

PHYLOGENY AND BIOGEOGRAPHY OF THE *PTILORIS* RIFLEBIRDS (AVES: PARADISAEIDAE)¹

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Abstract. We performed a phylogenetic and biogeographic study of the riflebird genus *Ptiloris* (Paradisaeidae). Our analysis, which includes sonograms documenting intertaxonomic variation in male advertisement vocalizations and a reassessment of key morphological characters, indicates that (1) the genus includes two distinct clades (*P. victoriae/paradiseus* and the *P. magnificus* complex); (2) within the *P. magnificus* complex, the eastern Papuan form may constitute a heretofore unrecognized sibling species; and (3) the biogeography of *Ptiloris* provides additional confirming evidence that the Torres Strait has been of minor importance as a biogeographic barrier for Australo-Papuan rainforest birds.

Key words: Systematics; biogeography; *Ptiloris*; *Paradisaeidae*; riflebirds.

INTRODUCTION

The riflebird genus *Ptiloris* (Paradisaeidae) includes the only group of birds of paradise that has speciated across the Torres Strait, the shallow water passage separating New Guinea from Australia (Walker 1972, Schodde and Calaby 1972, Kikkawa et al. 1981). Riflebirds are stocky, sexually dimorphic forest-dwellers that are best known for the persistent loud calls given by males from regular display perches (e.g., *P. victoriae*) or randomly throughout their forest territories (e.g., *P. magnificus*; Gilliard 1969, Beehler and Pruett-Jones 1983). The species are polygynous and promiscuous, the males establishing display courts and the females alone raising offspring without assistance (Cooper and Forshaw 1977, Diamond 1986).

Traditional systematic treatments (Mayr 1962, Gilliard 1969, Cooper and Forshaw 1977) recognize three allopatric species: the Magnificent Riflebird [*Ptiloris magnificus* (Vieillot)], comprising three subspecies (*P. m. magnificus*, *P. m. alberti* Elliot, and *P. m. intercedens* Sharpe) and inhabiting New Guinea and the Cape York Peninsula of Australia; Victoria's Riflebird (*Ptiloris victoriae* Gould); and the Paradise Riflebird (*Ptiloris paradiseus* Swainson). The last two are monotypic and inhabit small ranges in rainforest refuges in eastern Australia (Gilliard 1969).

Our attention was drawn to the riflebirds as part of the junior author's studies of variation in avian vocal dialects of species with populations on either side of Torres Strait. Unpublished field recordings made by the senior author indicated that analysis of regional variation in *Ptiloris* vocalizations could help clarify understanding of riflebird relationships (see Diamond 1972, Schodde 1974, Cooper and Forshaw 1977, Beehler et al. 1986, Coates 1990).

In our preliminary studies we also found that geographic variation in the pattern of feathering on the base of the culmen (see Mayr and Rand 1937, Schodde and Hitchcock 1968) appeared to corroborate the geographic trends in vocalization, and thus constituted an additional feature of unrecognized systematic significance. In light of the recent systematic and biogeographic analysis of Australasian passerines made by Cracraft (1986), we believe it is useful to present a revised assessment of the riflebirds, one of Cracraft's focal taxa.

We have reassessed: (1) character evolution in the genus *Ptiloris*, (2) the cladistic relationships in the five regional taxa, and (3) the impact of a revised generic phylogeny on species status of the Papuan forms and on the biogeographic significance of the Torres Strait.

MATERIALS AND METHODS

For our vocal analysis, we assembled tape recordings of male advertisement calls in five populations of *Ptiloris* from New Guinea (*interce-*

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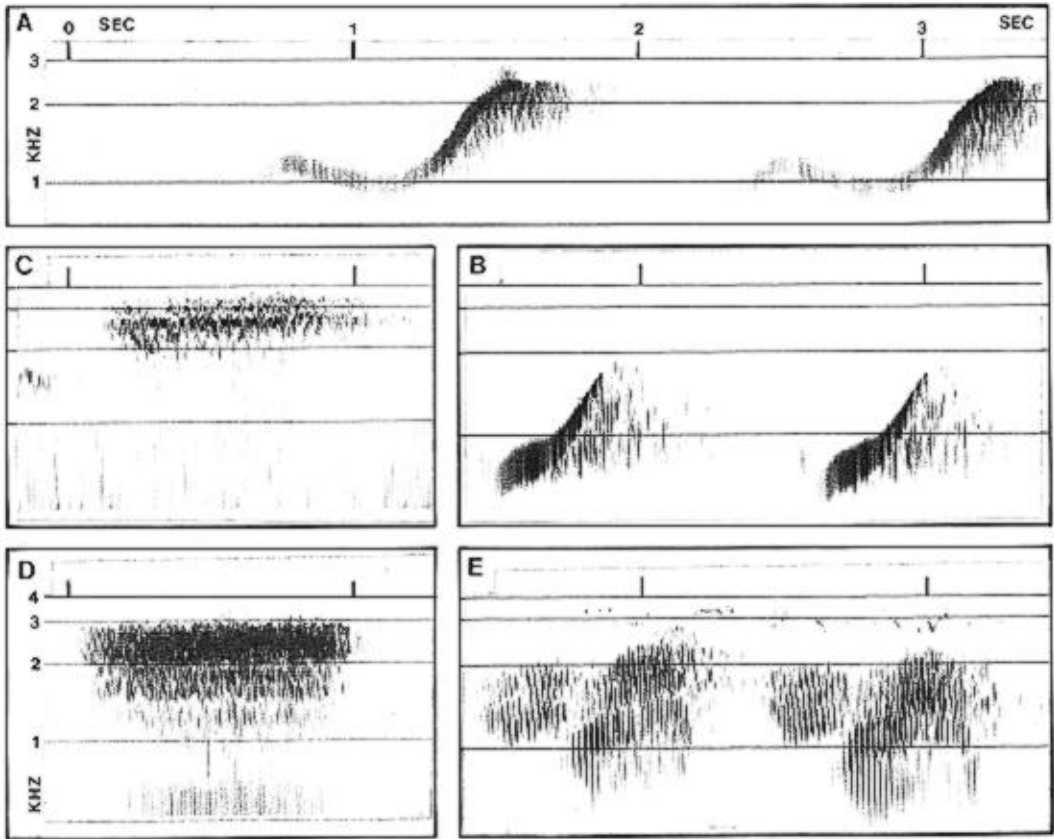


FIGURE 1. Sonograms of *Ptiloris* populations. A. *P. m. alberti* from Iron Range, Queensland. B. *P. m. magnificus*, Puwani, West Sepik Province, Papua New Guinea. C. *P. victoriae*, Paluma, Queensland. D. *P. paradiseus*, Bunya Mountains, Queensland. E. *P. m. intercedens*, Morobe Province, Papua New Guinea.

dens, *magnificus*) and Australia (*alberti*, *paradiseus*, and *victoriae*). The Australian recordings were made by RJS, the Papuan recordings were made by BMB. These were converted to sonograms (log scale, wide band) for visual comparison (Fig. 1) using a Kay Sonograph in the Department of Vertebrate Zoology, National Museum of Natural History (Washington, D.C.)

For cladistic analysis of *Ptiloris* we developed a character matrix for the five regional taxa (*magnificus*, *intercedens*, *alberti*, *paradiseus*, and *victoriae*) and two designated outgroups (*Parotia lawesii* and *Lophorina superba*). Our choice of outgroups follows Cracraft (1986) as well as traditional determinations of sister-groups to the riflebirds (e.g., Schodde 1976, Diamond 1972). We followed the methodology detailed in Cracraft (1986). For analysis, we used a series of thirteen plumage characters, three aspects of bill

morphology, and a single vocal character (Tables 1 and 2). This included a reassessment of six of Cracraft's characters and 11 additional traits. Plumage and bill morphology were coded after examining a series of five each of male and female specimens from collections of the American Museum of Natural History (New York) and National Museum of Natural History. We excluded characters that showed significant intra-population variation.

The data in our systematic character matrix were subjected to the PAUP branching algorithm, versions 2.4 and 3.0 (Swofford 1985, 1990). We performed series of PAUP runs both with characters unordered and ordered. We ordered characters based on putative primitive-derived sequences delineated with reference both to the outgroup taxa and the distribution of character states in other related taxa (Kluge 1976).

TABLE 1. Character states for the genus *Ptiloris*.

CHARACTER ONE: male advertisement vocalization—(0) one or more harsh notes; (1) two or several loud growl notes, (2) several upslurred, musical wolf whistles (see sonograms, Fig. 1).

CHARACTER TWO: feathering on base of culmen of male—(0) extended anteriorly, (1) small portion of base unfeathered, (2) unfeathered ridge deep and expanded posteriorly.

CHARACTER THREE: iridescent breast-shield of male—(0) winged, (1) small, unwinged, (2) large, unwinged.

CHARACTER FOUR: black velvety feathers posterior to breast shield of male—(0) absent, (1) forming a narrow band, (2) forming a broad band.

CHARACTER FIVE: green velvet feathering posterior to breast shield of male—(0) absent, (1) narrow, (2) extensive.

CHARACTER SIX: flank plumes—(0) absent, (1) very brief, (2) subequal or equal to length of tail, (3) longer than tail.

CHARACTER SEVEN: occipital plumes—(0) brief, (1) elongated.

CHARACTER EIGHT: central rectrices—(0) velvety purple-black, (1) blue-purple, (2) iridescent green.

CHARACTER NINE: female ventral pattern—(0) fine dark barring, (1) dark scalloping, (2) dark spotting.

CHARACTER TEN: female dorsal plumage color—(0) gray-brown, (1) medium brown, (2) reddish brown.

CHARACTER ELEVEN: pale streaking on crown of female—(0) prominent, (1) reduced, (2) much reduced or absent.

CHARACTER TWELVE: male flight feathers—(0) unspecialized, (1) blunt-tipped, sexually distinct, (2) with emarginate outer primaries.

CHARACTER THIRTEEN: upper throat pattern of female—(0) with fine dark speckling, (1) unspotted.

CHARACTER FOURTEEN: sexual dimorphism in bill length—(0) female's shorter than or nearly equal to the male's, (1) bill longer than male's.

CHARACTER FIFTEEN: rectrix shape of male—(0) narrow and typical, (1) broad and blunt-tipped.

CHARACTER SIXTEEN: male wing length (arc)—(0) less than 160 mm, (1) more than 180 mm.

CHARACTER SEVENTEEN: bill shape of female—(0) short and straight, (1) elongated and slightly decurved, (2) elongated and much decurved.

Characters were weighted equally, preventing us from unconsciously skewing the analysis by emphasizing characters that support personal biases. Because our analysis involved only seven taxa, using PAUP version 2.4 we were able to use the "alltrees" mode which produces an exhaustive search of all possible branching combinations. M. C. McKittrick ran the character matrix for us on PAUP version 3.0 using the "branch and bound" mode.

We plotted distributional records for the three allotaxa in the *magnificus* complex using data from the literature (Schodde and Hitchcock 1968, Gilliard 1969, Diamond 1972, Cooper and Forshaw 1977, Coates 1990); from specimen records from the American Museum of Natural History, National Museum of Natural History, and Australian National Wildlife Collection; and from unpublished distributional records based on voice (mostly of BMB). Our map showing distribution of the entire genus is based on the above sources plus data from MacDonald (1973) and Blakers et al. (1984).

RESULTS

CHARACTER ANALYSIS

Our analysis of vocalizations (Fig. 1) shows that (1) *Ptiloris victoriae* and *P. paradiseus* share the same coarse *yaaaaa*s call; (2) the regional taxa *alberti* and *magnificus* share the upslurred "wolf-whistle" call unlike that of any other riflebird. Transcribed as *woiiiieet—woi!*, the call is usually two notes but on occasion as many as four in a series; and (3) the growled voice of *intercedens* [*uRAUow—urauow*] shares some characteristics with that of *P. victoriae/paradiseus* but is distinct, and was classified as an intermediate character state. There is evidence of slight vocal variability within populations (Schodde in litt., for

TABLE 2. Character matrix for *Ptiloris*.

Taxa	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Parotia lawesit†</i>	0	0	1	0	0	2	1	0	0	1	2	2	0	0	1	0	0
<i>Lophorina†</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>P. victoriae</i>	0	1	1	2	2	1	0	2	2	0	0	1	1	1	1	0	1
<i>P. paradiseus</i>	0	1	1	2	2	1	0	2	1	0	0	1	1	1	1	0	2
<i>P. alberti</i>	2	2	2	1	1	3	0	1	0	1	1	1	1	0	1	1	1
<i>P. magnificus</i>	2	2	2	1	1	3	0	1	0	2	1	1	0	0	1	1	1
<i>P. intercedens</i>	1	1	2	1	1	2	0	1	0	2	2	1	1	0	1	1	1

† Outgroup taxa.

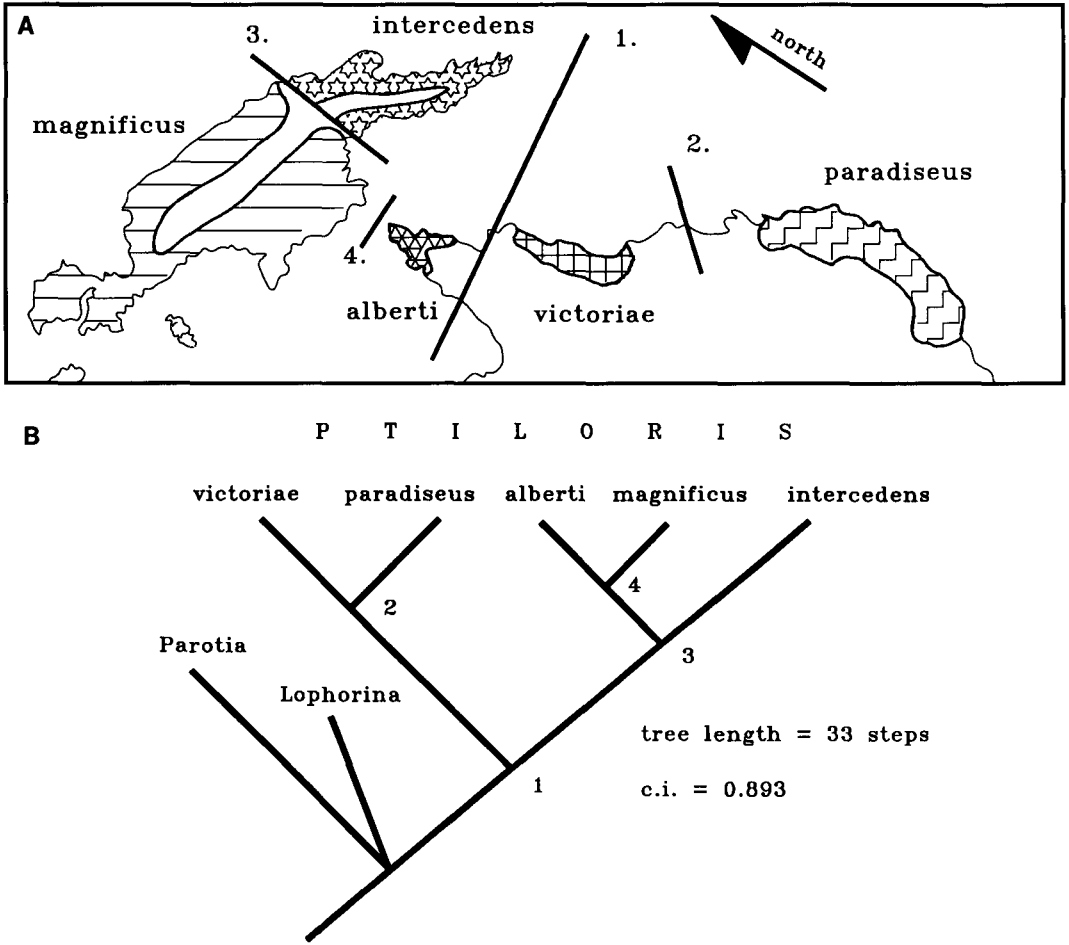


FIGURE 2. (A) Geographic distribution of the five basal taxa of *Ptiloris* in New Guinea and Australia, with postulated vicariance barriers corresponding to the numbered branching events in the cladogram.

(B) Phylogenetic hypothesis for the genus *Ptiloris*, rooted to the outgroups *Parotia lawesii* and *Lophorina superba*. Characters uniquely defining each node, numbered 1–4, are: (1) chars. 7, 15; (2) chars. 3, 4, 5, 6, 14; (3) chars. 3, 4, 5, 8, 16; (4) chars. 1, 2, 6, 11. Steps and consistency index (c.i.) based on unordered characters. C.i. generated with uninformative characters discounted.

P. m. alberti), but not to the extent that our classification of character states would be altered.

The pattern of culmen feathering showed a trend from heavily feathered anteriorly (primitive) to unfeathered along the ridge of the culmen (derived). *P. m. magnificus* and *P. m. alberti* shared the derived condition, and the other five *Ptiloris* tended toward the primitive condition exhibited by the outgroups *Lophorina* and *Parotia*. We are uncertain of the functional importance of this feathering pattern in *Ptiloris*, although it seems to be of importance to courtship display in the genus *Parotia* (Schodde and McKean 1974).

One plumage character, female dorsal color (character 11 of Cracraft 1986; our character 10) may be the product of character convergence related to the regional presence or absence of interspecific flocking. This character distinguishes the two Papuan populations (russet-backed females) from the three Australian populations (gray-brown-backed females). We believe that the evolution of female dorsal plumage has experienced regional plumage convergence, influenced by the considerable importance mixed foraging flocks in New Guinea and their absence in Australia. In New Guinea, there is evidence of striking plumage convergence among bird species that

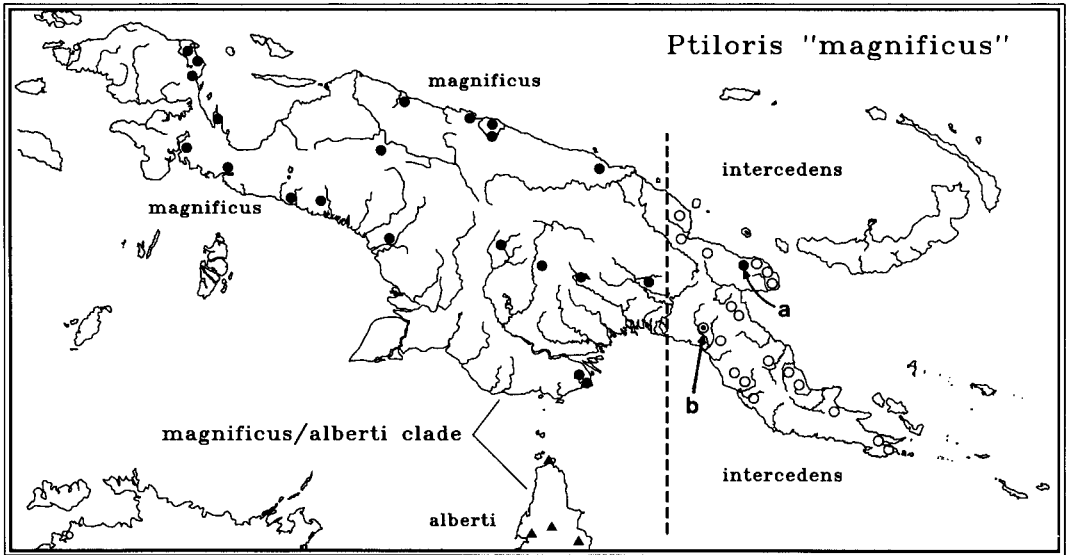


FIGURE 3. Geographic distribution of the *Ptiloris magnificus* complex in New Guinea and Australia. Black circles = *magnificus*; open circles = *intercedens*; black triangles = *alberti*. The easternmost black circle marked "a" represents a single vocal record of a male giving the *magnificus*-type advertisement call (Coates 1990). The circled dot indicated as "b" is location of the putative intermediate specimen (see text).

forage together in mixed flocks. These are Diamond's "brown and black flocks," which include birds of paradise, pitohuis, drongos, honeyeaters, and assorted other species (Diamond 1987).

Although we propose that the taxonomic distribution of female dorsal color may be the product of convergence, we still include the character in our matrix for two reasons. It allows for the possibility that we are wrong in our assumption about convergence, and it permits us to test the robustness of our novel branching pattern.

Our other characters were based on a revision and expansion of Cracraft's character list, and depends to a greater degree on those male plumage traits that are related to courtship display. In addition, we focus on traits that require straightforward objective measurement (length or shape) rather than minor variation in color or iridescence (Cracraft's characters 7, 8, 10, 12). We believe we have based our character matrix on a detailed knowledge of the biology of *Ptiloris*, based on extensive experience with the genus in the field.

CLADISTICS AND GEOGRAPHY

Our cladistic analysis produced a phylogenetic tree that pairs *P. paradiseus* with *P. victoriae* and forms a triplet of *P. m. alberti*, *P. m. magnificus*,

and *P. m. intercedens*. Within the latter clade, *P. m. intercedens*, the population from eastern New Guinea, comprises the sister-form to the *alberti/magnificus* pair (Fig. 2). With the characters unordered, the tree comprises 33 steps, with a consistency index (excluding uninformative characters) of 0.893. With all characters ordered, the tree is of 37 steps and has a consistency index (excluding uninformative characters) of 0.811. Both constituted the sole most parsimonious of 935 trees compared in each PAUP run, and there was no difference in branching order.

Our mapping of the distribution of the three allotaxa of the *magnificus* complex shows that *intercedens* differentiated as an eastern isolate (Fig. 2a, 3). Thus the main body of New Guinea, western New Guinea and northernmost Queensland comprise the range of the *magnificus/alberti* clade, and eastern New Guinea—primarily the Papuan peninsula—comprises the home of *intercedens*.

Because there are no *Ptiloris* populations in the high northwest-to-southeast trending cordillera of New Guinea, there are two contact zones where *intercedens* and its sister-form meet, one in the northern watershed (corresponding to the Ramu River) and another in the southern watershed (corresponding to the Purari River).

The populations of basal *magnificus* and *alberti*, situated on either side of Torres Strait, show only minor levels of morphological differentiation, and their vocalization and culmen-feathering character states are equivalent (Fig. 1, Table 2).

DISCUSSION

The difference between Cracraft's (1986) and our cladogram is the branching within the "*magnificus*" clade. Whereas Cracraft found *alberti* to be the outgroup of that triplet, we found *intercedens* to be the outgroup. Three characters not used by Cracraft and which support our revised branching were male voice, culmen feathering, and plume length. Because Cracraft's character matrix and its coding differed from ours it is not valid to grade the resulting cladograms by level of homoplasy. Nonetheless, our better-resolved tree employs new characters that are important features of the biology of the group, and thus we believe the branching shown in our cladogram is a closer approximation of the phylogenetic history of *Ptiloris*.

SPECIES STATUS OF ALLOTAXA

Cracraft (1986) used the "basal taxon" or "phylogenetic species" concept for morphologically distinct allotaxa. We agree that this is necessary for the purposes of cladistic analysis, but in some instances the resulting nomenclature is not concordant with current ornithological usage. Those who employ the "biological species concept" (*sensu* Mayr 1963) may wonder which of the five basal taxa treated in our analysis merit full species status in the Mayrian sense. We suggest that *Ptiloris paradiseus* and *P. victoriae* are closely related sister forms that each merit species status. The difference in female bill shape implies the evolution of distinct dietary or foraging habits. The situation with the *Ptiloris magnificus* complex is less clear. Certainly the populations *magnificus* and *alberti* are conspecific, but the parapatric disposition and vocal distinctness of *intercedens* and *magnificus* might suggest treatment of *intercedens* as a distinct sibling species.

PAPUAN DIFFERENTIATION

The initial phenomenon that focused our attention on *Ptiloris* was the strikingly different vocalizations of male riflebirds in eastern and west-central New Guinea (Figs. 1, 3). The guttural double-growl of the eastern population (*inter-*

cedens) shares few spectrographic similarities with the musical, upsweeping wolf whistles of *magnificus*, from central and western New Guinea. The contact zone of vocal dialects occurs in both the northern and southern watersheds. What, then, is its significance? Given that the species is promiscuous and that males compete for the right to mate with females, we suppose that vocalization may be of considerable biological importance. Notable, too, is that the call itself is very simple (Fig. 1) and that there is little or no individual or regional variation (Gilliard 1969, Beehler et al. 1986, Coates 1990). We doubt that either the growl or the musical whistle could be easily derived from the other by frequency modulation of the syrinx.

Because of the overall morphological similarity between the two Papuan populations, it is not clear whether any ecological differentiation has yet developed between the eastern and western allotaxa. There are no important differences in measurements between the two Papuan populations (Beehler, unpubl.).

The east-west boundary of the two Papuan forms corresponds to two major distributional barriers, the Ramu and Purari river basins. (The record of *intercedens* from Lake Kutubu, west of the Purari break, is in error [Schodde and Hitchcock 1968, Schodde, pers. comm.])

Coates (1990) reported hearing the western dialect near Yalumet, east of the Ramu, and near to where W. S. Peckover heard the eastern dialect (see Fig. 3). This implies that the two forms may be able to co-exist. In addition, Schodde (Coates 1990) reports a specimen with intermediate culmen feathering characteristics (a possible hybrid) at Futei, just east of the Purari barrier. It is obvious, then, that more fieldwork will be required to determine the nature of the interaction between the two Papuan forms. Is contact leading to coexistence, localized introgression, or interspecific territoriality? Are there populations with "hybrid" vocal characteristics? This would be relatively simple to determine by a field survey. We urge field workers to examine populations of *Ptiloris* in the vicinity of the Ramu and Purari basins in order to settle this question.

TORRESIAN BIOGEOGRAPHY

Our revised phylogeny suggests a minor reworking of Cracraft's (1986) general biogeographic hypothesis for the Australasian avifauna. As earlier postulated by Schodde and Calaby (1972), and

Kikkawa et al. (1981), the importance of the Torres Strait as a vicariance barrier should be considered minor. It appears that phylogenetic differentiation in taxa that range from the Papuan mainland southward to the eastern rainforests of Australia has been more heavily influenced by habitat barriers between the three eastern rainforest refuges within Australia than between Australia and New Guinea (Fig. 2). In *Ptiloris*, the major bouts of speciation apparently took place across continental nonforest habitat barriers (northern New South Wales/east-central Queensland/northern Queensland for *paradisus/victoriae/alberti*). Differentiation within the *magnificus* clade is only minor across Torres Strait (at the racial level), and is overshadowed by the degree of east-west differentiation on the Papuan mainland. Acknowledging that New Guinea and northern Australia were linked by a broad corridor of dry land during much of the Pleistocene (Walker 1972, Kikkawa et al. 1981), the geographic differentiation of the *Ptiloris magnificus* complex in Australia and New Guinea appears relatively straightforward. We envision that there existed a continuous Australo-Papuan distribution of the parent (ancestral) form, followed first by a vicariance event across the Ramu/Purari barrier (step 3 on Fig. 2), followed by a subsequent break of the trans-Torresian populations in the late Pleistocene (step 4 in Fig. 2).

East-west differentiation on the Papuan mainland is widespread in birds and other vertebrates (see, for example Mayr 1942, Schodde and Hitchcock 1972, Diamond 1972, Flannery 1990), and appears to outweigh the geographic differentiation that has occurred across the Torres Strait (Schodde and Calaby 1972, Kikkawa et al. 1981, Beehler, unpubl. analysis of forest birds). The remarkable genetic homogeneity of the tree *Acacia mangium* on either side of Torres Strait (Moran et al. 1989) corroborates this pattern. As indicated by the pattern of speciation in the riflebirds (Fig. 2), for Australasian rainforest birds geographic differentiation has occurred primarily between humid forest refuges in eastern Australia and in an east-west pattern in New Guinea (Diamond 1972). Torres Strait is a modern feature that has been of minor importance in this process.

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