* (formerly part of the Southeast Asian species *C. fortipes*; Wells, 1982), from which it differs in both external proportions and vocalizations. The distribution of this genus as a whole is of interest, as "… this [is] the only southwest Pacific land bird genus definitely derived from Asia but absent from either New Guinea or Australia" (Orenstein and Pratt, 1983: 196).

NEW SPECIES FROM BOUGAINVILLE ISLAND

As long ago as 1972, Diamond (1975: 21) recognized that an unknown montane bird occurred on Bougainville Island, North Solomons Province, Papua New Guinea. Its song was heard on Mt. Balbi between 1140 and 1340 m. Local residents, speakers of the Rotokas language, called it *kópipi* and said it was a resident of mountains. Nasioi-speaking people inland from Kieta called it *ódedi*. Diamond noted that the song consisted "of two-note and three-note rising phrases at time intervals of a few seconds. The pitch is high, and occasional notes are slightly trilled. In pattern and in quality the song suggests that of the Hermit Thrush of North America (*Catharus guttatus*)." He made no guesses as to its identity but suggested that it was "apparently montane, shy, not uncommon, and possibly solitary and territorial."

In 1977 Don Hadden first heard the beautiful, clear whistle of the *ódedi* while bird-watching along the old overgrown Port Mine Access Road. From that time to the end of 1980 when he left Bougainville, he heard the bird calling in that area, particularly when the weather was misty and/or wet, but was unable to capture an individual. Later (1979), Bruce Beehler (1983: 114–115) visited Bougainville at Hadden's invitation and heard the *ódedi* in the mountain forest west of Panguna. He became convinced that the *ódedi* was probably a member of the genus *Vitia* (= *Cettia*), but conflicting accounts by local field assistants of its appearance and habits made this uncertain. Hadden (1981: 93) reviewed its status up until that time. Other visiting bird-watchers to Bougainville heard the *ódedi* during the 1980s.

In 1989, rebels who seized control of the copper mine forced its closure, and during the 1990s no outsiders were able to visit Bougainville. Hadden returned to Bougainville in July 1999, after the civil war was largely over and Australian and New Zealand Peace Monitoring troops were deployed. Nevertheless, the area in the Crown Prince Range where the *ódedi* lived was still controlled by rebels, making expeditions to the area almost impossible. Hadden contacted John Toroura, who had assisted him with his bird studies in the 1980s. He proved extremely knowledgeable and helpful. With his advice on exactly where to place the mist nets, eventually the first *ódedi* was captured, and subsequently two additional birds were netted in steep, undisturbed rainforest (D. Hadden, personal commun.). A watercolor

Fig. 1. The Odedi (*Cettia haddeni*, new species), bottom, with its relatives *C. ruficapilla funebris* from Taveuni Island, Fiji (top), and *C. parens* from Makira Island, Solomon Islands (middle). Original watercolor by John Anderton.

by John Anderton shows this new bird and its nearest relatives (fig. 1). A photograph of a hand-held bird is presented in Hadden (2004: 195).

Beehler's prediction that the *ódedi* would prove to be a *Vitia* (= *Cettia*) has proven true, and the distinctiveness of this form is such that we propose to name it a new species in honor

of Don Hadden, whose long search for the bird has finally been rewarded. We suggest that this species be called the Odedi, the name of the bird in the Nasioi language and by which it has been called since 1972, when Jared Diamond first heard its voice.

Cettia haddeni, new species
English name: Odedi

DIAGNOSIS: Adults (one male, one unknown sex) with body mass greater than 21 grams—about four grams greater than any other *Cettia* known (table 1; Dunning 1993). All three individuals, including an immature of unknown sex, have bill width at the posterior margin of the nostril $\geq$ 7 millimeters, at least 2 millimeters greater than any other *Cettia* measured (table 1). Underparts darker than any other *Cettia* (closest being *C. ruficapilla funebris*, see below).

HOLOTYPE: AMNH 835234, adult male, collected between Kupei and Moreni villages, 1000 m, Crown Prince Range, Bougainville Island, North Solomons Province, Papua New Guinea, on 16 September 2000, prepared by Andrew Mack (no. 1380). Flattened wing 66.0 mm, tail [43.0] worn, tarsus 29.0, bill length from base 19.0, bill length from anterior edge of nostril 10.0, bill width at posterior edge of nostril 7.0. Colors of soft parts: tarsus yellowish-ochre (straw), browner on front; base of mandible yellowish-ochre, rest of bill dark brown; inside of mouth yellow. Testes 7 $\times$ 4 mm; skull ossified; no molt; tissues preserved in EtOH. The weight at time of skinning was recorded as 25 g, but the specimen had been frozen for some time.

PARATYPES: AMNH 833347, adult sex ?, Crown Prince Range, Bougainville Island, North Solomons Province, Papua New Guinea, January 2000, prepared by Andrew Mack (no. 1218). Flattened wing 66.0, tail [43.0] worn, tarsus 29.0, bill length from base 19.0, bill length from anterior edge of nostril 10.0, width of bill at posterior edge of nostril 8.0. Colors of soft parts: tarsus brown with yellowish cast to digits; bill dark brown, base of lower mandible paler, yellow-brown cast to tomentia. Skull 85% ossified; tissue preserved in EtOH. The weight at time of skinning was recorded as 24.5 g, but the specimen had been frozen for some time.

AMNH 836189, immature sex ?, Crown Prince Range, 1400 m, Bougainville Island, North Solomons Province, Papua New Guinea, 11 August 2001, prepared by Andrew Mack, no. 1571. Flattened wing [60.0] molt, tail missing, tarsus 26.5, bill length from base 19.0, bill length from anterior edge of nostril 10.0, width of bill at posterior edge of nostril 7.0. Colors of soft parts: iris dark, bill very dark brown, almost black, mouth lining dull yellow brown. Skull 10% ossified; tissue preserved in EtOH. This specimen had also been frozen for some time.

DESCRIPTION OF THE HOLOTYPE

Upperparts: Head dark chestnut with faint lighter streaks in the center of the feathers, back very dark brown with wings and tail more chestnut, ten rectrices, wings very rounded and unmarked (primary 10 half the length of 9, primary 9 ten mm shorter than 8, primary 8 five mm shorter than 7, primary 7 slightly shorter than 6, primaries 6 and 5 subequal, remainder of the primaries differ little in length from 6 and 5, those being slightly longer). Head: Sides of head brown with lighter streaks in the center of the feathers, dark loral spot, no eye-stripe, but feathers over the eye are slightly lighter; rictal bristles prominent; bill strong, broadened at base. Underparts with black feather bases tipped with gray, giving a mottled appearance, throat lighter. Flank feathers long and brownish olive; both tarsi and phalanges noticeably elongate. Paratype AMNH 833347 is similar, but feathers missing on the underparts make this specimen appear even blacker below. The almost identical measurements of these two specimens lead us to believe that it is perhaps also a male, as females are usually considerably smaller in this genus (see table 1). Paratype AMNH 836189 has very similar plumage. The presence of wing and body molt and the largely unossified skull indicate that this specimen is immature. The shorter tarsus may also indicate that this is a female and that there is a sexual size difference in this species as in others in the genus, as tarsus length in immature birds usually equals that of the

TABLE 1

Measurements of *Cettia haddeni*, *C. parens*, *C. ruficapilla*, and *C. carolinae* (from Rozendaal, 1987: 187)

Measurements in brackets indicate wear on the measured specimen, means for samples greater than two and sample sizes given in parentheses. Total culmen = culmen measured from base at skull; Culmen = culmen measured from anterior margin of nostril; Posterior bill width = width measured at posterior margin of the nostril.

Cettia species	Sex	Mass	Flattened wing	Tail	Tarsus	Total culmen	Culmen	Posterior bill width
haddeni	male (type)	[25.0]	66.0	[43.0]	29.0	19.0	10.0	7.0
	adult, sex ?	[24.5]	66.0	[43.0]	29.0	19.0	10.0	8.0
	immature, sex ?	—	[60.0]	—	26.5	19.0	10.0	7.0
parens	male	18.5–19.0	59.0–61.5	49.0, 50.0	26.0	18.5–19.0	10.0–11.0	5.0
		(18.8, 3)	(60.1, 3)	(2)	(3)	(18.8, 3)	(10.7, 3)	(3)
	female	14.0, 14.0	49.0–55.0	43.5–47.0	23.0–26.0	17.0–18.5	9.0–10.5	3.5–5.0
		(2)	(53.0, 4)	(44.8, 3)	(23.7, 4)	(17.5, 4)	(9.5, 4)	(4.5, 4)
r. funebris	male	—	61.0–65.0	50.0–60.0	25.0–27.0	18.0–19.5	9.5–11.0	4.5–5.0
			(62.7, 9)	(56.5, 9)	(26.4, 9)	(18.7, 9)	(10.2, 9)	(4.9, 9)
	female	—	55.0, 57.0	49.0	25.0, 25.5	19.0, 19.0	10.0, 11.0	5.0
			(2)	(1)	(2)	(2)	(2)	(1)
r. castaneoptera	male	—	57.0–63.0	54.5–62.0	24.5–27.0	17.5–20.0	10.0–11.0	4.5–5.0
			(60.2, 10)	(58.8, 10)	(25.4, 10)	(19.1, 10)	(10.5, 10)	(4.9, 10)
	female	—	54.0–60.0	54.0–55.0	24.0–25.0	17.5–19.0	9.5–11.5	4.5–5.0
			(55.9, 5)	(54.8, 4)	(24.7, 5)	(18.6, 4)	(10.5, 4)	(4.9, 5)
r. ruficapilla	male	—	57.0–61.0	52.5–58.0	24.5–26.0	18.0–20.0	10.0–11.0	4.5–5.0
			(59.4, 9)	(55.8, 9)	(25.1, 9)	(19.0, 9)	(10.4, 9)	(4.9, 9)
	female	—	53.0–55.0	48.0–51.0	23.0–24.0	18.0–19.0	9.5–10.5	4.5–5.0
			(53.7, 8)	(49.5, 7)	(23.5, 7)	(18.3, 6)	(10.0, 6)	(4.8, 6)
r. badiceps	male	—	57.0–61.0	52.0–58.5	24.0–25.5	17.0–19.0	9.0–11.0	4.5–5.0
			(58.2, 12)	(55.5, 11)	(24.8, 12)	(18.0, 12)	(9.75, 12)	(4.9, 12)
	female	—	50.0–56.5	48.0–49.5	21.0–24.0	16.0–18.5	8.0–9.5	4.0–5.0
			(52.5, 6)	(48.4, 5)	(22.6, 5)	(16.8, 6)	(8.8, 6)	(4.6, 6)
annae	male	—	71.0–79.0	61.0–68.0	27.0–30.0	21.0–23.0	12.5–13.0	5.0–5.5
			(74.8, 6)	(63.5, 6)	(29.0, 6)	(21.7, 5)	(12.8, 5)	(5.2, 5)
	female	—	61.0–75.0	52.0–63.0	26.5–30.0	20.0–22.0	10.5–12.0	4.5–5.0
			(66.7, 7)	(57.2, 5)	(28.2, 7)	(21.0, 7)	(11.5, 7)	(4.9, 7)
carolinae	male	18.6–20.6	68.0–71.0	45.0–49.0	22.0–25.0	20.0	11.0–11.5	4.3–5.1
		(19.5, 4)	(69.0, 4)	(47.5, 4)	(23.75, 4)	(4)	(11.25, 4)	(4.6, 4)
	female	13.5–15.0	59.0–61.0	39.0, 41.0	21.0–24.0	19.0	10.0–11.5	4.4–4.5
		(14.3, 3)	(60.0, 3)	(2)	(22.3, 3)	(3)	(10.8, 3)	(4.5, 3)

adult in ground dwelling species (M.L., personal obs.). The digits are also noticeably shorter in this specimen.

Related Species

When Ramsay (1876) named *Vitia* and its type species, *V. ruficapilla*, he noted that it had only 10 rectrices. Mayr (1935: 4–5, 1936: 15–16) did not mention the number of rectrices when he named *V. parens*, but it also has 10 (personal obs.). Delacour (1942) noted that species in the genus *Cettia* have 10 rectrices. Later, Orenstein and Pratt (1983) discussed the relationships of the southwest Pacific genera *Vitia* and *Psamathia* and concluded, based on song structure, egg color, and external morphology, that these genera with 10 rectrices should be included in *Cettia*. This arrangement has been followed by subsequent authors, including Watson et al. (1986: 11), Sibley and Monroe (1990: 609) and Dickinson (2003: 579). This new species from Bougainville also possesses the 10 rectrices of *Cettia* (sensu lato).

Geographically, the closest representative of *Cettia* is *C. parens* from Makira Island, Solomon Islands. Compared with that species, the Bougainville bird is larger with a shorter tail. Its upperparts are a darker, richer brown (not olive-brown). Below it lacks the yellowish brown tint of *parens*, the feather tips being gray. Because the gray tips are not as broad, the black (not gray) feather bases are much more apparent. The flanks are a much darker brownish olive. The rictal bristles are more prominent, and the tarsi are longer and heavier with longer digits. Mayr (1936: 15–16) noted that the juvenile of "*Vitia*" *parens* (younger than the immature specimen of *haddeni*) was very different from the adult, with the "middle of throat yellowish; breast, belly, and flanks grayish olivaceous, lower belly and under tail-coverts with a brownish wash; forehead and crown fuscous; back, wings, and tail fuscous brown; under wing-coverts yellowish; the whole plumage very soft." Interestingly, the upperparts of this bird are much more similar to all three specimens of *C. haddeni* than to adult *parens*, but the crown and sides of the face are almost entirely fuscous, showing only a very few narrow, lighter tips on the forehead feathers. It is very different from both forms in the coloration of the underparts. Orenstein and Pratt (1983: 190) called attention to similarities in the coloration of the underparts of this juvenile specimen to the underparts of adults of *C. annae*.

Comparison with the four subspecies of *Cettia ruficapilla* from Fiji, shows that *C. haddeni* is most similar to *C.r.funebris* from Taveuni Island in color of the upperparts, but somewhat more brownish on the lower back and tail. The lighter shaft streaks present on the head of *C. haddeni* are lacking in *funebris*. The side of the face is browner than in *funebris* and there are only slightly lighter feathers over the eye, whereas *funebris* has a readily visible tan eyestripe. The underparts of *haddeni* appear much darker because the feather tips are darker and narrower and expose more of the blacker, rather than gray, feather bases. The flank feathers are longer and darker than those of *funebris*. Overall, *haddeni* appears much darker, almost melanistic, when compared with *funebris*, and it differs most strikingly in its shorter tail, its longer and heavier tarsus and longer phalanges, and its wider bill.

Cettia carolinae from Yamdena Island in the Tanimbar Islands, South Moluccas, Indonesia (Rozendaal, 1987) was found by Rozendaal to be morphologically closest to *Cettia ruficapilla*, differing in details of coloration, and in possessing a marked sexual dimorphism and longer bill. Although specimens of *C. carolinae* were not available for direct comparison, measurements given for *C. carolinae* (Rozendaal, 1987: 187) show that the wing, tail, and bill measurements of the holotype of *C. haddeni* approach those of *carolinae* (table 1). However, tarsal measurements and body mass are much greater in *haddeni*.

Morphometric Analysis

We made standard external morphological measurements of *C. haddeni* as well as of the geographically and morphologically closest representatives of genus *Cettia* (table 1). The lengths of wing (flattened), tail, tarsus, and culmen (both from base of bill at the skull and

Fig. 2. Specimens of southwest Pacific island species of *Cettia*: left to right, *Cettia annae* (AMNH 332082), *C. ruficapilla funebris* (AMNH 251966), *C. parens* (AMNH 228063), and *C. haddeni* (AMNH 835234).

from the anterior edge of the nostril) were measured to the nearest 0.5 mm. Individuals of both sexes of *C. annae*, *C. parens*, and four subspecies of *C. ruficapilla* (*funebris*, *castaneoptera*, *ruficapilla*, and *badiceps*) were included (see table 1, fig. 2, and appendix 1). In addition, we obtained comparable measurements (excepting bill width) of the recently described species *C. carolinae* from Rozendaal (1987). We made two quantitative comparisons of *C. haddeni* with other species of *Cettia*. Due to the lack of a positively identified female *C. haddeni*, and the poorer available sample of females from other species, these comparisons were limited to male measurements alone, treating both the holotype and the paratype AMNH 833347 of *haddeni* as males (their measurements are nearly identical, in any case).

In the first comparison, we performed a principal components analysis on the species means for the external measurements, as reported in Orenstein and Pratt (1983), together with those for the subsequently described *C. haddeni* and *C. carolinae*. In addition to *C. ruficapilla*, *C. annae*, and *C. parens*, the data presented by Orenstein and Pratt (1983) included the mainland forms *C. fortipes*, *C. major*, and *C. diphone*, as well as the Luzon endemic *C. seebohmi* (sometimes considered a subspecies of *diphone*). The measurements reported in Orenstein and Pratt (1983) were taken differently from ours (e.g., they measured wing chord and exposed culmen) and included measurements of bill width and depth at the anterior edge of the nostril. In order to use their data, we obtained measures of wing chord, as well as of bill width and depth at the anterior edge of the nostril, from *C. haddeni* and *C. carolinae* (the latter courtesy of R. Dekker and H. van Grouw, National Museum of Natural History, Leiden; table 2). We excluded the measurement Orenstein and Pratt called "culmen total length" (= exposed culmen). All variables were scaled to mean zero and unit variance, and the principal components calculated using the *prcomp( )* function of R v1.9.0 (R Development Core Team, 2004).

The analysis of species means (table 2) yielded two principal components with eigenvalues greater than one, which together explained 82% of the variation in the original set of six variables. The eigenvalues and eigenvectors are reported in table 3. Coefficients of the first component were of

TABLE 2

Mean Measurements of *C. haddeni* and *C. carolinae* for Comparison with Data of Orenstein and Pratt (1983)

Sample sizes in parentheses. Both the type and AMNH 833347 were treated as males for this analysis. Data for *C. carolinae* provided courtesy of R. Dekker and H. van Grouw (National Museum of Natural History, Leiden). Wing chord = length of wing (unflattened); Anterior bill width = width measured at anterior margin of the nostril; Anterior bill depth = depth measured at anterior margin of the nostril.

Species	Sex	Wing chord	Anterior bill width	Anterior bill depth
C. haddeni	male	63.0 (2)	4.0 (2)	4.0 (2)
C. carolinae	male	69.0 (4)	3.1 (4)	3.3 (4)
	female	60.0 (3)	3.2 (3)	3.2 (3)

identical sign and similar magnitude, suggesting its interpretation as a ''general size'' variable, while the second component primarily contrasted bill and tail length. Plotting of species values on these two components (fig. 3) indicated that the two individuals of *C. haddeni* are among the most distinctive forms of *Cettia* investigated. In fact, *C. haddeni* had the third highest Euclidean distance from the origin of the component space (3.16), exceeded only by *C. fortipes pallidus* (3.85) and *C. diphone canturians* (3.71). On these components, *C. carolinae* (Tanimbar, Indonesia), *C. parens* (Makira, Solomon Islands), and *C. annae* (Palau) were closest to *C. haddeni*. Taking all components into account, *C. haddeni* was closest to *C. ruficapilla funebris*, followed by *C. parens* (not shown).

The second comparison made was a principal components analysis of individual external measurements from specimens reported in table 1 and appendix 1. For these analyses, culmen from base and culmen from anterior edge of nostril, the latter of which is a subset of the former, were made into two structurally independent variables by subtracting the latter from the former: the difference (the distance from the base of the bill to the anterior edge of the nostril) was defined as the ''upper culmen'', and was analyzed in lieu of the full culmen measurement. In this comparison, we used the bill width at the posterior margin of the nostril, rather than at the anterior, as this appeared to be measured more reliably on the specimens examined (widths for *C. carolinae* were provided courtesy of Dekker and van Grouw). As above, all variables were scaled to mean zero and unit variance, and the principal components calculated using *prcomp( )*. The eigenvalues and eigenvectors are reported in table 4, and the individual values are plotted on selected components in figure 4.

Analysis of the individual data (table 4) yielded a reduction of variables similar to the species mean analysis, with three components having eigenvalues greater than one, which together explained 82% of the original variance. The coefficients of the first component

TABLE 3

Results of Principal Components Analyses of *Cettia* Species Means

All measurements except for *C. haddeni* and *C. carolinae* from Orenstein and Pratt (1983: 188–189).

Component	Coefficients (eigenvectors)						Eigenvalue	Variance (%)
	Wing chord	Tail	Tarsus	Culmen[a]	Bill width	Bill depth		
PC1	0.410	0.211	0.465	0.372	0.471	0.460	3.851	64.2
PC2	−0.135	−0.828	0.191	0.459	0.120	−0.187	1.063	17.7
PC3	−0.756	−0.017	0.127	−0.302	0.471	0.314	0.467	7.8
PC4	0.390	−0.478	0.212	−0.686	−0.094	0.308	0.410	6.8
PC5	−0.088	0.202	0.777	−0.185	−0.094	−0.552	0.165	2.8
PC6	−0.288	0.024	0.288	0.235	−0.724	0.504	0.044	0.7

[a]Culmen (from nostril) of Orenstein and Pratt (1983).

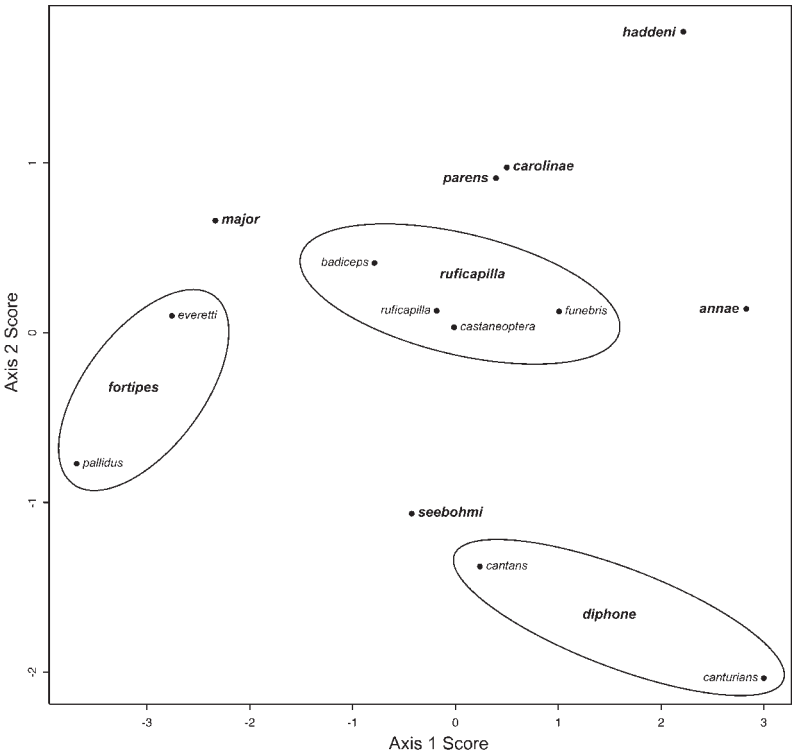

Fig. 3. Scatterplot of *Cettia* species and subspecies on the first two principal components derived from analysis of species means for six external measurements (tables 1, 2, and 3).

suggested interpretation as a size variable (table 4), while the second component contrasted bill width and tail length, and the third component was primarily determined by the relative proportions of the bill proximal and distal to the anterior margin of the nostril. Plotting of individuals on the first two components (fig. 4A) indicated a clear separation of *C. haddeni* and *C. annae* from the remaining species. Component three appeared to correlate with intrapopulation variation within the *C. ruficapilla* complex, although

TABLE 4
Results of Principal Components Analyses of Individual Variation in External Measurements of *Cettia* Species

	Coefficients (eigenvectors)							
Component	Flattened wing	Tail	Tarsus	Upper culmen[a]	Culmen	Bill width[b]	Eigenvalue	Variance (%)
PC1	0.558	0.230	0.544	0.154	0.512	0.234	2.531	42.2
PC2	−0.035	−0.605	0.167	0.145	−0.242	0.725	1.364	22.7
PC3	0.084	−0.285	−0.040	−0.896	0.321	0.061	1.025	17.1
PC4	−0.404	0.593	0.401	−0.332	−0.310	0.345	0.733	12.2
PC5	−0.117	0.321	−0.653	0.097	0.407	0.530	0.185	3.0
PC6	0.710	0.213	−0.295	−0.180	−0.561	0.129	0.163	2.7

[a]Total culmen – culmen from anterior of nostril.
[b]Bill width taken at posterior margin of the nostril.

clear distinctions among individual taxa were not apparent (fig. 4B). Although the fourth component explained relatively little additional variation (12.2%), it clearly distinguished *C. carolinae* from the other forms sampled (fig. 4B). Clustering analysis of individuals in component space yielded clear species clusters for *C. annae*, *C. carolinae*, and *C. haddeni*, but nested *C. parens* within variation among *C. ruficapilla* subspecies (fig. 5). In this analysis, *C. haddeni* appeared to be the most distinctive of the forms sampled.

Phylogenetic Relationships

Although the new species agrees with *Cettia* in its coloration and morphometry, we also sought to establish its relationships using molecular data. To this end, we obtained sequences from two genes from two of the three available samples. As a wide range of comparative material was available for the RAG1 locus (e.g., Barker et al., 2004; Beresford et al., 2005), we attempted to isolate this gene from all three samples. However, either handling of the samples in the field prior to freezing or the long period of storage at relatively high temperatures led to degradation of their DNA, and we were able to obtain only a partial sequence from the 3′ end of the gene (GenBank accession DQ066452; 1182 bp, the region amplified by primers R21/R24 and R23/R2I; Groth and Barrowclough, 1999) from a single sample (the holotype AMNH 835234; see Barker et al., 2002, for methods). Phylogenetic analysis of this partial sequence was performed (using PAUP* v4.0b10, equally weighted parsimony, TBR branch swapping after 50 random addition sequence replicates; Swofford, 2002), including previously published RAG1 sequences (as listed in Beresford et al., 2005). This analysis placed the partial RAG1 sequence as sister to *Cettia brunnifrons* (fig. 6), and bootstrap analysis (100 replicates; Felsenstein, 1985) indicated strong support for this placement (found in 100% of replicates).

In addition to the nuclear sequence, we also obtained complete mitochondrial cytochrome *b* sequence from a second individual (the paratype AMNH 836189; see Barker, 2004 for methods, although the 5′ primer used was L14857, 5′-AGGATCATTCGCCCTATCC-AT-3′). We compared this sequence to Acrocephaline and Megalurine (sensu Sibley and Monroe, 1990) sequences available in GenBank (including samples from the genera *Acrocephalus*, *Bradypterus*, *Cettia*, *Cisticola*, *Hippolais*, *Locustella*, *Megalurus*, *Orthotomus*, *Phylloscopus*, *Prinia*, *Seicercus*, and *Urosphena*). Three Asian species of *Cettia* (*cetti*, *fortipes*, and *diphone*) and *Urosphena squameiceps* were represented by sequences in the database. Of the sequences surveyed, the *C. haddeni* sequence clustered unambiguously (under both parsimony and distance criteria; results not shown) with seven haplotypes of *Cettia diphone*, at an average of 5.0% uncorrected sequence divergence. In order to estimate the relationship of *C. haddeni* to other island as well as mainland forms, we also obtained partial cytochrome *b* sequences from two individuals each of three additional species: *C. ruficapilla*, *C. parens*, and *C. annae* (see appendix 1 for individuals). For these individuals, genomic DNA was extracted from slivers of toe pad using the DNeasy extraction protocol (Qiagen, Maryland), modified by addition of 30 μL of 100 mg/mL dithiothreitol (ISC BioExpress, Utah) to the digestion mix, and by final DNA elution in 50 μL of elution buffer. Based on the complete *C. haddeni* sequence and other published *Cettia* sequences, taxon-specific primers were designed (table 5) to target 640 bp of cytochrome *b*. PCR conditions and sequencing protocols were the same as for tissues. All DNA extraction and PCR setup was performed in a lab and building separate from that used for other avian molecular work. The complete cytochrome *b* sequence of *C. haddeni* and the partial sequences for the remaining species have been deposited in GenBank (accession DQ066451 and accessions DQ288966-DQ288971).

The novel *Cettia* sequences were analyzed in conjunction with the continental species represented in GenBank, and *Urosphena*, using two sequences of *Aegithalos* and *Psaltriparus* as outgroups (fig. 6, and unpublished data; see fig. 7 for GenBank accessions). Parsimony analysis of the 640 bases obtained from the skin samples yielded a single most-parsimonious tree (not shown; L = 386, CI = 0.65, RI =

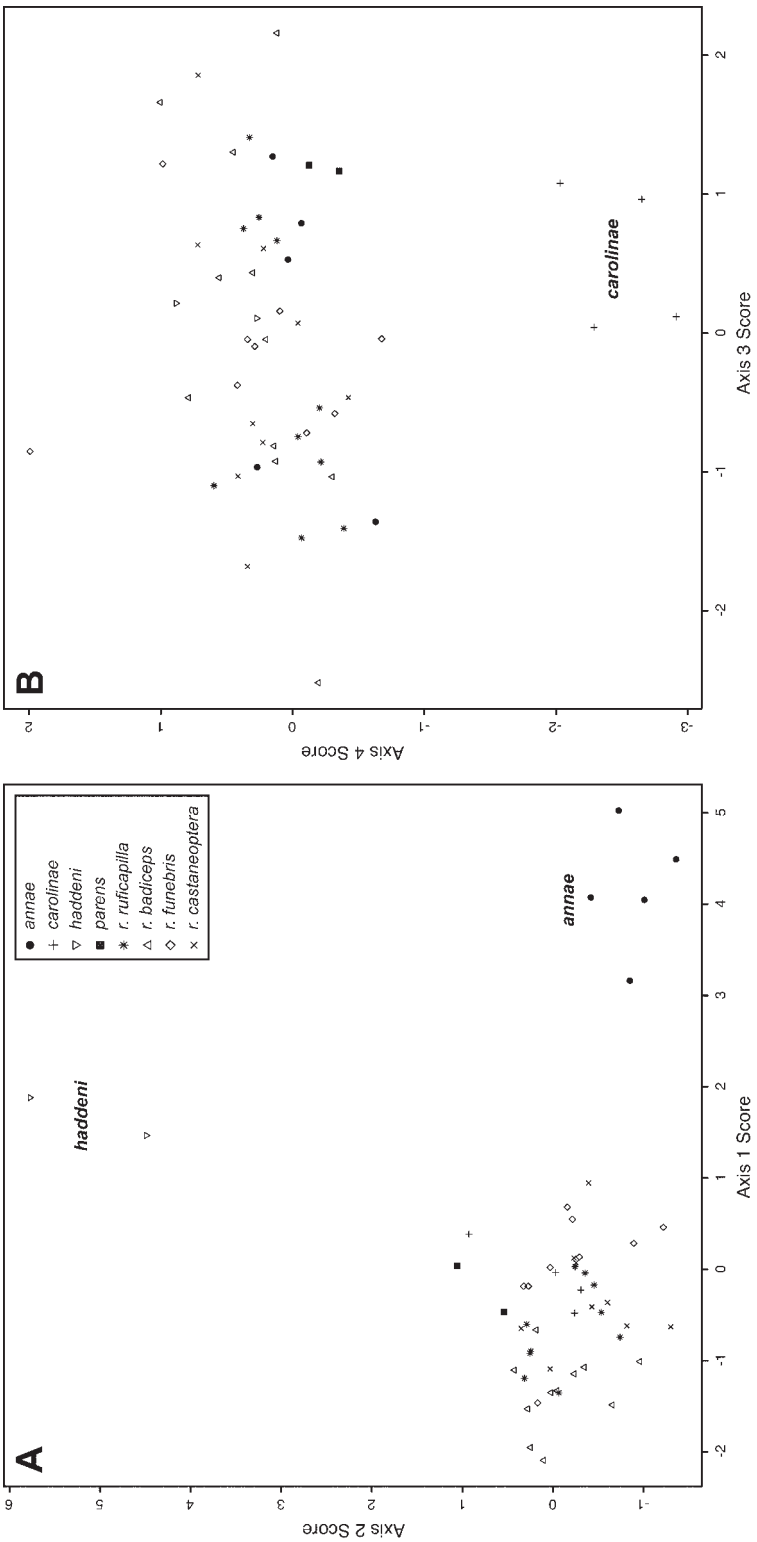

Fig. 4. Scatterplots of individual *Cettia* on the first and second (A) and third and fourth (B) principal components derived from analysis of five external measurements (tables 1 and 4).

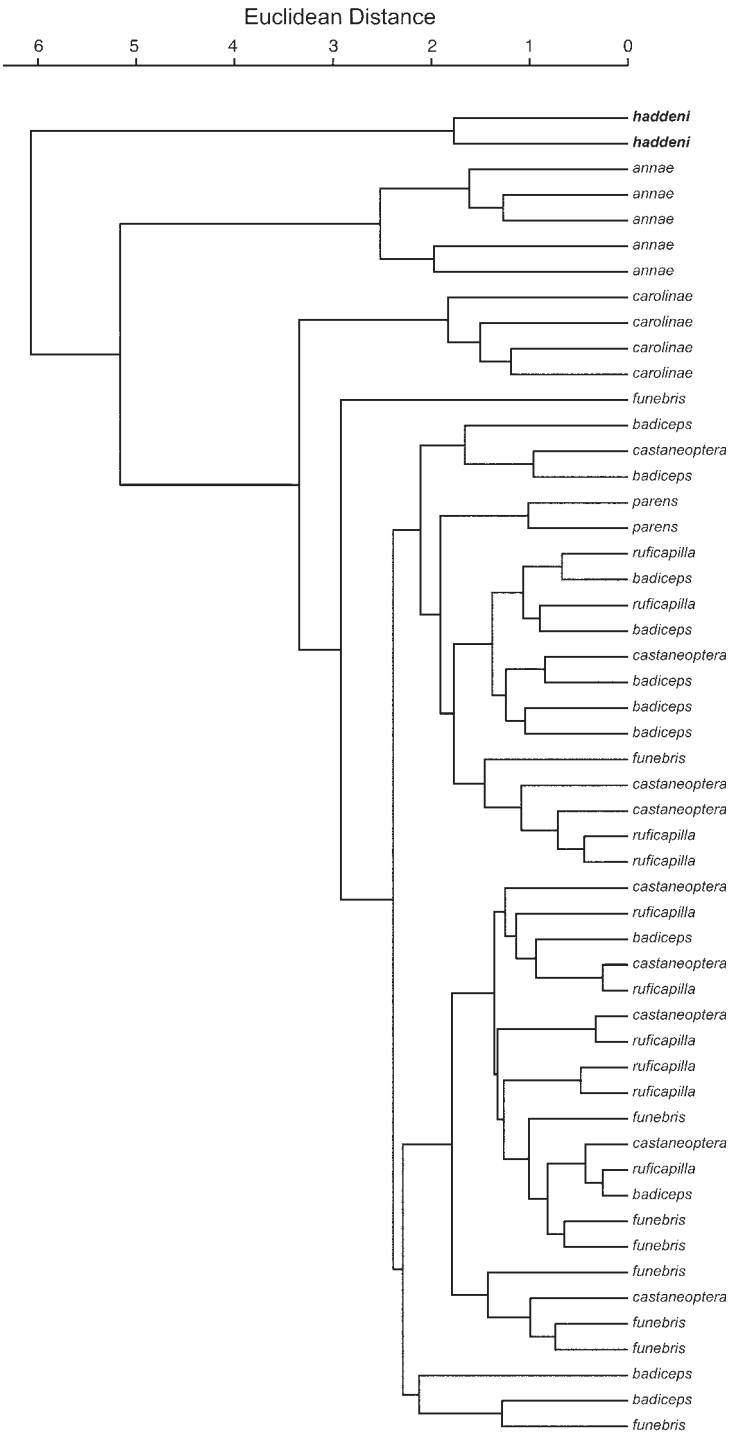

Fig. 5. UPGMA clustering of individual *Cettia* specimens based on pairwise Euclidean distances measured in the space defined by principal components rotation of five external morphological measurements (tables 1 and 4).

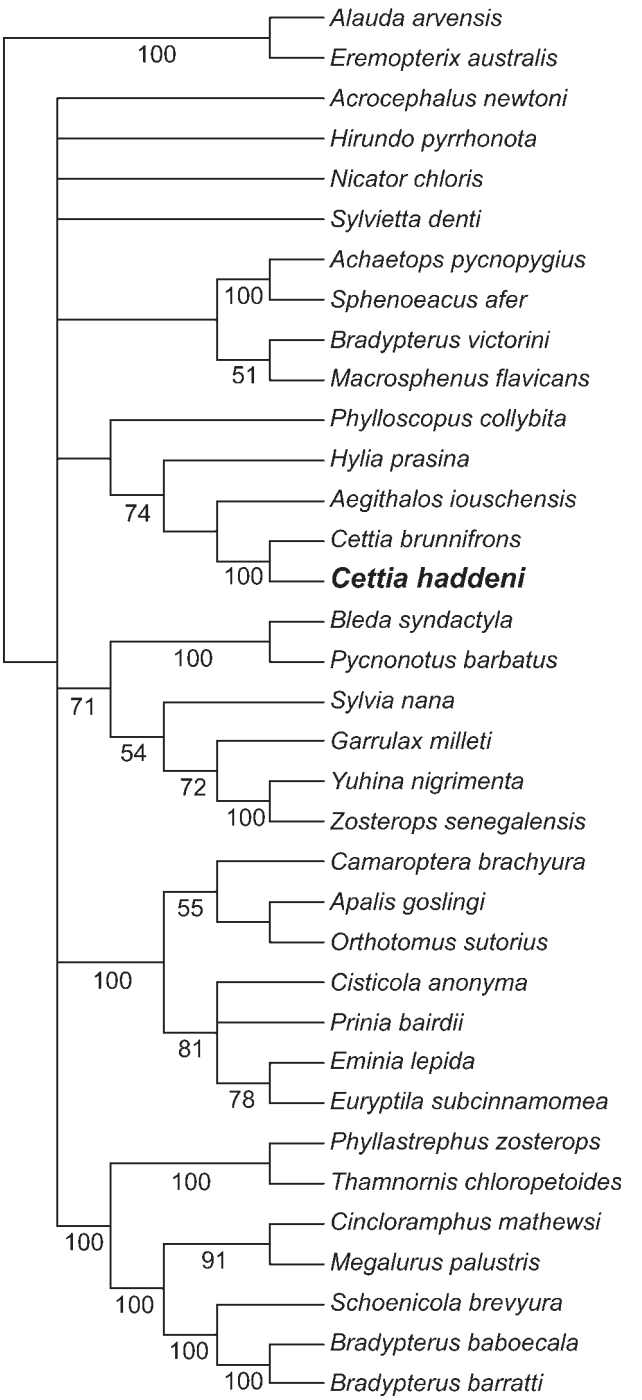

Fig. 6. Strict consensus of nine equally parsimonious trees (L = 1287 steps, CI = 0.664, RI = 0.557) obtained from analysis of partial RAG1 sequences from *Cettia haddeni* and putative sylvioid relatives (Beresford et al., 2005). Numbers below branches indicate bootstrap values ≥ 50% (see text).

TABLE 5
Primers Used in Amplification of Cytochrome *b* from Museum Skin Specimens

Primer	Sequence	Source
L15068	CTA GCC ATR CAC TAY ACA GCA GA	Groth, 2000 (modified)
L15410 *Cettia*	TGA GGC GGA TTC TCR GTA GAY AA	Groth, 2000 (modified)
H15460 *Cettia*	GTG GAC TAA TGT AAG TCC YRC GAT	Groth, 2000 (modified)
H15709 *Cettia*	GCR TAG GCR AAT AGG AAG TAT CA	Barker, 2004 (modified)

0.81). Likelihood model fitting on this tree suggested analysis with the HKY+Γ model (Hasegawa et al., 1985) of evolution (estimated using DT-ModSel; Minin et al., 2003). Figure 7 shows a phylogram of the maximum likelihood estimate of relationships among the sampled species (from a heuristic search with 10 random sequence additions and TBR branch swapping), with support for individual nodes based on parsimony and likelihood bootstrap (1000 and 200 replicates, respectively), and a Bayesian analysis of the data using the same model (default priors, two runs with four incrementally heated chains run for $2 \cdot 10^6$ generations, discarding $5 \cdot 10^5$ generations prior to the chains achieving stationarity). This topology differs from the parsimony tree in its arrangement of island forms (*C. annae* and *parens* switch positions), and in recovering a monophyletic *Cettia* (parsimony places *C. cetti* with *Urosphena*). Support for the relationship of *C. haddeni* with *Cettia* was strong (99% bootstrap under parsimony and 1.00 estimated Bayesian posterior). Within the genus, *C. haddeni* was recovered as part of a monophyletic group of island forms (including *C. ruficapilla*, *parens*, and *annae*), which was sister to the continental *C. diphone*. Support for the *C. diphone*/island clade was strong with parsimony and Bayesian analysis (99% and 1.00), but much weaker under maximum likelihood (54%), and monophyly of the island clade was weakly supported (68% and 50% for parsimony and likelihood respectively, estimated posterior 0.73). Although support for monophyly of *C. diphone* was good (85 and 69% under parsimony and likelihood, estimated posterior 1.00), the two subspecies (the migratory mainland *C.d. borealis*, and sedentary Japanese *C. d. cantans*) were significantly differentiated (separated at 2.5% uncorrected sequence divergence) and monophyletic (Nishiumi and Kim, 2004). Divergence among the island forms was substantial, averaging 4.1% among species, compared to 5.1% between the island forms and *C. diphone*, and 0.2% polymorphism within the island forms with multiple sequences available.

DISCUSSION

Morphometric analyses of *Cettia* species and individuals indicate that the birds from Bougainville are distinctive (tables 1, 3, and 4; figs. 3 and 4), most notably in having large overall size (including substantially higher body mass, table 1), a relatively short tail, and longer more robust tarsi. These traits, as well as a relatively rounded wing shape suggest an adaptive shift toward a more terrestrial habit in the Bougainville birds. Molecular data agree with morphology in establishing that these birds are at least as distinct from the other island forms of *Cettia* as those forms are from each other, and that this differentiation far exceeds intraspecific variation, to the extent it has been sampled. These data, in combination with the geographic isolation of the population due to its restricted distribution in montane regions of Bougainville, strongly support recognition of a new species, *Cettia haddeni*.

As noted above, few phylogenetic analyses of terrestrial vertebrates endemic to the southwest Pacific have been performed. Recently, however, analysis of phylogenetic relationships among monarch flycatchers (tribe Monarchini)—a group with much wider distribution than *Cettia*, throughout the south Pacific—has provided novel insights into the history of avian diversification in this region (Filardi and Moyle, 2005). This study strongly supports the importance of the Pacific as

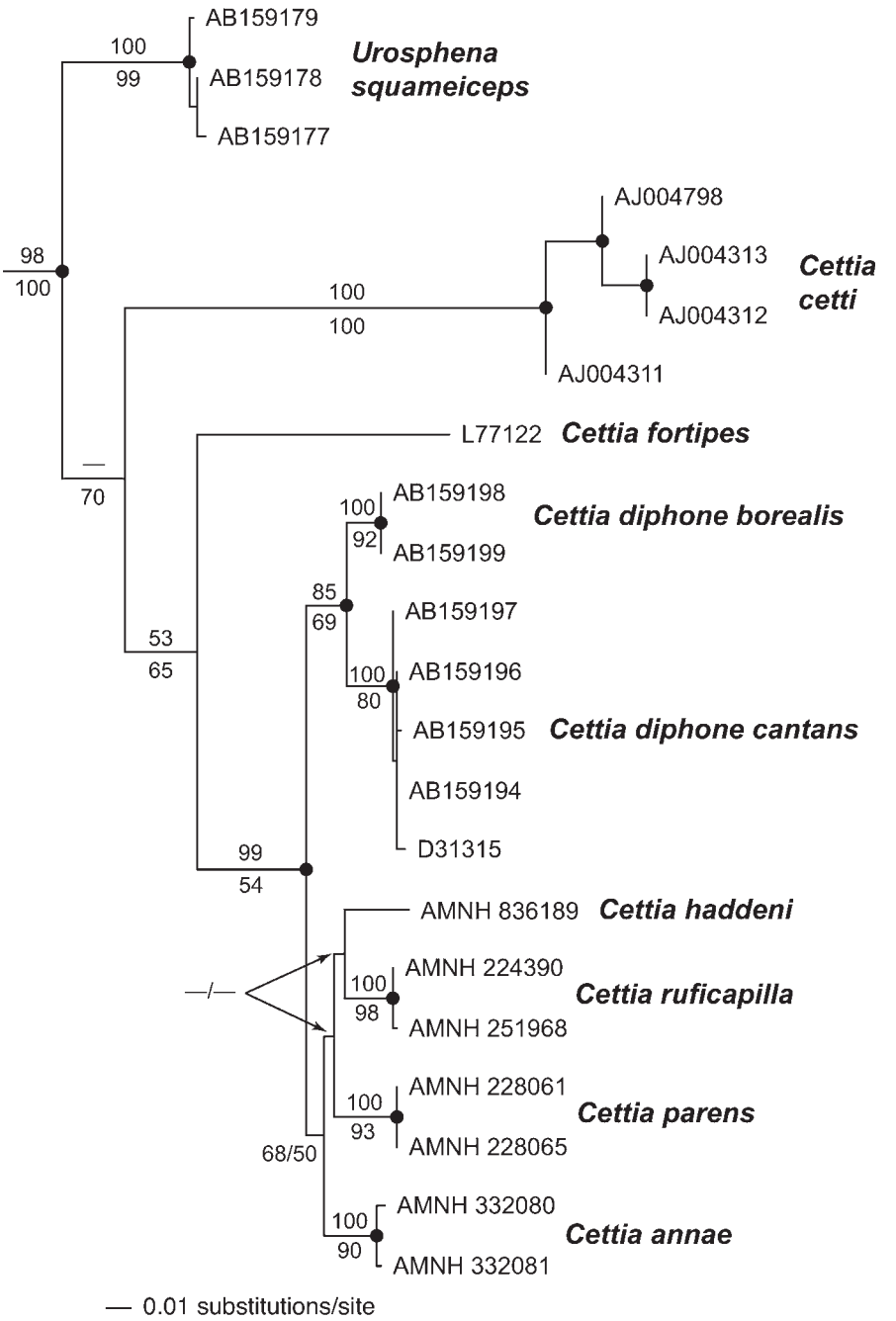

Fig. 7. Maximum likelihood tree ($-\ln L = 2615.7$, $\pi_A = 0.28$, $\pi_C = 0.38$, $\pi_G = 0.11$, $\pi_T = 0.22$, $\kappa = 11.3$, $\alpha = 0.16$) of cytochrome *b* sequences from *Cettia* and *Urosphena*. The tree was rooted using *Psaltriparus minimus* (GenBank accession AF074597) and *Aegithalos caudatus* (accession AB159169) as outgroups. Numbers at each terminal are GenBank accessions, numbers above and below each branch are bootstrap support (parsimony/likelihood, 1000 and 200 replicates respectively), and filled circles at selected nodes indicate estimated Bayesian posterior probabilities ≥ 0.95.

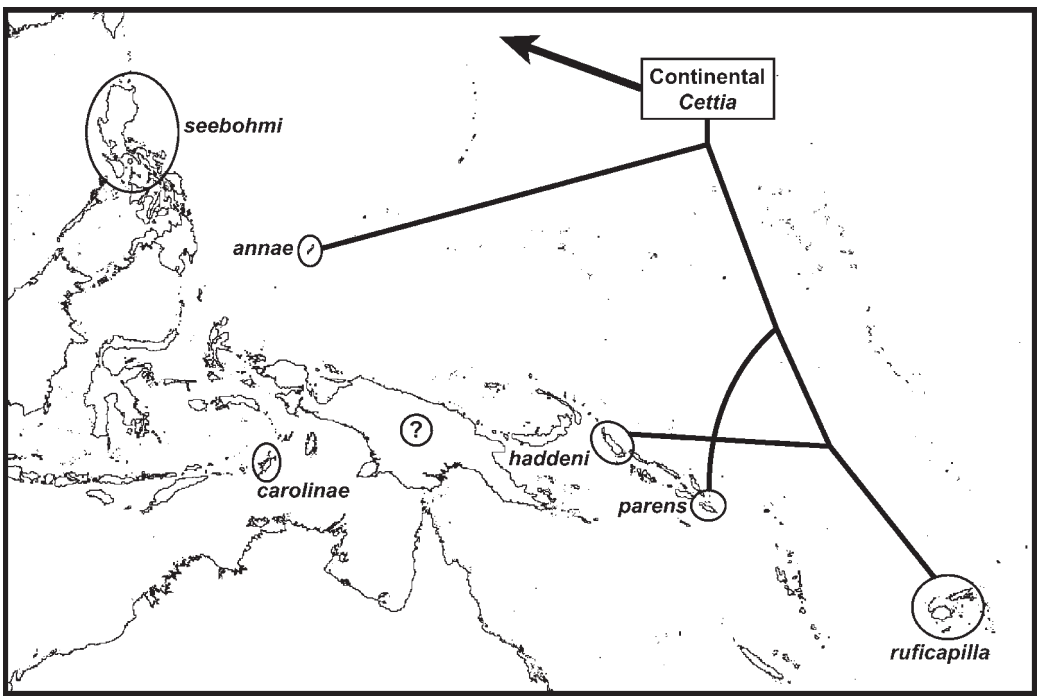

Fig. 8. Distribution of *Cettia haddeni* and relatives in the southwest Pacific. The distribution of sampled species and the putative close relatives *C. carolinae* and *C. seebohmi* are shown by circled islands or island groups, and the maximum likelihood relationships among sampled forms are superimposed. Although resolved, support for relationships among the island forms is poor (fig. 7).

a center of differentiation for the monarchs, recovering monophyly of a wide array of differentiated Pacific forms, nested within the single traditional genus *Monarcha*. Importantly, this study also finds evidence of dispersal from the south Pacific back into continental areas, suggesting that this region has served not only as a downstream ''sink'' for continental forms, but as an active source of new colonists. At present, we find no evidence for similar patterns in the relatively species-poor genus *Cettia*, which appears to conform more closely to the traditionally conceived model of stepwise dispersal from a continental source (fig. 8; Mayr and Diamond, 2001).

In their paper on the distribution and relationships of *Cettia*, Orenstein and Pratt (1983) suggested that the southwest Pacific *Cettia* were derived from a widespread colonizing ancestor that subsequently differentiated into locally adapted forms. They argued that ''gaps in the present distribution of *Cettia* in the southwest Pacific cannot be entirely explained by accidents of dispersal or unsuitability of habitat on the unoccupied islands,'' (p. 195) and attributed the patchy distribution of this genus at least in part to diffuse competition (Mayr and Diamond, 1976, and Diamond and Marshall, 1977) with other birds, such as the Australasian *Gerygone* ''warblers''. Interestingly, they also suggested that the patchy distribution of the genus, and the highland distribution of some of its forms (e.g., *C. parens*, *C. ruficapilla funebris*) might be due to competitive exclusion by more recently dispersed southwest Pacific taxa, invoking the taxon cycle (Wilson, 1961; Ricklefs and Cox, 1972, 1978; Mayr and Diamond, 2001; Ricklefs and Bermingham, 2001).

The data reported here offer one test of this explanation for the distribution of Pacific *Cettia* (fig. 8). Namely, their hypothesis requires that these forms be derived from a single common ancestor, rather than being

independently derived from one or more mainland forms. For instance, long distance migrants such as the New World *Buteo swainsonii* appear to have been the source for establishment of multiple endemic island forms (*B. galapagoensis* and possibly *B. solitarius*; Riesing et al., 2003), and a similar mechanism could be invoked for migratory continental *Cettia* (specifically, *C. diphone*). Analyses of the cytochrome *b* data unequivocally support monophyly of the sampled island forms, regardless of optimality criterion (fig. 7). However, support for this relationship varies significantly among methods, and should not be considered conclusive. Interestingly, relationships among these forms are not well supported (fig. 7), consistent with rapid differentiation from a widespread ancestor. These results are consistent with the contention that the southwest Pacific species are in the latter stages of a taxon cycle. However, it is difficult to argue that this result must be the consequence of this controversial process. For instance, it is well known that human-mediated extinction has had a profound effect on the composition of South Pacific avifaunas (Steadman 1995), and this could have contributed to the apparently relict distribution of *Cettia*. In particular, Steadman (1993, 1995) has recorded the prehistoric extinction or extirpation of *Cettia* (a form he describes as closely related to or conspecific with *Cettia ruficapilla* from Fiji) from 'Eua in Tonga. Likewise, the effects of recent (i.e., Pliocene/Pleistocene) climate change on habitat structure and distribution in the South Pacific are only now being documented (Hope et al. 2004), and the impact of such changes on the avifauna is not clear. As is being done for many Caribbean groups (Ricklefs and Bermingham, 1999, 2001), more detailed analysis of the ecology of these species, their interactions with other island forms, and the relationships of those forms should be performed. In addition, we have yet to obtain molecular data for two other forms hypothesized to compose part of this group (*C. seebohmi* and *C. carolinae*). The relationships of these forms, as well as those of more distinctive endemic Pacific warblers (e.g., *Trichocichla*, *Ortygocichla*), should be a focus of future work.

The recent discovery of *Cettia haddeni*, as well as the similarly recent discovery of *C. carolinae*, in combination with the evidence that at least some species of island *Cettia* are descended from a more widespread common ancestor, suggests that additional forms await discovery in poorly known areas of the southwest Pacific, especially on large high islands such as Guadalcanal. Because earlier surveys, including those of the Whitney South Sea Expedition, spent relatively short periods at high altitudes and operated without mist nets, the future discovery of secretive forest birds such as *Cettia* is a distinct possibility. However, this begs the question of why *Cettia* is absent from mainland New Guinea. It remains an open question whether this absence is an artifact of sampling or, possibly, evidence that the *Cettia* clade in the Pacific is an island lineage unable to penetrate the rich New Guinea biota.

ACKNOWLEDGMENTS

We are pleased to name this new species for Don Hadden. In addition to producing his two volumes on the birds of Bougainville and the North Solomons (1981, 2004), illustrated largely with his own spectacular field photographs, he has discovered two other new forms on Bougainville: *Cichlornis llaneae* Hadden, 1983, now *Megalurulus whitneyi llaneae* (see Dickinson, 2003: 587), and *Zoothera talaseae atrigena* Ripley and Hadden, 1982.

We are most grateful to Andrew Mack for preparing the specimens; to John Anderton for his illustration of *C. haddeni* and its relatives; to R. Dekker and H. van Grouw for measuring specimens of *Cettia carolinae* at the National Museum of Natural History, Leiden; to Paul Sweet for measuring specimens of *Cettia parens* at the Natural History Museum, Tring, United Kingdom; to Katrina Cook for sending digital photos of those specimens to us; and to Craig Chesek, James Dean, Llane Hadden, Shannon Kenney, A. Townsend Peterson, Mark Robbins, and E. Scholes for their assistance in various important ways. Bruce Beehler, Joel Cracraft, Jared Diamond, Christopher Filardi, and Richard

Schodde read earlier drafts of this paper and made helpful comments. FKB thanks George Weiblen (University of Minnesota) for graciously hosting the museum skin extraction and PCR work.

REFERENCES

Barker, F.K. 2004. Monophyly and relationships of wrens (Aves: Troglodytidae): a congruence analysis of heterogeneous mitochondrial and nuclear DNA sequence data. Molecular Phylogenetics and Evolution 32(2): 486–504.

Barker, F.K., G.F. Barrowclough, and J.G. Groth. 2002. A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. Proceedings of the Royal Society of London, B 269: 295–308.

Barker, F.K., A. Cibois, P.A. Schikler, J. Feinstein, and J. Cracraft. 2004. Phylogeny and diversification of the largest avian radiation. Proceedings of the National Academy of Sciences 101(30): 11040–11045.

Beehler, B. 1983. Thoughts on an ornithological mystery from Bougainville Island, Papua New Guinea. Emu 83: 114–115.

Beresford, P., F.K. Barker, P.G. Ryan, and T.M. Crowe. 2005. African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary 'enigmas.' Proceedings of the Royal Society of London, B 272: 849–858.

Cockburn, A. 2003. Cooperative breeding in passerines: does sociality inhibit speciation? Proceedings of the Royal Society of London B 270: 2207–2214.

Delacour, J. 1942. The bush-warblers of the Genera *Cettia* and *Bradypterus*, with notes on allied genera and species. Ibis, ser. 14, 6: 509–519.

Diamond, J. 1975. Distributional ecology and habits of some Bougainville birds (Solomon Islands). Condor 77: 14–23.

Diamond, J.M., and A.G. Marshall. 1977. Niche shifts in New Hebridean birds. Emu 77: 61–72.

Dickinson, E.C. (editor). 2003. The Howard & Moore complete checklist of the birds of the world, 3rd ed. London: Christopher Helm, 1039 pp.

Dunning, J.B., Jr. 1993. CRC handbook of avian body masses. Boca Raton, FL: CRC Press, 371 pp.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783–791.

Filardi, C.E., and R.G. Moyle. 2005. Single origin of a pan-Pacific bird group and upstream colonization of Australasia. Nature 438: 216–219.

Filardi, C.E., and C.E. Smith. 2005. Molecular phylogenetics of monarch flycatchers (genus *Monarcha*) with emphasis on Solomon Island endemics. Molecular Phylogenetics and Evolution 37: 776–788.

Groth, J.G. 2000. Molecular evidence for the systematic position of *Urocynchramus pylzowi*. Auk 117: 787–791.

Groth, J.G., and G.F. Barrowclough. 1999. Basal divergences in birds and the phylogenetic utility of the nuclear RAG-1 gene. Molecular Phylogenetics and Evolution 12: 115–123.

Hadden, D. 1981. Birds of the North Solomons. Wau Ecology Institute Handbook No. 8.Wau, Papua New Guinea: Wau Ecology Institute, 107 pp.

Hadden, D. 2004. Birds and bird lore of Bougainville and the North Solomons. Alderley, Queensland: Dove Publications, 312 pp.

Hasegawa, M., H. Kishino, and T. Yano. 1985. Dating the human-ape splitting by a molecular clock of mitochondrial DNA. Journal of Molecular Evolution 22: 160–174.

Hope, G., A.P. Kershaw, S. van der Kaars, S. Xiangjun, P.-M. Liew, L.E. Heusser, H. Takahara, M. McGlone, N. Miyoshi, and P.T. Moss. 2004. History of vegetation and habitat change in the Austral-Asian region. Quaternary International 118–119: 103–126.

Jansa, S.A., F.K. Barker, and L.R. Heaney. In press. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. Systematic Biology.

Lovette, I.J., E. Bermingham, and R.E. Ricklefs. 2002. Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. Proceedings of the Royal Society of London B 269: 37–42.

MacArthur, R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press.

Mayr, E. 1935. Birds collected during the Whitney South Sea Expedition. XXX. Descriptions of twenty-five new species and subspecies. American Museum Novitates 820: 1–6.

Mayr, E. 1936. Birds collected during the Whitney South Sea Expedition. XXXI. Descriptions of twenty-five species and subspecies. American Museum Novitates 828: 1–19.

Mayr, E., and J.M. Diamond. 1976. Birds on islands in the sky: origin of the montane avifauna of northern Melanesia. Proceedings of the National Academy of Sciences 73: 1765–1769.

Mayr, E., and J. Diamond. 2001. The birds of northern Melanesia: speciation, ecology and biogeography. Oxford: Oxford University Press, 492 pp.

Minin, V., Z. Abdo, P. Joyce, and J. Sullivan. 2003. Performance-based selection of likelihood models for phylogeny estimation. Systematic Biology 52: 674–683.

Nishiumi, I., and C.H. Kim. 2004. Little genetic differences between Korean and Japanese populations in songbirds. National Science Museum Monographs (Tokyo) 24: 279–286.

Orenstein, R.I., and H.D. Pratt. 1983. The relationships and evolution of the southwest Pacific warbler genera *Vitia* and *Psamathia* (Sylviinae). Wilson Bulletin 95: 184–198.

Paxinos, E.E., H.F. James, S.L. Olson, M.D. Sorenson, J. Jackson, and R.C. Fleischer. 2002. mtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada goose (*Branta canadensis*). Proceedings of the National Academy of Sciences 99: 1399–1404.

R Development Core Team. 2004, R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ramsay, E.P. 1876. Characters of a new genus and species of Passerine bird, from the Fiji Islands, proposed to be called *Vitia*. Proceedings of the Linnean Society of New South Wales 1: 41–42.

Ricklefs, R.E., and E. Bermingham. 1999. Taxon cycles in the Lesser Antillean avifauna. Ostrich 70: 49–59.

Ricklefs, R.E., and E. Bermingham. 2001. Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. Science 294: 1522–1525.

Ricklefs, R.E., and G.C. Cox. 1972. Taxon cycles in the West Indian avifauna. American Naturalist 106: 195–219.

Ricklefs, R.E., and G.C. Cox. 1978. Stage of taxon cycle, habitat distribution, and population density in the avifauna of the West Indies. American Naturalist 112: 875–895.

Riesing, M.J., L. Kruckenhauser, A. Gamauf, and E. Haring. 2003. Molecular phylogeny of the genus Buteo (Aves: Accipitridae) based on mitochondrial marker sequences. Molecular Phylogenetics and Evolution 27: 328–342.

Rozendaal, F.G. 1987. Description of a new species of bush warbler of the genus *Cettia* Bonaparte, 1834 (Aves: Sylviidae) from Yamdena, Tanimbar Islands, Indonesia. Zoologische Mededelingen 61: 177–202.

Sibley, C.G., and B.L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. New Haven: Yale University Press, 1111 pp.

Slikas, B., I.B. Jones, S.R. Derrickson, and R.C. Fleischer. 2000. Phylogenetic relationships of Micronesian white-eyes based on mitochondrial sequence data. Auk 117: 355–365.

Steadman, D.W. 1993. Biogeography of Tongan birds before and after human impact. Proceedings of the National Academy of Sciences, USA 90: 818–822.

Steadman, D.W. 1995. Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. Science 267: 1123–1131.

Swofford, D.L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), v4.0b10. Sunderland, MA: Sinauer.

Watson, G.E., M.A. Traylor, Jr., and E. Mayr. 1986. Family Sylviidae. *In* E. Mayr and G.W. Cottrell (editors), Check-list of birds of the world 11: 3–294. Cambridge, MA: Museum of Comparative Zoology, 638 pp.

Wells, D.R. 1982. Biological species limits in the *Cettia fortipes* complex. Bulletin of the British Ornithologists' Club 102: 57–62.

Wilson, E.O. 1961. The nature of the taxon cycle in the Melanesian ant fauna. American Naturalist 95: 169–193.

Zerega, N.J.C., D. Ragone, and T.J. Motley. 2004. Complex origins of breadfruit (*Artocarpus altilis*, Moraceae): Implications for human migrations in Oceania. American Journal of Botany 91: 760–766.

APPENDIX 1
Specimens Examined

Daggers indicate holotypes; gene symbols in brackets indicate that sequence was obtained from the corresponding individual. All specimens are housed in the collections of the American Museum of Natural History (AMNH), or the Natural History Museum, Tring, United Kingdom (BMNH).

Cettia haddeni

AMNH 833347, 835234†[RAG1] 836189 [mtcyb]

Cettia annae

AMNH 213233, 332076, 332078, 332079, 332080[mtcyb], 332081[mtcyb], 332082, 332083, 332084, 332085, 332086, 332087, 332088.

Cettia parens

AMNH 228061[mtcyb], 228063†, 228064, 228065[mtcyb], 228066. BMNH 1959.21.559, 1959.21.560.

Cettia ruficapilla ruficapilla

AMNH 224388, 251946, 251947, 251948, 251949, 251950, 251951, 251952, 251953, 251954, 251955, 251956, 251958, 251959, 251960, 251961, 251963, 252014.

Cettia ruficapilla badiceps

AMNH 251986, 251987, 251989, 251990, 251992, 251994, 251995, 251996, 251997, 251998, 251999, 252003, 252004, 252005, 252006, 252007, 252009, 588948.

Cettia ruficapilla castaneoptera

AMNH 251011†, 251973, 251976, 251977, 251978, 251979, 251980, 251981, 251982, 251983, 251984, 252010, 252012, 252013, 252015.

Cettia ruficapilla funebris

AMNH 224390[mtcyb], 251965, 251966, 251967, 251968[mtcyb], 251969, 251970†, 251971, 251972, 252016, 252019.