GENETIC AND MORPHOLOGICAL DIFFERENTIATION AND PHYLOGENY IN THE AUSTRALO-PAPUAN SCRUBWRENS (*SERICORNIS*, ACANTHIZIDAE)

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ABSTRACT.—The interrelationships of 13 of the 14 species currently recognized in the Australo-Papuan oscinine scrubwrens, *Sericornis*, were assessed by protein electrophoresis, screening 44 presumptive loci. Consensus among analyses indicated that *Sericornis* comprises two primary lineages of hitherto unassociated species: *S. beccarii* with *S. magnirostris*, *S. nouhuysi* and the *S. perspicillatus* group; and *S. papuensis* and *S. keri* with *S. spilodera* and the *S. frontalis* group. Both lineages are shared by Australia and New Guinea. Patterns of latitudinal and altitudinal allopatry and sequences of introgressive intergradation are concordant with these groupings, but many features of external morphology are not. Apparent homologies in face, wing and tail markings, used formerly as the principal criteria for grouping species, are particularly at variance and are interpreted either as coinherited ancestral traits or homoplasies.

Distribution patterns suggest that both primary lineages were first split vicariantly between Australia and New Guinea, and then radiated independently on each land mass under the influence of paleoclimatic change. Dispersal between Australia and New Guinea is indicated only in the *magnirostris* sublineage and is either very recent or just broken. *Received 13 April 1987, accepted 18 April 1988.*

WITH thornbills (*Acanthiza*) and gerygones (*Gerygone*), scrubwrens of the genus *Sericornis* Gould form one of three major assemblages of species within the Australo-Papuan family Acanthizidae. In its strictest sense (RAOU Checklist Committee 1926; Mayr 1986), the group comprises small, brown, thin-billed insectivores that live sedentarily in pairs or small communal groups in the middle- and understrata of subtropical and temperate forests in montane New Guinea and coastal Australia (Figs. 1 and 2).

General agreement on the composition and relationships of *Sericornis* was reached in the revisions of Mayr (1937), Mayr and Rand (1937), Mayr and Serventy (1938), and Keast (1978a). Their concepts of the genus were maintained in essence by Mayr (1986), who accepted 14 species. Six are endemic to New Guinea, seven endemic to Australia and one (*S. beccarii*) is shared (Figs. 1 and 2). Schodde (1975) expanded *Sericornis* to include 5 allied mono- and di-typic generic groups from drier sclerophyllous habitats in Australia (cf. Schodde and McKean 1976). Although this reorganization was controversial, it has not been subjected to testing other than by brief and conflicting comparisons of morphological and behavioral traits (Keast 1978a, b; Schodde 1981).

We studied the relationships among the species of *Sericornis* sensu Mayr (1986) as determined by allozymic variation at 44 presumptive loci. The monophyly of this group, corroborated by DNA-DNA hybridization (Sibley and Ahlquist 1985), is not in question. Material of all but one species was examined, but we present data for only 11 of the 14. Of the 3 excluded or missing, the Tasmanian Scrubtit (*S. magnus*) was found to be unrelated to the core lineages of *Sericornis* (Christidis and Schodde in prep.); the Spotted Scrubwren (*S. maculatus*) is not accepted here as a species because it intergrades with the White-browed Scrubwren (*S. frontalis*; cf. Condon 1951) and shows no significant allozymic differentiation from it (Christidis and Schodde in press); and tissues of the Vogelkop Scrubwren (*Sericornis rufescens*) were unavailable.

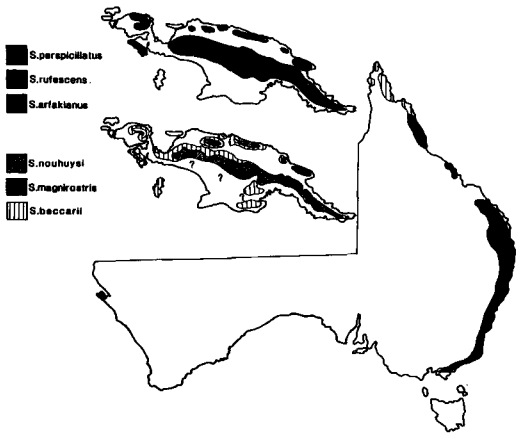

Fig. 1. Geographical distribution of taxa of the *Sericornis magnirostris* primary lineage.

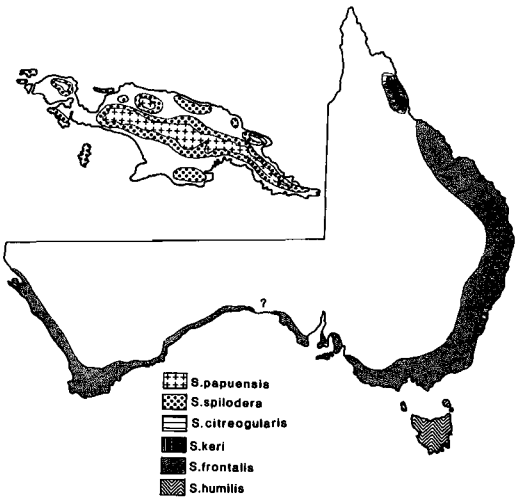

Fig. 2. Geographical distribution of taxa of the *Sericornis frontalis* primary lineage.

Methods

Liver, breast muscle and heart tissues, stored in liquid nitrogen, were examined from 127 individuals of 11 species, together with those of 6 geographically spread individuals of the Brown Thornbill (*Acanthiza pusilla*). Geographically isolated subspecies of the Large-billed Scrubwren (*S. m. magnirostris, S. m. viridior*) and Yellow-throated Scrubwren (*S. c. citreogularis, S. c. cairnsi*) were included to provide a frame for differentiation across all taxonomic levels. The samples and their collection localities are itemized in Table 1.

Individuals were screened electrophoretically for 37 enzyme systems representing 44 presumptive loci (Christidis and Schodde in press). Initially, representatives of 5 diverse acanthizid genera, including *Sericornis*, were analyzed to determine optimal conditions for each enzyme system. It allowed us to maximize resolution of the allelic bands and so detect most of the variation in our subsequent screening of *Sericornis*. Genetic distances between taxa were estimated by the measures of Nei (1978) and Rogers (1972), from which UPGMA phenograms (Sneath and Sokal 1973) and distance-Wagner trees (Farris 1972) were constructed. A further analysis of fixed (nonpolymorphic) differences among electromorphs was performed by the cladistic method of Hennig (1966). Highly polymorphic loci and low frequency allelomorphs shared across lineages were culled, to reduce confusion from unclarified plesiomorphic states and convergence (cf. Patton and Avise 1983). Accordingly *Gpdh, Est-1, Est-3*, and the low frequency allelomorphs at *Pep L-Pro* and *Acon-2* were excluded. The rationale and modes of these procedures were outlined in Christidis (1987).

Acanthiza pusilla was used to root the Wagner tree and as the out-group for cladistic analysis (Patton and Avise 1983) because it is a member of the genus considered closest to core sericornine lineages (Meise 1931, Mayr 1937), but falls outside the sericornine assemblage. In-group comparisons were also made within the sericornine assemblage of Schodde (1975), but because they did not affect the monophyly of *Sericornis* as defined here, they are reported elsewhere (Christidis and Schodde in prep.).

Morphometric and qualitative morphological data for comparison were collated from specimens in the Australian National Wildlife Collection, Canberra (ANWC), augmented with material from the Queensland Museum, Brisbane (QM), Australian Museum, Sydney (AM), and, for *S. rufescens*, American Museum of Natural History, New York (AMNH). Information on altitudinal distribution in New Guinea was drawn from specimen records in ANWC and AM, and from banding records in the Australian Bird Banding Scheme, Australian National Parks and Wildlife Service, Canberra.

Results

Allelic frequencies, heterozygosities, and genetic distances.—Of the 44 loci screened, 12 were monomorphic in all species (E.C. numbers in parentheses): *Got-2* (2.6.1.1), *Idh-2* (1.1.1.42), *Tpi* (5.3.1.1), *Sod* (1.15.1.1), *Fum* (4.2.1.2), *Ak* (2.7.4.3), *Ck-3* (2.7.3.2), *Gdh* (1.4.1.3), *Gpt-2* (2.6.12), *Acon-1* (4.2.1.3), *Mdh-1* and *Mdh-2* (1.1.1.37). Allelic frequencies at the other 32 varying loci are given in Table 2, excluding those of 5% or less. For the species of *Sericornis*, mean heterozygosity calculated by the direct count estimate (Nei 1975) was 0.035, and the average proportion of polymorphic loci 18.4% (Table 2). The mean genetic

TABLE 1. Localities and sample sizes (*n*) of species examined. Voucher specimens in Australian National Wildlife Collection, CSIRO, Canberra; and in Australian Museum, Sydney.

	Symbol[a]	Locality	*n*
Sericornis perspicillatus	SPE	Efogi, Papua New Guinea	13
S. arfakianus	SAR	Karimui and Tari, Papua New Guinea	4
S. magnirostris magnirostris	SMA	Kangaroo Valley, New South Wales	2
		Cambridge Plateau, New South Wales	6
		Conondale Range, Queensland	3
		Dawes Range, Queensland	1
		Clarke Range, Queensland	2
S. m. viridior	SMV	Atherton, Queensland	4
		Helenvale district, Queensland	1
S. beccarii	SBE	Silver Plains, Cape York Peninsula, Queensland	3
		McIlwraith Range, Queensland	6
		Tari district, Papua New Guinea	3
S. nouhuysi	SNO	Efogi, Papua New Guinea	10
S. papuensis	SPA	Efogi, Papua New Guinea	3
S. spilodera	SSP	Tari district, Papua New Guinea	2
S. citreogularis citreogularis	SCI	Kangaroo Valley, New South Wales	2
		Cambridge Plateau, New South Wales	6
		Conondale Range, Queensland	3
S. c. cairnsi	SCC	Atherton, Queensland	6
S. keri	SKE	Atherton, Queensland	2
		Mt. Lewis, Queensland	4
S. humilis	SHU	Tasmania[b]	6
S. frontalis	SFR	South-eastern Australia[b]	28
Acanthiza pusilla	APU	Eastern Australia, Tasmania	6

[a] Symbols used in Figs. 4 and 5.

[b] A complete listing of localities is given in Christidis and Schodde (in press).

distance (Nei 1978) among all 11 species was 0.197 (SD 0.068, SE 0.001); and that between them and *Acanthiza pusilla* was 0.345 (SD 0.054, SE 0.005), indicating substantial differentiation. In comparison, the average interspecific and intergeneric distances in Parulidae, Emberizidae, Muscicapidae and Icteridae were 0.10 and 0.26 respectively (Avise and Aquadro 1982).

As expected, genetic distances were greater among species than subspecies (Table 3), but several values were contradictory. Nei's (1978) distances were only 0.046 between the allospecific Brown and White-browed scrubwrens (*S. humilis, S. frontalis*), and were 0.02–0.03 among the Australian Large-billed Scrubwren (*S. m. magnirostris*), morphologically dissimilar Tropical Scrubwren (*S. beccarii*), and New Guinean Large Scrubwren (*S. nouhuysi*). In contrast, the pairs of subspecies of the Large-billed and Yellow-throated (*S. citreogularis*) scrubwrens, which are almost identical in appearance (Mayr 1937), differed by distances of 0.032 and 0.036. Compared to measures within other avian species (Corbin 1977, Avise and Aquadro 1982), these values were rather high and equivalent to protein differentiation at species level in parulid warblers (Avise et al. 1980).

Genetic differentiation.—The UPGMA phenograms derived from both Rogers' (1972) and Nei's (1978) distances were identical and separate *Sericornis* into 5 groups of species, all of which are closer to one another than to *Acanthiza pusilla* (Fig. 3). The first group comprises the Pale-billed Scrubwren (*S. spilodera*) and Papuan Scrubwren (*S. papuensis*), between which the distance was greater than any among the other 4 groups. Thus these 2 species were clustered because of their distinctiveness from remaining taxa. The other 4 groups were: *S. citreogularis*; New Guinean *S. perspicillatus-S. arfakianus*; *S. magnirostris-S. beccarii-S. nouhuysi*; and Australian *S. frontalis* and its allies. The last assemblage comprised *S. frontalis*, the Tasmanian *S. humilis*, and the Atherton Scrubwren (*S. keri*), and was closest to the *magnirostris* cluster. In the *magnirostris* group, *S. m. viridior* of northeast Queensland was the most distant member allozymically (see above).

Phylogenetic clustering.—Derived from values for Rogers' (1972) genetic distance, the distance-Wagner tree (Fig. 4) is rooted by *Acanthiza pusilla*. Unlike the UPGMA procedure, the Wagner algorithm does not assume a constant rate of protein evolution, and this is reflected

in the differing branch lengths among taxa (Figs. 3 and 4). It implies, for example, that *S. citreogularis cairnsi* in northeast Queensland has undergone a 2.5-fold faster change in proteins since divergence than its allosubspecies, *S. c. citreogularis*, in central east Australia. Despite this basic difference, the Wagner network identified the same 5 clusters of species as in the phenetic analysis. One major discrepancy was the position of the *S. frontalis* assemblage which was aligned most closely with *S. citreogularis*, leaving the Buff-faced Scrubwren (*S. perspicillatus*) and Olive Scrubwren (*S. arfakianus*) as the sister-group of the *magnirostris* assemblage.

Cladistic analysis distinguished further between ancestral and derived states among the allozymes (Fig. 5). Plesiomorphies were identified from comparison with *Acanthiza pusilla*, and the synapomorphies defining each clade are listed in Table 4. They corroborated once more the 5 terminal clusters identified by both UPGMA and distance-Wagner analyses and split them into two primary lineages. On one side of the split were the *S. perspicillatus* and *S. magnirostris* groups; the remainder were on the other. A close connection between the *perspicillatus* and *magnirostris* groups was supported by the Wagner tree (Fig. 4), and, to a lesser extent, by the UPGMA phenogram (Fig. 3). Moreover, the synapomorphy at locus *Gda*(a), which defined this clade, did not occur in any of the other species which were all fixed for the ancestral state, indicating that convergence at this locus is unlikely.

Members of the other primary lineage (comprising *S. citreogularis*, the *frontalis* group and *S. papuensis-S. spilodera*) were not so close, as indicated in the UPGMA phenogram and distance-Wagner tree (Figs. 3 and 4). Although their clade is also defined by a single synapomorphy, *6 Pgd*(c), the allele was present in *S. nouhuysi*, together with state (d). This may reflect convergence. Convergence may explain much of the observed variation at this locus in *Sericornis* (Table 2), but it does not strengthen the hypothesis of monophyly of the group.

Discussion

Concordance of lineages.—The 3 different analyses of electrophoretic data define interspecific alliances that are largely concordant. *Sericornis* comprises 5 clear-cut terminal clusters of species. There is some discord, however, in the links among the 5 clusters. Here the alignment of *S. magnirostris* with the *S. frontalis* group in the UPGMA phenogram was distorted because plesiomorphies linking them were not eliminated by out-group comparison. The alternative arrangement corroborated by both distance-Wagner and cladistic analysis is the more likely phylogeny. It indicates two primary lineages in the genus. In one, the close-knit *magnirostris* lineage, the *S. perspicillatus* and *S. magnirostris* groups form two sublineages. The other, the *frontalis* lineage, is more diffuse. It includes *S. keri* as a close ally of *S. frontalis*, and *S. citreogularis* and *S. papuensis* group as more divergent sublineages.

Plumage patterns, hitherto the principal criteria for grouping the species taxonomically, are at variance with this phylogeny. By consensus, they align the species in two different clusters (Mayr 1937, 1986; Galbraith and Parker 1969; Parker 1970; Keast 1978a; and Diamond 1985). In one, sharing plain plumage with red iris and unbarred or faintly barred tail, *S. papuensis*, *S. spilodera*, and *S. keri* are grouped with the *perspicillatus* and *magnirostris* sublineages. In the other, with seemingly homologous white marks on face and wing coverts and sexual dimorphism in the duskiness of the lores, *S. beccarii* is aligned with the *S. frontalis* group and *S. citreogularis*. There are, nevertheless, anomalies consistent with the protein phylogeny. *S. beccarii* has the red iris and plain tail of the *magnirostris* sublineage; and *S. spilodera* shares dusky breast spotting with some members of the *S. frontalis* superspecies. The plain plumage of other species, moreover, may mask relationships (Galbraith and Parker 1969). It is tempting to dismiss the morphological clusters as unsound, based on undiscriminated plesiomorphies and homoplasies of unknown genetic background and adaptive value. Because protein phylogenies may be distorted by convergences (Stewart et al. 1987), we examined additional evidence from geographical and ecological distribution and genetic intergradation.

Distribution and foraging niche.—Patterns of allopatry and sympatry, associating taxa inversely to their affinities, separate *S. papuensis* and *S. spilodera* from the *perspicillatus* and *magnirostris* groups, align *S. beccarii* with *S. nouhuysi*, and are consistent with links between *S. keri* and the *frontalis* sublineages, and between *S. beccarii* and the *magnirostris* sublineage.

In New Guinea, species that coexist—up to

TABLE 2. Frequencies of electromorphs at the 32 variable loci, proportion of polymorphic loci[1] (P), and mean heterozygosity ($\bar{H}$) in all species examined. Alphabetic designations of alleles refer to their anodal mobilities, where A > B > C. Unless indicated otherwise, alleles are present at a frequency of 100%.

	Locus (E.C. no.)					
Species	Pep L-A (3.4.11)	GPDH (1.1.1.8)	Pep L-PrO (3.4.11)	GOT-1 (2.6.1.1)	Pep L-G-G (3.4.11)	6PGD (1.1.1.44)
Sericornis frontalis	B(0.96)	C(0.06) D(0.83) G(0.10)	C	A	C(0.89) D(0.06)	C(0.98)
S. humilis	B	D	C	A	C(0.92) D(0.08)	A(0.17) B(0.08) C(0.75)
S. keri	A(0.14) B(0.86)	D(0.50) G(0.50)	C	A	B	B(0.07) C(0.93)
S. m. magnirostris	B	D(0.71) H(0.14)	C	A(0.93) B(0.07)	A(0.18) B(0.11) C(0.71)	B
S. m. viridior	B	D(0.20) G(0.60) H(0.10) I(0.10)	A(0.40) C(0.60)	A	B(0.90) C(0.10)	B
S. beccarii	A(0.13) B(0.87)	G	C	A	B(0.33) C(0.67)	B
S. c. citreogularis	A(0.36) B(0.64)	G	A(0.18) C(0.82)	A	A(0.32) B(0.14) C(0.50)	C
S. c. cairnsi	B	G	A(0.17) C(0.83)	A	A(0.17) B(0.25) C(0.58)	C
S. nouhuysi	B	D(0.85) G(0.15)	C(0.96)	A	B(0.81 C(0.19)	B(0.46) C(0.54)
S. perspicillatus	B	A(0.50) G(0.50)	C(0.54) D(0.46)	A	B(0.85) C(0.15)	D
S. papuensis	B	A(0.17) H(0.83)	C	A	A(0.17) B(0.83)	C
S. spilodera	B	A(0.25) H(0.75)	C	C	B	C
S. arfakianus	B(0.88) C(0.12)	A	C(0.88) E(0.12)	A	C	D
Acanthiza pusilla	B	E(0.08) H(0.17) I(0.75)	C	A	A(0.08) B(0.84) C(0.08)	B

three at any one site—are members of different protein lineages and forage in separate forest strata. Those that belong to the same or sister sublineage glean in the same strata and replace one another altitudinally (Fig. 6, Table 5, cf. Fig. 5). Diamond (1969, 1972, 1985) aligned *S. papuensis* and *S. spilodera* with the *perspicillatus* group because he recorded them in a successive altitudinal sequence, but our data from six discrete mountain systems show a different pattern (Fig. 6). Only members within the *perspicillatus* and *papuensis* groups were consistently allopatric. Between *S. papuensis* and *S. perspicillatus*, as between *S. spilodera* and *S. arfakianus*, there was too much altitudinal overlap to be explained by competitive exclusion between closely related congeners. The first pair appeared to be partitioned at least partly by feeding zone (Beehler et al. 1986). In the second, *S. spilodera*, larger in size and with a longer and heavier bill than *S. arfakianus* (Table 5), may also forage differently (cf. Schoener 1965, Willson 1971).

Members of the third group in New Guinea, *S. beccarii* and *S. nouhuysi*, also replace one another

TABLE 2. Continued.

	Locus (E.C. no.)							
Species	ENOL (4.2.1.11)	GA3PD (1.2.1.12)	PK (2.7.1.40)	GPT-2 (2.6.1.12)	CK-4 (2.7.3.2)	GP1 (5.3.1.9)	MP1 (5.3.1.8)	EST-1 (3.1.1.1)
S. frontalis	B	B	C(0.96)	C	B(0.13) C(0.87)	C(0.96)	A	A(0.08) B(0.92)
S. humilis	B	B	C	C	C	C	A	B(0.67) C(0.25) D(0.08)
S. keri	B	B	C	A	B(0.29) C(0.71)	C	A(0.71) B(0.29)	B(0.50) C(0.43) D(0.07)
S. m. magnirostris	B	B	C	C	A(0.11) C(0.89)	C	A(0.89) B(0.11)	B(0.96) C(0.04)
S. m. viridior	B	B	C	C	A(0.30) C(0.70)	C	A(0.80) B(0.20)	B(0.90) C(0.10)
S. beccarii	B	B	C	C	A(0.21) C(0.79)	C	A(0.79) B(0.13) C(0.08)	B
S. c. citreogularis	C	B	C	C	A(0.09) C(0.91)	C(0.86) D(0.14)	A(0.96)	A(0.77) B(0.23)
S. c. cairnsi	C	B	C	C	A(0.33) C(0.67)	C	A	A(0.58) B(0.42)
S. nouhuysi	B	B	C	C	A(0.15) C(0.85)	B(0.19) C(0.81)	A(0.96)	B(0.77) C(0.23)
S. perspicillatus	B	B	C	B(0.15) C(0.85)	A(0.37) C(0.73)	B	A(0.96)	B(0.09) D(0.50) E(0.41)
S. papuensis	A	B	A	C	C	B	A(0.83) B(0.17)	C(0.50) D(0.50)
S. spilodera	B	A	A	C	C	A	A	B(0.50) D(0.50)
S. arfakianus	B	B	C	C	C	B	A	C
A. pusilla	B	B	C	C	A(0.25) C(0.75)	B(0.92) C(0.08)	A(0.92) B(0.08)	B(0.25) C(0.75)

[1] A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99.

[2] "Nothing" dehydrogenase, i.e. NADP specific bands, was observed without the addition of any substrate to the staining mixture.

[3] General protein stained with Coomasie Blue.

TABLE 2. Extended.

Locus (E.C. no.)								
G6PD (1.1.1.49)	NADP nDH[2]	GDA (3.5.4.3)	PGM-1 (2.7.5.1)	PGM-2 (2.7.5.1)	PGM-3 (2.7.5.1)	ACON-2 (4.2.1.3)	NP (2.4.2.1)	
B	D(0.98)	B	A(0.96)	B(0.06) C(0.86) D(0.06)	C(0.92)	C	D(0.98)	
A(0.17) B(0.83)	D	B	A(0.92) C(0.08)	C	A	A(0.25) B(0.75)	D	
B	A(0.43) B(0.43) C(0.14)	B	A	C	C	C	D	
B(0.79) C(0.07) D(0.14)	D	A	A(0.79) C(0.21)	A(0.64) C(0.36)	C	C	D(0.96)	
B(0.40) C(0.60)	D	A	A	A(0.20) C(0.80)	C	C	D	
B	D	A	A	A(0.96)	C	C	D(0.96)	
A(0.14) B(0.82)	D	B	A(0.96)	C	C	C(0.77) D(0.18)	D(0.86) F(0.09)	
A(0.08) B(0.92)	D	B	A(0.67) B(0.33)	C	C	C(0.17) D(0.83)	C	
B	D	A	A	A	C	C	D	
B	D(0.96)	A	A	C	C	C	D(0.92) E(0.08)	
B	D	B	A	C	C	C(0.83) D(0.17)	D	
B	D	B	A	C	C	C	D	
B	D	A	A	C	C	B(0.13) C(0.87)	D	
A(0.83) B(0.17)	D	B	A	C	C	B(0.08) C(0.92)	D(0.25) E(0.33)	

altitudinally (see below) and overlap with members of the other two protein lineages at all levels. In Australia, *S. beccarii* is allopatric with both *S. frontalis* and *S. magnirostris* (Parker 1970, Keast 1978a, Boles 1979) where its mode of foraging (it creeps over stems and lianas in the lower-mid strata of forest) is like that of *magnirostris*, not *frontalis* (Table 5). *S. nouhuysi* also feeds in the same manner but lower, usually within 2 m of the ground (Beehler et al. 1986).

Among Australian taxa, *S. magnirostris* is sympatric with every other species in mainland rain forests, all of which are members of the *frontalis* protein lineage (Figs. 1 and 2, cf. Figs. 4 and 5). Within the *frontalis* group allopatry is more ecological than geographical. *S. frontalis* is replaced by *S. humilis* in Tasmania, and overlaps *S. keri* and *S. citreogularis* completely (Fig. 2). Ecological separation is greatest between *keri* and *frontalis*, and verges on local allopatry. *S. keri* is endemic to the substage of closed rain forest above ca. 650 m altitude in northeast Queensland and *frontalis* occupies the uncano-

TABLE 2. Extended.

Locus (E.C. no.)												
EST-2 (3.1.1.1)	EST-3 (3.1.1.1)	IDH-1 (1.1.1.42)	ALD (4.1.2.13)	LDH-1 (1.1.1.27)	LDH-2 (1.1.1.27)	GP-1[3]	GP-2[3]	GP-3[3]	GP-4[3]	P	$\bar{H}$
B(0.92)	B	A(0.06) C(0.92)	D	A	B	B	A	B	B	34.1	0.035
B	B	C	D	A(0.83) B(0.17)	B	B	A	B	B	20.5	0.038
A(0.43) B(0.57)	B	C	D	A	B	B	A	B	B	18.2	0.055
B	B	A(0.07) C(0.93)	C	A	B	B	A	B	B	25.0	0.054
B	B	C	C	A	B	B	A	B	B	18.2	0.068
B	B	C	C	A	B	B	A	B	B	13.6	0.034
B	B	C	E	A	B	B	A	B	A	25.0	0.033
B	B	C	E	A	B	B	A	B	A	15.9	0.045
B	B	C	C	A	B	B	A	B	B	18.2	0.035
B(0.96)	A	C(0.96) D(0.04)	B	A(0.92) B(0.08)	B	B	A	B	B	27.3	0.049
B	A	C	A	A	B	A	A	A	B	11.4	0.038
B	B	C	—	A	B	B	A	B	B	4.5	0.011
B	B	C	—	A	B	B	A	B	B	6.8	0.017
B	C	C	F	C	A	C	B	B	B	22.7	0.042

TABLE 3. Genetic distance measures. Upper matrix, Rogers (1972) genetic distance; lower matrix, Nei (1978) unbiased genetic distance.

Species	1	2	3	4	5	6	7	8	9
1. *Sericornis frontalis*	—	0.082	0.111	0.112	0.147	0.134	0.150	0.178	0.116
2. *S. humilis*	0.046	—	0.165	0.162	0.195	0.192	0.190	0.206	0.165
3. *S. keri*	0.075	0.129	—	0.196	0.173	0.187	0.200	0.232	0.166
4. *S. m. magnirostris*	0.085	0.131	0.165	—	0.076	0.053	0.204	0.230	0.064
5. *S. m. viridior*	0.114	0.164	0.141	0.032	—	0.070	0.202	0.224	0.082
6. *S. beccarii*	0.116	0.173	0.170	0.022	0.033	—	0.189	0.216	0.062
7. *S. c. citreogularis*	0.116	0.166	0.167	0.186	0.172	0.176	—	0.071	0.202
8. *S. c. cairnsi*	0.152	0.189	0.208	0.222	0.209	0.212	0.036	—	0.230
9. *S. nouhuysi*	0.091	0.143	0.137	0.023	0.041	0.031	0.183	0.220	—
10. *S. perspicillatus*	0.182	0.234	0.202	0.164	0.135	0.163	0.228	0.271	0.144
11. *S. papuensis*	0.237	0.291	0.252	0.312	0.278	0.300	0.241	0.285	0.267
12. *S. spilodera*	0.166	0.224	0.183	0.232	0.201	0.225	0.212	0.257	0.197
13. *S. arfakianus*	0.168	0.203	0.179	0.148	0.127	0.162	0.221	0.268	0.122
14. *Acanthiza pusilla*	0.323	0.359	0.355	0.322	0.297	0.352	0.391	0.421	0.333

pied shrubberies of the forest edge and streams at the same levels there. Because *frontalis* enters rain forests wherever else they occur in its range and forages in the same zone as *keri* (Table 5), this partitioning may be enforced by competition. *S. citreogularis* coexists with *frontalis* and *keri* in the same forests where the larger and heavier-billed *citreogularis* feeds almost exclusively on the forest floor and may take prey of a different average range and size (Table 5; Keast 1978a; cf. Hespenheide 1973, 1975; Cody 1978). Here the degrees of sympatry are consistent with the greater genetic distance between *citreogularis* and the other 2 species (Figs. 3 and 4).

Genetic intergradation.—Intergradation through introgressive gene flow has been recorded only among members of the *S. frontalis* superspecies and between *S. magnirostris, S. beccarii* and *S. nouhuysi.* Its sequences in the *frontalis* group, which implicates *S. humilis,* were described by Mayr (1937), Condon (1951, 1954), Green (1969), and Ford (1985), and analyzed electrophoretically by Christidis and Schodde (in press). It is consistent with both the protein phylogeny and traditional morphological groupings.

Intergradation among members of the *magnirostris* protein lineages conflicts with morphology. In New Guinea where they abut (Fig. 1), *S. beccarii* is linked to *S. nouhuysi* by a suite of populations identified as "*S. virgatus*" (Rand and Gilliard 1967: 359; Diamond 1969, 1985; Gilliard and Le Croy 1970; cf. Mayr 1986). Despite sight observations of sympatry (Diamond 1985), it is our impression (from spot-sampled populations at different stages of intermediacy at different localities at different altitudes) that there is a patchy sequence of intergradation between *beccarii* and *nouhuysi* in western New Guinea. The more uniformly intermediate populations on isolated ranges away from the central cordillera may be stabilized hybrids, proportionate in their traits to the genetic input from respective parental members (cf. Hartert 1930).

In Australia, *S. beccarii* intergrades with *S. magnirostris,* not *S. frontalis* where it abuts on them on the eastern foot of Cape York Peninsula (Schodde and Ford in prep.; *contra* Parker 1970, Boles 1979). Boles (1979) recorded *beccarii* and *magnirostris* as sympatric, but our series revealed a complex zone of introgression between them in all differential traits, even color of bill (cf. Table 5).

Morphological correlations.—Patterns of geographical distribution, foraging niche, and genetic intergradation are consistent with the protein phylogeny wherever it was discrepant with traditional morphological groupings. Accordingly, we interpret those similarities in plumage marks that conflict with the protein phylogeny as unresolved plesiomorphies and homoplasies. Discriminating them and their polarity is not possible, except in terminal sublineages, until the phylogeny of the broader sericornine assemblage (Schodde 1975) is clarified because other members of the sericornine assemblage share both plain and analogously marked plumages with *Sericornis* (*sensu stricto*). For members of terminal sublineages, character states in sister lineages indicate that plain plumage was acquired secondarily in *S. keri* as were

TABLE 3. Extended.

10	11	12	13	14
0.198	0.235	0.175	0.175	0.326
0.243	0.277	0.222	0.209	0.353
0.220	0.253	0.194	0.195	0.350
0.190	0.293	0.235	0.169	0.287
0.160	0.270	0.215	0.153	0.260
0.181	0.277	0.226	0.169	0.292
0.240	0.241	0.223	0.220	0.369
0.267	0.278	0.255	0.258	0.386
0.162	0.259	0.201	0.139	0.282
—	0.214	0.233	0.111	0.269
0.199	—	0.206	0.229	0.326
0.231	0.210	—	0.196	0.341
0.079	0.232	0.196	—	0.260
0.316	0.334	0.355	0.300	—

patterned face and wing coverts and pale bill in *S. beccarii* (Table 5, cf. Fig. 5).

Variations in bodily proportions correlate best with niche occupied and environment (Table 5, cf. Schoener 1965, Hespenheide 1973). In tarsus, arboreal species were consistently shorter legged than those such as the Australian members of the *frontalis* group which forage near and on the forest floor. Those scrubwrens that probe the crannies of branches and stems (*magnirostris* sublineage) or feed on the ground (Australian *frontalis* group) have disproportionately longer and more slender beaks than higher level foliage- and twig-gleaners. Taxa at lower tropical latitudes have disproportionately shorter tails than those at higher temperate latitudes, a characteristic also recored in the related genus *Acanthiza* (Keast 1978c). In the *frontalis* group, *S. keri* has a shorter tail than southern *S. frontalis*, while in the *magnirostris* sublineage there is a south to north sequence in diminishing length, beginning in *magnirostris* in central east Australia and ending in *S. nouhuysi* in New Guinea. By these criteria, *S. rufescens*, of which no tissues were available but which is as small and slender-billed as *S. perspicillatus* and occupies the same niche, is the vicar of that species and not stubby-billed *S. papuensis* in the mountains of Cendrawasi, west New Guinea (also Mayr 1937, 1986; cf. Diamond 1985).

TABLE 4. Electromorphs defining clades in Fig. 5.

Clade	Apomorphic characters
1	Pep L-G-G (D)
2	CK-4 (B), ALD (D)[a]
3	GP-4 (A), ENOL (C)
4	PK (A)
5	6PGD (C)
6	G6PD (C)
7	PGM-2 (A), ALD (C)[a]
8	6PGD (D)
9	GDA (B)
10	GP-1 (B), GP-2 (B), LDH-1 (A), LDH-2 (B)

[a] Characters in which the plesiomorphic state could not be determined.

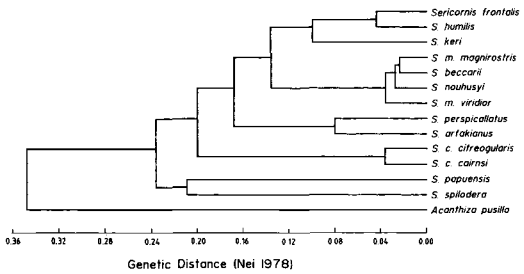

Fig. 3. UPGMA phenogram based on Nei's (1978) genetic distance values (Table 3).

Zoogeographical synthesis.—Ancestral *Sericornis* presumably first split into two primary lineages in cool rain forests on the formerly unbroken Australo-southern New Guinean continent, probably at some time within the last 5–10 million years (cf. Sibley and Ahlquist 1985). Then as the continent dried in the late Plio-Pleisto-

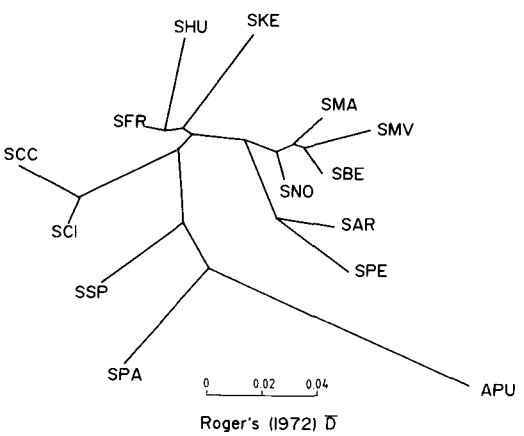

Fig. 4. Distance-Wagner tree based on Rogers' (1972) genetic distance values (Table 3). The tree is rooted by the out-group method of Farris (1972), to *Acanthiza pusilla* (APU). Other symbols refer to *Sericornis papuensis* (SPA), *S. spilodera* (SSP), *S. citreogularis citreogularis* (SCI), *S. c. cairnsi* (SCC), *S. keri* (SKE), *S. humilis* (SHU), *S. frontalis* (SFR), *S. arfakianus* (SAR), *S. perspicillatus* (SPE), *S. nouhuysi* (SNO), *S. magnirostris magnirostris* (SMA), *S. m. viridior* (SMV), *S. beccarii* (SBE).

TABLE 5. Morphological traits, foraging strata, and distribution of the species of *Sericornis* in comparison with those of *Acanthiza pusilla*. Data on foraging strata from Diamond 1972, Keast 1978a, Beehler et al. 1986 (p. 31), and personal records. Symbols in parentheses in Table indicate incomplete expression. The sample sizes of males and females, respectively, for statistical analysis of relative size and proportion are in parentheses following species names. Parenthetic numbers after size are wing measurements of male samples only; and those after the following ratios are for the sexes combined. Measurements are means ± 1 SD. Wing measured as the flattened chord; tail, from tip to base of central rectrices; bill, as the exposed culmen; and tarsus, from heel to fore-edge of last undivided scute at base of toes.

Trait	*S. rufescens* (7, 6)	*S. perspicillatus* (10, 10)	*S. arfakianus olivaceus* (10, 10)	*S. nouhuysi oorti* (10, 10)	*S. beccarii minimus* (10, 10)	*S. m. magnirostris* (10, 10)
Russet face wash	–	–	–	+	–	(+)
Russet frons scalloping (*Acanthiza*-like)	–	–	–	(+)	–	–
Black lores/frons	–	–	–	–	(+)	–
Pale superciliary stripe	–	–	–	–	+ (broken)	–
Pale subocular bar	–	–	–	–	+	–
Pale malar line	–	–	–	–	(+)	–
Black spotting/streaking on throat/breast	–	–	–	–	–	–
Diffuse olive-grey throat/breast streaking	–	–	+	(+)	–, (+)	(+)
White tipping on alula/primary coverts	–	–	–	–, (+)	+	–
Black subterminal tail bar	(+)	(+)	(–)	–	–	–
White tail tipping	–	–	–	–	–	–
Bill color	dark	dark	dark	dark	pale	dark
Iris color	chestnut	chestnut	chestnut	chestnut	chestnut	chestnut
Sexual dimorphism in face/throat marks	–	–	–	–	+	–
Sexual dimorphism in size	(+)	+	+	+	+	–
Size	small 53.0 ± 1.4	small 55.0 ± 1.3	small 54.5 ± 1.3	large 64.1 ± 2.0	medium 58.2 ± 1.3	medium-small 56.3 ± 1.6
Tail : wing ratio	short 0.69 ± 0.03	short 0.71 ± 0.03	short 0.71 ± 0.02	short 0.68 ± 0.02	short 0.70 ± 0.02	long 0.79 ± 0.03
Bill : wing ratio	medium 0.18 ± 0.01	medium 0.18 ± 0.01	medium 0.18 ± 0.01	long 0.19 ± 0.01	long 0.20 ± 0.01	long 0.21 ± 0.01
Tarsus : wing ratio	medium 0.35 ± 0.02	medium 0.36 ± 0.01	medium 0.36 ± 0.02	medium 0.37 ± 0.02	medium 0.36 ± 0.02	medium 0.37 ± 0.01
Foraging strata	arboreal	arboreal foliage (2–20 m)	arboreal	substage stems (0.5–3 m)	subarboreal stems (0.5–15 m)	arboreal stems (1–20 m)
Distribution	Cendrawasi, New Guinea	New Guinea	New Guinea	New Guinea	Cape York Peninsula	Central east Australia

cene, both lineages withdrew with the rain forests to its east and north fringes, taking refuge in the Australian Great Dividing Range and rising New Guinean cordillera. These events, developing a dry Arafura plain and, later, Torres Strait to separate the Australian and New Guinean ranges, initiated vicariant splits within both lineages. In montane New Guinea the *perspicillatus* and *papuensis* groups diverged from the Australian *magnirostris* and *frontalis-citreogularis*

TABLE 5. Extended.

S. p. papuensis (10, 6)	*S. spilodera guttatus* (10, 6)	*S. c. citreogularis* (10, 10)	*S. keri* (6, 10)	*S. h. humilis* (10, 10)	*S. f. frontalis* (10, 10)	*A. pusilla*
–	–	–	–	–	–	–
+	–	–	–	–	–	+
–	–	+	–	–	+	–
–	–	+	–	(+)	+	–
–	–	–	–	–	+	–
–	–	+	–	(+)	+	–
–	+	–	–	+	+	scallop-streaked
–	–	–	(+)	+	–	–
–	–	–	–	(+)	+	–
+, (+)	–	–	(+)	(+)	(+) (+ other races)	+
–	–	–	–	–	– (+ other races)	+, –
dark chestnut	pale chestnut	dark chestnut	dark chestnut	dark cream	medium cream	dark chestnut
–	–	+	(+)	+	+	–
–	+	+	+	+	+	+
medium 58.6 ± 1.0	medium 62.2 ± 1.0	large 68.6 ± 1.8	medium 60.3 ± 1.4	large 64.0 ± 1.6	medium 58.4 ± 2.6	
short 0.68 ± 0.02	medium 0.74 ± 0.02	long 0.79 ± 0.2	medium 0.73 ± 0.03	long 0.82 ± 0.03	long 0.80 ± 0.04	
short 0.15 ± 0.01	medium 0.17 ± 0.01	medium 0.17 ± 0.01	long 0.19 ± 0.01	long 0.20 ± 0.01	long 0.19 ± 0.01	
medium 0.35 ± 0.01	short 0.32 ± 0.00	long 0.40 ± 0.02	long 0.39 ± 0.02	long 0.40 ± 0.01	long 0.39 ± 0.02	
lower arboreal foliage (0.5–5 m)	arboreal	floor-substage (0–1 m)	substage-floor (0–1 m)	substage-floor (0–2 m)	substage-floor (0–2 m)	aboreal (0.5–10 m)
New Guinea	New Guinea	East Australia	North-east Australia	Tasmania	South-east Australia	Australia

groups, respectively. Since then, all 4 secondary lineages have undergone minor radiations separately in Australia and New Guinea, with only one, the *magnirostris* group, dispersed between the 2 land masses (see below, also Diamond 1969, Gilliard and Le Croy 1970). This reconstruction is generally concordant with the paleogeographic and environmental history of the Australo-Papuan continent of the times (Doutch 1972; Walker 1972; Bowler 1976, 1982; Dow 1977;

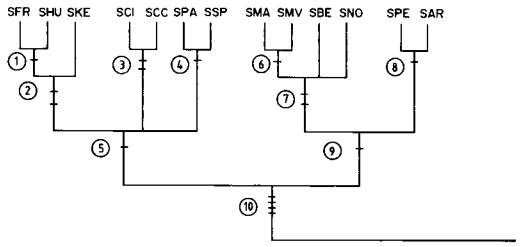

Fig. 5. Cladogram derived from electromorphs (Table 4), with *Acanthiza pusilla* as the out-group. Bars represent the number of synapomorphies that define each clade, and numbers at branch points identify synapomorphic allozymes (Table 4). Lettered symbols are identified in Fig. 4.

Kemp 1981; Schodde 1982; Hope 1983; Pieters et al. 1983; Dow and Sukatmo 1984). An alternative interpretation (Keast 1978a, b), postulating that *Sericornis* arose in New Guinea and dispersed to Australia in a complex series of waves, is less parsimonious and at variance with the protein phylogeny and known paleogeography.

Within New Guinea, the sequence of radiation in the secondary lineages reflects altitudinal replacement (Schodde and Hitchcock 1972; Diamond 1973, 1985). Ancestral stocks of the respective pairs *S. perspicillatus-S. arfakianus* and *S. papuensis-S. spilodera* were probably first separated from each other on different eastern and western or outlying sectors of the central New Guinean cordillera, perhaps as altitudinal life zones rose above valley floors during the warmer interglacial epochs of the Pleistocene. Then, as the zones fell during the next or subsequent glacial periods, the stocks spread out to come in contact and overlap one another at different altitudes where they had speciated. *Sericornis perspicillatus* moved over *S. arfakianus* and, before this, *S. papuensis* over *S. spilodera*, judged by

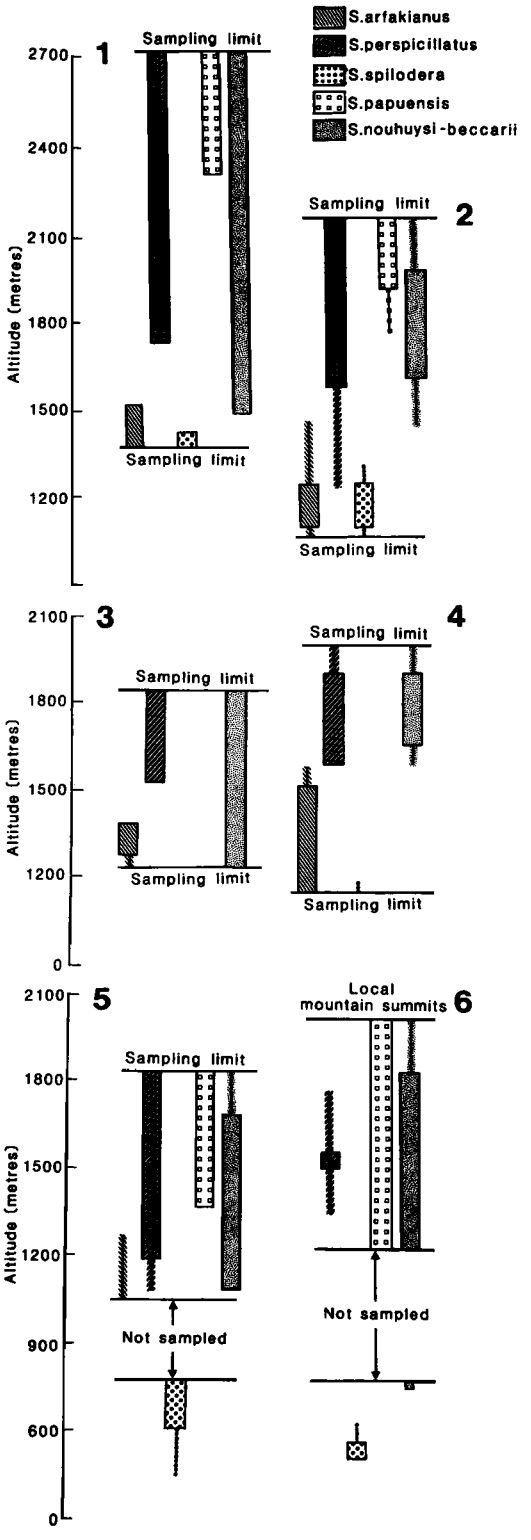

Fig. 6. Altitudinal ranges of species of *Sericornis* at six localities in eastern New Guinea: 1. Kuper-Kaindi Ranges; 2. Kukukuku Range; 3. Herzog Mountains; 4. Rawlinson Range; 5. south scarp, Owen Stanley Range; 6. Mt. Simpson-Mt. Dayman ranges. Narrow-width bands represent single records and broad-width bands 2 or more in the Australian National Wildlife Collection, CSIRO, and the Australian Bird Banding Scheme, Australian National Parks and Wildlife Service, Canberra.

their genetic, morphological and ecological distances (Figs. 3 and 6, Table 5). Because the members of both pairs are so widespread today, we cannot pinpoint their geographic origins. *Sericornis rufescens* has speciated since in isolation from *S. perspicillatus* after stocks of the latter reached the mountains of Cendrawasi when life zones were lower than now.

In Australia, radiation probably followed sequences of latitudinal isolation produced by fluctuating connections in habitat around the periphery of the continent by climatic oscillations during the Plio-Pleistocene (Gentilli 1949; Serventy 1953, 1972; Keast 1959, 1961). First to diverge in the *frontalis* primary lineage were the *frontalis* and *citreogularis* groups, split in enclaves of rain forest between northeast and southeast Australia by an early dry "glacial" epoch. We cannot identify either region as the source of either group because both groups are widely sympatric today. Within the *frontalis* group, *S. keri* then budded off in the northeast during a subsequent dry glacial period, followed by *S. humilis* in Tasmania. *S. citreogularis* was probably also split into northern and southern populations at about the same time or a little later, unless its members diverged at a slower rate. Within both *citreogularis* and *frontalis* groups, the rates of protein change (Fig. 4) was fastest in the populations isolated in northeast Queensland (*S. citreogularis cairnsi, S. keri*) and Tasmania (*S. humilis*), probably reflecting past bottlenecks in available habitat there. Because its populations north of Brisbane are as yet undifferentiated (Ford 1985; Christidis and Schodde in press; *pace* Mayr 1937, 1986), *S. frontalis* has apparently re-expanded north to fringe on *S. keri* very recently. This could have happened 6,000–8,000 years ago after the end of the last glacial epoch when for the first and only time in the last 25,000 years the northeast Queensland tablelands were linked by suitable rain forests to those in the south (Nix and Kalma 1972).

The *magnirostris* group apparently arose in Australia and dispersed to New Guinea, budding off *S. beccarii* and *S. nouhuysi* in the course of dispersal (also Diamond 1969, Gilliard and Le Croy 1970). It was accompanied by a shift in foraging zones, from the forest midstage to the substage, a reversal of the niche switch in the *frontalis* primary lineage between New Guinea and Australia. Consistent with this, *S. magnirostris*, the putative ancestral form, resembles members of the *perspicillatus* group more in form and feeding behavior than either of its sister species (Table 5). The intergradation between members of the *magnirostris* group wherever they abut, together with slight differentiation in their proteins (Table 3), indicates that they have not speciated completely. Their differences in external morphology, however, are as great as those between any species in *Sericornis* (Table 5). There are 2 likely but unresolved explanations: 1. In response to very recent dispersal to New Guinea, perhaps during the last glacial epochs when ancestral stocks of *beccarii* may have been confined to tiny pockets of rain forest on the Arafura plain (Nix and Kalma 1972), they may have evolved more rapidly. This would account for the divergence in plumage pattern but not the conformity in proteins. 2. *Magnirostris, beccarii* and *nouhuysi* are all older but their intergradation in current pluvial times has enabled alleles for proteins to spread more rapidly than the genes for morphological traits.

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We dedicate this paper to Professor Charles G. Sibley on the occasion of his 70th birthday for his pioneering example in the molecular study of phylogeny in birds.

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