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## Preliminary Results of an Ornithological Exploration of the North Coastal Range, New Guinea

BY JARED M. DIAMOND<sup>1</sup>

The present paper is preliminary to a full report on the birds that I collected in 1966 in the North Coastal Range of New Guinea (Bewani, Torricelli, and Prince Alexander mountains). As seen in figure 1, the backbone of New Guinea is formed by the central dividing range, which extends uninterruptedly from the base of the Vogelkop in the west to the tip of southeast New Guinea. To the north of the central ranges, and separated from them by the nearly coterminous lowland basins of the Markham, Ramu, Sepik, Idenburg, and Rauffaer rivers, are several isolated mountain ranges along the north coast. Earlier systematic exploration of three of these mountain "islands" (the Cyclops Mountains by Mayr, cf. Hartert, 1930; the Adelbert Mountains by Gilliard, cf. Gilliard and LeCroy, 1967; and the Huon Peninsula principally by Mayr, 1931) revealed marked differences at the subspecies and semi-species level between their montane avifaunas and the montane avifauna of the central ranges, and the same degree of endemism has now been found to characterize the montane avifauna of the North Coastal Range as well. Although a more detailed zoogeographical analysis of the North Coastal Range will be published elsewhere, the main patterns may be summarized here, as follows: the portion of the central ranges with

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<sup>1</sup> Department of Physiology, University of California Medical Center, Los Angeles, California.

which the hill-forest (2000–4500 feet) avifauna of the North Coastal Range has its closest affinities is the north slopes of the Snow Mountains 300 miles to the west and across the Idenburg Basin, rather than the eastern highlands 70 miles directly to the south across the Sepik Basin (cf. *Meliphaga orientalis citreola*); the depauperate mid-montane (> 4500 feet) avifauna shows the highest level of endemism and has

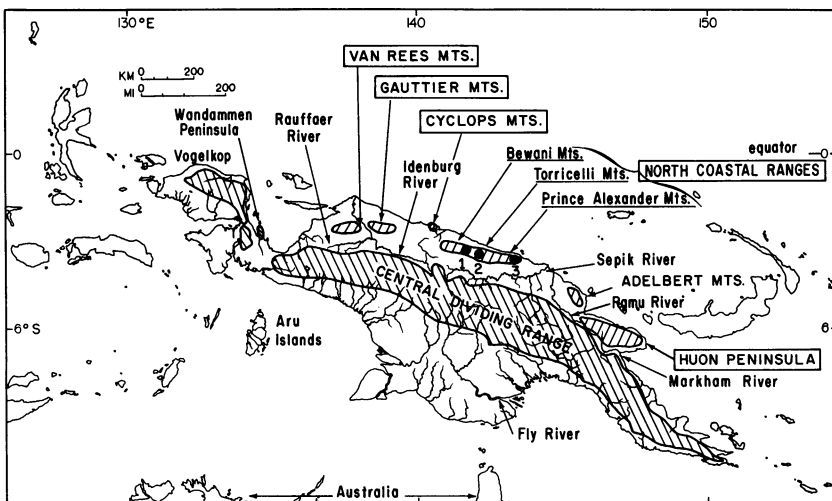


FIG. 1. New Guinea, showing some localities mentioned in the text. The principal mountain ranges over 4000 feet high are hatched: the mountains of the Vogelkop (Arfak and Tamrau mountains) and the central ranges, from upper left to lower right; the “northern mountain-islands” (Van Rees Mountains, Gauttier Mountains, Cyclops Mountains, North Coastal Range, Adelbert Mountains, Huon Peninsula), from lower left to upper right. Note that these “northern mountain-islands” are separated from the central ranges by lowland river basins. Collecting localities of the expedition are numbered: 1, Mt. Menawa and Utai in the Bewani Mountains; 2, Mt. Somoro, Mt. Nibo, and Miliom in the Torricelli Mountains; 3, Mt. Turu in the Prince Alexander Mountains.

arrived at random from the east (cf. *Eupetes leucostictus menawa*) and west (cf. *Crateroscelis robusta bastille*); affinities with the next mountain “island” to the east, the Adelbert Mountains, are negligible (cf. genus *Sericulus*); and there are closer affinities with the next mountain “island” to the west, the Cyclops Mountains, notably in the shared endemic species *Rallicula mayri* and *Ptiloprora mayri*, but also some marked differences (cf. races of *Crateroscelis robusta*).

Described here are eight new subspecies, the first record of the Golden

Bowerbird, *Sericulus aureus aureus*, for eastern New Guinea on the northern watershed, and the discovery that the *Meliphaga* race known as *citreola* and hitherto considered an altitudinal subspecies of *M. analoga* is actually a race of *M. orientalis*. Revisions are presented of the taxonomically difficult genera *Rallicula* and *Ptiloprora* and of the *Sericornis virgatus-beccarii-nouhuysi* complex, necessitated by problems in assessing the taxonomic status and affinities of the isolates in the North Coastal Range and Cyclops Mountains.

The localities mentioned below are:

Mt. Menawa (summit elevation 6185 feet), the highest peak in the North Coastal Range, lying in the Bewani Mountains at about latitude 3° 12' S., longitude 141° 40' E. Three of the endemic forms (*Eupetes leucostictus menawa*, *Epimachus fastosus ultimus*, and *Ptiloprora mayri acrophila*) are confined to the summit of Mt. Menawa, and numerous other species that have not differentiated occur in the North Coastal Range only on this peak.

Utai, a village and mission airfield to the southwest of Mt. Menawa and at its foot.

Mt. Somoro (summit elevation, 4620 feet), a peak in the Torricelli Mountains 10 miles northeast of Lumi Patrol Post, which is at latitude 3° 29' S., longitude 142° 2' E.

Mt. Nibo (summit elevation, 4955 feet), a peak in the Torricelli Mountains about 3 miles east of Mt. Somoro.

Miliom (elevation 1500 feet), a village 2 miles east of Lumi.

Mt. Turu (summit elevation, 3750 feet), a peak in the Prince Alexander Mountains at latitude 3° 37' S., longitude 143° 21' E.

Accounts of the expedition have been published elsewhere (Diamond, 1967b, 1968).

All measurements are in millimeters, and all weights are in grams.

### ***Rallicula mayri carmichaeli*, new subspecies**

TYPE: A.M.N.H. No. 789759; adult male; Mt. Nibo, Torricelli Mountains, Sepik District, Mandated Territory of New Guinea, 4500 feet; July 12, 1966; J. M. Diamond.

DESCRIPTION: In general, a large and dark form of *Rallicula* in which the loss of a black mantle has proceeded further in the male than in the female, so that the mantle is a mosaic of black and chestnut-brown in the female, and is a brown close to, but not the same as, the color of the forequarters in the male.

ADULT MALE: The upper parts appear at first glance to be uniformly dark chestnut-brown. In good light, the mid-back, lower back, and upper wing coverts (corresponding to the black area in *Rallicula forbesi*) are seen to be dull dark brown, replaced more or less abruptly by the chestnut-brown of the upper back and head; since both colors are dull,

the contrast is slight and easily overlooked. The nape is slightly darker, more charcoal-brown and less chestnut than the forehead, and with obscure dark tips to the feathers. The under parts (chin through upper belly) are dark chestnut-brown, somewhat lighter and brighter than the back. The lower belly and lower flanks are dull brown, with obscure light buff barring. The upper tail coverts and tail are chestnut-brown like the upper back and head, with obscure black barring on the upper tail coverts and distally on the tail. The upper surfaces of the remiges are blackish; the under sides are dark gray, with white bars on the inner webs at about 15-mm. intervals. A few obscure black and light buff bars or spots are present near the tips of the upper wing coverts. The legs are black, the bill is dark gray to blackish, and the iris is brown.

The adult female resembles the male, except that the dull dark brown dorsal region (mid-back and lower back, and upper wing coverts) has light buff spots at intervals of 5 to 10 mm., surrounded by black areas of varying extent which often merge with black areas surrounding adjacent spots, with the result that the mantle is a mosaic of black and brown areas. The proportion of black areas is highest on the upper wing coverts and scapulars (40 to 80% of the total area), so that the folded wing appears largely black rather than brown. The proportion is lower on the back, varying individually from slight (little more than in *Rallicula m. mayri*, where the proportion is only a few per cent) to about 20 per cent of the total area. Small buff spots are present on the outer web of the remiges corresponding to the position of the bars on the inner web. The obscure bars or spots near the tips of the upper wing coverts of the male are lacking in the female.

**RANGE:** Presently known only from the summits (4400 feet and upward) of Mt. Menawa and Mt. Nibo; probably occurs on the summits of a few of the other highest peaks in the Bewani and Torricelli mountains.

**MATERIAL:** Mt. Nibo (4500 feet), one male; Mt. Menawa (4400-6185 feet), three males, three females; July 12 to August 14, 1966.

**WEIGHTS AND MEASUREMENTS:** Wing, four males, 110, 111, 117 (type), 118; three females, 110, 111, 112. Tail, four males, 62 (type), 65, 66, 71; two females, 64, 67. Exposed culmen, four males, 25.5, 26 (type), 26, 26.5; three females, 23.5, 24, 26. Weight, two males, 131 (type), 136; two females, 111.8, 122.5.

#### DIFFERENTIAL DIAGNOSIS OF PRINCIPAL *RALLICULA* FORMS

This diagnosis is based on the examination of series of all named

*Rallicula* races, including all known specimens of *mayri* and *carmichaeli*, large series of *forbesi* and *rubra*, four specimens of *leucospila*, and the types of *R. rubra subrubra*, *R. rubra telefolminensis*, *R. forbesi steini*, *R. mayri mayri*, and *R. mayri carmichaeli*.

#### SIZE

The races of *R. rubra* are much smaller (table 1) than all the other forms.

#### PATTERN OF MANTLE

The ground color (i.e., not considering spots or streaks) is uniform chestnut-brown identical to the upper back in males of *R. rubra* and in both sexes of *R. m. mayri*; black, contrasting with the upper back, in both sexes of *R. leucospila*; blackish brown in females of *R. rubra* and generally in both sexes of *R. forbesi*; a mosaic of black and brown in females of *carmichaeli*; and dull dark brown, contrasting only slightly with the upper back, in males of *carmichaeli*. In many females of *R. forbesi* (but not of *R. rubra*) from southeast New Guinea (*R. f. forbesi*) and from the eastern highlands (*R. f. steini*) and in the type of *R. f. steini* from the Weyland Mountains, the mantle and wings are actually a mosaic of blackish brown and dark brown as in females of *carmichaeli*; the aggregate extent of the black areas is in some cases less than in *carmichaeli* on the wings but invariably more than in *carmichaeli* on the back, and the brown areas are darker than in *carmichaeli*. The mantle of males of *R. forbesi* both from southeast New Guinea and the eastern highlands is also quite variable, ranging from blackish brown contrasting strongly with the upper back to a brown scarcely darker than in *carmichaeli*. The transition between the blackish mantle and the chestnut-brown upper back is farthest anteriorly in *R. leucospila*, followed by *R. rubra* (females), and farthest posteriorly in *R. forbesi*.

#### SPOTS OR STREAKS

Spots or streaks on the mid-back and lower back and upper wing coverts are lacking in males of all forms except in males of *R. leucospila*, which have white streaks. Females of all forms have spots, which are white in *R. leucospila*; white or very pale buff in *R. rubra*; pale buff, occasionally but rarely white, in *R. forbesi*; most buffy in *R. m. mayri*; in *carmichaeli*, comparable with *R. m. mayri* in one female and to the buffiest *R. forbesi* in the other two. The number or density of the spots is higher in *R. rubra* (and perhaps in the one available *R. leucospila* female) than in *R. forbesi*, *mayri*, or *carmichaeli*. A few females of *R. rubra* but not those of *R. forbesi*, *mayri*, or *carmichaeli* have some of the spots extended into streaks, as in *R. leucospila* males.

#### DARKNESS

The darkness of the head and upper back is in the sequence *carmichaeli* (darkest) >> *mayri* = *forbesi* > *telefolminensis* = *leucospila* ≥ *rubra rubra* ≥ *rubra klossi* > *rubra subrubra* (lightest). The most marked difference is between the dark *carmichaeli* and the remaining forms, differences between which are relatively minor. The darkness of the under parts is in the sequence *carmichaeli* > *mayri* > *rubra rubra* = *leucospila* > *rubra telefolminensis* = *forbesi* > *rubra klossi* > *rubra subrubra*; these differences are minor.

TABLE 1  
COMPARATIVE MEASUREMENTS AND WEIGHTS OF THE GENUS *Rallacula*  
(Averages are given in parentheses.)

	Exposed Culmen	Wing	Tail	Weight
<i>mayri camichaeli</i>				
North Coastal Range				
4 males	25.5-26.5 (26)	110-118 (114.0)	62-71 (66.0)	131, 136
3 females <sup>a</sup>	23.5-26 (24.5)	110-112 (111.0)	63.5-67 (65.3)	112, 123
<i>mayri mayri</i>				
Cyclops Mountains				
4 males	23-25.5 (24.5)	111-115.5 (113.6)	65-71.5 (68.2)	123, 123, 129
1 female <sup>a</sup>	23	108.5	64.5	119
<i>leucospila</i>				
Vogelkop and Wandammen				
3 males	21-24 (22.3)	108-110 (109)	65.5-69 (67.5)	114, 125
1 female	23	105	58	—
<i>rubra rubra</i>				
Vogelkop				
2 males	24, 26	94, 97	63, 65	—
<i>rubra klossi</i>				
Weyland Mountains				
4 males	22-25 (23.7)	91-92 (91.2)	50.5-57.5 (54.8)	—
4 females	23.5, 24	85-94 (93.5)	46.5-56 (52.8)	—
<i>rubra subrubra</i>				
Snow Mountains				
11 males <sup>a</sup>	24-26 (25.0)	94-102 (97.4)	50.5-67 (60.5)	84, 88, 91
9 females	24-25 (24.6)	89-100 (96.2)	55-66 (60.4)	—

TABLE 1—(Continued)

	Exposed Culmen	Wing	Tail	Weight
<i>rubra telefolminensis</i>				
Telefomin				
2 males <sup>a</sup>	22, 23	93, 93	56.5	71, 76
<i>forbesi forbesi</i>				
Southeast New Guinea				
5 males	22.5–27.5 (25.5)	110–117 (112.3)	70.5–76 (73)	—
5 females	24–27 (25.2)	110–116 (113.4)	64.5–76 (69.5)	—
<i>forbesi dryas</i>				
Huon Peninsula				
2 males	23, 23.5	99–113	58–60	78–106 (88)
		104–111 <sup>b</sup>		
1 female	22.5	111	61	65–96 (82)
		101–109 <sup>b</sup>		
<i>forbesi steini</i>				
Eastern highlands, Telefomin,				
Snow and Weyland mountains				
7 males	24.5–26.5 (25.3)	106.5–115.5 (112.1)	62–71 (64.7)	88
9 females <sup>a</sup>	22–26 (24.1)	105–116 (107.9)	60–67 (63.0)	87–95 (91)

<sup>a</sup>Including type.

<sup>b</sup>From Mayr (1931, p. 709).

## BARRING OF TAIL

*Rallicula leucospila* has black bars on the upper tail coverts and tail, which are lacking in all races of *R. rubra*. *Carmichaeli*, *mayri*, and *R. forbesi* have barring but more obscure and variable than that of *leucospila*, and barring is nearly lacking in some *forbesi* specimens.

## NAPE

In males somewhat more than in females, the nape is generally darker, more brown, less chestnut, than the forehead and upper back and has obscure black tips; this coloration is most marked in *leucospila*, variably less so in *carmichaeli*, *mayri*, *forbesi*, *rubra rubra*, and *rubra telefolminensis*, and not at all in *rubra klossi*, *rubra subrubra*, and a few *forbesi* specimens.

## BARRING OF LOWER FLANKS AND UNDER TAIL COVERTS

Variably distinct light buff bars with black edges are present in all forms, except males of *R. rubra* in which they are very obscure or non-existent. This barring is more distinct in *carmichaeli* than in *mayri*.

## BARRING OF UNDER WING

The under wing has fairly broad white bars in most forms (including *carmichaeli*); these are reduced to large spots in some *forbesi* specimens, and are much reduced in the *rubra* races other than *rubra rubra*.

## UPPER WING COVERTS

The upper wing coverts have a few obscure black and light buff bars or spots at their tips in three out of four males of *carmichaeli* and in all four males of *mayri*, but not in other forms.

REMARKS: The taxonomy and evolution of the various forms of the endemic New Guinea genus *Rallicula* are placed in a new light by the discovery of this population, the most striking endemic form of the North Coastal Range.

As seen in figure 2, the distributions of *leucospila*, *mayri*, *carmichaeli*, and *forbesi* (including the races *forbesi*, *steini*, and *dryas*) are allopatric and cover all the principal mountain ranges of New Guinea. *Rallicula rubra* (including the races *rubra*, *klossi*, *subrubra*, and *telefolminensis*) shares the Vogelkop (at least the Arfak Mountains; no records from the Tamarau Mountains) with *leucospila*, and shares western New Guinea from the Weyland Mountains to Telefomin with *forbesi*. In most of western New Guinea *rubra* is more common than *forbesi*: the Third Archbold Expedition examined nearly 100 specimens of *rubra* and collected only one *forbesi* on the north slope of the Snow Mountains; various collectors on the south slopes of the Snow Mountains have obtained small numbers of *rubra* but no *forbesi*; Stein (1936, p. 57) found *rubra* "einer der häufigsten Vögel," *forbesi* "beträchtlich seltener" in the Weyland Moun-



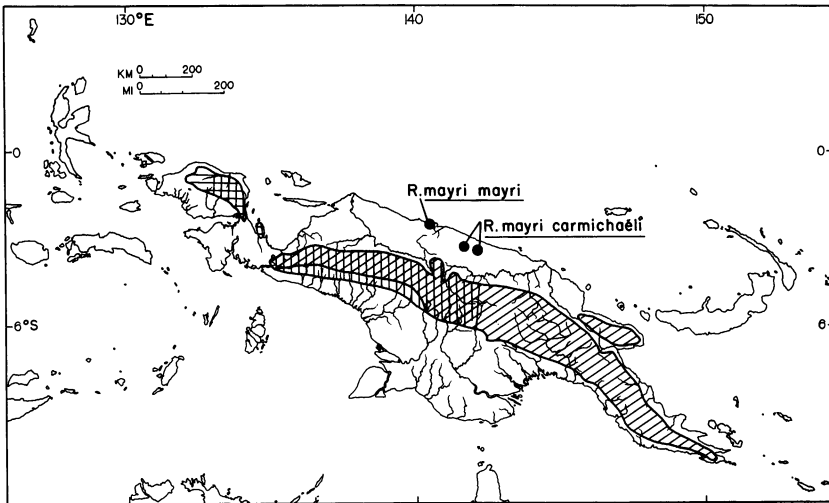


FIG. 2. Distribution of the principal forms of the endemic New Guinea genus *Rallricula*. Horizontal hatching, *R. leucospila*; vertical hatching, *R. rubra*; diagonal hatching, *R. forbesi*; solid dots, *R. mayri mayri* and *R. mayri carmichaeli*. All forms are allopatric to one another except for *R. rubra*, which shares the Vogelkop with *R. leucospila* and the western half of the central ranges with *R. forbesi*.

tains (northern watershed); but Gilliard considered *forbesi* more common than *rubra* at Telefomin, near the eastern limit of the range of *rubra*.

The ecological differences between *rubra* and *forbesi* are difficult to determine because almost all museum specimens of these shy rails were obtained by natives and the only published field observations are the fairly detailed ones of Stein (1936, pp. 56-57) and the brief remarks of Mayr and Rand (1937, p. 25). *Leucospila*, *forbesi*, *mayri*, and *carmichaeli* have been regularly collected down to 4000 to 4500 feet. All adequately documented specimens of *rubra* have been collected above 5700 feet (mainly above 6000 or 7000 feet) except on the south slope of the Snow Mountains, where *forbesi* is apparently missing and *rubra* was taken at 4200 feet (Ogilvie-Grant, 1915, p. 290). The limited available information suggests that niche differences may be largely altitudinal. Stein stated so explicitly (Stein, 1936, pp. 56-57; Hartert, Paludan, Rothschild, and Stresemann, 1936, p. 239) for the sympatric populations in the Weyland Mountains, where *rubra* lived at 5900 to 8200 feet and *forbesi* at 4900 feet. Similarly, in the area of sympatry at Telefomin, Gilliard's two specimens of *rubra* came from 7200 and 7300 feet, and his three specimens of *forbesi* from around 5850 feet (Gilliard and LeCroy,

1961, p. 35). No information is available about the altitudinal preference of *rubra* in the area of sympatry with *leucospila*, which lives at about 4300 to 6000 feet.

In addition to being sympatric with *leucospila* and *forbesi*, *rubra* differs in several morphological respects from *leucospila*, *forbesi*, *mayri*, and *carmichaeli*, which agree among themselves in these respects: in the smaller size of *rubra*, the absence of black barring on the upper tail coverts and tail of *rubra*, the reduction of barring on the lower flanks and under tail coverts, the reduction of the white bars in the under wing, and, less consistently, the less-dark nape.

Initially, an affinity of *mayri* and *carmichaeli* to *rubra* rather than to *forbesi* seemed indicated by the uniform dorsal coloration and absence of a dark mantle in *rubra* and *mayri*, characters that at first glance also seemed to hold for *carmichaeli*. A more detailed examination and the differential diagnosis given above show, however, that *mayri* and *carmichaeli* are related to *forbesi* rather than to *rubra* in this respect as well, and that *mayri* has lost and *carmichaeli* is losing its black mantle independently of *rubra*. Males of *carmichaeli* have a dull mantle which is abruptly demarcated from the upper back but contrasts so little with it as to be noticeable only in good light, when it is seen readily in two of the males and with great difficulty in the other two. This loss of contrast in *carmichaeli* is due to two factors: the mantle itself is lighter and much less blackish than in *forbesi*, and the forequarters are darker chestnut-brown than in any other *Rallacula* form. *Forbesi* itself shows much individual variation in the darkness of the mantle, which in some specimens of *forbesi* approaches but does not equal *carmichaeli*. In females of *carmichaeli* the loss of the mantle has proceeded much less far than in males. The loss of contrast in females is due partly to the dark forequarters, but mainly to the breaking up of the mantle into a black and brown mosaic, with the black areas surrounding each of the pale buff spots. This disruption of the mantle into a mosaic is also present, although to a less-marked degree, in many females of *forbesi*. The loss of the contrasting mantle in *mayri* is complete in the male, and nearly complete in the female, in which there is only a narrow black margin to each buff spot. Thus, in respect to the distinctness of the mantle, which provides the most obvious difference between *mayri* and *forbesi*, *carmichaeli* is intermediate, but much closer to *mayri* in the male and variable but on the average equidistant in the female. *Carmichaeli* differs from both *mayri* and *forbesi* in the much darker forequarters.

In the respects mentioned in the previous paragraph but one, the affinities of *leucospila* are with *forbesi*, *mayri*, and *carmichaeli* rather than

with *rubra*. *Leucospila* differs from all other forms in the streaked back of the male. In a number of other minor features it resembles *rubra* more than the other forms, viz., the anterior position of the border of the mantle, the white rather than buff dorsal spots of the female, perhaps the relatively high density of these spots, and the dorsal streaks in a few females of *rubra* foreshadowing the male of *leucospila*.

Compared with the differences between the five main divisions of *Rallicula* (*carmichaeli*, *forbesi*, *leucospila*, *mayri*, *rubra*), the differences among the races of *rubra* (*rubra*, *klossi*, *subrubra*, and *telefolminensis*) and among the races of *forbesi* (*forbesi*, *steini*, and *dryas*) are very minor. The large series of *R. forbesi* in particular shows great individual variability of coloration in all populations, and the only consistent racial characters appear to be the slighter bill, short tail, and short wing of *dryas* and the long tail of *forbesi*. *Dryas* has been contradictorily characterized as much darker than *forbesi* (Mayr, 1931, p. 709), much more brownish, less blackish, dorsally (Mayr and Gilliard, 1954, p. 335), and dark olive-brown rather than black dorsally (Rand and Gilliard, 1967, p. 115), but the three *dryas* specimens available to me differ among themselves in this respect and can each be well matched by darker or lighter specimens of *forbesi*.

It seems likely from the above discussion that all the *Rallicula* forms previously constituted a superspecies or polytypic species, with the ancestor of *leucospila* on the Vogelkop, and *rubra* and *forbesi* on the central range in western and eastern New Guinea, respectively; that *rubra* reinvaded most of the range of *leucospila*, and *forbesi* reinvaded most of the original range of *rubra*; that, as with so many cases of recently completed speciation in New Guinea montane birds, sympatry involves altitudinal exclusion; that in the areas of sympatry *rubra* was displaced upward from the original *Rallicula* altitudinal range and diverged furthest from the common ancestor morphologically in size and in the other respects mentioned previously; and that *mayri* and *carmichaeli* are clearly closer to *forbesi* than to *rubra*, whereas the position of *leucospila* is more difficult to decide.

The somewhat arbitrary decision whether to regard the allopatric forms *leucospila*, *mayri*, *carmichaeli*, and *forbesi* as equal members of a superspecies or to rank some as subspecies of others involves at best a guess about the isolating mechanisms, which are completely unknown in *Rallicula*. The fact that members of both sympatric pairs (*leucospila-rubra*, *rubra-forbesi*) have very similar females but very different dorsal patterns in the males (streaked on black in *leucospila*, uniform brown in *rubra*, unstreaked black mantle in *forbesi*) suggests that the male dorsal

pattern might be important. The pattern of *leucospila* (as unlike *forbesi* as *rubra* is unlike either), as well as the above-mentioned minor features, suggests that *leucospila* would behave as a good species toward *forbesi-mayri-carmichaeli*, and I favor retaining it as a species. The latter three might at one extreme be considered three distinct species, at the other extreme as conspecific. Females of *forbesi*, *mayri*, and *carmichaeli* differ much more obviously from one another than do females of the sympatric pairs (*leucospila-rubra* and *rubra-forbesi*). Most males of *forbesi* differ nearly as much from those of *mayri* and *carmichaeli* in the dorsal pattern as from males of *rubra*, so that *forbesi* is also best kept separate. Whereas *mayri* and *carmichaeli* differ from each other significantly in general darkness and in the extent of reduction of the mantle (strikingly so in the female), they are clearly closer to each other than either is to *forbesi* or than *forbesi* is to *leucospila* or *rubra*. The obscure mantle in males of *carmichaeli* but not of *mayri*, although interesting in tracing the descent from *forbesi*, could hardly serve to distinguish males of *mayri* from those of *carmichaeli* in the eyes of a female. Thus, *mayri* and *carmichaeli* are best considered conspecific with each other, and in the same superspecies as *forbesi* and *leucospila*, yielding the following classification:

*Rallicula leucospila*: Arfak, Tamrau, and Wandammen mountains

*Rallicula rubra* (races *rubra*, *subrubra*, *klossi*, *telefolminensis*): Arfak Mountains and central ranges from Weyland Mountains to Telefomin

*Rallicula forbesi* (races *forbesi*, *steini*, *dryas*): Central ranges from Weyland Mountains to southeast New Guinea and Huon Peninsula

*Rallicula mayri mayri*: Cyclops Mountains

*Rallicula mayri carmichaeli*: Bewani and Torricelli mountains

It is a pleasure to name this interesting new form in honor of Dr. Leonard Carmichael, Vice President for Research and Exploration, the National Geographic Society, as a token of my gratitude to him and to the Society for their encouragement and generous support of my explorations in New Guinea.

#### ***Aegotheles wallacii manni*, new subspecies**

TYPE: A.M.N.H. No. 789760; adult female; Mt. Menawa, Bewani Mountains, Sepik District, Mandated Territory of New Guinea, 3200 feet; August 2, 1966; J. M. Diamond.

DIAGNOSIS: In size *manni* is intermediate between *wallacii* and *gigas*. As seen in table 2, which summarizes measurements of all known specimens of the species, the wing of both *manni* males is longer than the wing in all *wallacii* males and shorter than that in both *gigas* males, and the wing of the *manni* female is longer than the wing in all *wallacii*

TABLE 2  
COMPARATIVE MEASUREMENTS OF *Aegotheles wallacii*

	Wing	Tail
<i>manni</i>		
North Coastal Range		
2 males	125.5, 126	101, 107
1 female <sup>a</sup>	130.5	104
<i>gigas</i>		
Weyland Mountains		
2 males <sup>a</sup>	128, 130 <sup>a</sup>	116 <sup>a</sup> , 117
6 females	127, <sup>b</sup> 132, 133, 134, 135, 137	102, <sup>b</sup> 109.5, 115, 115, 116, 117
<i>wallacii</i>		
Vogelkop		
1 male	122.5	106
2 females <sup>a</sup>	121, <sup>c</sup> 123 <sup>a, d</sup>	103 + X, <sup>a, d</sup> 105 <sup>c</sup>
South New Guinea		
2 males	118, 122	108, 109
2 females	117, 126	94, 106 <sup>d</sup>
Aru Islands		
2 males	115.5, 117 <sup>d</sup>	95, 103 <sup>d</sup>
2 females	113, <sup>d</sup> 117	99, 100 <sup>d</sup>
1 (sex?)	124	101

<sup>a</sup>Including type.  
<sup>b</sup>From Hartert, Paludan, Rothschild, and Stresemann (1936, p. 225).  
<sup>c</sup>From Mayr and de Schauensee (1939, p. 116).  
<sup>d</sup>From Mayr and Rand (1936, p. 241).

females and shorter than that in all but one *gigas* female. The tail is shorter than that of *gigas* and comparable with that of *wallacii*. The superciliary stripe, the ground color of the under parts, and the spots on the outer webs of the primaries are more whitish, less buffy, than in the other two races. The upper parts are darker, more blackish brown, less brown, than in the other two races. The Karimui specimen of *wallacii*, collected in 1965, is no darker than four *wallacii* specimens collected 30 to 60 years ago, making foxing unlikely as an explanation. Suggestions of a white collar on the hind neck are present in two *manni* specimens and more faintly indicated in the third; present in two *gigas* specimens, absent from five; faintly indicated in one *wallacii* specimen (an Aru Island male), absent from four.

RANGE: Presently known only from Mt. Menawa at the western end and Mt. Turu at the eastern end of the North Coastal Range; presumably the intervening parts of the North Coastal Range as well.

**MATERIAL:** Mt. Menawa (3200 feet), one male, one female; Mt. Turu (3600 feet), one male; August 2 to September 11, 1966.

**WEIGHTS AND MEASUREMENTS:** For measurements, see table 2. Weight, one male, 50.5; one female (type), 52.

**COMPARATIVE MATERIAL:** *Aegotheles w. gigas*: Weyland Mountains, two males, five females (collected by Shaw-Mayer). *Aegotheles w. wallacii*: four males (Manokwari, collected by Stein; Fly River, collected by Archbold, Rand, and Tate; Karimui, collected by Diamond; Aru Islands, collected by Kühn), two females (Eilanden River, collected by Meek; Aru Islands, collected by Frost), one (sex?) (Aru Islands). All these specimens are in the American Museum of Natural History, except for two of the Aru Islands specimens which are in the Museum of Comparative Zoology, Harvard University. In addition to these 14 specimens and the three *manni* specimens, six other specimens of this species are known to exist, and their measurements as reported in the literature are included in table 2: *gigas*, one female (Weyland Mountains, collected by Stein); *wallacii*, one male (Aru Islands, collected by Goodfellow), four females (Vogelkop, type, collected by Wallace; Vogelkop, collected by Ripley; Wataikwa River, collected by the British Ornithological Union Expedition; Aru Islands, collected by the Challenger Expedition).

**REMARKS:** All three specimens of the new subspecies were caught in mist-nets.

*Aegotheles wallacii* has hitherto been considered to have a perplexingly discontinuous altitudinal distribution, with a small-size population (*wallacii*) in the lowlands of the Vogelkop and southwest New Guinea, and a large-sized population (*gigas*) at 5000 feet in the Weyland Mountains. Given this peculiar range, Rothschild's inclination (1931, p. 268) to regard *gigas* as a district species is understandable. With the discovery of the new population, which is intermediate in altitudinal range (3200 to 3600 feet) as well as in size between *wallacii* and *gigas*, *Aegotheles wallacii* begins to make sense as a species. Re-examination of the available information about this rare bird yields the following picture (see fig. 3 for localities mentioned):

*Aegotheles w. gigas* is known from only seven specimens collected in the Weyland Mountains by Shaw-Mayer, stated to be from 5000 feet (Rothschild, 1931, p. 268), and one specimen collected in the Weyland Mountains by Stein, stated to be from 1200 meters (= 3940 feet) (Hartert, Paludan, Rothschild, and Stresemann, 1936, p. 226). Stein regularly noted the elevation of his Weyland specimens to the nearest 100 meters, and his field notes (Stein, 1936) show that he paid careful attention to

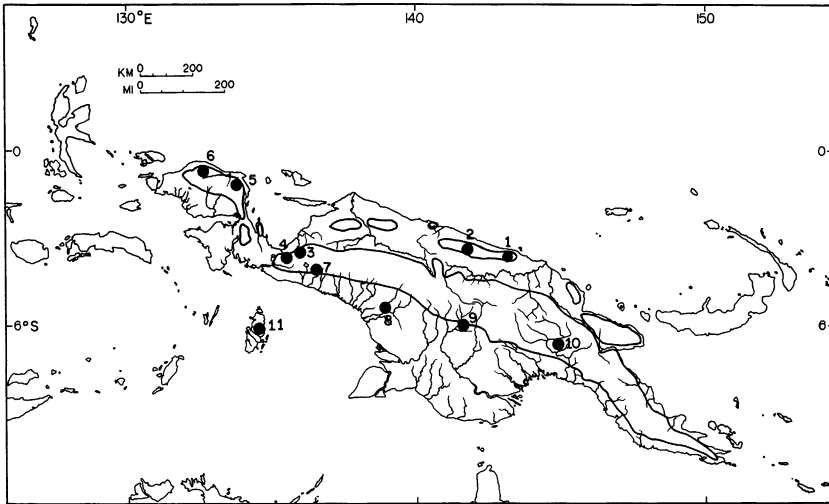


FIG. 3. Localities at which *Aegotheles wallacii* has been collected, superimposed on outlines of the principal mountain ranges of New Guinea. *A. w. manni*: 1, Mt. Turu; 2, Mt. Menawa, North Coastal Range. *A. w. gigas*: 3, Gebroeders Range; 4, Mt. Kunupi, Weyland Mountains. *A. w. wallacii*: 5, Manokwari (Arfak Mountains); 6, Tamrau Mountains, Vogelkop; 7, Wataikwa River; 8, Eilanden River; 9, Fly River; 10, Karimui; 11, Aru Islands. Localities 9, 11, and possibly 8 are near sea level; the remainder are in mountains (about 1500 to 5000 feet).

altitudinal distribution. Shaw-Mayer's Weyland labels give elevations to the nearest 1000 feet, and examination of these records for species of well-known altitudinal distribution suggests that some of his altitudes may be overestimates.

*Aegotheles w. wallacii* is known from 12 specimens from the Vogelkop, southern New Guinea west of longitude 145° E., and the Aru Islands. The five Aru Islands specimens certainly came from near sea level; the Archbold-Rand-Tate specimen, from 330 feet; my Karimui specimen, from 3650 feet; and Ripley's specimen, from 1725 feet. The altitudes of the remaining four specimens are surely under 3000 feet but are not known more exactly.

The conclusions these records suggest are that *Aegotheles wallacii* is basically the owlet-nightjar of hill forest (about 2000 to 5000 feet), living in an altitudinal band above its lowlands congener *A. bennettii* and below its mid-montane congeners *A. insignis* and *A. albertisii*; and that it descends to sea level in the faunally distinct south New Guinea area (Fly River, Merauke District, and Aru Islands) that lay on the main route

of faunal exchange with Australia when the Sahul Shelf was above sea level and formed a land bridge. There are at least 20 other species or superspecies (see Rand and Brass, 1940, p. 378; Mayr, 1941, p. x; and pp. 29, 37, 38 of this paper, for some examples) that are confined to the hills or mountains elsewhere in New Guinea but that have populations at sea level in the lowlands of south New Guinea and the Aru Islands. At least nine of these (not including *Aegotheles wallacii*) still have isolated populations on the Cape York Peninsula of Australia.

It is a pleasure to name this new race for the Honorable Sir Alan Mann, Chief Justice of the Supreme Court of Papua and New Guinea, in honor of his contributions to faunal exploration as well as to jurisprudence in New Guinea.

***Coracina montana bicinia*, new subspecies**

TYPE: A.M.N.H. No. 789761; adult female; Mt. Nibo, Torricelli Mountains, Sepik District, Mandated Territory of New Guinea, 2800 feet; July 15, 1966; J. M. Diamond.

DIAGNOSIS: *Coracina m. bicinia* is distinguished by being larger than the largest population of *montana*, and by having the black patch on the chin and throat of the female of considerably greater extent.

RANGE: Medium elevations (above about 2700 feet) in the Torricelli Mountains, Bewani Mountains, and Cyclops Mountains.

MATERIAL: Mt. Somoro, eight males, five females, one immature female; Mt. Nibo, four males, four females, one immature female; Mt. Menawa, seven males, six females, one immature male, two immature females; July 4 to August 13, 1966.

WEIGHTS AND MEASUREMENTS: Wing, 17 males, 140 (three), 141, 142, 143 (three), 144 (two), 145, 146, 147, 148, 150 (two), and 152; 13 females, 134, 135 (two), 137 (four), 138 (two), 139, 140 (two, including type), and 141; two immature males, 135 and 137; four immature females, 132 (two), 134, and 139. Weight, 15 males, 72, 75, 77, 77.4, 80, 80.3, 80.5, 81, 82.3, 83.5 (three), 86, 86.5, and 88; 13 females, 72, 73.2, 73.5, 74, 74.5, 74.8, 75.5, 79, 80.3, 81, 81.8, 82, and 85; one immature male, 72.4; three immature females, 68.5, 70, and 72.8.

REMARKS: As summarized in table 3, the size decreases clinally from west to east (Vogelkop to southeast New Guinea) on the central range. The small southeast New Guinea birds have been separated as *minus*, but this race has not been recognized by recent authors (e.g., White, 1948) because the change in size is clinal. The isolated populations of *bicina* are larger than the largest (i.e., westernmost) populations of *mon-*



*tana*, with very little overlap. Of 88 *montana* specimens measured, only one Vogelkop male (142 mm.), one Vogelkop female (135 mm.), and two Snow Mountains females (135 mm.) had longer wings than the smallest male (140 mm.) and female (134 mm.) of *bicinia*. There is no overlap between *bicinia* and the *montana* population on the central range at the same longitude (Telefomin). In addition, it should be noted that size increases with altitude at a given locality (Rand, 1942b, p. 463).

TABLE 3  
COMPARATIVE MEASUREMENTS OF THE WING OF *Coracina montana*  
(Averages are given in parentheses.)

	Males	Females
<i>montana</i>		
Vogelkop, 11 males, 3 females	135-142 (138.5)	131-135 (132.7)
Weyland Mountains, 3 males, 3 females	133-138 (136.0)	125-134 (130.0)
Snow Mountains, 9 males, 10 females	134-140 (136.0)	127-135 (129.8)
Telefomin, 5 males, 3 females	124-133 (131.0)	127-131 (129.0)
Eastern highlands, 14 males, 8 females	127-135 (130.9)	124-131 (126.4)
Southeast New Guinea, 10 males, 9 females	125-133 (130.4)	121-128 (126.0)
<i>bicinia</i>		
North Coastal Range, 15 males, 13 females	140-152 (144.5)	134-141 (137.5)
Cyclops Mountains, 2 males, 2 females	142, 143 (142.5)	138, 139 (138.5)

Virtually all *montana* specimens measured were collected between 4000 and 9000 feet, whereas all *bicinia* specimens were collected between 2800 and 5400 feet. The geographical difference in size between *bicinia* and *montana* is therefore even greater than indicated by the average values of table 3, if comparisons are made at the same altitude.

In adult females from the North Coastal Range the black area on the chin and throat extends on the average about 25 mm. along the ventral midline from the base of the bill and varies between 19 and 35 mm. The patch is also large in the two females from the Cyclops Mountains (22 and 26 mm.), as already noted by Hartert (1936, p. 90). Although a few females of *montana* from the Snow Mountains have patches comparable in extent with the average for *bicinia*, the average extent for *montana* is much less (about 10 mm.). The difference is not due to variations in skinning technique, since the difference is still an obvious one when specimens of both *bicinia* and *montana* stuffed by Mayr or by my native assistants are compared.

This race is named *bicinia* for its precisely synchronized and conspicuous duets, which are among the most distinctive sounds of the New Guinea forest (Diamond and Terborgh, 1968).

***Crateroscelis robusta bastille*, new subspecies**

TYPE: A.M.N.H. No. 789762; adult male; Mt. Nibo, Torricelli Mountains, Sepik District, Mandated Territory of New Guinea, 4750 feet; July 14, 1966; J. M. Diamond.

DIAGNOSIS: The new race is nearest *sanfordi*, but differs from topotypical *sanfordi* of the Wandammen Peninsula (six specimens compared, including type) in that the upper parts are dull dark olive instead of rich brown to olive-brown, and in that the under parts are slightly paler. From *sanfordi* of the Weyland Mountains (12 specimens compared, including type of "*steini*") *bastille* differs in that the upper parts are more olive and less brown, the under parts are slightly darker and richer brown, less gray, and there is less contrast between the light throat and darker breast and belly. *Robusta*, *deficiens*, *peninsularis*, and *ripleyi* are quite different in that the under parts are gray rather than brown.

RANGE: Presently known only from the summits (4500 feet and upward) of Mt. Menawa and Mt. Nibo; probably the summits of a few of the other highest peaks in the Bewani and Torricelli mountains.

MATERIAL: Mt. Nibo, two males; Mt. Menawa, seven males, one female, two (sex?); July 12 to August 14, 1966.

WEIGHTS AND MEASUREMENTS: Wing, seven males, 58, 59, 60 (type), 60, 61, 61, and 62; one female, 60; two (sex?), 59 and 60. Weight, six males, 18.0, 18.2, 19.0 (type), 19.0, 19.3, and 19.7; one female, 19.5; one (sex?), 18.8.

REMARKS: The populations of this mid-montane species fall into two groups, the distribution of which forms a peculiar mosaic (see fig. 4). The gray-breasted group inhabits the central range in eastern New Guinea (*robusta*), the easternmost "north mountain-island" (Huon Peninsula: *robusta*), a "north mountain-island" in west New Guinea (Cyclops Mountains: *deficiens*), and the Arfak (*peninsularis*) and Tamrau (*ripleyi*) mountains of the Vogelkop at the western extremity of New Guinea. The brown-breasted group was previously known from the central range and outlying Wandammen Peninsula of western New Guinea (*sanfordi*), and now turns up on "north mountain-islands" of eastern New Guinea (*bastille*) between the gray-breasted populations of the Huon and Cyclops "islands."

The Weyland population was separated as *steini* and, taken alone, would in fact be just separable from topotypical *sanfordi* of the Wandammen Peninsula on the basis of paler under parts, paler throat contrasting with the darker breast and belly, and slightly more olive, less

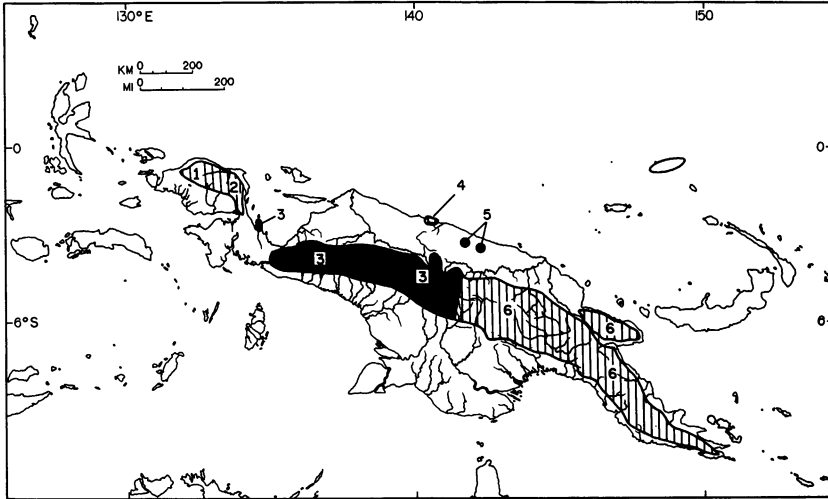


FIG. 4. Ranges of the subspecies of *Crateroscelis robusta*. Vertical hatching, gray-breasted races: 1, *ripleyi*, Tamrau Mountains; 2, *peninsularis*, Arfak Mountains; 4, *deficiens*, Cyclops Mountains; 6, *robusta*, Huon Peninsula and eastern half of the central ranges. Solid shading, brown-breasted races: 3, *sanfordi*, Wandammen Peninsula and western half of central ranges; 5, *bastille*, North Coastal Range.

brown, upper parts. When the Third Archbold Expedition collected in the Snow Mountains a large and variable series, some of which were as rich brown as *sanfordi* and others of which were as olive-brown dorsally and as pale ventrally as *steini*, Rand (1942b, p. 468) synonymized *sanfordi* with *steini*. Comparison of 70 of Rand's Snow Mountains specimens with *bastille* shows that, although most Snow Mountains birds are darker and richer brown ventrally than *bastille*, a few of the palest Snow Mountains birds are comparable, but that the Snow Mountains birds with the palest under parts and most olive backs are still less olive, less dark, and browner dorsally than *bastille*, and that most of Rand's series differs more markedly in these respects. *Bastille* thus represents one extreme of dorsal coloration, with the Wandammen population and the brownest Snow Mountains birds at the other extreme and the Weyland population intermediate but nearer the Wandammen series. There is no difference between the Mt. Menawa and Mt. Nibo specimens.

***Eupetes leucostictus menawa*, new subspecies**

TYPE: A.M.N.H. No. 789763; adult male; Mt. Menawa, Bewani

TABLE 4  
COMPARATIVE MEASUREMENTS (IN MILLIMETERS) OF THE WING OF *Eupetes leucostictus*  
(Averages are given in parentheses.)

	Males	Females
<i>menawa</i>		
Mt. Menawa, 2 males, 2 females	79, 79	76, 76
<i>loriae</i>		
Southeast New Guinea, 14 males, 7 females	78-84 (80.6)	77-79 (77.9)
<i>loriae</i>		
Eastern highlands, 4 males, 4 females	84-86 (85.0)	77-79 (78.0)
<i>amabilis</i>		
Huon Peninsula, 4 males, 2 females	80-87 (83.5)	77, 80 (78.5)
<i>sibilans</i>		
Cyclops Mountains, 8 males, 6 females	79-82 (80.6)	75-80 (77.8)

Mountains, Sepik District, Mandated Territory of New Guinea, 4500 feet; August 8, 1966; J. M. Diamond.

DIAGNOSIS: The new race is nearest toptotypical *loriae* of southeast New Guinea, but differs in that the extensive olive wash of the under parts, which covers most of the breast and flanks, to leave only a small area along the midline of the belly blue, is brighter and more pronounced in both sexes and particularly in the males; and in the slightly darker chestnut crown, brighter olive back, and smaller size (see table 4). The differences are more marked when compared with *loriae* of the eastern highlands, which has the olive wash of the under parts considerably smaller in extent and the back duller olive. *Sibilans* of the Cyclops Mountains differs in having the olive wash of the under parts limited to the sides of the flanks and a distinct breast band, leaving most of the belly and lower breast blue; and in the lighter, duller olive back and the slightly lighter and brighter chestnut crown. *Amabilis* of the Huon Peninsula differs in being blue below with almost no olive wash, and considerably less bright olive above. *Leucostictus* of the Vogelkop differs in having white spots on the black triangle on the upper breast, in the less extensive and duller olive wash below, and in the lighter and duller olive back. *Centralis* of the Snow Mountains and *mayri* of the Wandammen Peninsula differ strikingly in that the back is chestnut, not olive.

RANGE: Known only from the summit (4100 feet and upward) of Mt. Menawa.

MATERIAL: Mt. Menawa, two males, two females; August 8 and 12, 1966.

WEIGHTS AND MEASUREMENTS: Wing, two males, 79 (type) and 79; two females, 76 and 76. Exposed culmen, one male (type), 20; two females, 17.5 and 19. Weight, one male, 47.5; one female, 49.2.

REMARKS: In this species, as in *Crateroscelis robusta*, the western races *centralis* and *mayri* are very unlike the eastern races *loriae* and *amabilis*, and the Cyclops population *sibilans* and (surprisingly) the Vogelkop population *leucostictus* resemble the eastern populations. However, the Mt. Menawa population belongs to the eastern group in *Eupetes leucostictus*, whereas it belongs to the western group in *Crateroscelis robusta*.

### ***Sericornis virgatus boreonesioticus*, new subspecies**

TYPE: A.M.N.H. No. 789764; adult male; Mt. Somoro, Torricelli Mountains, Sepik District, Mandated Territory of New Guinea, 4450 feet; July 8, 1966; J. M. Diamond.

DIAGNOSIS: The new race is a member of the *virgatus-beccarii-nouhuysi* species groups. It is closest to the race *jobiensis* and is also related to *virgatus* and *imitator*, e.g., in that the forehead, loreal region, and eye ring are ochraceous and in that light tips to the upper wing coverts are either narrow (16 specimens) or lacking (25 specimens). *Boreonesioticus* differs from *jobiensis*, *virgatus*, and *imitator* in the greater extent and depth of the ochraceous wash on the chin (virtually lacking in *imitator*, reduced in *virgatus* and *jobiensis*) and in the darker bill, which is blackish from above and blackish to medium horn-colored from below. The back is more olive, less brown, than that of *virgatus* (which scarcely contrasts with the brown crown), slightly darker than that of *imitator*, and close to that of *jobiensis* but a trifle darker. A lemon wash on the belly, which is present in almost all specimens of *jobiensis* and *imitator* and is absent from *virgatus*, is present in half of the *boreonesioticus* specimens, absent from or indistinct in the others. The dusky wash on the breast averages darker than that in *jobiensis* and slightly darker than that in *imitator*. *Imitator* differs, in addition, in the reduction of the ochraceous color of the forehead and face, in the presence of obscure frontal spots, and in that the light tips to the upper wing coverts are almost invariably present. The size of *boreonesioticus* is like that of *jobiensis* and that of *virgatus*, and is slightly smaller than that of *imitator* (cf. table 5).

The races *cyclopum*, *wondiwoi*, and *weylandi* ("cyclopum group") all differ from *virgatus*, *jobiensis*, *imitator*, *pontifex*, and *boreonesioticus* ("*virgatus* group") in the more distinct, dark, upper wing coverts, with contrasting white tips in all specimens, the distinct white pattern of the forehead and lores, the whitish throat, the distinct lemon wash on the

TABLE 5  
COMPARATIVE MEASUREMENTS AND WEIGHTS OF *Sericornis virgatus*,  
"virgatus" GROUP OF RACES

	Culmen (from Base)	Wing	Weight
<i>boreonesioticus</i>			
North Coastal Range			
29 males <sup>a</sup>	13.5–16.5	55–61	10.4–14.5
16 females	12.5–17	52–58	10.8–14.7
<i>jubiensis</i>			
Japen Island			
3 males	15.5, 16, 16	55, 60, 62	12, 12.5, 13.5
4 females	14, 15, 15.5	55, 55, 56, 56	11.5, 12, 12.5, 12.6
<i>imitator</i>			
Vogelkop			
3 males <sup>a</sup>	15, 15, 16	60, 62, 63	12.5, 13.5, 14
1 female	14.5	55	11
4 females <sup>b</sup>	15–16	55, 55.5, 58, 59	
<i>virgatus</i>			
Sepik Mountains			
1 female	15.5	55	—
4 males <sup>c</sup>	—	58, 59, 59, 60	—
6 females <sup>c</sup>	—	54, 55, 55, 56, 57, 58	—

<sup>a</sup>Including type.

<sup>b</sup>From Mayr (1937, p. 12).

<sup>c</sup>From Stresemann (1923, p. 13).

belly, and the very pale bill. *Idenburgi*, which approaches the *virgatus* group, differs in the much duskier under parts, in the presence of a somewhat indistinct white pattern and lack of ochraceous color on the forehead and lores, and in the absence of ochraceous color from the chin, which is often whitish with obscure speckles. *Pontifex* was not available for comparison, but, from published descriptions (Stresemann, 1921, p. 34, and 1923, p. 12; Mayr, 1937, p. 19), it must be larger, browner above and yellower below, and it has a pale bill.

It is interesting that *boreonesioticus* is more similar to *jubiensis* than to the geographically much closer *cyclopus*, *idenburgi*, and *virgatus* populations. Mayr (1937, p. 5) has commented on the irregular geographical variation in this superspecies.

RANGE: The North Coastal Range (Bewani, Torricelli, and Prince Alexander mountains) between 2100 and 4500 feet, rarely to 4800 feet.

MATERIAL: Mt. Menawa (2200 to 4500 feet), 12 males, four females,

one juvenile female, five (sex?); Mt. Somoro (3200 to 4500 feet), seven males, six females; Mt. Nibo (2500 to 4750 feet), four males, two females, three (sex?); Mt. Turu (2800 to 3750 feet), six males, four females, three (sex?).

**WEIGHTS AND MEASUREMENTS:** Wing, 24 males, 55, 56 (two), 57 (eight), 58 (five), 59 (four, including type), 60 (three), and 61; 13 females, 52 (two), 53, 54 (two), 55 (two), 56 (three), 57, and 58 (two); five (sex?), 54 (two), 55, 57, and 58. Culmen (from base), 24 males, 13.5 (two), 14, 14.5 (two), 15 (three), 15.5 (six), 16 (eight, including type), and 16.5 (two); 13 females, 12.5, 13.5, 14, 14.5 (two), 15 (six), 15.5, and 17; five (sex?), 12.5, 15 (three), and 15.5. Weight, 27 males, 10.4, 11.0, 11.4, 11.6, 11.7, 11.8, 12.0 (two), 12.2, 12.3 (two), 12.4 (two), 12.6, 12.7 (three), 12.8, 13.0 (two), 13.3 (two), 13.5 (four), and 14.5; 15 females, 10.8, 11.0, 11.4, 11.5, 11.7, 11.8 (two), 12.3, 12.5, 12.6, 12.8, 13.5, 13.7 (two), and 14.7; one juvenile female, 9.6; five (sex?), 10.3, 10.7, 10.8, 11.0, and 11.9.

**IRIS:** Usually orange-brown, often red-brown or reddish, infrequently dull brown.

**COMPARATIVE MATERIAL:** *Sericornis v. jobiensis*: Three males (including type), four females; Japan, collected by Stein. *Imitator*: Three males (including type), one female, three (sex?); Vogelkop, collected by Mayr. *Virgatus*: One female; Mäanderberg, collected by Bürgers. *Idenburgi*: Three males (including type), three females, one (sex?); north slopes of Snow Mountains, collected by Rand. *Cyclopus*: Four males (including type), one female, one (sex?); Cyclops Mountains, collected by Mayr. *Wondiwoi*: Three males (including type), one female; Wandammen Peninsula, collected by Mayr. *Weylandi*: Five males (including type), three females; Weyland Mountains, collected by Stein. Detailed comparisons of the races *beccarii*, *randi*, *dubius*, *minimus*, *nouhuysi*, *cantans*, *stresemanni*, *oorti*, *monticola*, *magnirostris*, and *viridior*, which appear not to be conspecific with *boreonesioticus*, *virgatus*, *idenburgi*, or other members of the “*cyclopus*” or “*virgatus*” groups, were also made, but these races are not rediagnosed here because their morphology was thoroughly reviewed by Mayr (1937).

**REMARKS:** The warbler genus *Sericornis* of the Australian and Papuan region has continued to pose difficult problems for taxonomists. Many of these problems were clarified in a review by Mayr (1937), but some remain, particularly in regard to 18 races which may be termed the *virgatus-beccarii-nouhuysi* complex. Most or all of these 18 races clearly arose from the superspecies which includes the allopatric Australian semispecies *frontalis*, *maculatus*, and *humilis*. Representatives of the com-

plex occur on all the mountains of New Guinea and in the lowlands of south New Guinea, the Aru Islands, and the Cape York Peninsula of Australia. Since sympatric pairs of forms occur together along the northern watershed of New Guinea's central range and on the Vogelkop, at least two species must be involved. The sources of difficulty in drawing species limits are that morphological differences among the forms vis-a-vis one another and vis-a-vis other New Guinea *Sericornis*

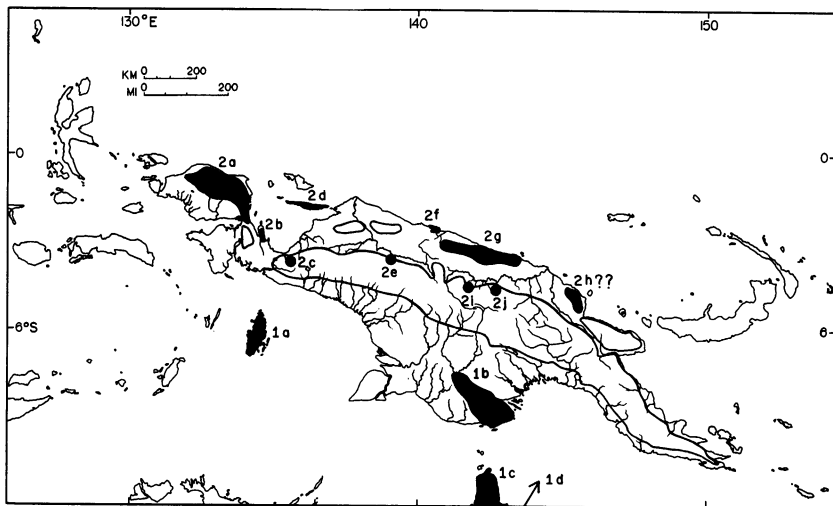


FIG. 5. Ranges of the subspecies of *Sericornis beccarii* (1a-1d) and *Sericornis virgatus* (2a-2j), superimposed on outlines of the principal mountain ranges of New Guinea. For names of the races, see text. *Sericornis beccarii* occurs at sea level in south New Guinea, the Aru Islands, and the Cape York Peninsula of Australia; *S. virgatus* lives between about 2100 and 4600 feet in northern New Guinea and on the Vogelkop.

species are fairly small, that geographical variation in morphology appears irregular, and that allopatric forms, of which similar habitats suggest they may be conspecific, are often much less similar in appearance than sympatric forms which are surely distinct species. Mayr (1937, 1941) proposed two slightly different schemes for drawing species lines involving two species. Recently Rand and Gilliard (1967) reclassified the forms among three species but stressed the uncertainty of the arrangement.

In my field studies of *Sericornis* in several different areas of New Guinea, I was struck by the simple and consistent ecological differences between the two to six *Sericornis* forms coexisting in a given area, which



suggests the plausibility, as a working hypothesis, of a new classification in which such ecologically equivalent races are assumed to be conspecific. The arrangement differs from that of Mayr (1937, 1941) in recognizing three species rather than two as a result of dividing his *S. beccarii* into *S. beccarii* plus *S. virgatus*, and in transferring the race *pontifex* from *S. nouhuysi* to *S. virgatus* and the race *cantans* from *S. beccarii* to *S. nouhuysi*. It differs from the three-species arrangement of Rand and Gilliard (1967) in transferring *cantans* from *S. virgatus* to *S. nouhuysi* and in transferring *cyclopum*, *weylandi*, *wondiwoi*, and *idenburgi* from *S. beccarii* to *S. virgatus*. The proposed classification follows (the numbers refer to fig. 5, which shows the geographical ranges of the races of *S. virgatus* and *S. beccarii*):

- 1a. *S. beccarii beccarii*: Aru Islands.
- 1b. *S. beccarii randi*: Fly River lowlands of South New Guinea.
- 1c. *S. beccarii minimus*: Northern part of Cape York Peninsula, Australia.
- 1d. *S. beccarii dubius*: Southern part of Cape York Peninsula, Australia.
- 2a. *S. virgatus imitator*: Vogelkop.
- 2b. *S. virgatus wondiwoi*: Wandammen Peninsula.
- 2c. *S. virgatus weylandi*: Weyland Mountains.
- 2d. *S. virgatus jobiensis*: Japen Island.
- 2e. *S. virgatus idenburgi*: Northern watershed of the Snow Mountains above the Idenburg River.
- 2f. *S. virgatus cyclopum*: Cyclops Mountains.
- 2g. *S. virgatus boreonesioticus*: North Coastal Range.
- 2h. *S. virgatus* (?) subsp.: Adelbert Mountains (may be a race of *S. nouhuysi*; see page 29).
- 2i. *S. virgatus virgatus*: Mäanderberg, Sepik Mountains
- 2j. *S. virgatus pontifex*: Lordberg and Hunsteinspitze, Sepik Mountains.
- 3a. *S. nouhuysi cantans*: Vogelkop.
- 3b. *S. nouhuysi nouhuysi*: Weyland and Snow mountains.
- 3c. *S. nouhuysi stresemanni*: Mountains of eastern New Guinea, approximately between latitudes 141 and 145° E.
- 3d. *S. nouhuysi oorti*: Huon Peninsula, and southeast New Guinea west approximately to latitude 145° E.
- 3e. *S. nouhuysi monticola*: High altitudes in southeast New Guinea.

The ecological basis of this classification is that New Guinea *Sericornis* forms fall into two distinct groups on the basis of bill size and preferred foraging level within the vegetational column, and that the forms of each group segregate altitudinally. The *virgatus-beccarii-nouhuysi* complex consists of large-billed forms (average value for whole culmen ranges from 15.1 to 15.4 mm. in several populations measured) which do almost all of their foraging in the under story. The other group consists of small-billed forms (average value for whole culmen ranges from 12.0 to 12.8 mm. in several populations measured) and includes *S. spilodera*,

*S. arfakianus*, the *S. perspicillatus*-*S. rufescens* superspecies, *S. papuensis*, and an ecologically similar warbler of a different but very closely related genus otherwise confined to Australia, *Acanthiza murina*. This small-billed group forages not only in the lower story but also commonly up to about 30 to 40 feet above the ground. [The remaining species of *Sericornis* in New Guinea, *S. nigroviridis*, has a very distinct color pattern, is known only from the unique type obtained in the well-explored Herzog Mountains (Miller, 1964), and must be exceedingly local, close to extinction, and *hors concours* as regards niche occupancy.] The differences in foraging levels between the two groups showed up clearly in my mist-netting results: the members of the first group I encountered (*S. nouhuysi stresemanni*, *S. nouhuysi oorti*, and *S. virgatus boreonesioticus*) were netted proportionally twice as often, in relation to their abundance as estimated by censusing techniques, as were the members of the second group. These differences between the two groups in foraging levels, which I noted in the eastern highlands and North Coastal Range, agree with Rand's observations in southeast New Guinea that *S. nouhuysi* fed "in the lower strata of the forest, while *A. murina* fed in the upper strata" (Mayr and Rand, 1937, p. 132); and with Stein's (1936, p. 43; Hartert, Paluden, Rothschild, and Stresemann, 1936, p. 216-217) observation that the six *Sericornis* forms in the Weyland Mountains fall into two groups on the basis of behavior, one consisting of *S. virgatus weylandi* and *S. nouhuysi nouhuysi*, the other consisting of *S. spilodera spilodera*, *S. arfakianus*, *S. perspicillatus*, and *S. papuensis bürgersi*. Probably there are other niche differences between the two groups besides preferred foraging level, e.g., associated with bill size, since the small-billed group still spends a good deal of time in the lower-story domain of the large-billed group.

The New Guinea avifauna contains many examples of pairs, and several examples of trios, of closely related species with mutually exclusive altitudinal ranges. The small-billed *Sericornis* forms provide one of the few instances of an altitudinally segregating quartet or quintet (see fig. 6). On all mountains where I have collected, *S. spilodera* was replaced abruptly with increasing altitude by *S. arfakianus*, replaced in turn by *S. perspicillatus*. Except for occasional immatures collected beyond the usual altitudinal limits of adults, the transitions were sharp and took place within a vertical range of less than 100 feet. On Mt. Karimui, 8165 feet high, *S. perspicillatus* was abruptly replaced above 6400 feet by *S. papuensis*, and *Acanthiza murina* was missing, so that there was a strict four-species altitudinal sequence. On Mt. Michael, 12,500 feet high, *S. papuensis* was replaced at the highest altitudes by *Acanthiza*

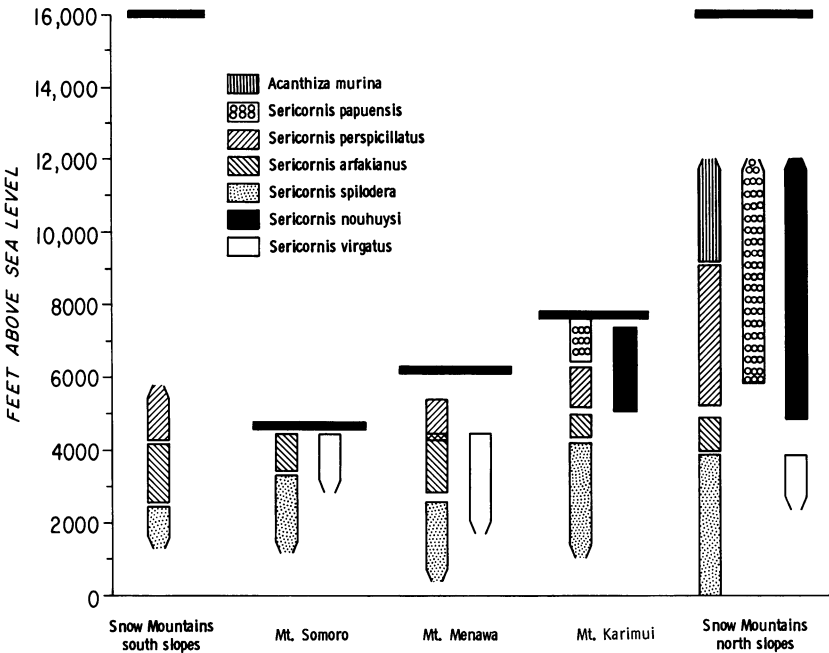


FIG. 6. Altitudinal ranges of seven closely related warblers on five New Guinea mountains. *Sericornis virgatus* and *S. nouhuysi* are large-billed warblers of the under story; the other five species are small-billed and forage up to 40 feet above the ground. Note that altitudinal ranges within each group are mutually exclusive except for *S. papuensis* in the presence of *Acanthiza murina* (Snow Mountains, north slopes). Results for Mt. Somoro and Mt. Menawa (North Coastal Range) and Mt. Karimui (eastern highlands) are based on my field work; for the north slopes of the Snow Mountains, on the Third Archbold Expedition (Rand, 1942b, pp. 472-475); and for the south slopes of the Snow Mountains, on the Wollaston Expedition (Ogilvie-Grant, 1915, pp. 111, 171; virtually no collecting above 5500 feet). The elevation of the summit of each mountain is indicated by the heavy horizontal line. If collecting was not carried out continuously up to the summit or down to sea level so that an altitudinal limit of a species is not known exactly, the limit of the range is left open.

*murina*, but my records were too scanty for me to determine the sharpness of the *S. perspicillatus*-*S. papuensis* and *S. papuensis*-*Acanthiza murina* transitions on Mt. Michael. The results of the First and the Third Archbold Expeditions (Mayr and Rand, 1937; Rand, 1942b) for mountains in southeast and western New Guinea high enough to support *Acanthiza murina* suggest that under these circumstances *S. perspicillatus*

is replaced abruptly by *Acanthiza murina*, with *S. papuensis* overlapping both (fig. 6).

Figure 6 shows that the altitudinal range of each large-billed form overlaps that of two or three small-billed forms, indicating that the altitudinal range of a given form depends on the ranges of the members of its own group (large-billed or small-billed) but not on the ranges of the members of the other group. For altitudinal relations within the large-billed group, I rely on the experience of Stein, Rand, and Mayr in areas where two large-billed forms were sympatric, since each of my study areas contained only one large-billed form. The most explicit statement is that of Stein (1936, p. 43, in translation): "It is particularly striking that the two species [*S. virgatus weylandi* and *S. nouhuysi nouhuysi*] appear to exclude each other altitudinally. *S. nouhuysi* lives higher, from about 1800 meters upward, while I always encountered *S. beccarii* [= *S. virgatus*] below 1800 meters. Only at this zone of contact can one find both species together, sometimes even in the same moss-covered tree! I had repeated opportunity to satisfy myself of these facts on my climbs to the summit of Mt. Kunupi." On the north slopes of the Snow Mountains Rand (1942b, pp. 472-473) collected *S. virgatus idenburgi* between 2800 and 3900 feet and *S. nouhuysi nouhuysi* between 4900 and 11,800 feet, with no altitudinal overlap (fig. 6). On the Vogelkop Mayr (1937, p. 13) collected *S. virgatus imitator* from 2600 to 4600 feet and *S. nouhuysi cantans* from 4600 (rarely 3950) to 6600 feet. Thus, sympatry within the *virgatus-beccarii-nouhuysi* complex involves altitudinal replacement of the hill-forest species *S. virgatus* by the mid-montane *S. nouhuysi*, in analogy to the quadruple or quintuple succession in the small-billed series.

These altitudinal interrelations among *Sericornis* forms result from competitive exclusion, as shown by the sharpness of the altitudinal transitions in the absence of sharp vegetational changes. The different average vertical preferences within the vegetational column for the two groups also involve competition: on Mt. Turu (summit elevation 3750 feet), where the small-billed *S. arfakianus* was absent and *S. virgatus boreo-nesioticus* was the only *Sericornis* at the summit, *S. virgatus* spent more of its time in the middle story and was netted proportionally three times less often (relative to its censused abundance) than on other mountains of the North Coastal Range, where *S. arfakianus* was present. Relief from competition may also be expressing itself in the fact that *S. spilodera*, the only small-billed form with most of its altitudinal range not shared by a large-billed form, has the largest bill of the small-billed series, intermediate in size between the other members of the small-billed series

and the members of the *virgatus-beccarii-nouhuysi* complex.

The forms that I group together under *S. virgatus* fall into three groups morphologically. *Cyclopum*, *weylandi*, and *wondiwoi* have distinct facial markings; *virgatus*, *jobiensis*, *boreonesioticus*, *imitator*, and *pontifex* have indistinct or no facial markings; and *idenburgi* is intermediate in its facial pattern (but duskier in general coloration). *Imitator*, which has the most distinct pattern of the "*virgatus*-group," and *wondiwoi*, which has the least distinct pattern of the "*cyclopum*-group," link each group to *idenburgi*. I provisionally consider all these forms conspecific because *weylandi*, *idenburgi*, and *imitator*, representing each of the three groups, are clearly occupying the same niche, viz., that of the low-altitude member of a sympatric, large-billed, lower-story species pair, and because the other six forms have the same altitudinal range (about 2500 to 4500 feet). I provisionally consider *cantans* a race of *S. nouhuysi* because it is clearly the high-altitude member of such a species pair and hence occupying the *nouhuysi* niche.

The five principal unsolved problems are the following:

1. The remaining four races of the large-billed complex (*beccarii*, *randi*, *minimus*, and *dubius*), which I group as a distinct species, *S. beccarii*, live near sea level in the lowlands of south New Guinea, the Aru Islands, and the Cape York Peninsula of Australia. As discussed under *Aegothales wallacii* and *Sericulus aureus*, there are many species or superspecies distributed in the mountains of New Guinea, the lowlands of south New Guinea, and the lowlands of Australia, having spread either from the New Guinea mountains to Australia or vice versa over the former Sahul Shelf land bridge joining south New Guinea and the Cape York Peninsula at the present Torres Strait. *Sericornis virgatus* in the mountains of New Guinea, *S. beccarii* in the Sahul Shelf lowlands, and *S. frontalis*, *S. maculatus*, and *S. humilis* in Australia form a superspecies with this distribution. The *S. virgatus* races to which *S. beccarii* bears the greatest similarity are the *cyclopum* group. Whether to consider *S. virgatus* and *S. beccarii* conspecific or separate members of a superspecies is a somewhat arbitrary decision, but the latter choice seems preferable in view of the ecological discontinuity (hill forest versus lowland rain forest) and large geographical discontinuity between the two groups and the close similarity between sympatric forms of *S. virgatus* and *S. nouhuysi*.

2. In the Adelbert Mountains there exists a population of the *virgatus-beccarii-nouhuysi* complex known only from a single specimen labeled as having been collected at 4000 feet and listed by Gilliard and LeCroy (1967, p. 67) as *S. nouhuysi oorti*. Examination shows that this specimen has a black bill and lacks light tips to the upper wing coverts, is less

yellow below than *S. n. oorti* or *S. n. stresemanni* but more yellow than *S. virgatus jobiensis* or *S. v. imitator*, and is apparently close to *S. v. pontifex*, of which I have no material, except for the black bill. The altitude of 4000 feet would be within the normal range of *S. virgatus* and slightly low for *S. nouhuysi*, but the exactness of the altitudinal assignment of the specimen is not known. Without more information and material it is impossible to decide whether the Adelbert population belongs to the species *S. virgatus* or *S. nouhuysi*.

3. In the field Mayr (1937, p. 13) concluded that the sympatric Vogelkop forms *cantans* and *imitator* represented two separate species. Both forms are somewhat variable (as are most other members of the complex), and the apparent intermediacy of a few specimens has led some subsequent authors, including Mayr and de Schauensee (1939, p. 124) and Rand and Gilliard (1967, pp. 359–366), to consider *cantans* and *imitator* as conspecific altitudinal races. In the material available to me (seven or eight specimens of each, including the type of *imitator*) the differences in well-prepared adult specimens concern the throat (whitish in *imitator*, buff in *cantans*), the breast-band (gray in *imitator*, buff in *cantans*), the light tips of the upper wing coverts (distinct in most individuals of *imitator*, obscure in all of those of *cantans*), and the more distinct and less ochraceous supraloral spots, yellowish belly, lighter bill, and slightly lighter back of *imitator*. I cannot assign five of the 16 available specimens which are in poor condition or not fully adult. Although further field studies are required to settle the point, the facts that well-prepared adult *imitator* specimens resemble specimens of *S. virgatus* and good *cantans* specimens resemble specimens of *S. nouhuysi*, that *S. nouhuysi* is present on all other major mountain ranges of New Guinea (including the Huon Peninsula), and that *cantans* is altitudinally occupying the *nouhuysi* niche make it probable that *cantans* is a race of *S. nouhuysi*, not an altitudinal race of *S. virgatus*.

4. On mountains too low to support *Acanthiza murina*, *S. papuensis* and *S. perspicillatus* have mutually exclusive altitudinal ranges, whereas on high mountains suitable for *Acanthiza murina*, *S. papuensis* shares the lower half of its altitudinal range with *S. perspicillatus* and the upper half with *Acanthiza murina* (compare Mt. Karimui and the Snow Mountains north slopes, fig. 6). Presumably *S. papuensis* and *S. perspicillatus* exhibit a narrower range of foraging behaviors in the presence than in the absence of *Acanthiza murina* to permit this broad altitudinal overlap on high mountains. What this behavioral contraction involves is unknown.

5. Although present distributions are too complex to permit unequivocal reconstruction of the evolutionary history of the *virgatus*-

*beccarii-nouhuysi* complex, one possibility is that a double invasion of New Guinea by the Australian *frontalis-humilis-maculatus* superspecies is involved, with *nouhuysi* the older invader. The invasion route of the more recent invader, *S. virgatus*, may have been across the low-altitude gap in the central range south of the Wandammen Peninsula, the only north-south pass under 5000 feet in New Guinea, since there is an apparent pattern to the geographical variability of *S. virgatus* in that the populations become less like those of *beccarii* and more like those of *nouhuysi* as one proceeds west and east of the gap (fig. 6).

Studies of voice are likely to provide the best test of the proposed classification scheme. The songs and calls I have heard from all four small-billed *Sericornis* species are dry and harsh. The songs of *S. virgatus boreonesioticus* and *S. nouhuysi stresemanni* are melodious warbles but with readily distinguishable patterns which may be useful in determining affinities of the problem races.

#### ***Epimachus fastosus ultimus*, new subspecies**

TYPE: A.M.N.H. No. 789765; adult female; Mt. Menawa, Bewani Mountains, Sepik District, Mandated Territory of New Guinea, 5200 feet; August 10, 1966; J. M. Diamond.

DIAGNOSIS: The new race differs from other populations in the relatively and absolutely short bill, in the relatively long tail of the female (table 6), and in the darker, less bright, rufous crown of the female. The adult male of *ultimus* has a shorter bill than all 21 males of other races measured; all females of *ultimus* have shorter bills than 19 out of 21 females of other races measured. The tail of the female is considerably longer than that of *fastosus* and that of *atratus*, and comparable with that of *stresemanni* (see table 6). The wing length is considerably shorter than that of *stresemanni*, and comparable with that of *fastosus* and that of *atratus*. *Ultimus* differs from *fastosus*, and agrees with *atratus* and *stresemanni*, in the more black, less brown, under parts of the adult male and in the more olive, less rufous, upper tail of the adult female. The light barring on the under parts of the adult female is buffy, as in *atratus* from Mt. Goliath and the Wandammen Peninsula, rather than whitish, as in *fastosus* and the Telefomin and Weyland Mountains populations.

RANGE: Known only from the summit (4500 feet and upward) of Mt. Menawa.

MATERIAL: Mt. Menawa, one male, nine females, five immature males (including birds obtained by natives and measured in the field).

WEIGHTS AND MEASUREMENTS: Wing, one male, 191; nine females,

TABLE 6  
COMPARATIVE MEASUREMENTS OF ADULTS OF *Epimachus fastosus*  
(Averages are given in parentheses.)

	Male	Bill <sup>a</sup>	Female	Male	Wing	Female	Male	Tail	Female
<i>ultimus</i>									
Mt. Menawa	55.5		53-57.5 (55.3)	191	157.5-167 (162.7)		704	229, 294-331 (303)	
1 male, 9 females <sup>b</sup>									
<i>fastosus</i>									
Vogelkop	56-61 (58.4)	52-61 (58.0)		191-197 (194.3)	154-172 (161.6)		583-756 (653)	258-283 (272)	
8 males, 8 females									
<i>atratus</i>									
Wandammen and									
Weyland mountains									
8 males, 8 females	58.5-62 (59.6)	57-62 (59.5)		186-204 (191.3)	152-167 (161.5)		634-670 (662)	170-268 (224)	
Snow Mountains <sup>c</sup>									
4 males, 6 females	—	—		199-211 (204.5)	168-182 (174.7)		773-845 (819)	226-302, 355 (280)	
Mt. Goliath									
1 male, 3 females	60.5	60-63 (61.5)	200	169-172 (170.3)			761	226-286 (264)	
<i>stresemanni</i>									
Telefomin									
1 male, 1 female	65	60	208	176			824	350	
Schrader Range <sup>d</sup>									
6 males, 5 females	62-66.5 (64.4)	63.5-72 (66.1)	210-222 (214.7)	175-182 (177)			810-940 (848)	289-325 (302)	

<sup>a</sup> From anterior edge of nostril.

<sup>b</sup> Including type.

<sup>c</sup> From Junge (1939, p. 8).

<sup>d</sup> From Stresemann (1923, p. 34).



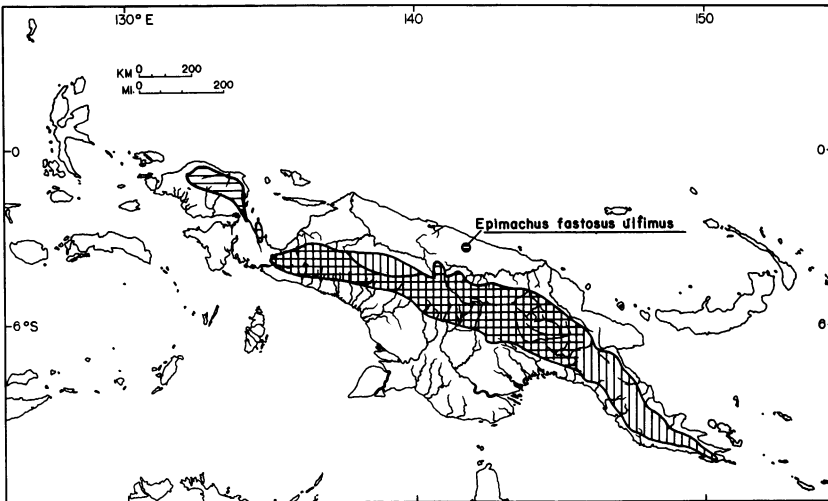


FIG. 7. Ranges of the two species of *Epimachus*: *E. fastosus*, horizontal hatching; *E. meyeri*, vertical hatching. The two species are sympatric over most of their ranges, but *E. meyeri* is missing on the Vogelkop, Wandammen Peninsula, and Mt. Menawa, and *E. fastosus* is missing in southeast New Guinea and apparently in the northern part of the Snow Mountains.

157, 159, 162, 162, 163, 164, 165, 166, and 167 (type); five immature males, 183 (four) and 186. Tail, one male, 704; eight females, 229, 294, 302, 304, 305, 328, 330, and 331 (type); five immature males, 317, 336, 337, 355, and 369. Bill (from anterior edge of nostril), one male, 55; nine females, 53, 54 (two), 55 (two, including type), 56, and 57 (three); five immature males, 53 (two), 55, 56, and 57. Weight, one male, 280; six females, 184, 185, 186, 187, 191, and 207; five immature males, 228, 239, 245, 248, and 252.

REMARKS: *Epimachus fastosus ultimus* is the sole population of a montane bird of paradise in the North Coastal Range, where the discovery of this isolated and very restricted colony came as a surprise. As is apparent from figure 7, the two species of *Epimachus* appeared previously to be confined to the central range and were absent even from the Huon Peninsula, which many other montane birds of paradise (*Drepanornis albertisii geisleri*, *Astrapia rothschildi*, *Parotia wahnesi*, *Lophorina superba latipennis*, *Paradisaea guilielmi*) had colonized.

A review of the relationships among the various populations of *Epimachus fastosus* shows that they fall into three groups. First, the populations of the central ranges from the Wandammen Peninsula to the east-

ern highlands are all very similar in proportions and in color, except for the geographically irregular minor variation in the buffiness of the pale ventral barring of the female. The only variable character of significance in this group is size (table 6), which appears to increase clinally from west to east (from the Wandammen Peninsula and Weyland Mountains, to the south slope of the Snow Mountains and Mt. Goliath, to Telefomin, to the Schrader Range). The Mt. Goliath population, which lies in the middle of the cline, was initially separated from *fastosus* of the Vogelkop as *atratus*, and the larger Schrader population later separated as *stresemanni*. If the size increase between Mt. Goliath and the Schrader Range proves to be clinal, it may not be possible to maintain *stresemanni*. Second, the isolated Mt. Menawa race *ultimus* generally agrees with *atratus* in color except for the crown of the female, and agrees with the smallest (westernmost) *atratus* population in wing length, but is different in proportions, viz., it is short-billed and long-tailed. Finally, the Vogelkop population *fastosus* is similar to the smallest *atratus* population in size and proportions except apparently in having a longer tail in the female, but differs from both *atratus* and *ultimus* in the color of the upper tail of the female and the color of the under parts of the adult male. The dark ventral barring of the female and the under parts of the adult male are obviously affected by foxing and become more brown, less black, postmortem, so that the Menawa male (collected in 1966) has the blackest under parts, and the only other post-war adult males available for comparison (Telefomin, 1954, and Mt. Hagen, 1952) are the next blackest. However, comparison of *fastosus* and *atratus* specimens collected in the same year (1928) shows that the browner under parts of *fastosus* are a valid racial character.

The two species of *Epimachus* are rather similar in appearance but have quite different calls, suggesting a role of vocalizations in the isolating mechanisms. The calls of adult males of *Epimachus fastosus stresemanni* which I heard in the eastern highlands consisted of two identical, loud, liquid notes, similar to calls Gilliard heard at Telefomin. I am not personally familiar with the call of *Epimachus meyeri*, but Gilliard described it as a loud, staccato rattling like a machine-gun or pneumatic drill (Mayr and Gilliard, 1954, p. 355; Rand and Gilliard, 1967, p. 474). On Mt. Menawa I frequently heard the calls of *Epimachus fastosus ultimus*. Some consisted of two liquid notes as in the eastern highlands, but others consisted of a very rapid, staccato, machine-gun-like burst followed immediately by a single liquid note, i.e., intermediate between the calls of *E. fastosus* and those of *E. meyeri* in the area of sympatry. Perhaps this call of the isolated Mt. Menawa population is close to that

TABLE 7  
COMPARATIVE MEASUREMENTS OF THE GENUS *Sericulus* IN NEW GUINEA

	Exposed Culmen	Wing	Tail	Weight
<i>aureus aureus</i>				
Vogelkop, Wandammen, Weyland Mountains, and Idenburg slopes				
9 adult males	21, 22 (five), 23	135, 139, 140 (two), 141, 142, 143 (two), 145	75, 78, 79 (two), 80, 81, 82, 83, 86	175, 180
6 subadult males	21, 22, 23 (three), 24	142, 143, 145 (two), 146, 147	79 (two), 80, 81, 82, 87	165
3 immature males <sup>a</sup>	22, 23	138, 139 (two)	76, 88, 89	135
3 females	22, 24	138 (two), 140	83, 87	165, 175
4 (sex?) <sup>a</sup>	22, 23, 24 (two)	142, 145, 147, 149	82, 87, 88 (two)	—
Mt. Turu				
1 subadult male	22	144	74	176
2 immature males <sup>a</sup>	22, 24	133, 137	76, 87	156 (two)
1 female	23	142	96	171
<i>aureus ardens</i>				
Wataikwa and Fly rivers				
5 adult males	23 (two)	134, 137, 138, 139 (two)	60, 62, 63, 65, 68	—
1 immature male <sup>a</sup>	24	136	68	—
<i>bakeri</i>				
Adelbert Mountains				
3 adult males	—	137, 138, 143	77, 78, 84	178, 180, 183
1 immature male <sup>a</sup>	—	140.5	86	170
5 females	—	132, 136.5, 139 (two), 142	88, 89, 92	164, 165, 173, 177, 184

<sup>a</sup> In female-like plumage.

<sup>b</sup> Measurements from Gilliard and LeCroy (1967, p. 74).

of the common ancestor, from which the calls of *E. fastosus* and those of *E. meyeri* on the central range diverged to furnish an isolating mechanism when each form reinvaded the geographical range of the other.

*Sericulus aureus aureus* (Linné)

MATERIAL: Mt. Turu: one subadult male (*a*), two immature males (*b*, *c*), one female; September 8 and 9, 1966.

WEIGHTS AND MEASUREMENTS: See table 7.

COLOR OF SOFT PARTS: Bill black. Legs gray. Gape orange. Iris, lemon (subadult male *a*), pale green (immature male *c*), or brown (female and immature male *b*).

REMARKS: The specimens were collected between about 3000 and 3600 feet on Mt. Turu. These bowerbirds were also seen between 3000 and 3200 feet on Mt. Nibo, but were apparently absent from Mt. Somoro and Mt. Menawa. They moved through the forest between 40 feet above the ground and the treetops in parties of two or three, remaining silent except for an occasional faint call, "ksh." Both on Mt. Turu and Mt. Nibo my native assistants Paran and Kariniga saw adult males, which proved too shy to be collected despite all efforts. The female and subadult and immature males nevertheless suffice to prove that the North Coastal Range population is closest to that of *aureus*, not to that of *ardens*, on the basis of the black areas on the face of the subadult male (lacking in *ardens*), the length of the tail (longer than in *ardens*; see table 7), and the color of the crown, which is somewhat darker brown in females and immature males of topotypical *aureus* from the Vogelkop and of the Mt. Turu series than that of *ardens*. The Mt. Turu series differs from the Vogelkop population in that the under parts of the female are considerably deeper orange (nearly as deep as those of Vogelkop males), in that the same difference holds for immature males, and in that the upper parts are somewhat lighter and duller. Whether these minor differences are sufficiently consistent to be of taxonomic significance is uncertain.

No information was obtained as to whether or not the population in the North Coastal Range builds a bower. The bowers of *ardens* on the Strickland River and those of *aureus* on the Vogelkop were recently discovered by H. L. Bell and the late E. T. Gilliard, respectively.

This is apparently the first definite record of the Golden Bowerbird for the Mandated Territory and extends the range 300 miles to the east. Figure 8 summarizes our present distributional knowledge of the three populations of the genus *Sericulus* in New Guinea. *Sericulus bakeri* is con-

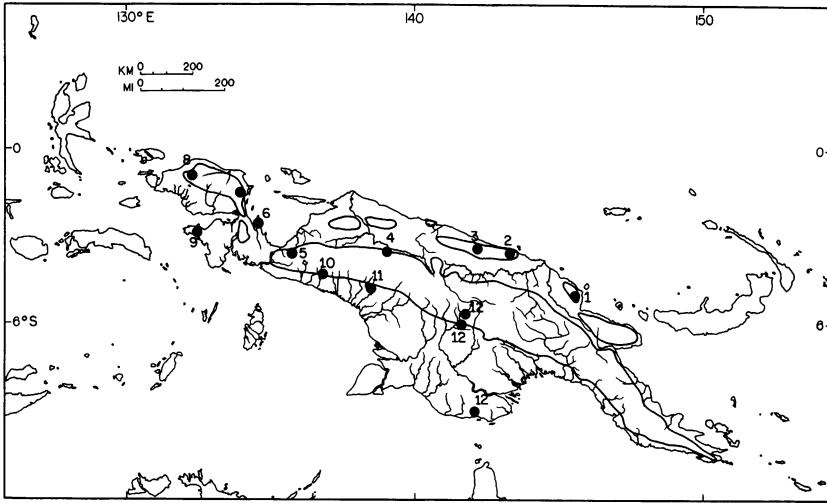


FIG. 8. Localities at which *Sericulus* bowerbirds are known to occur in New Guinea, superimposed on outlines of the principal mountain ranges. *S. bakeri*: 1, Adelbert Mountains (collected by Beck, 1928, and Gilliard, 1959). *S. aureus aureus*: 2, Mt. Turu (collected by Diamond, 1966); 3, Mt. Nibo (observed by Diamond, 1966); 4, Idenburg slopes (collected by Third Archbold Expedition, 1939); 5, Weyland Mountains (collected by Shaw-Mayer, 1930); 6, Wandamen Peninsula (collected by Mayr, 1928); 7, Arfak Mountains (collected by Guillemard, 1883; Mayr, 1929; Bergman, 1949; and earlier records); 8, Tamrau Mountains (collected by Gilliard, 1964); 9, Onin Peninsula (cited in Mayr, 1941). *S. aureus ardens*: 10, Wataikwa River (collected by British Ornithological Union Expedition, 1910); 11, Noord River (collected by Lorentz, 1907); 12, Fly and Strickland rivers (collected by D'Albertis, 1877; Second Archbold Expedition, 1936; Bell, 1967; additional records by Nevermann from the Merauke District, 200 miles west of the Fly River). All localities are at about 2800 to 4000 feet except for 12 and perhaps 11, which are near sea level.

finned to elevations above 3000 feet in the Adelbert Mountains. *Sericulus aureus aureus* lives between about 2800 and 4000 feet on the Vogelkop and is very patchily distributed (five locality records) at the same elevations along the northern watershed east to Mt. Turu. *Sericulus aureus ardens*, the plumage of which is quite distinct from that of *S. a. aureus* in the adult male, inhabits the hill forest and lowlands of the southern watershed east to the Fly and Strickland rivers. The remaining *Sericulus*, *S. chrysocephalus*, occurs in eastern Australia. This distribution clearly illustrates the faunal distinctness of the Adelbert Mountains from the North Coastal Range. The pattern (mountains of New Guinea, lowlands of south New Guinea, eastern Australia) is typical of species or

superspecies invading Australia from the mountains of New Guinea or vice versa, as discussed under *Aegotheles wallacii manni* and *Sericornis virgatus boreonesioticus*.

The color of the iris, which is brown in the adult female and immature male, evidently becomes yellow in the adult male, as shown also by colors recorded on labels of specimens collected by Mayr, Shaw-Mayer, and Rand.

The immature male with the pale green eye is in the same plumage as adult females. The other immature male, which may be a younger bird on the basis of the smaller and black testes, longer tail, and brown eye, differs from the adult female only in having one orange feather on the shoulder and a few scattered yellow feathers on the mid-back. The subadult male has the lores and the circumocular region (except immediately posterior to the eye) black, bordered dorsally with red-orange in the superciliary region and area above the lores, some black feathers on the chin, the crown blackish anteriorly, darker brown than in the female posteriorly and with some scattered scarlet feathers, and the upper parts darker and richer brown than those of the female. Examination of other subadult males shows that the head is the first part to reach fully adult plumage, followed by the upper back, and finally by the lower back, wings, and tail.

*Meliphaga analoga flavida* Stresemann and Paludan

MATERIAL: Utai (650 feet), five males, four females; Miliom (1500 feet), nine males, two females; July 21 to August 27, 1966.

WEIGHTS AND MEASUREMENTS: Wing, 14 males, 78 (four), 79 (two), 80 (three), 81 (four), and 82; six females, 71, 74 (two), 75, 76, and 78. Tail, 14 males, 60, 63 (three), 64, 66 (three), 67 (three), 67.5, 68, and 69; six females, 56, 59, 61, 62, 64, and 65. Whole culmen, 12 males, 20.5, 21.5, 22 (two), 22.5 (three), 23, 23.5 (three), and 24; six females, 20.5 (two), 21, 21.5, and 22 (two). Exposed culmen, 11 males, 16, 16.5, 17, 17.5 (three), 18 (four), and 20.5; six females, 15.5, 16 (two), 16.5 (two), and 17. Weight, 14 males, 18.8, 20.2, 20.2, 20.5, 20.6, 21.4, 21.5, 21.8, 21.8, 22.5, 22.5, 22.6, 22.7, 23.5; six females, 17.8, 18.3, 18.7, 19, 20, and 20.2.

REMARKS: See under next species.

*Meliphaga orientalis citreola* Rand

MATERIAL: Mt. Menawa (2650 to 4300 feet), four males, seven females; Mt. Somoro (3000 to 4500 feet), three females; Mt. Nibo (3200

to 4700 feet), three males, six females; Mt. Turu (2700 to 3750 feet), four males, four females, one immature female; July 5 to September 10, 1966.

WEIGHTS AND MEASUREMENTS: Wing, 11 males, 75, 76 (three), 77 (five), 78, and 79; 20 females, 69, 70, 71 (9), 72 (four), 73 (four), and 74. Tail, nine males, 55, 57 (two), 58, 58.5, 59, 60, 61, and 62; 20 females, 51, 53 (two), 55 (five), 56 (two), 56.5 (two), 57 (four), 58; 59 (two), and 60. Whole culmen, 10 males, 20.5 (three), 21 (five), 22, and 22.5; 19 females, 18, 18.5 (two), 19.5 (two), 20 (eight), 20.5 (four), 21, and 22. Exposed culmen, 10 males, 16.5 (two), 17 (five), 18 (two), and 19; 19 females, 15 (two), 15.5 (three), 16 (eight), 16.5 (three), 17, 17.5, and 18.5. Weight, 10 males, 17.5, 18, 18.2 (two), 18.3, 19 (two), 19.4, 19.5, and 20; 20 females, 14.8, 15.8, 16.5 (two), 16.6, 17 (two), 17.3, 17.5 (two), 17.7, 18, 18.3 (three), 18.5 (two), 19.2, 19.5, and 20.

REMARKS: The group of approximately nine sibling species that includes *Meliphaga analoga* and *M. aruensis* poses the most complex taxonomic questions among New Guinea passerines. The basic problem is that morphological differences between all forms are slight, that as many as six forms may be found living sympatrically, and that differences between sympatric forms can be more trivial than the differences between allopatric forms considered conspecific, making the grouping of forms into species difficult. A fine morphological study by Rand (1936) cleared up much of the earlier confusion and provided the foundation for present understanding of the group. As emphasized by Rand and Gilliard (1967, p. 558), study of ecological differences among the meliphagas is essential to further progress in unraveling their relationships. The case discussed below illustrates the difficulty or impossibility of deciding species affiliation in this group solely on the basis of study skins.

On the north slopes of the Snow Mountains above the Idenburg River the Third Archbold Expedition (Rand, 1942b) collected five kinds of meliphagas: the forms known as *M. aruensis sharpei* at sea level to 2800 feet, *M. montana sepik* at 2600 to 3900 feet, *M. flavirictus crockettorum* at 160 feet, *M. analoga flavida* at sea level to 160 feet, and a new form at 2800 to 3900 feet. The new form was very similar to *M. analoga flavida* and was therefore considered to be an altitudinal subspecies and described as *M. analoga citreola* (Rand, 1941, p. 14). In the North Coastal Range I collected the same five forms: *M. aruensis sharpei* at 650 to 3500 feet, *M. montana sepik* at 1915 to 4750 feet, *M. flavirictus crockettorum* at 1500 to 2330 feet, *M. analoga flavida* at 650 to 1600 feet, and *citreola* at 2650 to 4700 feet. Detailed comparative descriptions were made of each specimen before it was stuffed, the exact altitude at which each

TABLE 8  
COMPARATIVE MEASUREMENTS AND WEIGHTS OF *Meliphaga analoga flavida* AND RACES OF *M. orientalis*  
(Averages are given in parentheses.)

	Exposed Culmen	Whole Culmen	Wing	Tail	Weight
<i>orientalis citreola</i>					
North Coastal Range					
11 males	16.5-19 (17.3)	20.5-22.5 (21.1)	75-79 (76.8)	55-62 (58.6)	17.5-20 (18.7)
20 females	15-18.5 (16.2)	18-22 (20.0)	69-74 (71.6)	51-60 (56.0)	14.8-20 (17.5)
Snow Mountains, north slopes					
14 males <sup>a</sup>	17-19 (17.8)	20-22.5 (21.2)	72-79 (76.6)	57-63 (60.3)	—
2 females	16, 17	19, 20.5	72, 75	56, 57	—
<i>orientalis beeki</i>					
Huon Peninsula					
1 male <sup>a</sup>	17	22	75	63	—
2 females	15.5, 16	19.5, 20	71.72	58, 59	—
Morobe District <sup>b</sup>					
9 males	—	—	78-81 (79.9)	—	—
2 females	—	—	74, 75	—	—
<i>orientalis facialis</i>					
Vogelkop, Weyland Mountains					
2 males	17.5, 19	21, 22	80, 80	63, 64	—
3 females	17, 17	21, 22	72-78 (75.7)	57-60 (59)	—
Snow Mountains, south slopes					
1 male	—	22	74	55	—
2 females	—	20, 20	69, 71	56, 57	—



TABLE 8—(Continued)

	Exposed Culmen	Whole Culmen	Wing	Tail	Weight
Eastern highlands					
10 males	17.5-19.5 (18.4)	20.5-23 (21.6)	71-78 (74.8)	56-62 (59.9)	15.7-20.4 (18.6)
11 females	16-18.5 (17.5)	19, 21 (20.2)	66-71 (68.8)	52-58 (56.4)	15.5-19.5 (17.6)
<i>analoga flavida</i>					
North Coastal Range					
14 males	16-20.5 (17.7)	20.5-24 (22.6)	78-82 (79.7)	60-69 (65.5)	18.8-23.5 (21.5)
6 females	15.5-17 (16.2)	20.5-22 (21.4)	71-78 (74.7)	56-65 (61.2)	17.8-20.2 (19.0)
Snow Mountains, north slopes					
7 males	—	—	77-82 (80.2)	60-66 (64.0)	—
6 females	—	—	74-77 (74.7)	57-62 (60.2)	—
Japen, north New Guinea coast					
12 males	—	—	78-85 (81.2)	66-71 (68.6)	—
9 females	—	—	73-78 (75.4)	59-66 (62.6)	—
<i>analoga analoga</i>					
Eastern highlands					
3 males	18-18.5 (18.3)	23, 24 (23.5)	80-83 (82.0)	64-70 (66.3)	24-25.5 (24.9)
4 females	16-18.5 (17.3)	21, 22 (21.5)	75-78 (76.2)	60-64 (62.0)	21, 22 (21.3)

<sup>a</sup>Including type.

<sup>b</sup>Measurements from Rand (1936).

specimen was taken was noted, and attention was paid to vertical distribution in the vegetational column of the forest. Both the morphological evidence and the ecological evidence indicate that *flavida* and *citreola* represent separate species rather than altitudinal subspecies and that *citreola* is a race of *Meliphaga orientalis*. The morphological similarity between the populations of *M. orientalis* and *M. analoga* living together in other areas of New Guinea has already been noted by Rand (1936, p. 16) and is particularly close in the *citreola-flavida* case because of the yellowish coloration of both forms.

The *citreola* population of the North Coastal Range appears indistinguishable from Rand's type series of *citreola* in every feature of size and color compared. The *flavida* population of the North Coastal Range is very close to *flavida* from Hollandia, and slightly less yellow below than *flavida* from the Idenburg River. The morphological differences between the high-altitude (*citreola*) and low-altitude (*flavida*) populations in the North Coastal Range are as follows: (1) *Flavida* has a very distinct yellow rictal streak, more pronounced than in *M. aruensis sharpei* and somewhat less pronounced than in *M. flavirictus crockettorum*, which has the most marked rictal streak of the New Guinea meliphagas. *Citreola* has the rictal streak greatly reduced or nearly absent. I found this an absolute and infallible character for distinguishing live birds or fresh specimens (not yet skinned) of the two forms in the hand. In stuffed skins it is a useful but frequently not reliable character, because even slight distortion of the rictal region during skinning may obscure the streak in *flavida*, as apparent from comparison of some of my skins with my field descriptions of the same specimens before they were stuffed. Many of Rand's *flavida* skins, but none of his *citreola* skins, have distinct rictal streaks, but some of his *flavida* skins lack distinct streaks, presumably as an artifact of preparation despite the high quality of Rand's specimens. (2) *Flavida* has a greater weight and longer wing and tail, particularly in the male (table 8). Thirteen of my 14 *flavida* males have heavier weights and longer tails than all my *citreola* males, whereas nine of 11 *citreola* males have shorter wings than all *flavida* males. *Flavida* females also average larger and heavier than *citreola* females, but there is more overlap in the females. *Citreola* has a very slightly shorter and more slender bill. (3) The under wing coverts and the inner edges of the remiges are yellow-olive in both forms but slightly lighter and more yellow in *citreola*. (4) In life and in fresh specimens the under parts of *citreola* had a slight unevenness and streakiness which was quite absent from *flavida*. This is usually not a useful character in my or Rand's study skins, and Rand did not cite it in his diagnosis of *citreola*. (5) *Fla-*

*vida* has a very slightly more gray and dense rump tuft than *citreola*. (6) *Citreola* is brighter and yellower above. It should be appreciated that the degree of all these differences would be considered very minor in other New Guinea genera.

That two species rather than altitudinal subspecies are involved is clear from the discontinuous altitudinal range in a continuous forested habitat, from the absence of change in either population with altitude, and from the absence of morphological intergrading. In the Torricelli Mountains I collected *flavida* while working between 1450 and 1600 feet at the village of Miliom. As I started up Mt. Nibo, I began collecting at 2330 feet but met neither *flavida* nor *citreola* until I reached 3200 feet, where *citreola* appeared and continued up to 4700 feet. On Mt. Somoro both forms were similarly absent from 2620 to 3000 feet, where *citreola* appeared and continued to 4500 feet. In the Bewani Mountains *flavida* was common at Utai (650 feet) at the foot of Mt. Menawa. *Flavida* was absent when I resumed collecting at 1910 feet on Mt. Menawa, and *citreola* first appeared at 2650 feet and went up to 4300 feet, above which limit *Ptiloprora mayri* (absent from the other mountains surveyed) appeared to take over its niche. On Mt. Turu in the Prince Alexander Range only *citreola* was encountered (2700 to 3750 feet) because no collecting was done at low elevations. Thus, there is a gap between the lower limit of *citreola* (varying locally between 2650 and 3200 feet) and the upper limit of *flavida* (somewhere between 1600 and 1910 feet) despite intensive collecting in this gap with particular attention to meliphagas, of which three other readily distinguishable species (*M. montana*, *M. aruensis*, and *M. flavirictus*) were secured in the gap. Neither form approaches the other with change in altitude: specimens of *flavida* from Utai (650 feet) and Miliom (1450 to 1600 feet) are the same in appearance and in range of measurements, as are specimens of *citreola* from near its lower and upper limit on all four mountains. In fresh specimens there were no intergrades in the character of the rictal streak. In addition, as Mayr and Gilliard (1954, p. 369) reasoned in assessing the status of altitudinally representative forms in the genus *Ptiloprora*, "If both forms were members of a single species, which is strongly subject to altitudinal variation, one would suspect that the species is also subject to much geographical variation." The Hollandia, Idenburg River, and North Coastal Range populations of the low-altitude form *flavida* do differ slightly in yellowness or grayness of the under parts, but the Idenburg and North Coastal Range populations of the high-altitude form *citreola* are identical.

Since *citreola* is not an altitudinal race of *M. analoga flavida*, what is

it? The following ecological considerations suggest that it is a subspecies of *M. orientalis*. In the eastern highlands I had found that the altitudinal ranges of *M. analoga analoga* and *M. orientalis facialis* were mutually exclusive, the former ranging up to 3250 feet and the latter down to 3650 feet; and that they replaced each other altitudinally as the slender-billed meliphaga of the middle and upper stories, leaving the lower story to the stouter-billed *M. mimikae bastille*, *M. montana auga*, and *M. aruensis aruensis*. For example, the latter three forms were regularly caught in mist nets, the former two seldom or never. In the North Coastal Range the forms *flavida* and *citreola* replaced each other altitudinally in the middle and upper stories, leaving the lower story to the stouter-billed *M. montana sepi* and *M. aruensis sharpei* (the latter two netted regularly, *flavida* only once, *citreola* only three times). Forms of *M. orientalis* have been collected on most of the mountain ranges of New Guinea at elevations above those inhabited by *M. analoga* but would be inexplicably missing from the North Coastal Range and north slopes of the Snow Mountains if *citreola* were not a race of *M. orientalis*. In fact, *citreola* in these two areas occupies the same ecological niche which (other) races of *M. orientalis* do elsewhere in New Guinea, viz., as the slender-billed meliphaga of the middle and upper stories at altitudes above ca. 3000 feet.

The assignment of *citreola* to *M. orientalis*, although it could not have been made with confidence on morphological grounds alone, is morphologically reasonable. Except for the yellowish coloration most of the characters by which *citreola* differs from *M. analoga* are those that distinguish the other races of *M. orientalis* from *M. analoga*, viz., the greatly reduced rectal streak, the shorter wing and tail, the lighter weight, the slightly more slender bill, and the unevenness of the under parts (Rand, 1936). The races of *M. orientalis* to which *citreola* is closest are *becki* (Huon Peninsula) and *facialis* (Weyland Mountains and Vogelkop), from which it differs principally in the more yellow, less gray, under parts and the brighter upper parts (nearer *facialis* than *becki*). The inner edges of the remiges in *citreola* are similar to *becki* and less ochraceous than in *facialis*. The size of *citreola* is comparable with *facialis* of the eastern highlands and south slope of the Snow Mountains and with *becki* of the Huon Peninsula, and smaller than *facialis* of the Vogelkop and Weyland Mountains and *becki* of the Morobe District (table 8). The race *orientalis* of southeast New Guinea differs from *becki*, *facialis*, and *citreola* in the more pronounced unevenness of the under parts, the grayer upper parts, the more ochraceous under wing, and the blackish postocular region.

Other instances of altitudinally representative pairs of New Guinea

bird forms which were described as subspecies or long considered conspecific but have proved to be separate species include *Peltops blainvillii* and *P. montanus* (Stresemann, 1923, p. 92), *Ptiliprora guisei* and *P. perstriata* (Mayr and Gilliard, 1954, p. 368), *Melidectes rufocrissalis* and *M. belfordi* (Gilliard, 1959; Diamond, 1967a, p. 12; Gilliard and LeCroy, 1968), *Epimachus fastosus* and *E. meyeri* (Rothschild, 1931, p. 253), *Rallacula rubra* and *R. forbesi* (Stein, 1936, p. 56; Hartert, Paludan, Rothschild, and Stresemann, 1936, p. 239), and perhaps *Aegotheles albertisii* and *A. archboldi* (Junge, 1953, p. 38; Ripley, 1964, p. 39).

Two new races of *Meliphaga analoga* have been named in a recent paper by Salomonsen (1966) who preliminarily named a total of 28 new races of meliphagids, based on re-examination of older material. The six of these races the types and type series of which I have so far had the opportunity to study proved to be based on specimens that were collected or analyzed by Rand, Mayr, Gilliard, or all three. They pointed out minor characters which they believed did not warrant naming, such as differential wear and fading in areas with different climates (*Philemon novaeguineae fretensis*), clinal variation in size (*Melidectes fuscus gilliardi*, *Philemon novaeguineae fretensis*), irregular and slight color variation (*Meliphaga analoga connectens*, *M. a. papuae*, *Oedistoma pygmaeum flavipectus*, *O. p. olivascens*), and those of older comparative types which were aberrant and may have foxed (*Meliphaga analoga connectens*: see Gilliard and LeCroy, 1967, p. 78). Re-examination of this older material on which the six descriptions were based, plus the more recent material of these species in my collections from northern and southern New Guinea and the eastern highlands, confirms the conclusions of Rand, Mayr, and Gilliard that the characters on which these six races are based do not justify taxonomic recognition: *Meliphaga analoga connectens* Salomonsen = *M. a. flavida* Stresemann and Paludan (see Rand, 1936, p. 14; Rand, 1942b, p. 508; Gilliard and LeCroy, 1967, p. 78), *Meliphaga analoga papuae* Salomonsen = *M. a. analoga* Reichenbach (see Rand, 1936, p. 14), *Philemon novaeguineae fretensis* Salomonsen = *P. n. novaeguineae* (Müller) (see Mayr and Rand, 1937, p. 234; Rand, 1942a, p. 364), *Oedistoma pygmaeum flavipectus* Salomonsen = *O. p. pygmaeum* Salvadori, *Oedistoma pygmaeum olivascens* Salomonsen = *O. p. pygmaeum* Salvadori, and *Melidectes fuscus gilliardi* Salomonsen = *M. f. fuscus* (DeVis) (see Mayr and Gilliard, 1954, pp. 367-368; Sims, 1956, p. 432). Gilliard and LeCroy [MS] will show that the race *Melilestes megarhynchus brunneus* Salomonsen, the type of which I was unable to examine, is synonymous with *M. m. megarhynchus* (Gray) because the brownish coloration attributed to the type resulted from foxing. A number of the remaining 21 races de-

scribed in the same paper appear similarly to be doubtfully distinct and in need of confirmation. More detailed discussion of these populations will be given elsewhere (Diamond, MS).

***Ptiloprora mayri acrophila*, new subspecies**

TYPE: A.M.N.H. No. 789766; adult male; Mt. Menawa, Bewani Mountains, Sepik District, Mandated Territory of New Guinea, 5200 feet; August 12, 1966; J. M. Diamond.

DIAGNOSIS: The new race differs from *mayri* in that the edges of the upper wing coverts are light rufous olive (in some cases more rufous, in others more olive) not pure light gray; in that the edges to the feathers of the top of the head are not uniformly light gray, but are a slightly darker gray than in *mayri* from the forehead extending distally for half or two-thirds of the distance to the start of rufous edging on the back, and dull olive for the remainder of the distance; in that the dark centers to the feathers of the under parts are lighter, more gray and less black, contrasting less with the light edges, so that the under parts appear less spotted; and in that the edges of the feathers of the back are darker, duller, and with an olive tone lacking in the pure rufous edges of *mayri*. Immatures of both *mayri* and *acrophila* are washed ventrally with olive.

RANGE: Known only from the summit (4200 to 6185 feet) of Mt. Menawa, where it is the most abundant bird.

MATERIAL: Mt. Menawa, 24 males, 14 females, two (sex?), two immature males, one immature (sex?); August 1 to 13, 1966.

WEIGHTS AND MEASUREMENTS: Wing, 15 males, 98.5, 99.5, 101 (four, including type), 101.5 (two), 102 (four), 102.5, 103, and 104; eight females, 88.5, 90, 91 (two), 91.5 (two), 93.5, and 94; one (sex?), 91.5; two immature males, 96.5 and 97; one immature (sex?), 95.5. Tail, 15 males, 77, 78, 79.5, 80.5, 81, 81.5, 82 (type), 82.5 (two), 83 (three), 83.5, 84, and 84.5; seven females, 75, 77.5 (three), 78 (two), and 79; one (sex?), 76; two immature males, 75.5 and 84; one immature (sex?), 75.5. Exposed culmen, 15 males, 24.5 (two, including type), 25 (two), 25.5 (three), 26 (four), and 26.5 (four); seven females, 22.5, 23, 23.5 (two), and 24 (three); two immature males, 26 and 26.5; one immature (sex?), 25. Weight, 15 males, 29.3, 29.7, 30, 31, 31.6, 31.7 (type), 32.2, 32.6 (two), 32.7, 32.8 (two), 33.6, 36, and 36.3; 10 females, 25.5, 26.3, 26.5, 27.3, 27.5, 28, 28.3, 28.4, 29, and 29.2; one (sex?), 31.6; two immature males, 30.5 and 31; one immature (sex?), 31.

COLOR OF IRIS: Green.

## DIFFERENTIAL DIAGNOSIS OF *PTILOPRORA GUISEI*, *PTILOPRORA MAYRI*, *PTILOPRORA PERSTRIATA*, AND *PTILOPRORA ERYTHROPLEURA*

### SIZE

As shown by the wing lengths and weights listed in table 9, *P. mayri* and *P. perstriata* are large (wing near 100 mm. in males, 90 mm. in females), *P. guisei* (wing near 90 mm. in males, 80 mm. in females) and *P. erythropleura* (wing near 86 mm. in males, 78 mm. in females) are small. Apparently no specimen of *P. guisei* or *P. erythropleura* has as long a wing as any specimen of *P. mayri* or *P. perstriata* of the same sex. It should be noted in addition that wing length increases considerably with altitude in *P. p. perstriata* (Rand, 1942b, p. 509), and that the mountain ranges on which *P. m. mayri*, *P. m. acrophila*, and *P. p. praedicta* live are isolated and low (< 7000 feet). Comparison with *perstriata* from elevations of 6000 to 8000 feet shows that at a given altitude *mayri*, *acrophila*, and *praedicta* are the largest populations, followed by *perstriata*, followed after a gap by the races of *P. guisei* and *P. erythropleura*.

### DORSAL COLORATION

*Ptiloprora mayri* and *P. guisei* may be termed "brown-backed," *P. perstriata* and *P. erythropleura* "black-backed," on the basis of the color of the edges of the black-centered back feathers. In *P. guisei* these edges are bright rufous (slightly brighter in *P. g. guisei* than in *P. g. umbrosa*), so that the back appears predominantly rufous. In *P. m. mayri* the edges are a paler rufous than those in *P. guisei*, and those in *P. m. acrophila* are a rufous olive much closer to rufous than to olive but still with a definite olive tone quite lacking in *P. m. mayri* or *P. guisei*. The edges are gray anteriorly in *P. perstriata*, becoming very dull brown or olive-brown on the lower back and rump, and very dull olive in *P. erythropleura*, so that the back appears predominantly black.

### DISTINCTNESS OF VENTRAL SPOTTING

The feathers of the under parts have gray to black centers, with whitish edges. In the *P. guisei* races and in *P. p. perstriata* the spots are equally black, but the white edges are broader in comparison with the black center in *P. guisei*, giving it a more distinctly spotted appearance. In *P. mayri* and in *P. p. praedicta* the edges are narrow as in *P. p. perstriata*, but in *P. m. mayri* and *P. p. praedicta* the centers are less black and more gray than those in *P. p. perstriata*, they are lighter gray in *acrophila*, and still lighter gray in *P. erythropleura*, contrasting less with the light periphery and yielding a less-spotted appearance. The extreme of this progressive reduction of the spots (*P. guisei* > *P. p. perstriata* > *P. m. mayri* = *P. p. praedicta* > *P. m. acrophila* > *P. erythropleura*) is *P. plumbea*, in which the under parts are nearly uniform gray, with very obscure light feather tips.

### RUFIOUS OF THE FLANKS

The rufous of the flanks is brightest in *P. guisei*, duller and paler in *P. p.*

TABLE 9  
COMPARATIVE MEASUREMENTS AND WEIGHTS OF THE GENUS *Philoprona*  
(Averages are given in parentheses.)

	Wing	Tail	Exposed Culmen	Weight
<i>mayri acrophila</i>				
North Coastal Range, 4200–6185 feet				
15 males <sup>a</sup>	98.5–104 (101.5)	77–84.5 (81.7)	24.5–26.5 (25.7)	29.3–36.3 (32.3)
10 males	88.5–94 (91.4)	75–79 (77.5)	22.5–24 (23.5)	25.5–29.2 (27.6)
<i>mayri mayri</i>				
Cyclops Mountains, 4300–7100 feet				
8 males <sup>a</sup>	96–102 (99.3)	80.5–86 (83.1)	23.5–25 (24.4)	30–37.5 (34.1)
7 females	88–94.5 (89.7)	76.5–79.5 (78.1)	22–23 (22.3)	24–29 (27.2)
<i>perstriata praedicta</i>				
Wandammen, 4900–6600 feet				
3 males <sup>a</sup>	101.5–104.5 (103)	87.5–94 (91.2)	23, 24 (23.5)	29.5–32 (30.7)
1 female	89.5	82	21	26
<i>perstriata perstriata</i>				
Weyland Mountains, 5900–7900 feet				
2 males	95, 97 (96)	81.5, 85 (83.2)	25.5	—
2 females	87, 94 (90.5)	79, 80 (79.5)	23	—
Snow Mountains, 10,600–12,100 feet				
3 males	97–106 (100.7)	90–95.5 (93.2)	21–23 (22)	—
4 females	90–95 (93.2)	78–85.5 (81.7)	20–22 (21.3)	—
Snow Mountains, 5900–7100 feet				
8 males	96–102 (98.5)	82.5–90 (87.7)	23–25.5 (24.1)	—
7 females	86–88 (87.3)	77–81 (78.3)	20–22 (21.1)	—
Telefomin, 7200–7600 feet				
6 males	94–99.5 (97.6)	82–87 (84.5)	20.5–24 (22.2)	23.5–30 (27.1)
6 females	87–89 (87.8)	71.5–79 (75.6)	20–22.5 (21.2)	21–25.5 (23.1)



TABLE 9—(Continued)

	Wing	Tail	Exposed Culmen	Weight
Eastern highlands, 8000–11,000 feet				
4 males	95–103 (99.2)	81–93 (89.5)	23–25 (23.9)	—
3 females	91–92 (91.7)	83–83.5 (83.2)	20–23 (21.7)	—
Southeast New Guinea, 12,100 feet				
4 females	88.5–93 (91.0)	82.5–85 (83.6)	20–20.5 (20.3)	—
<i>guisei guisei</i>				
Southeast New Guinea, 6600–9300 feet				
6 males	88–93 (90.5)	73–78 (75.8)	22–23 (22.4)	—
6 females	77–81.5 (78.5)	62.5–67 (65.3)	18.5–21 (20.0)	—
<i>guisei umbrosa</i>				
Huon Peninsula <sup>b</sup>				
19 males	87–93 (90.2)	—	—	21–27 (24.0)
6 females	79–84 (82.5)	—	—	19–22 (20.8)
Eastern highlands, 4400–8165 feet				
39 males	86.5–90 (88.4)	71–75.5 (73.2)	20–21.5 (21.0)	21.3–27.7 (24.2)
45 females	77–84 (79.7)	65–70 (66.5)	18–21 (19.3)	17.6–24 (20.4)
<i>erythroleura erythroleura</i>				
Arfak Mountains				
2 males	83, 86 (84.5)	68.5, 72 (70.2)	17.5, 18.5 (18)	21–23 (22)
4 females	76–79 (78.0)	62–70 (66.8)	16–16.5 (16.3)	18.5–20.5 (19.5)
Tamrau Mountains				
6 males	84–89 (87.0)	69.5–77.5 (73.0)	20–20.5 (20.2)	21.5–25 (23.3)
1 female	79	66	17.5	18.8

TABLE 9—(Continued)

	Wing	Tail	Exposed Culmen	Weight
<i>erythropleura dammermanni</i>				
Weyland, Snow mountains				
2 males	87, 87 (87)	67.5, 69.5 (68.5)	17.5, 18.5 (18)	—
4 females	80–81 (80.7)	62.5–67 (65.7)	17–18 (17.5)	—
<i>meekiana meekiana</i>				
Southeast New Guinea				
5 males	82–87 (83.6)	68–72 (69.8)	16–17 (16.2)	18.5
2 females	73, 75 (74)	60, 61 (60.5)	15, 17 (16)	—
<i>meekiana occidentalis</i>				
Snow Mountains				
5 males	82–92 (86.6)	67–77 (71.4)	15, 16 (15.3)	—
9 females	78–84 (79.9)	61–71 (66.2)	14.5–16.5 (15.4)	—
<i>plumbea plumbea</i>				
Southeast New Guinea				
5 males	71–78 (75.2)	60–65 (62.5)	16–16.5 (16.3)	13.5, 14
3 females	69–74 (60.7)	58–61 (59.8)	16	12.5
<i>plumbea granti</i>				
Telefomin				
1 male	83	57	18	16.5
Utakwa River <sup>c</sup>				
2 males	83, 86 (84.5)	—	—	—
2 females	74, 75 (74.5)	—	—	—

<sup>a</sup>Including type.

<sup>b</sup>Measurements from Mayr (1931, p. 665).

<sup>c</sup>Measurements from Ogilvie-Grant (1915, p. 75).

*perstriata*, and slightly more dull and pale in *P. mayri* and *P. p. praedicta*.

#### CROWN COLORATION

The edges of the feathers of the top of the head (forehead to nape) are entirely olive in *P. g. guisei* of southeast New Guinea; olive posteriorly, gray anteriorly in *P. g. umbrosa* and *P. m. acrophila* with the extent of gray edging greatest in *P. m. acrophila*; entirely gray in *P. m. mayri*, *P. p. perstriata*, and *P. p. praedicta*; and very dull olive-gray in *P. erythropleura*, somewhat more olive posteriorly and more gray anteriorly. The gray edges are considerably lighter (virtually whitish) in *P. m. mayri* than in *P. m. acrophila* or *P. p. praedicta*, and slightly darker again in *P. p. perstriata*, giving *P. m. mayri* the appearance of the lightest and most-spotted crown.

#### EDGES OF THE UPPER WING COVERTS

The edges of the upper wing coverts are whitish, with an olive to yellow-olive wash, in *P. guisei*; rufous to rufous olive in *P. perstriata*; light rufous olive (in some more rufous, in others more olive) in *P. m. acrophila*; varying from distinctly rufous to very light olive in *P. erythropleura*, spanning the range of *P. guisei* and *P. perstriata*; and light gray, with no suggestion of olive or rufous, in *P. m. mayri*.

#### COLOR OF IRIS

The iris is green in *P. guisei*, *P. perstriata*, and *P. mayri*, red or red-brown in *P. erythropleura* (light gray in *P. meekiana* and in *P. plumbea*).

#### VOICE

Detailed descriptions of the songs and calls of *P. guisei*, *P. perstriata*, and *P. mayri*, which I have heard frequently, will be given in the systematic accounts of my collections in the eastern highlands and North Coastal Range. Suffice it to say for the present that the vocalizations of all three forms consist of plaintive whistles which are often indistinguishable, and that Stein's (1936, p. 32) description of the call of *P. erythropleura* seems similar.

#### LOWER LIMIT OF ALTITUDINAL RANGE

In the area of sympatry with *P. guisea*, *P. perstriata* does not descend below the upper limit of *P. guisei*, which varies locally from 8000 to 10,000 feet. The lower limit is 4200 feet for *P. m. acrophila* on Mt. Menawa; 4300 feet for *P. m. mayri* in the Cyclops Mountains; 4900 feet for *P. p. praedicta* on the Wandammen Peninsula; and varies locally between 4000 and 8000 feet for *P. guisei*, *P. erythropleura*, and *P. perstriata* outside the range of *P. guisei*. My field observations indicate that this lower limit is closely correlated with the local elevation at which heavily mossed conditions first occur, rather than varying clinally or with the species as appeared earlier (Gilliard and LeCroy, 1961, p. 80). Thus, altitudinal range is not a guide to species affiliations.

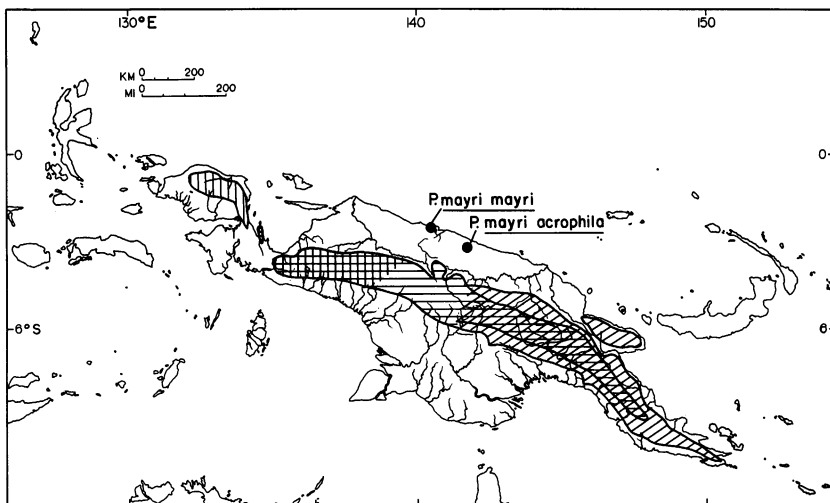


FIG. 9. Ranges of *Ptiloprora erythropleura* (vertical hatching), *P. perstriata* (horizontal hatching), *P. guisei* (diagonal hatching), and *P. mayri* (no hatching). *Ptiloprora perstriata* is sympatric with *P. erythropleura* in much of western New Guinea and with *P. guisei* in much of eastern New Guinea.

REMARKS: As rediagnosed, the endemic New Guinea genus *Ptiloprora* consists of six (formerly five) similar species, four of which (*guisei*, *perstriata*, *erythropleura*, and *mayri*; see fig. 9 for ranges) are particularly similar and were for some time thought to be allopatric and conspecific. In 1913 the Wollaston expedition found *erythropleura* and *perstriata* together on the south slopes of the Snow Mountains, necessitating the separation of *erythropleura* from the other forms. *Ptiloprora erythropleura* and *P. perstriata* are now known to be sympatric over a distance of at least 250 miles in western New Guinea, with broad altitudinal overlap but with *perstriata* extending to higher altitudes than *erythropleura*. In 1954 Mayr and Gilliard (1954, p. 369) showed that *guisei*, of which *perstriata* had been considered a high-altitude race, is actually a distinct species. *Ptiloprora guisei* and *P. perstriata* are now known to be sympatric over a distance of at least 350 miles in eastern New Guinea (Gilliard and LeCroy, 1961, p. 80), with mutually exclusive altitudinal ranges. Since *P. guisei* is "brown-backed" but *P. perstriata* "black-backed" and since the isolated population *mayri* of the Cyclops Mountains is brown-backed, Mayr and Gilliard considered *mayri* a race of *P. guisei* in redrawing species limits. Discovery of the new population *acrophila* from the North Coastal Range, which is closest to *mayri*, prompted the more de-

tailed comparison of this group given above. This comparison suggests that *P. mayri* should be recognized as a separate species, with *acrophila* a subspecies of it, yielding the following arrangement (see fig. 9 for a distributional map and table 9 for comparative measurements):

*Ptiloprora erythropleura erythropleura*: Vogelkop.

*Ptiloprora erythropleura dammermanni*: Central ranges from the Weyland Mountains east to the Oranje Mountains.

*Ptiloprora perstriata perstriata*: Central ranges from the Weyland Mountains east to the Wharton Range in southeast New Guinea.

*Ptiloprora perstriata praedicta*: Wandammen Peninsula.

*Ptiloprora mayri mayri*: Cyclops Mountains.

*Ptiloprora mayri acrophila*: Mt. Menawa.

*Ptiloprora guisei guisei*: southeast New Guinea.

*Ptiloprora guisei umbrosa*: Schrader Range and eastern highlands (Huon Peninsula population intermediate between *guisei* and *umbrosa* but nearer *umbrosa*).

Seven morphological characters (see differential diagnosis above), of which size and dorsal coloration are the most marked, distinguish members of this group. Large size places *mayri* and *acrophila* with *P. perstriata* and separates them from the smaller *P. guisei* and *P. erythropleura*. Dorsal coloration allies *mayri* and *acrophila* with *P. guisei* as opposed to *P. perstriata* and *P. erythropleura*. In some minor characters (ventral spotting, depth of rufous on flanks, crown of *mayri*) *mayri* and *acrophila* are closer to *P. perstriata* than to *P. guisei*, in another minor character (crown and upper wing coverts of *acrophila*) they are intermediate, and in the other minor characters (gray-edged upper wing coverts of *mayri*, olive tone to the dorsal rufous edges of *acrophila*) they differ from both *P. guisei* and *P. perstriata*. In one minor character (ventral spotting) the deviation of *mayri* and *acrophila* from *P. perstriata* is in the direction of *P. erythropleura* rather than of *P. guisei*. The race *P. p. praedicta* agrees with *mayri* and *acrophila* in three of the minor features that separate *mayri* and *acrophila* from *P. p. perstriata* (larger size at low altitudes, reduced ventral spotting, paler and duller rufous flanks).

Distribution (see fig. 9) and morphology suggest the following reconstruction of the evolutionary history of the *erythropleura-perstriata-mayri-guisei* complex. The ancestral form was probably distributed over the Vogelkop and the whole length of the central ranges and showed a clinal decrease from east to west in distinctness of ventral spotting and in brightness of rufous on the flanks, as indicated by the present distribution of these traits in the daughter species. After the ancestral form had broken up into isolates on the various mountain ranges of New Guinea, the first form to acquire reproductive isolation and to reinvade the range of other populations was *P. erythropleura*, expanding from the

Vogelkop into the main body of western New Guinea. The greater age of this range expansion is suggested by the fact that ecological differences between *P. erythropleura* and *P. perstriata* are now sufficient to permit broad altitudinal as well as geographical overlap (and may also be suggested by the distinctive red eye of *P. erythropleura*). Subsequently the Snow Mountains population, the range of which *P. erythropleura* had invaded, the ancestor of *P. perstriata*, expanded into virtually the whole range of the eastern New Guinea representative, *P. guisei*, but *guisei* and *perstriata* are still too similar ecologically to coexist at the same altitude. The isolated *P. mayri* may have remained closest to the common ancestor of *guisei-mayri-perstriata*, from which *guisei* diverged by becoming smaller and *perstriata* by losing the rufous edges of the dorsal feathers. *Ptiloprora meekiana* (the adult of which *erythropleura-perstriata-mayri-guisei* all resemble in their olive-washed immature plumage) and *P. plumbea* resulted from still earlier speciations, as indicated by their greater morphological distinctness and their wide but fragmented relict-like ranges.

In an assessment of the taxonomic status of *mayri* and *acrophila*, the relevant considerations are that they are nearly equidistant from *P. guisei* and *P. perstriata*, but slightly closer to the latter on the basis of minor characters, and closer to the race *P. p. praedicta* than to *P. p. perstriata*. The differences between *P. g. guisei* and *P. g. umbrosa*, or between *P. p. perstriata* (*lorentzi* is considered not separable) and *P. p. praedicta*,<sup>1</sup> or between *mayri* and *acrophila*, or between *P. e. erythropleura* and *P. e. dammermanni* are much less than those separating *mayri-acrophila* from *P. guisei* or from *P. perstriata*. The morphological differences between *mayri-acrophila* and *P. guisei* (size plus minor characters) are comparable with those between the sympatric forms *P. perstriata* and *P. erythropleura*. Thus, the best guess one can make at present is that *mayri-acrophila* may be reproductively isolated from *P. guisei* or *P. perstriata* and should tentatively be considered a distinct species. The eventual

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<sup>1</sup> I have not examined the unique type of *P. p. incerta* from the Wissel Lakes, which from the description resembles a hybrid between *P. p. perstriata* and *P. erythropleura dammermanni* (Junge, 1953, p. 72; Peters, 1967, p. 414). Against the possibility of this hybrid origin Junge pointed out that specimens of *P. erythropleura dammermanni* but not of *P. p. perstriata* were taken at the Wissel Lakes. However, *perstriata* may still be present in low numbers, since it was present but very uncommon immediately to the west in the Weyland Mountains (Stein, 1936, p. 32) and common to the east in the Snow Mountains. "Many of the known hybrids of animal species are found at the margin of the normal geographic range of one of the two parent species" (Mayr, 1963, p. 127), because the rare species has difficulty finding a mate of its own species. There is no other suspected instance of hybridization in the genus *Ptiloprora*.

test of the correctness of this guess will depend on whether or not new forms are discovered in West Irian linking *P. mayri* and *P. perstriata praedicta*.

### CHANGE OF NAME

I take this opportunity to provide a new name for the race of *Melidectes rufocrissalis* on the southern slopes of the eastern highlands, since, as Mrs. Mary LeCroy has kindly called to my attention, the name *gilliardi* is preoccupied.

#### **Melidectes rufocrissalis thomasi**, new name

This new name is proposed in honor of the late E. Thomas Gilliard, to replace *Melidectes rufocrissalis gilliardi* Diamond (1967, p. 9), preoccupied by *Melidectes fuscus gilliardi* Salomonsen (1966, p. 10), a synonym of *Melidectes fuscus fuscus* (DeVis).

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