VARIATION, RELATIONSHIPS AND EVOLUTION IN THE *PACHYCEPHALA PECTORALIS* SUPERSPECIES *(AVES, MUSCICAPIDAE)*

BY

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SYNOPSIS

The Australasian species *Pachycephala pectoralis* is remarkable for the great number and variety of geographical representatives which, since they intergrade, must be included in it. Although cited in recent evolutionary literature (Meise 1936, Dobzhansky 1937, Mayr 1942, Ripley 1945, Cain 1954a), the species has not previously been revised as a whole. It presents a wealth of geographically-variable plumage characters, whose relative systematic importance can be assessed from their co-variation. The complicated character-geography of the *P. pectoralis* superspecies is here interpreted in terms of colonizations by two major stocks, followed by divergence in isolation, great expansions of range, and extensive secondary intergradation. Whether two forms, on meeting, will interbreed or coexist as distinct species, seems to depend less on their degree of relationship than on internal and external ecological factors.

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INTRODUCTION

Pachycephala pectoralis, the Golden Whistler, is probably unique in the richness of its geographical variation. More than seventy subspecies can be recognized, extending from Java and the Moluccas to Tasmania and Tonga. Many of these are so unlike that they would certainly be considered as distinct species, were it not for the more or less complete intergradation between them.

There has been no comprehensive checklist of the species since that proposed by Mathews (1930), in which forms now generally recognized as subspecies of *P. pectoralis* are separated into eleven species. But as early as 1908 Rothschild and Hartert had suggested that the distinctive races of the Solomons are conspecific with more characteristic *P. pectoralis*, and this was confirmed twenty years later (Hartert, 1929) by the discovery of hybrid populations. Rensch (1931) included the Sumban race and its relatives, but not those of the northern Moluccas. Mayr (1932a, b) placed even the aberrant forms of northern Fiji in *P. pectoralis*, because they are connected with that species by intermediate forms. The conspecificity of diverse forms has been accepted in subsequent lists (van Bemmel, 1948 ; Mayr, 1941a, 1945, 1954a, 1955), which together cover almost the whole range of the species. All these forms are accepted here as belonging to *P. pectoralis*.

P. soror in the hill forest of New Guinea is very like nearby races of *P. pectoralis*. Over most of its range it replaces this species ; but a race of *P. pectoralis* lives so close to populations of *P. soror* (Rand, 1940) that the barriers between them are probably intrinsic (p. 166). Thus two very similar forms seem to be genetically sympatric (Cain, 1953), and must be considered as distinct species ; while others which differ much more, and seem to be actually less closely related, intergrade and must be considered conspecific. This situation is not unknown in other animals (e.g. *Acanthiza*, Mayr, 1942, 174), but the striking example in *Pachycephala* has been pointed out only by Cain (1954a) as a result of the present review.

Scope and presentation

Four species are considered, which form a single superspecies with a triplet (see p. 172) in New Guinea:

> *P. schlegelii* Schlegel, New Guinea mountain forest from 4,000 or 5,000 to 12,000 ft.
> *P. soror* Sclater, New Guinea hill forest from 2,200 to 5,200 ft.
> *P. pectoralis* (Latham), Lesser Sunda Isles and Moluccas to Tasmania and Tonga; but absent from New Guinea except for the south-east coast, and disturbed habitats in the Snow Mountains between 5,200 and 8,000 ft.
> *P. flavifrons* (Peale), Samoa.

No linear arrangement can be satisfactory, since *P. pectoralis* connects the other three species.

Text-figure 6 (end-fold) gives the ranges of the species and subspecies, and of the subspecies-groups of *P. pectoralis*. The latter seem to be natural groups, though because of gene-interchange their boundaries are not sharp and have to be shown rather arbitrarily (see Text-fig. 8):

> Lesser Sundan subspecies-group A (subspecies 1–5).
> Moluccan subspecies-group B (subspecies 6–8).
> Solomons subspecies-group C (subspecies 9–17).
> Fijian subspecies-group D (subspecies 18–21).
> Northern Australian subspecies-group E (subspecies 22–27).
> Southern Australian subspecies-group F (subspecies 28–33).
> Southern Melanesian subspecies-group G (subspecies 34–38).
> Widespread subspecies-group H (subspecies 39–57).

P. schlegelii and *P. soror* have three subspecies each, while *P. flavifrons* is monotypic. Many forms recognized as distinct subspecies by recent authors have been combined in this presentation (see p. 175), although a number of these are distinct enough to be separated according to current usage (list on p. 205).

The use of subspecies names is not helpful to the reader unless he is already familiar with the group under discussion. Nor is it usually necessary, since most subspecies are easily characterized by their geographical ranges (cf. Wilson & Browne, 1953). In this paper the range citation, given in a condensed and approximate form, is followed by a cipher for direct reference to the map (Text-fig. 6). This cipher consists of the number of the subspecies within its species, preceded by the subspecies-group letter for subspecies of *P. pectoralis*. Where infrasubspecific variation is discussed, parts of the subspecies range are indicated by lower-case suffixes. Thus "Sumbawa to Alor A3" indicates the form of *P. pectoralis* on Sumbawa, Flores, Lomblen, Pantar and Alor (which from "Lomblen to Alor A3b" is slightly larger and larger-billed). The exact range of any form can be found from the checklist (p. 195), which is lettered and numbered to correspond.

Subspecies names are useful in referring to forms whose geographical ranges are diffuse or difficult to define: "*dahli* E25" is used for the subspecies of *P. pectoralis* which ranges from south-eastern New Guinea and Fergusson Island to many small islands in the Bismarck Archipelago. The range of *dahli* is shown inset on the map.

Material

I have seen at least one adult male and one adult female of every subspecies recognized by recent authors, except for the following : no specimens of H46 and H50 ; no adult male of D21; no adult female of C15, G37a & b, H49, H52 and H56 (juveniles seen) and E25c (female unknown). I have examined the following types in the British Museum (Natural History): *fulvotincta* Wallace A3a, *mentalis* Wallace B6, *neglecta* Layard (= D18b), *aurantiiventris* Seebohm D19a, *torquata* Layard D20a, *fuliginosa* Vigors & Horsfield F28b, *fusca* Vigors & Horsfield (= F30b), *variegata* Gray (= G34), *cucullata* Gray G36, *chlorurus* Gray G37a, *intacta* Sharpe G37d, *fuscoflava* Sclater H42, *xanthocnemis* Gray (= H43b), *clio* Wallace H45, *collaris* Ramsay H47a, *vitiensis* Gray H55, *klossi* Ogilvie-Grant and *bartoni* Ogilvie-Grant (*P. soror* 2 & 3).

Unfortunately, many of the available series were very short, and the measurement tables compiled (p. 212) are inadequate for proper statistical treatment. Individual variation and fine geographical variation are therefore not considered in this paper. Where the available material was inadequate full use has been made of published descriptions and measurements, especially those of Mayr (1932a, b, and 1954a).

I have studied *P. pectoralis* in the field on Guadalcanal C11 and San Cristobal C17a, and seen and heard it near Sydney F30b, on Lord Howe and Norfolk Islands F32 & 33, and on Efate and Santo G37b & d. I have also studied *P. implicata* (which is rather closely related to the *pectoralis* superspecies) in the mountains of Guadalcanal (Cain & Galbraith, 1956).

PLUMAGE PATTERNS

Pigments

All the colours in the various plumages of the superspecies are produced by combinations of yellow, black and brownish pigments (Table I). The yellow pigment is soluble in boiling alcohol or pyridine, and turns a transient blue-green with concentrated sulphuric acid. It is therefore a carotenoid (Cain, 1950, 104). Carotenoid

TABLE I.—*Composition of Plumage Colours.*

Melanins.	Carotenoid.			
	None.	V. pale.	Pale.	Deep.
None	White	Pale yellow	Lemon-yellow	Golden- to orange-yellow
Eumelanin :				
Barbs clear, barbules saturated	Grey	Olive-grey	Olive-green	Golden-olive
Granules in barbs, barbules saturated	Dull black	—	Olive-black	—
Saturated	Black	—	—	—
Phaeomelanins :				
Pale	Sandy to dull pink	Cream	Cinnamon to vinous	Citrine
Deep	Brown to rufous	Russet	Tawny-orange	—

tends to be more concentrated in the barbs than in the barbules of the feather. The other pigments, if not saturated in both elements of the vane, are more concentrated in the barbules than in the barbs. They are granular. Under the microscope black granules still appear intense black, while brown ones vary considerably in hue and intensity. The black and brown pigments are presumably eumelanins and phaeomelanins. Parts of the vane devoid of melanins are filled with minute bubbles, which by multiple internal reflection add to the brilliance of the whites and yellows. Most contour feathers are grey basally, with the black granules forming bands across the barbules.

Patterns

It is convenient to describe the variation of the male pattern throughout the superspecies in terms of departure from a standard. The descriptions will be briefest, and the peculiarites of the various forms most clearly apparent, if the pattern chosen as standard combines all the variants which are more common than their alternatives. This condition is fulfilled by the pattern of males of *P. pectoralis* in the Bismarcks H48–51, which is shown diagrammatically in Text-fig. 1 (top), and described below.
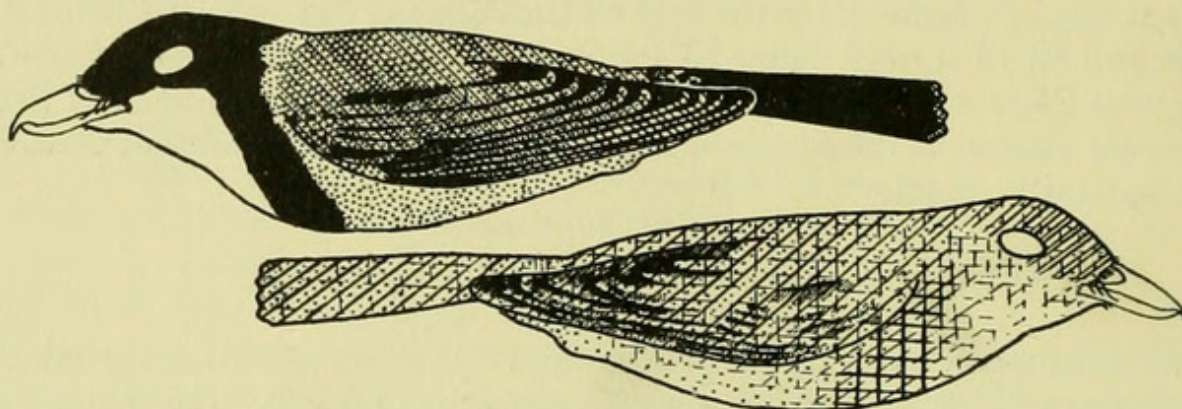
FIG. 1.—Diagram of the standard plumage patterns for the superspecies. Male (above, facing left) H48–51 ; female (below, facing right) H52. Not to scale. Colour key : diagonal hatching, grey (without stipple) or olive (with stipple) ; cross-hatching, brown and rufous hues ; stipple, yellow ; black, black ; white, white. The same conventions are used in all the diagrams of plumage pattern (Text-figs. 1–3 and 5).

ADULT MALE. White chin and throat separated by black gorget, between auriculars, from golden-yellow underparts; fore-edge of gorget formed by black tips of white feathers, hind-edge by black feathers overlying yellow ; black cap and auriculars separated by yellow collar across hind-neck from golden-olive mantle ; wings dull black with olive outer edges to all feathers, fading to grey towards tips of outer primaries ; inner edges of quills whitish ; tail and upper tail-coverts black with olive tips, and olivaceous traces at bases of outer quills.

It is harder to select a standard for the female plumage, since the patterns are much vaguer than those of the males, and the variation is more quantitative than qualitative. The following description and the diagram (Text-fig. 1, bottom) best fit some females of the widespread group H, and especially those from Ndeni H52.

ADULT FEMALE.   Throat pale buff with faint dark fringes at sides ; gorget brownish,

vaguely defined, grading into brownish wash on breast and flanks ; mid-belly and under tail-coverts free from melanins ; under tail-coverts pale yellow, breast and belly washed with yellow ; upper parts citrine ; collar, rump and tail brighter ; cap greyer than mantle, auriculars cinnamon ; wings blackish-brown with citrine outer edges to all feathers, fading to greyish towards tips of outer primaries ; inner edges of quills whitish.

Retarded and juvenile plumages

Males are sometimes found in plumage like that of the adult females (" II Phase " of Mayr, 1932a, b), though commonly with more intense carotenoid. They agree with adults in tail shape and in having black bills, and their testes are often enlarged (Baker, Marshall & Harrison, 1940). They are evidently adult males in a " retarded " plumage (Mayr, 1933) : in Victoria and Tasmania at least they are known to breed in this condition (Chandler, 1912 ; Howe, 1927 ; Lawrence, 1952).

Juveniles of both sexes have brown or straw-coloured bills, and softer wings and more pointed tail-feathers than adults. In pattern they resemble adult females, except that they have the edges of the wing feathers rufous, the cap olivaceous, the mantle often browner and the carotenoid pigment more dilute (I Phase). Nestlings are commonly rufous all over ; but in the lesser Sunda Isles (nestling of A3b seen) are greyish with darker shaft-streaks beneath. Only Mayr (1932a, b) has systematically described immature plumages, and I have not examined sufficient immature skins from parts of the range not treated by him to attempt a survey of their variation.

At first sight the female and juvenile patterns seem very different from that of the adult male. But the distribution of pigments is much the same—except that carotenoids are greatly diluted, there are no solid blacks, and eumelanins are more or less replaced by phaeomelanins. As a result, these patterns are less sharply defined and stereotyped than that of the male, and show a greater range of colours.

Visual significance

In many birds the upperparts are cryptic, while the underparts bear a conspicuous pattern which plays a part in intraspecific display. The standard male pattern of *P. pectoralis* is a good example of this. Both the ventral and the dorsal pattern embody transverse bands which contrast strongly with the ground-colour (see Cott, 1940). The bright underparts contrast with the forest background, so that the black gorget (exploiting maximal tone-contrast against the white, and an especially effective colour-contrast against the yellow) is an emphatic feature. The olive upperparts, on the other hand, conform with the background, and the yellow collar is disruptive in effect. Females and juveniles tend to be inconspicuously coloured, with neither emphatic nor markedly disruptive features.

This common species has been largely neglected by Australian ornithologists (except Lawrence, 1952), and nothing seems to be known of the part played in intraspecific display by the conspicuous male ventral pattern. Although we saw neither courtship nor aggressive displays in the Solomons, the general behaviour of

these birds (Cain and Galbraith, 1956) is much what might be expected from a study of their colour-patterns. The males show themselves freely to a ground observer as they move about below the canopy, whistling loudly. But although they will sing from bare branches overhung by foliage, they avoid all perches exposed to the sky.

Females of *P. pectoralis* on Guadalcanal C11, like those of many other subspecies, are dull in colour. They are very silent and skulking, seldom seen as they move about in dense thickets near the ground. Those on San Cristobal C17 are as bright yellow beneath as the males, but lack the black gorget. They are often seen in company with the males in the upper substage, usually silent, but occasionally heard to give alarm calls and quiet whistles. A related species in the mountains of Guadalcanal (*P. implicata*) has the females actually more conspicuous than the males. They are not more retiring than the males, and are more vocal than the females of *P. pectoralis*. The males of *P. implicata* are inconspicuously coloured in olive and blackish, and are much more silent and retiring than those of *P. pectoralis*. On the other hand, a pair of this species was seen feeding exposed in the tops of small trees: perhaps the direction of predation is less important to these more uniformly-coloured birds.

VARIATION

Geographical variation in the superspecies is conspicuous and complex. Marked sexual dimorphism is normal, but in three widely-separated races of *P. pectoralis* the males are permanently hen-feathered, while *P. flavifrons* has cock-feathered females. The sporadic occurrence, in sexually dimorphic forms, of breeding males in female plumage shows that hen-feathering is not very important here, either as an indicator of genetical change or as a potential barrier to interbreeding.

The bold pattern of the male is subject to striking variation. For example, in some forms the throat is yellow instead of white, and some of these lack the black gorget. These differences are not unifactorial, since for almost every pair of contrasted characters intermediate states are to be found. Single characters cannot be used to delimit natural groups, since not one variant is confined to a single subspecies-group of *P. pectoralis* (as distinguished by the whole constellation of characters of both sexes) and shown by every race belonging to that group. Most are both polyphyletic in origin and labile within groups. The marked geographical variation of the female pattern does not present the same appearance of discontinuity, and there is less temptation to erect a classification based on single characters of the females.

Size variation

The largest subspecies of *P. pectoralis* have wings over 30% longer than the smallest. If their proportions are the same, they should therefore be more than twice as heavy. Unfortunately, weight measurements are available for very few forms in the super-species, so that wing lengths are for the present the best indication of body size. Certain subspecies which are evidently very closely related differ markedly in size, which is therefore not generally of much importance in assessing relationships ; but some of the discontinuities between subspecies-groups are marked by sharp changes

in size as well as in other characters. A coarse grading into size-classes adequately expresses the major variation, which more detailed treatment would tend to obscure. In any case, too few specimens of many forms were available for quantitative treatment to be satisfactory. Snow (1954) has pointed out that quantitative differences (in size, proportions, intensity of pigmentation, etc.) are often adaptive, and cannot be used as clues to relationships and past history until their present environmental relations have been worked out. Conversely, where the past history has been as complex as in the *pectoralis* superspecies, such differences cannot be shown to be adaptive until relationships have been established (by studying the co-variation of more stable characters). Two forms on neighbouring islands might differ in size, not because the climates were different but because they were the same, if the forms belonged to different subspecies-groups whose size/temperature relationships (Snow, 1954, 22) had been evolved under different climates.

The various forms are graded into five classes on the average wing lengths of adult males. But the arbitrarily-selected limits of these classes have in a few cases been relaxed, to avoid separating closely-related forms whose small difference in size happens to transgress them. The southernmost Australian forms are classed as " large ", not as " very large ", because the appearance of the skins (prepared by many different collectors) strongly suggests that they are considerably smaller birds, though with relatively long wings (perhaps in relation to their nomadic habit) than the " very large " ones of the Solomons and elsewhere. This can only be decided when weight measurements are available. The middle class, containing the most forms, is of wing lengths from 90 to 95 mm.; those from 80 to 85 mm. are graded as " very small ", from 85 to 90 as " small ", from 95 to 100 as " large " and over 100 as " very large ". The following forms fall outside the middle class :

VERY SMALL BIRDS. Sumba, Java to Alor, and Flores Sea and Salayer A1–5 ; midwestern Australia E22 a–c (size increasing north-eastwards).

SMALL BIRDS. Rennell and San Cristobal C16–17 ; northern Australia to southern New Guinea E22d–24 ; New Caledonia, New Hebrides and Vanikoro G34 & 36–38 ; Timor to Damar H39–41 ; Sula and Peleng Isles H45–46 ; large islands in the Bismarcks H48 ; Kandavu H54 ; *P. soror* ; *P. schlegelii* ; *P. flavifrons*.

LARGE BIRDS. Ternate, Tidore and Obi B7–8 ; Vella Lavella to Gatukai C13 & 15 ; Tasmania and southern Australia F28–30, size decreasing northwards ; Tabar H50 ; Lau archipelago H56.

VERY LARGE BIRDS. Bougainville to Malaita, and Rendova and Tetipari C9–12 & 14 ; Loyalty Isles G35 ; Tenimber Isles H42 ; Lihir H49 ; Tonga H57.

Differences in bill size are even more marked, with the largest bills some 60% longer than the smallest, and the bill may be stubby, stout or slender. However, closely related forms differ in bill size even more than in wing length, and the accuracy of this measurement is not sufficient for the forms to be graded with any degree of certainty from the scanty data available. Tail and tarsus lengths are only comparable when expressed as relative lengths, which vary between individuals much more than the absolute measurements. Therefore none of these measurements is dealt with comprehensively, though there is some discussion of climatic correlation in certain parts of the range (p. 186).

Male character-geography

Some of the most conspicuous variations appear to be qualitative and discontinuous, but hybrid forms often show intermediate states. Probably most of the variations are in fact potentially continuous—but it is convenient to deal with the geographical distribution of the more important variations in terms of discontinuous "characters", at the same time mentioning the occurrence of intermediate conditions.

(1) HEN-FEATHERED. Rennell C16, Norfolk Island F33 (sexes almost indistinguishable) ; Salayar A5 (male in a female type of plumage, but more advanced in character than its own female).

The hen-feathered races were considered as separate species until Mayr (1932a, 5) pointed out the relative unimportance of the character. Since individual males of dimorphic subspecies can breed in female plumage, hen-feathering involves neither a radical change in the genome nor complete breakdown of courtship and territorial displays. Variations of the male pattern such as " no gorget ", " no collar ", " cap pale " and " tail pale " may be considered as partial hen-feathering, and the San Cristobal form C17 especially shows several such indications.

The three fully hen-feathered forms are not considered further in the male character-geography.

(2) CHIN BLACK. Sumba A1 ; Morotai to Batjan B6–7 ; Solomons except San Cristobal C9–15 ; *P. schlegelii*, *P. flavifrons*.

(3) THROAT AND CHIN BLACK. Tonga H57.

In *P. flavifrons* there is much black at the base of the throat feathers, which shows as irregular barring. Another approach to the black-throated condition is shown in the reduction of the throat patch on Sumba A1 (where black malar feathers intervene between it and the auriculars), from Java to Alor A2–3, and in *P. soror* and *P. schlegelii*.

(4) THROAT YELLOW. Solomons C9–17 (variable in hybrids on small islands off Shortland E26) ; northern and central Fiji D18–21 ; Tenimber Isles H42 ; *P. flavifrons* (individually variable).

Juveniles on Vanikoro G38 have yellow throats, and there is a tendency for the throats of juveniles in the New Hebrides G37 and on Utupua H53 to be yellowish (Mayr, 1932b). A few yellow feathers occasionally appear in the white throats of adult males. I have seen these in males of *P. pectoralis* from Teste Island E25b, Lord Howe Island F32, New Caledonia G34, Loyalty Islands G35, Aneitum G36 and Kandavu H54, and in *P. soror* from the Snow Mountains 2a. But they seem to occur most frequently in *P. schlegelii*—in eight of thirty-one adult males examined.

(5) BASES OF THROAT-FEATHERS WHITE. Obi B8 ; Solomons C9–17 ; northern and central Fiji D18–21 ; midwestern Australia to small islands in the Bismarcks, and hybrids off Shortland E22–26 ; Vanikoro G38 ; Tenimber Isles H42 ; Sula and Peleng Isles H45–46 ; Louisiades H47 ; Ndeni, Santa Cruz islets and Utupua H52–53.

(6) NO GORGET. Malaita C12 ; Viti Levu and Vanua Levu D18a and 19a ; *P. flavifrons*.

The gorget is more or less broadly interrupted in individual males on the islands between Koro and Taviuni on the one hand, and Viti Levu and Vanua Levu on the other—D18b, 19b & c.

(7) FORE-EDGE OF GORGET DEFINED BY PALE FEATHERS. Sumba and Java to Alor A1–3 ; northern Moluccas B6–8 ; Solomons except San Cristobal (and the gorgetless forms on Malaita and Rennell) C9–11 & 13–15 ; Ceram H43 ; Ndeni and Santa Cruz islets H52 ; *P. schlegelii.*

In these forms the black of the gorget deeply undercuts the white or yellow of the throat, whereas in the standard pattern the edge of the gorget is defined on the underlying layers of feathers at about the same level. On San Cristobal C17, in the hybrids on the outliers of Shortland E26, and on Buru H44, the gorget undercuts the throat-patch, but there are also some black tips.

(8) GORGET CUT OFF FROM AURICULARS. Northern Moluccas B6–8 ; New Caledonia G34 ; Ceram H43 ; Ndeni and Santa Cruz islets H52.

In all these forms the throat-feathers are unusually long, extending further back than the auriculars. They are best developed from Morotai to Batjan B6–7 (where they cover most of the gorget), and least so on New Caledonia G34 (where only the lateral feathers are appreciably lengthened). In B6–7 and G34 the gorget is itself reduced, and does not join the auriculars even beneath the white feathers. On Vella Lavella and Ganonga C13 the yellow feathers extend behind the auriculars, but the gorget is too broad to be cut off.

(9) GORGET VERY BROAD. Vella Lavella and Ganonga C13 ; *P. schlegelii.*

(10) GORGET VERY NARROW. New Caledonia G34 ; Kandavu H54 ; *P. soror.*

(11) BREAST RUFOUS. Sumba A1 (intense, extending to flanks and belly), Java A2a (less intense, especially on belly), Bali A2b (still less intense on flanks and belly), Sumbawa to Alor A3 (confined to band behind gorget), islands in Flores Sea A4 (very faint, barely detectable on belly and flanks) ; Santa Anna C17b and individuals on San Cristobal C17a (patch behind gorget) ; New Caledonia G34 (patch behind gorget) ; *P. schlegelii* (extending to flanks and belly ; very intense from Snow Mountains to south-eastern New Guinea 3, somewhat less so in Vogelkop and Cyclops Mountains 1 & 2).

There is a rufous wash centred on the vent on Taviuni, Koro and Vatu vara D20–21, Ceram H43, Ngau H55, and in individuals on Aneitum G36.

Where very pale rufous phaeomelanin combines with pale yellow carotenoid (as in the Flores Sea A4), the tawny-orange produced is rather like the orange-yellow of very intense carotenoid (as on Vanua Levu D19). The difference is easily seen through the microscope, since the phaeomelanin appears granular.

(12) CAROTENOID VERY DEEP (ORANGE-YELLOW). Vella Lavella and Ganonga C13 ; Vanua Levu to Koro and Vatu vara D19–21 ; Louisiades H47 ; Lihir H49 ; Manus H51.

(13) CAROTENOID PALE (LEMON-YELLOW AND GREENISH-OLIVE). Mid- and north-western Australia E22, deepening northwards E22a to 23 ; Tasmania and southern Australia F28–30, deepening northwards F29 to 31 ; New Caledonia, New Hebrides and Vanikoro G34 & 36–38 ; Babar H40 ; Utupua H53 ; *P. soror.*

(14) FOREHEAD YELLOW. Viti Levu, Vanua Levu and Vatu vara D18a, 19a & b & 21 (sometimes a few yellow feathers on Ovalau, Rambi and Kio D18b & 19c) ; *P. flavifrons* (sometimes white, in white-throated individuals).

(15) CAP PALE. Santa Anna C17b (olive, with blackish lores and auriculars) and

San Cristobal C17a (variable, from olive to black) ; New Caledonia G34 (grey) ; Aneitum G36 (dull black with more or less olive scalloping).

(16) No COLLAR. Vella Lavella and Ganonga C13, Ndeni and Santa Cruz islets H52, *P. flavifrons* (melanic forms with no trace of a collar) ; Fiji, except for Vatu vara and Kandavu, D18–20, H55–56 (black of cap extends far down on hind-neck, followed by a yellowish trace) ; Malaita C12, New Caledonia G34, *P. soror* (yellowish trace) ; San Cristobal C17 (yellowish trace on hind-neck, clear yellow patches at sides of neck).

The collar is very vague and narrow on the islands in the Flores Sea A4, from Kulambangra to Gatukai C15 and on the Tenimber Islands H42. It is narrow and washed with olive on the nape on Sumba and from Java to Alor A1–3, on Rendova and Tetipari C14, in mid- and north-western Australia E22, in Tasmania, southern and eastern Australia and on Lord Howe F28–32, from the Loyalty Isles to Vanikoro G35–38, on Timor H39a, the Louisiades H47, Utupua H53 and Kandavu H54.

(17) MANTLE BLACK. Vella Lavella and Ganonga C13, Ndeni and Santa Cruz islets H52, *P. flavifrons* (wholly black) ; islands in Flores Sea A4, Rendova and Tetipari C14, Taviuni and Koro D20, Ngau and Lau archipelago H55–56 (feathers black-centred, individually variable from olive with concealed black spots to black with olive scalloping).

(18) WING BLACK. Islands in Flores Sea A4 ; Vella Lavella, Ganonga, Rendova and Tetipari C13–14 ; *P. flavifrons* ; *P. schlegelii*.

In these forms the pale edges to the wing-feathers are absent or exceedingly narrow. The pale edges are narrow, and the primary-coverts entirely black, on Taviuni, Koro and Vatu vara D20–21, in *dahli* E25, on Ceram and Buru H43–44, Ndeni and Santa Cruz islets H52 and Ngau and the Lau archipelago H55–56.

(19) OLIVE VERY DARK. Kulambangra to Gatukai C15 ; Fiji D18–21 & H54–56 ; Ceram and Buru H43–44 ; *P. soror* ; *P. schlegelii*.

Normally the bases of the barbules, as well as the barbs, are yellow, giving a more or less pronounced herring-bone pattern under the microscope. In the above forms the barbules are black down to their junctions with the barbs.

(20) OLIVE TINGED WITH BROWNISH. San Cristobal C17 ; Koro and Taviuni D20 ; Ceram H43 ; Louisiades H47 ; individuals on Aneitum G36.

The phaeomelanic wash is deepest on tail, upper tail-coverts, rump and secondaries.

(21) WING QUILLS GREY-EDGED. Midwestern Australia to small islands in the Bismarcks E22–25 ; Tasmania F29 ; Damar H41 ; *P. soror* in Snow Mountains 2a.

The wings are unusually grey in southern Australia F28 & 30, becoming more olive northwards ; and in eastern Fiji D19 & 21 & H56, becoming more olive westwards (towards Viti Levu and Kandavu D18 & H54). They are also unusually grey in all populations of *P. soror*. They are variable in colour in the hybrids on outliers of Shortland E26.

(22) UPPER WING-COVERTS YELLOW-EDGED. Viti Levu and Vanua Levu D18–19 ; midwestern Australia to small islands in the Bismarcks E22–25 ; Tasmania, southern and eastern Australia and Lord Howe F28–32 ; Loyalty Islands G35.

The upper wing-coverts are edged with yellower olive than the mantle in many forms ; those listed above show this most conspicuously.

(23) UPPER TAIL-COVERTS ALL-OLIVE. Kulambangra to Gatukai C15; San Cristobal C17; northern Fiji, except Koro and Vatu vara, D18–20a; mid- and north-western Australia E22; Tasmania, southern and eastern Australia and Lord Howe F28–32; New Caledonia to Banks Islands G34–37; Timor H39; Tenimber Isles H42; Louisiades H47; Kandavu H54; Tonga H57; *P. soror*.

(24) TAIL PALE. Tasmania F29, New Caledonia, Loyalty Islands and Aneitum G34–36, Timor H39, western Louisiades H47a (no solid black); San Cristobal C17 (more or less black); south-western and South Australia F28, New Hebrides from Erromango northwards G37, Misima H47b, Kandavu H54, *P. soror* except the Snow Mountains 1 & 3 (black subterminal patch); south-eastern Australia and Lord Howe F30 & 32, Babar H40, Rossel H47c (more than half black); mid-western Australia E22a–c, southern Queensland F31a, Damar H41, *P. soror* in Snow Mountains 2 (wide olive edges basally); north-western Australia E22d, northern Queensland F31b (narrow olive edges basally).

The pale part of the tail, usually olive, is grey from south-western Australia to Tasmania and Victoria F28–30a, and sometimes greyish in northern Queensland F31b.

(25) UPPER TAIL-COVERTS ALL-BLACK. Sumba, Java to Alor, and islands in Flores Sea A1–4; Morotai to Obi B6–8; Vella Lavella and Ganonga C13; Ceram, Sula and Peleng Islands H43 & 45–46; Ndeni and Santa Cruz islets H52; *P. schlegelii*; *P. flavifrons*.

Even in these forms, the shortest coverts usually have narrow olive tips. Males on Buru H44, and from some other localities, have the tips of all the coverts extremely narrow.

(26) TAIL ALL-BLACK. Sumba A1; Morotai to Batjan B6–7; Vella Lavella and Ganonga C13; Ndeni and Santa Cruz islets H52; *P. schlegelii*; *P. flavifrons*.

There are sometimes narrow and obscure olivaceous tips to the lateral tail feathers, even in these forms. The tips are unusually narrow from Java to Alor A2–3, on Obi B8, in most of the Solomons C9–12 & 14–15, and from Ceram to Peleng H43–46.

Female character-geography

(1) COCK-FEATHERED. *P. flavifrons* (throat and forehead patterns less sharply defined than in the male).

Certain single characters of the female (such as a white throat, a sharply defined gorget, bright yellow underparts, a pure grey cap and pure olive mantle, and a partly black tail) tend perhaps towards the male pattern. Often they appear independently, but on San Cristobal C17, and also in northern members of group E and in *P. soror*, most of the characters mentioned occur together—these forms have an advanced type of female plumage. Individual females of the race on Vella Lavella C13a (whose males are all-black above) have black gorgets (Mayr, 1932a, 17). A partly cock-feathered female from Malaita C12 is reported by Mayr (1932a, 21). I have seen several specimens which (though sexed as females) are partly or wholly in the plumage of the adult male, but consider it unwise to rely on the sexing of these, since they carry no indication that the collector had noticed the discrepancy between gonads and plumage.

P. flavifrons is not considered further in the female character-geography.

(2) BILL PALE. Solomons C9–17 (palest from Guadalcanal to Kulambangra and on Rennell C10c–11 & 15–16, darkest on Malaita, Vella Lavella and Ganonga C12 & 13) ; Rambi and Kio D19c.

(3) THROAT WITHOUT MELANIC WASH. Islands in Flores Sea and Salayer A4–5, midwestern Australia E22a–c, New Caledonia to Banks Islands G34–37, Timor and Babar H39–40, Louisiades H47, Utupua H53, *P. soror* (wholly white) ; north-western Australia to small islands in the Bismarcks, hybrids near Shortland and the Snow Mountains E22d–27, Vanikoro G38, *P. schlegelii* in the Vogelkop and Cyclops Mountains 1 & 2 (white, more or less mottled) ; San Cristobal C17 (pure yellow).

(4) THROAT YELLOW. Choiseul to Russel Isles, central Solomons, Rennell and San Cristobal C10 & 13–17 ; Tenimber Isles H42.

(5) CHEEKS YELLOWER THAN THROAT. Bougainville, Guadalcanal and Malaita C9, 11 & 12 ; Viti Levu and Vanua Levu D18a & 19a.

(6) THROAT BARRED. Morotai to Obi B6–8 ; Bougainville, Guadalcanal and Malaita C9, 11 & 12 ; Viti Levu and Vanua Levu D18a & 19a, and individuals on Ovalau, Rambi and Kio D18b, 19b–c ; north-western Australia to small islands in the Bismarcks, hybrids near Shortland, and the Snow Mountains E22d–27 ; Tasmania, southern and eastern Australia, Lord Howe and Norfolk Islands F28–33 ; Damar H41 ; Sula and Peleng Islands H45–46 ; Tonga H57 ; *P. schlegelii* (faintly in the Vogelkop 1).

There is no sharp distinction between subterminal barring and terminal fringing of the feathers. There is a tendency towards heavy fringing, not entirely confined to the sides of the throat, from New Caledonia to the Banks Islands G34–37, in the Louisiades and Bismarcks H47–48, and on Utupua H53.

(7) THROAT AND BREAST SHAFT-STREAKED. *P.p. dahli*, hybrids near Shortland, and Snow Mountains E25–27 ; Vanikoro G38 ; Manus H51.

(8) UNDERPARTS SHAFT-STREAKED. Solomons except San Cristobal C9–16 ; Viti Levu and Vanua Levu D18a & 19a, and individuals on Ovalau, Rambi and Kio D18b & 19b–c.

(9) GORGET EUMELANIC. Morotai to Batjan B6–7, *P. schlegelii* east of the Vogelkop 2–3 (pure grey) ; Choiseul and Kulambangra to Florida, Rennell and San Cristobal C10 & 15–17, Loyalty Islands and Vanikoro G35 & 38 (olive) ; Bougainville and Malaita C9 & 12, northern Australia E22–23, Tasmania and southern Australia F28–30, New Caledonia, and New Hebrides from Erromango northwards G34, 37a–c & e (considerably greyer than standard).

(10) GORGET YELLOW-WASHED. Choiseul to Russel Islands, central Solomons, Rennell and San Cristobal C10 & 13–17 ; Loyalty Islands and Vanikoro G35 & 38 ; Babar and Tenimber Isles H40 & 42 ; Louisiades H47.

(11) BREAST AND FLANKS OLIVE. Morotai to Batjan B6–7 ; Choiseul and Kulambangra to Florida, and Rennell C10 & 15–16 (pale) ; Snow Mountains E27 (pale, confined to narrow band behind gorget) ; *P. soror* (pale) ; *P. schlegelii* (deep in Snow Mountains and south-eastern New Guinea).

Many forms have a combination of carotenoid and phaeomelanins on the underparts, but this ventral olive is rare.

(12) UNDERPARTS UNIFORM. Koro and Vatu vara D20b–21, and individuals on Ovalau and Taviuni D18b & 20a ; Tenimber Isles H42 ; Mussau and Lihir H48d–49; southern Fiji H54–56.

On Ceram and Buru H43–44 and in the Bismarcks H48a–c, the gorget is little darker than the throat and mid-belly.

(13) BELLY WASHED WITH MELANINS. Islands in Flores Sea A4 (pinkish) ; Bougainville, Guadalcanal and Malaita C9 & 11–12 (greyish or rufous buff) ; Rendova and Tetipari C14 (deep rufous) ; Fiji D18–21, H54–56 (greyish on Viti Levu and Vanua Levu D18a & 19a, cinnamon on Koro, Vatu vara and in southern Fiji D20b–21 & H54–56, individually variable between Koro and the large islands D18b & 19b– 20a) ; south-western and South Australia F28a–b (pinkish), Tasmania, Victorian mallee and northern Queensland F28c, 29 & 31b (buffy) ; New Caledonia G34 (pale buffy) ; Timor H39 (pinkish) ; Damar, Tenimber Isles, Ceram to Sula Isles, Bismarcks except Tabar H41–45 & 48–49 (brownish, more or less mixed with yellow).

(14) BREAST AND BELLY DEEP YELLOW. Morotai to Obi B6–8 (deepest on Obi B8) ; Choiseul and Vella Lavella to Florida, and San Cristobal C10, 13, 15 & 17 ; northern Australia, *dahli* and Snow Mountains E23, 25 & 27 ; Loyalty Islands and Vanikoro G35 & 38 ; Babar H40, Peleng Isles H46, Louisiades H47, Tabar H50, Manus H51, Utupua H53, Tonga H57 ; *P. soror* ; *P. schlegelii*.

(15) BREAST AND BELLY SCARCELY YELLOW. Sumbawa to Alor and islands in Flores Sea A3–4 ; Bougainville, Guadalcanal and Malaita C9, 11 & 12 (juveniles may be yellower) ; Fiji except Kandavu D18–21, H55–56 ; midwestern Australia E22a–c ; Tasmania and southern Australia F28–30 ; Malekula and Santo G37d ; Timor, Damar and Buru H39, 41 & 44.

(16) UNDER TAIL-COVERTS NOT YELLOW. Tasmania and southern Australia F28–30.

Here the female plumage is almost devoid of carotenoid, except for a circlet of pale yellow feathers at the vent.

(17) CAP OLIVE. Solomons C9–17 (may be obscured by heavy rufous wash).

(18) CAP GREY. Salayer A5 ; Morotai to Batjan B6–7 ; midwestern Australia to small islands in the Bismarcks E22–25 ; Tasmania, southern and eastern Australia, Lord Howe and Norfolk Island F28–33 ; Vanikoro G38 ; Tabar H50, Lau archipelago and Tonga H56–57 ; *P. schlegelii* east of the Vogelkop 2–3.

(19) AURICULARS GREY. Morotai to Batjan B6–7 ; Vanikoro G38 ; *P. schlegelii* east of the Vogelkop 2–3.

(20) MANTLE GREY. Tasmania and Victoria F29–30a (wholly grey) ; south-western and South Australia and New South Wales F28 & 30b (individuals with olive wash on rump or scapulars) ; midwestern Australia E22a–c (rump olive) ; north-western Australia E22d (rump and lower back olive).

(21) TAIL GREY. Tasmania and southern Australia F28–30.

(22) MANTLE PURE OLIVE OR GREY (WITHOUT PHAEOMELANINS). Sumba and Salayer A1 & 5 ; Morotai to Batjan B6–7 ; San Cristobal C17 ; midwestern Australia to *dahli* and Snow Mountains E22–25 & 27 ; Vanikoro G38 ; Tabar H50 ; Tonga H57 ; *P. schlegelii* in Cyclops Mountains 2.

(23) UPPERPARTS BROWN. Northern and central Fiji D18–21 ; Ceram H43, Louisiades H47, Mussau H48d, Lihir H49.

The mantle is distinctly brownish-olive on Aneitum and from Mai to Santo G36 & 37c–d, from Timor to the Tenimber Isles H39–42 (tail pure olive on Babar H40), from Buru to the Peleng Isles H44–46, in the rest of the Bismarcks and on Manus H48a–c & 51, on Ndeni, Santa Cruz islets and Utupua H52–53, in southern Fiji H54–56, and in *P. soror* in the Vogelkop 1.

(24) UPPERPARTS SOMETIMES RUFOUS-WASHED. Choiseul to Guadalcanal, and Vella Lavella to Tetipari C10–11 & 13–14 ; northern and central Fiji D18–21.

(25) WINGS RUSSET-EDGED. Solomons except San Cristobal C9–16 (mixed with olive from Choiseul and Kulambangra to Florida C10 & 15) ; northern and central Fiji D18–21 (mixed with olive on Koro D20b).

(26) TAIL PARTLY BLACK. San Cristobal C17 ; north-western and northern Australia, *dahli* and Snow Mountains E22d–23, 25 & 27 ; *P. soror*.

The variable hybrid populations on the small islands off Shortland E26 have largely been omitted from the character-geography. They are discussed on p. 156.

NATURAL GROUPS

Co-variation and character-complexes

Single characters might be used to link populations into as many sets of overlapping assemblages as there are characters under consideration. If these bore no relation to one another, or were strictly correlated with environmental features, little could be inferred about relationships and evolutionary history. In many groups, the few characters available in ordinary museum material may be too sporadic or too liable to parallel evolution to be helpful. But where there are many characters, capable of independent variation and not exclusively related to environmental differences, major discontinuities can be detected despite the local elimination or independent origin of single characters.

In the *P. pectoralis* superspecies, both the male and the female patterns are subject to a great deal of variation. The distribution of each character is different, so that all are at least partly independent. They are of very unequal systematic value ; great when their boundaries coincide with major discontinuities in the constellation of characters, small when they occur in forms not otherwise connected. Thus the loss of the male gorget is an important character, since in other respects also the Malaitan race C12 connects with those of northern Fiji D18–19, and these with *P. flavifrons*. Hen-feathering, on the other hand, is unimportant, since the hen-feathered races A5, C16 and F33 resemble, not one another, but the females of neighbouring dimorphic forms. A character may be important in one part of the range though not in another. For example, grey-winged males distinguish the closely-related forms (group E) which range from midwestern Australia to the Bismarcks E22–25, from others whose ranges they approach closely and whose males are otherwise very similar (F31, H47–50, *P. soror* 3) : but such grey wings are found also in eastern Fiji D19 & 21 & H56, in Tasmania and southern Australia F28–30, on Damar H41 and in *P. soror* 2 ; and not in the Snow Mountain race E27, which also belongs to group E.

Striking variants of the male pattern, which seem to be relatively stable, mostly mark off local groups of populations with rather compact geographical boundaries. However, many of them are associated with very different character-complexes in different parts of the species range, and even locally a single character is seldom precisely co-extensive with the complex. The major discontinuities cannot be adequately defined by using these few more or less clear-cut characters alone. The much greater number of obviously quantitative differences must be considered as well. Although all are liable to parallel evolution and extensive intergradation, discontinuities are marked by concordant changes in a number of characters.

Intergradation

Few of the discontinuities are sharply defined. Almost everywhere, very distinct forms are connected by populations which are intermediate in range and character. Sometimes the changes are more or less regular in all the characters concerned, sometimes they are abrupt or out of step. At a few points (p. 160) the intermediate populations are highly variable, and it is clear that the intergradation is secondary—forms which differentiated in isolation have met and exchanged genes in a hybrid zone. Where the individual populations do not show exceptional variability, the intergradation may be primary or secondary. Primary intergradation could result from selection in relation to environmental gradients, or from incomplete isolation between diverging populations, or (conceivably) from the expression of orthogenetic trends after successive expansions of range (cf. Mayr & Moynihan, 1946, 1). Secondary intergradation without increased variability would imply that the hybrid populations had been stabilized by subsequent selection. In *P. pectoralis* the geographical patterns of intergradation, and the characters involved, make it seem highly probable that the most striking examples of intergradation have resulted from the hybridizing of differentiated forms, with subsequent stabilization (p. 160). In other areas, however, character gradients seem to be correlated with climatic differences (p. 186).

Subspecies-groups

There are all degrees of phenotypic discontinuity, from differences between individuals of the same population upwards. The precise scope and rank of any natural group of populations must be to some extent a matter of opinion, except that sympatry introduces an objective criterion at the species level. The useful scope of the subspecies is discussed on p. 175. For convenience, such a richly diverse species as *P. pectoralis* must be broken up into subspecies-groups. These will not be of equal distinctiveness and homogeneity. Where a rather compact range is occupied by closely related forms, yet divided by considerable discontinuities, the number of groups to be recognized is to some extent a matter of choice. For example, the Australian subspecies-groups E and F might be combined into one, since the differences between them are much less sharp than those which mark off some other groups (cf. Mayr, 1954a, 19).

Where unlike forms intergrade they should not be separated if the connecting cline seems to be environmentally determined. Mathews (1930) not only removed the

Northern Australian group E from *P. pectoralis* but split it into two species, on the basis of characters which strongly suggest selective adaptation to climate (p. 187). But where the intergradation seems to be secondary and the end-forms are sufficiently unlike, they should be separated even though the position of the dividing line will have to be arbitrarily decided.

The situation in *P. pectoralis* is extremely complex. It seems to result from great plasticity in plumage characters combined with unusual ethological and genetic tolerance, and high mobility in successive waves of colonization combined with philopatry in local populations. As a result, very unlike forms have evolved and then met and interbred freely, and the resulting character-gradients mimic the true adaptive clines which also occur. It is unlikely that two students will ever agree on every detail of this confused situation.

In the following descriptions, the superspecies has been divided into eleven groups. These are treated in an order determined by higher grouping according to characters and trends (p. 168), regardless of the implications of sympatry and intergradation. The use of binomens for some of these groups (e.g. " *P. schlegelii* ") and informal designations for others (e.g. " Solomons group C ") anticipates the findings of later sections. A description of the divergence of each group as a whole from the standard patterns is followed by character-geographies of departures from the group patterns so determined. In general, group patterns have been arrived at (like the standard patterns of the whole superspecies) by combining those characters which are found in a majority of the contained forms, excluding those which are obviously intermediate with other groups. But in the Lesser Sunda Isles, Moluccas and Fiji, it seems clear that few forms have escaped contamination by gene-exchange. Here the group patterns are taken to be those of the apparently pure forms A1, B6–7, and D18a & 19a.

P. schlegelii (Text-fig. 3, p. 167)

Small birds. Male chin black, throat-patch small ; gorget very broad, fore-edge defined by white feathers ; breast, flanks and belly rufous-washed ; mantle very dark ; wing, upper tail-coverts and tail black. Female throat barred grey and white, gorget grey, breast and flanks olive ; belly lemon-yellow ; cap and auriculars grey, mantle pure olive.

MALE VARIATION. Throat-patch larger and gorget narrower in Vogelkop 1. Rufous very deep in south-eastern New Guinea 3b, paling steadily westwards to 3a ; much paler in Vogelkop and Cyclops Mountains 1–2.

FEMALE VARIATION. Throat white with grey bars, gorget and breast pale in Vogelkop and Cyclops Mountains 1–2 ; throat grey with white bars, gorget and breast dark from Weyland Mountains to south-eastern New Guinea 3.

Greys and olives brownish in Vogelkop 1.

Lesser Sundan group A (Text-fig. 2, p. 161)

Very small birds. Male chin black, throat-patch small and separated by black feathers from auriculars ; gorget narrow, fore-edge defined by white feathers ; breast, belly and flanks rufous-washed ; collar narrow and olive-washed ; upper

tail-coverts and tail black. Female throat whitish ; gorget greyish, pale and vague ; cap sandy-grey ; mantle pale sandy-olive.

MALE VARIATION. Hen-feathered on Salayer A5—male differs from female in larger throat-patch, greyer gorget and cap, grey auriculars, and darker and greener mantle.

Throat-patch touches auriculars from Java to Alor and in Flores Sea A2–4 ; patch not small, and fore-edge of gorget with black tips, in Flores Sea A4.

Rufous pale on belly in Java A2a, more so on Bali A2b, restricted to band behind gorget from Sumbawa to Alor A3, very pale and barely detectable below breast in Flores Sea A4.

Wing black and mantle mottled with black in Flores Sea A4 (individually variable).

Tail with narrow pale tips from Java to Alor and in Flores Sea A2–4.

FEMALE VARIATION. Throat pure white in Flores Sea and on Salayer A4–5, pinkish-buff from Java to Alor A2–3.

Gorget rather pinkish from Java to Alor and on Salayer A2–3 & 5 ; breast and belly uniformly pinkish in Flores Sea A4.

Breast and belly with very little yellow from Java to Alor and in Flores Sea A2–4.

Cap almost pure grey and mantle pure olive on Salayer A5, distinctly sandy from Sumbawa to Alor and in Flores Sea A3–4, less so on Sumba and Java A1–2.

Except for their smaller size, females from the Flores Sea A4 are very like those of Timor H39.

Moluccan group B (Text-fig. 2)

Medium-sized to large birds. Male chin black ; throat feathers long, partly covering gorget and cutting it off from auriculars ; gorget narrow from side to side, without black tips in the fore-edge ; upper tail-coverts and tail black. Female throat barred grey and white, gorget grey, breast and flanks pale olive ; belly lemon-yellow ; cap and auriculars grey, mantle pure olive.

SIZE VARIATION. Large birds on Ternate, Tidore and Obi B7–8.

MALE VARIATION. Chin white, throat feathers shorter, and tail with narrow and obscure pale tips on Obi B8.

FEMALE VARIATION. Throat-bars and gorget buff, breast and flanks ochraceous, belly golden-yellow, cap and mantle brownish on Obi B8.

Greys slightly paler and olives yellower on Ternate and Tidore B7 than from Morotai to Batjan B6.

The Obi form B8 is precisely intermediate between those of Ternate and Tidore B7 and Ceram H43, except that the female belly is deeper yellow than in either.

Solomons group C (Text-fig. 2)

Very large birds. Male chin black ; throat-patch yellow, rather small ; gorget broad, fore-edge defined by yellow feathers ; collar washed with olive. Female bill pale ; gorget broad and vague ; breast and flanks washed with melanins ; cap olive ; wing-feathers edged with russet.

SIZE VARIATION. Small birds on Rennell and San Cristobal C16–17, large (not very large) from Vella Lavella to Gatukai C13 & 15.

MALE VARIATION.   Hen-feathered on Rennell C16—male almost indistinguishable from female, but with slightly more carotenoid on the average.

Chin yellow on San Cristobal C17.

Throat-feathers long (extending behind auriculars), gorget very broad on Vella Lavella and Ganonga C13.

Gorget absent, but throat-feathers sometimes black-fringed, on Malaita C12.

Some black tips in fore-edge of gorget on San Cristobal C17.

Rufous patch below gorget on Santa Anna C17b and in individuals on San Cristobal C17a.

Head olive with blackish lores and auriculars on Santa Anna C17b, varies from olive (auriculars brownish) to black on San Cristobal C17a.

Collar absent on Vella Lavella and Ganonga C13 ; reduced to a trace on Malaita and from Kulambangra to Gatukai and Tetipari C12 & 14–15 ; reduced to a trace on the hind-neck, but with broad patches laterally, on San Cristobal C17.

Entire upperparts and flanks black on Vella Lavella and Ganonga C13 (individuals on Ganonga C13b have narrow olive edges on the wings) ; wing black and mantle more or less mottled with black on Rendova and Tetipari C14 ; centres of mantle-feathers blackish, and olive dark greenish, from Kulambangra to Gatukai C15 ; olive rather greenish on San Cristobal C17.

Upper tail-coverts olive from Kulambangra to Gatukai and on San Cristobal C15 & 17 ; olive edges broad on Malaita C12. Tail more or less olive on San Cristobal C17.

FEMALE VARIATION.   Bill straw-coloured from Kulambangra to Guadalcanal and Rennell C10c–11 & 15–16 ; blackish brown elsewhere.

Individuals on Vella Lavella C13a are melanistic, with black gorgets and more or less black upperparts.

Underparts faintly washed with yellow, cheeks yellower than throat, on Bougainville and Guadalcanal (juveniles sometimes much yellower) and Malaita C9, 11 & 12 ; yellow pale on Rendova, Tetipari and Rennell C14 & 16 ; lemon-yellow elsewhere (when unmixed with melanins).

Throat faintly barred on Malaita C12 ; underparts (except mid-belly) conspicuously shaft-streaked on Malaita C12, more faintly on Bougainville, Choiseul and Guadalcanal, and from Kulambangra to Gatukai C9–10a, 11 & 15.

Gorget greyish on Bougainville and Malaita C9 & 12 ; olive from Choiseul and Kulambangra to Florida, and on Rennell and San Cristobal C10 & 15–17 (fairly narrow and distinct on San Cristobal C17) ; rufous on Guadalcanal and from Vella Lavella to Tetipari C11 & 13–14.

Underparts washed with deep rufous on Rendova and Tetipari C14 ; rufous very variable in extent and depth on Vella Lavella and Ganonga C13 ; confined to gorget, breast and flanks on Ysabel and Guadalcanal C10b & 11 (deep, pale or absent), and Choiseul, Russel Isles and Rennell C10a & c & 16 (pale).

Breast and flanks pale olive from Kulambangra to Gatukai and on Rennell C15–16, and in individuals from Choiseul to Florida C10.

Cap citrine, mantle olive on San Cristobal C17 ; cap brownish or rufous olive, mantle olive from Kulambangra to Gatukai and on Rennell C15–16 ; cap brownish

citrine, mantle citrine from Buka to Malaita C9–10 & 12 (sometimes with a rufous wash on Ysabel C10b, less common on Choiseul C10a) ; cap rufous, scapulars and mantle strongly washed with rufous (most consistently on Rendova and Tetipari C14) on Guadalcanal and from Vella Lavella to Tetipari C11 & 13–14. Indications of a collar from Buka to Guadalcanal and on Vella Lavella and Ganonga C9–11 & 13.

Olive dark from Kulambangra to Gatukai C15, darker still on Rennell C16.

Olive dull (little carotenoid) on Rennell C16 ; richer on Guadalcanal, Rendova and Tetipari C11 & 14 ; richer on Bougainville and from Kulambangra to Gatukai C9 & 15 ; richer from Choiseul to Malaita and on Vella Lavella and Ganonga C10, 12 & 13 ; rich on San Cristobal C17.

Wing-feathers edged with olive on San Cristobal C17 ; russet mixed with olive from Russel Isles to Kulambangra C10c & 15, less strongly from Choiseul to Florida C10a–b.

Tail pure olive, with variable black subterminal patch, on San Cristobal C17 ; citrine from Buka to the central Solomons and Guadalcanal C9, 13–15 & 10c–11 ; olivaceous brown from Choiseul to Malaita C10a–b & 12 ; dull brown on Rennell C16.

Fijian group D (Text-fig. 2)

Medium-sized birds. Male chin and throat yellow ; no gorget ; forehead yellow ; black of cap continued on to hind-neck, collar reduced to a trace ; olive very dark ; upper wing-coverts yellow-edged ; upper tail-coverts olive ; olive tips of tail-feathers dull but wide. Female forehead, circumoculars, cheeks and under tail-coverts faintly washed with yellow, underparts otherwise without carotenoid (buffy-grey, with throat and mid-belly slightly paler) ; underparts streaked with brown, and throat and breast barred also ; upperparts dull olive-brown, wing-feathers edged with dark russet ; individuals are dark rufous all over.

MALE VARIATION. Underparts lemon-yellow on Viti Levu and Ovalau D18, orange-yellow elsewhere.

More or less complete gorget, individually variable, on Ovalau and from south-western Vanua Levu to Kio D18b & 19b–c ; gorget complete (though somewhat irregular) on Taviuni, Koro and Vatu vara D20–21.

Breast, belly and under tail-coverts washed with brown on Vatu vara D21 ; under tail-coverts ochraceous on Koro D20b, decreasingly so towards Vanua Levu D20a to 19b.

Collar narrow but uninterrupted on Vatu vara D21.

Wing-quills edged with greyish on Vanua Levu and Vatu vara D19 & 21, becoming more olive eastwards, towards Viti Levu and Koro D18 & 20.

Upper tail-coverts with black centres on Koro and (larger) on Vatu vara D20b–21.

FEMALE VARIATION. Bill brown on Rambi and Kio D19c.

Underparts evenly-coloured on Koro and Vatu vara D20b & 21 ; mottling becomes more common and emphatic towards the large islands D18b to a, and 20a to 19a. Ground-colour of underparts cinnamon on Koro D20b and (rather paler) Vatu vara D21, individually variable, becoming greyer, towards the large islands D18b to a, and 20a to 19a.

Forehead, circumoculars and cheeks not yellow on Koro and Vatu vara D20b–21 ; increasingly so towards the large islands D18b to a, and 20a to 19a.

Females on Koro and Vatu vara D20b–21 are very like those in southern Fiji H54–56.

P. flavifrons (Text-fig. 5, p. 173)

Small birds. Male chin dull black, throat dull black with broad yellow or white tips; no gorget ; underparts lemon yellow ; forehead yellow or white ; upperparts dull black (slightly washed with olive), primaries with obscure narrow greyish edges. Female cock-feathered—like the male, but throat pale grey with narrow yellow or white tips, forehead blackish (with or without a yellow wash).

INDIVIDUAL VARIATION. The tips of the throat feathers are usually yellow, but may be white ; two specimens in the British Museum (Natural History) have mixed yellow and white tips. Some white-throated birds have the forehead white (in females, without a yellow wash). The distribution of these phases in the collections of the British Museum (Natural History), and the American Museum of Natural History (from Mayr, 1932b), is shown in Table II : there is no evidence of a significant difference in representation of the colour phases, either between the sexes or between Savaii and Upolu. All the B.M. (N.H.) specimens are from Upolu.

TABLE II.—*Colour Phases in* P. flavifrons.

| | Forehead. | |
Throat.	Yellow.	White.
Yellow	48	—
Yellow and white . .	2	—
White	8	9

P. soror (Text-fig. 3)

Small birds. Male throat-patch rather small ; gorget narrow ; underparts lemon-yellow ; breast and flanks faintly olivaceous ; collar reduced to a trace ; mantle very dark greenish olive ; edges of wing quills greyish ; upper tail-coverts olive, tail partly olive. Female throat-patch white and small ; gorget narrow, clear and brownish ; breast and flanks pale citrine, yellow wash extending high on breast ; belly pale lemon-yellow ; cap olivaceous-brown ; tail partly black.

MALE VARIATION. Mantle increasingly golden-olive towards the west 3 to 1. Wing quills greyest in the centre 2.

Tail olive, with a variable black subterminal patch, in the west and east 1 & 3 ; black, with wide olive edges basally, in the centre 2.

FEMALE VARIATION. Upperparts much browner in Vogelkop 1 ; increasingly purer olive towards the east 2 to 3.

Northern Australian group E

Very small to medium-sized birds. Male throat-feathers white to their bases ; edges of wing-quills grey ; edges of upper wing-coverts yellow ; primary-coverts black. Female throat white, with barring ; gorget well defined, buffy-grey ; breast,

flanks and belly whitish to golden-yellow, without melanins ; cap rather pure grey, mantle pure olive (or grey) ; tail partly black.

SIZE VARIATION. Very small birds in mid-western Australia E22a–c, size increasing through north-western Australia E22d to small in northern Australia and southern New Guinea E23–24. Like the Snow Mountain birds E27, those grouped together as *dahli* E25 are mostly medium-sized—but there is considerable variation between the scattered populations, with the birds of Fergusson E25c (and Teste and Long Islands E25b & d) rather large, and those of south-eastern New Guinea and Witu E25a & e apparently rather small.

MALE VARIATION. Throat-feathers grey-based in Snow Mountains E27 (Text-fig. 3).

Breast and belly lemon-yellow in mid-western Australia E22a, gradually becoming deeper northwards E22b to d, golden-yellow from northern Australia eastwards E23–27.

Collar narrow in midwestern Australia E22a (widening northwards E22b to 23), and Snow Mountains E27.

Mantle greenish-olive in midwestern Australia E22a (becoming yellower northwards E22b to 23), and Snow Mountains E27.

Edges of wing-quills olive in Snow Mountains E27.

Primary-coverts olive in mid-western and north-western Australia and Snow Mountains E22 & 27 ; sometimes with very narrow pale edges from northern Australia to southern New Guinea E23 to 24.

Upper tail-coverts olive in mid-western and north-western Australia E22.

Tail with broad olive edges basally in midwestern Australia E22a, decreasing northwards E22b to d.

FEMALE VARIATION. Females from Teste and Fergusson E25b–c are unknown.

Throat unbarred in mid-western Australia E22a–c, barring pale in north-western and northern Australia E22d–23 ; throat and gorget shaft-streaked (in addition to barring) from Cape York to southern New Guinea E24 (faintly) and in *dahli* and Snow Mountains E25 & 27.

Breast and flanks pale olivaceous in Snow Mountains E27 ; ochraceous from Cape York to southern New Guinea E24.

Breast and belly whitish and under tail-coverts pale yellow in mid-western Australia E22a–c ; breast and belly pale yellow, under tail-coverts lemon-yellow, in north-western Australia, and from Cape York to southern New Guinea E22d & 24 ; under-parts lemon-yellow in northern Australia E23, golden-yellow in *dahli* and Snow Mountains E25 & 27.

Cap brown in Snow Mountains E27.

Mantle grey, only rump olivaceous, in mid-western Australia E22a–c, becoming olive northwards E22d to 23. Olive bright in Snow Mountains E27.

Edges of wing feathers, rump and base of tail brownish on Witu, Malie and Nissan E25e & j–k.

Tail olive in mid-western Australia, and from Cape York to southern New Guinea E22a–c & 24 ; with a variable amount of black in north-western and northern Australia E22d–23 ; more than half black in *dahli* E25 ; black with olive edges in Snow Mountains E27.

Mayr has shown (1932a) that the birds on small islands west of Shortland E26

form a hybrid population. The nine known males show almost every degree of intermediacy between *dahli* E25 and the Bougainville-Shortland race C9—except that they do not have black chins like those of the Solomons group C. In this series the largest birds have the yellowest throats, and the smallest ones the whitest. Other characters seem to vary independently, so far as can be judged from this short series. There is rather less variation between the nine females, which are also intermediate between those of E25 and C9.

The females from Cape York to southern New Guinea E24 differ from those on either side (E23 & 25) in characters which approach those of the Queensland form F31—breast and flanks ochraceous, little ventral yellow, tail without black (Mayr, 1954a).

The Louisiades form H47 is intermediate between groups E and H. It is here placed in the latter because the male has olive edges to the wings, and the female is brownish ; but the white throat, sharp and narrow gorget and bright yellow underparts of the female are untypical of group H. The Tabar form H50 may be similarly intermediate (p. 164).

Southern Australian group F

Large birds, with long wings and tails, small bills and soft plumage. Male breast and belly lemon-yellow ; collar rather narrow and washed with olive ; upper wing-coverts yellow-edged ; upper tail-coverts olive, base of tail olive or grey. Female throat barred ; gorget, breast and flanks buffy-grey, belly more or less washed with melanins ; yellow absent from underparts, or only in under tail-coverts ; cap grey, mantle dull sandy-olive.

SIZE VARIATION. Large birds with long tails and very small bills in Tasmania F29, size and relative tail-length decreasing and bills lengthening northwards—smallest birds near Cairns F31b, longest bills on Lord Howe and Norfolk Islands F32–33.

MALE VARIATION. Hen-feathered on Norfolk Island F33—indistinguishable from female.

Yellow somewhat paler from south-western Australia to Tasmania F28–29.

Collar broader and clearer on Lord Howe F32.

Wing quills blackish brown with grey edges in Tasmania F29, centres blackening and edges becoming more olive northwards F28 and 30 to 31.

Tail without black in Tasmania F29 ; about one-third black from south-western Australia to South Australia F28a–b ; increasing through Victorian mallee F28c to two-thirds black in south-eastern Australia F30 ; two-thirds black on Lord Howe F32 (olive tips very wide) ; mainly black, olive varying from wide edges to a wash at the extreme base, in Queensland F31 (averaging blacker near Cairns F31b).

Pale part of tail grey in Tasmania and southern Australia F28–30a ; olive elsewhere, but often greyish near Cairns F31b.

FEMALE VARIATION. Belly pinkish from south-western Australia to South Australia F28a–b, fading to buffy in Victorian mallee, Tasmania and near Cairns F28c–29 & 31b ; whitish in south-eastern Australia F30 ; often faintly yellowish in

southern Queensland F31a, and always on Lord Howe F32 ; distinctly yellow on Norfolk Island F33.

Under tail-coverts whitish in Tasmania and southern Australia F28–30.

Upperparts rather brownish in Tasmania F29, and more or less brownish in most individuals near Cairns F31b ; rather pure grey in south-western Australia F28a.

Mantle grey in Tasmania F29 ; sometimes with a faint olive wash in southern Australia F28 & 30 ; dull olive elsewhere.

Tail grey in Tasmania and southern Australia F28–30 ; dull olive near Cairns F31b ; olive elsewhere.

Southern Melanesian group G

Small birds. Male gorget narrow ; breast and belly lemon-yellow ; collar narrow and washed with olive ; centres of wing-feathers blackish-brown ; upper tail-coverts and tail olive. Female throat white ; gorget greyish ; breast and belly without melanins.

SIZE VARIATION. Very large birds on Loyalty Islands G35.

MALE VARIATION. Lateral throat feathers long, separating gorget from auriculars, on New Caledonia G34 (Text-fig. 5).

Gorget dull black, and very narrow, on New Caledonia G34 ; dull black on Aneitum G36 ; rather broad on Vanikoro G38.

Pale rufous patch below gorget on New Caledonia G34.

Flanks and under tail-coverts ochraceous, rump, tail and edges of secondaries washed with brownish, in individuals on Aneitum G36.

Breast and belly golden-yellow on Loyalty Islands G35.

Cap and auriculars grey on New Caledonia G34 ; dull black, cap more or less scalloped with olive, on Aneitum G36.

Collar reduced to a trace on New Caledonia G34, very narrow on Erromango G37a.

Mantle greenish-olive on Erromango, and from Raga to Vanikoro G37a & 37e–38 ; golden-olive on Loyalty Islands, and Malekula and Santo G35 & 37d.

Upper tail-coverts black-centred, tail black, on Vanikoro G38 ; tail with black patches (on inner webs of all but central quills) from Erromango to Banks Islands G37.

FEMALE VARIATION. Throat and gorget shaft-streaked on Vanikoro G38.

Gorget olive on Loyalty Islands and Vanikoro G35 & 38 ; greyest on Erromango, Efate and Banks Islands G37a–b & f ; brownish on Aneitum G36.

Gorget extends into buffy-grey wash on breast and belly on New Caledonia G34.

Underparts golden-yellow on Loyalty Islands G35, lemon-yellow on Vanikoro G38 ; elsewhere, under tail-coverts pale yellow, breast and belly faintly washed with yellow (palest on Malekula and Santo G37d).

Cap and auriculars grey on Vanikoro G38 ; cap greyish on Efate and Banks Islands G37b & f ; brownish on Aneitum G36.

Mantle pure golden-olive on Loyalty Islands G35, pure greenish-olive on Vanikoro G38 ; elsewhere dull olive, purest on Efate and Banks Islands G37b & f, brownish on Malekula and Santo G37d ; very brown on Aneitum G36.

Tail and edges of secondaries browner than mantle on Loyalty Islands G35, somewhat so on Aneitum and Erromango G36–37a.

JUVENILE VARIATION. Throat lemon-yellow on Vanikoro G38, sometimes yellow-washed in New Hebrides (recorded from G37c & f by Mayr, 1932b). Juveniles on Vanikoro G38 are remarkably like those on San Cristobal C17, except for the shaft-streaking of their throats and gorgets.

The New Hebrides G36–37 are a region of incipient subspeciation, with the females of almost every island distinguishable in series (Mayr, 1932b). The Aneitum population G36 is rather distinct, and that on Erromango G37a more so than the others.

Widespread group H (close to standard patterns, Text-fig. 1)

Small to very large birds. Male of standard pattern. Female underparts rather uniform, brownish, with little yellow; upperparts brownish, cap not contrasting, edges of wing feathers distinctly browner than mantle.

SIZE VARIATION. Very large birds on Tenimber Isles, Lihir and Tonga H42, 49 & 57; large on Tabar and Lau archipelago H50 & 56; small on Timor and Damar, Sula and Peleng Isles, large islands in the Bismarcks, and Kandavu H39, 41, 45–46, 48 & 54.

MALE VARIATION. Chin and throat black in Tonga H57 (Text-fig. 5); yellow on Tenimber Isles H42.

Throat-feathers long, cutting gorget off from auriculars (fore-edge of gorget defined by white feathers) on Ceram, and Ndeni and Santa Cruz islets H43 & 52; gorget very narrow near auriculars, with few black tips, on Buru H44.

Gorget streaked with white on Babar H40; dull black and very narrow on Kandavu H54, narrow on Ngau H55.

Underparts lemon-yellow from Timor to Tenimber Isles and on Utupua, Kandavu and Tonga H39–42, 53–54 & 57; orange-yellow in Louisiades and on Lihir and Manus H47, 49 & 51.

Under tail-coverts ochraceous on Ngau H55.

Upperparts (except for narrow olive edges on wing-feathers) black on Ndeni and Santa Cruz islets H52; mantle mottled with black in Lau archipelago H56, somewhat so on Ngau H55.

Primary-coverts black on Ceram and Buru, Ndeni and Santa Cruz islets, and Lau archipelago H43–44, 52 & 56.

Collar absent on Ndeni and Santa Cruz islets H52; reduced to a trace on Tenimber Isles H42, and Ngau and Lau archipelago H55-56 (black of cap extends on to hind-neck); washed with olive from Timor to Damar, in the Louisiades and on Utupua and Kandavu H39–41, 47 & 53–54.

Olive dark and greenish on Buru, Ngau and Lau archipelago H44 & 55–56; dull on Kandavu H54.

Olive washed with brownish (especially on rump, tail and edges of secondaries) on Ceram and Louisiades H43 & 47.

Edges of wing quills grey on Damar H41, and greyish in Lau archipelago H56.

Upper tail-coverts olive on Timor, Tenimber Isles, Louisiades, Kandavu and Tonga

H39, 42, 47, 54 & 57 ; black from Ceram to Peleng Isles H43–46 (very narrow olive edges on Buru H44).

Tail olive on Timor and western Louisiades H39 & 47a ; olive with blackish subterminal patches on Misima and Kandavu H47b & 54 ; olive basally on Babar and Rossel H40 & 47c ; with broad olive edges basally on Damar H41.

Pale tip of tail very broad and yellowish in Tonga H57.

FEMALE VARIATION. Throat white on Timor and Babar, Louisiades and Utupua H39–40, 47 & 53 ; whitish on Damar, Ceram, Sula and Peleng Isles, Tabar, Manus, Ndeni and Santa Cruz islets H41, 43, 45–46 & 50–52.

Throat washed with yellow on Tenimber Isles H42.

Throat barred on Damar, Sula and Peleng Isles H41 & 45–46, and faintly in Tonga H57.

Throat and gorget streaked on Manus H51, and faintly on Tabar H50.

Underparts uniformly cinnamon in southern Fiji H54–56 (very richly so on Ngau H55). Gorget scarcely darker than throat and belly on Mussau and Lihir H48d–49 ; little darker on Tenimber Isles, large islands of the Bismarcks, and Ndeni and Santa Cruz islets H42, 48a–c & 52. Gorget little darker than breast, but greyer, on Timor and Damar and from Ceram to Peleng Isles H39, 41 & 43–46. Gorget pale and narrow on Babar and Louisiades H40 & 47 (vinous), Tabar, Manus and Tonga H50–51 & 57 (cinnamon) ; broad on Utupua H53 (dark brown).

Breast and belly without melanins in Louisiades H47 ; belly without melanins, breast faintly cinnamon on Tabar and Tonga H50 & 57 ; belly without melanins, breast and flanks brownish on Utupua H53 ; breast and belly faintly washed with cinnamon on Babar and Manus H40 & 51.

Breast and belly without yellow on Ngau and Lau archipelago H55–56 ; faintly washed with yellow on Timor, Damar, Buru and Kandavu H39, 41, 44 & 54, more strongly on Tenimber Isles, Ceram and Sula Isles H42–43 & 45 ; yellow pale on Babar, Bismarcks except Tabar, and Ndeni and Santa Cruz islets H40, 48–49 & 52 ; deep in Peleng Isles and Louisiades H46 & 47, and especially on Tabar and Manus H50–51.

Cap grey on Tabar, Ngau and Tonga H50, 55 & 57 ; distinctly greyer than mantle on Manus, Utupua, Kandavu and Lau archipelago H51, 53, 54 & 56 ; distinctly browner than mantle on Bismarcks except Tabar H48–49.

Mantle bright citrine on Tabar, Manus and Tonga H50–51 & 57 ; dull sandy-olive on Timor, Damar, Tenimber Isles, Kandavu and Lau archipelago H39, 41–42, 54 & 56 ; brownish olive on Babar H40 (tail pure olive), Peleng Isles, Louisiades, large islands of the Bismarcks, Utupua and Ngau H46, 47, 48a–c, 53 & 55 ; browner and duller from Ceram to Sula Isles and on Ndeni and Santa Cruz islets H43–45 & 52 ; olive-brown on Mussau and Lihir H48d–49.

Edges of wing feathers scarcely browner than mantle on Tabar, Manus and Tonga H50–51 & 57.

Not only are the distinctive characters of the group few and slight, but most of the forms are intermediate in some respects with neighbouring groups. Besides penetration by characters proper to other groups, intermediate forms seem to be liable to special changes (p. 165). The wide range of this group has enabled it to meet and

intergrade with five of the seven other subspecies-groups, and there seems to have been gene-flow into it in the following areas :

From group A to Timor and Babar H39–40.
From group B to Ceram, Peleng and Sula Isles H43 & 46–45.
From group D to southern Fiji H54–56.
From group E to Louisiades H47 (and possibly Damar, Tabar and Manus H41 & 50–51).
From group G to Utupua H53.

When the effects of this gene-exchange have been allowed for, three forms stand out conspicuously from the remarkably uniform remainder :

Tenimber Isles H42 (very large, throat yellow).
Ndeni and Santa Cruz islets H52 (male upperparts black, throat-feathers long).
Tonga H57 (very large, male throat black, female with little brown and much yellow).

INTERGRADATION AND BRIDGELESS GAPS

Gene-exchange between subspecies-groups

The eight subspecies-groups of *P. pectoralis* approach one another in several areas, in all of which there are signs of intergradation between them (Text-fig. 8). Groups A and H intergrade in the Lesser Sunda Isles, B and H in the southern Moluccas, C and E in the western Solomons, C and G in the eastern Solomons, D and H in central Fiji, E and F in southern New Guinea, E and H in the Louisiades, and G and H in the Santa Cruz archipelago. In most of these areas, it is not immediately obvious whether the intergradation is primary or secondary.

Only in the western Solomons is there indisputable evidence of hybridization between very dissimilar forms. The populations on three islets west of Shortland (E26) are highly variable. Extreme individuals closely resemble the Shortland race C9 on the one hand and *dahli* E25 on the other, while every degree of intermediacy is found (p. 156).

On San Cristobal C17a also there is considerable variation between males, in the amount of rufous on the breast and of black on the head and tail. Their song, too, is remarkably variable (Cain & Galbraith, 1956). Though the San Cristobal race agrees with the rest of group C in the yellow throat, and the olive cap and pale bill of the female, it differs from the standard pattern of that group in most other characters. It is much smaller. The male has a yellow chin, black tips in the fore-edge of the gorget, a rufous breast-patch, and partly olive head and tail. The female is bright yellow underneath, with a narrow gorget and no melanic wash, lacks rufous on the upperparts (including the wings), and has a partly black tail. Many of these characters of the males are retarded, and of the females advanced.

Avifaunally San Cristobal is distinct from the rest of the Solomons, with several endemic forms showing markedly reduced size (*Collocalia esculenta makirensis*, *Ptilinopus solomonensis solomonensis*, *Halcyon chloris solomonis*, *Rhipidura rufifrons russata*, *Monarcha vidua*, *Myiagra cervinicauda* and *Aplonis grandis dichrous*), reduced sexual dimorphism (*Coracina tenuirostris salamonis*, *C. lineata makirae*,
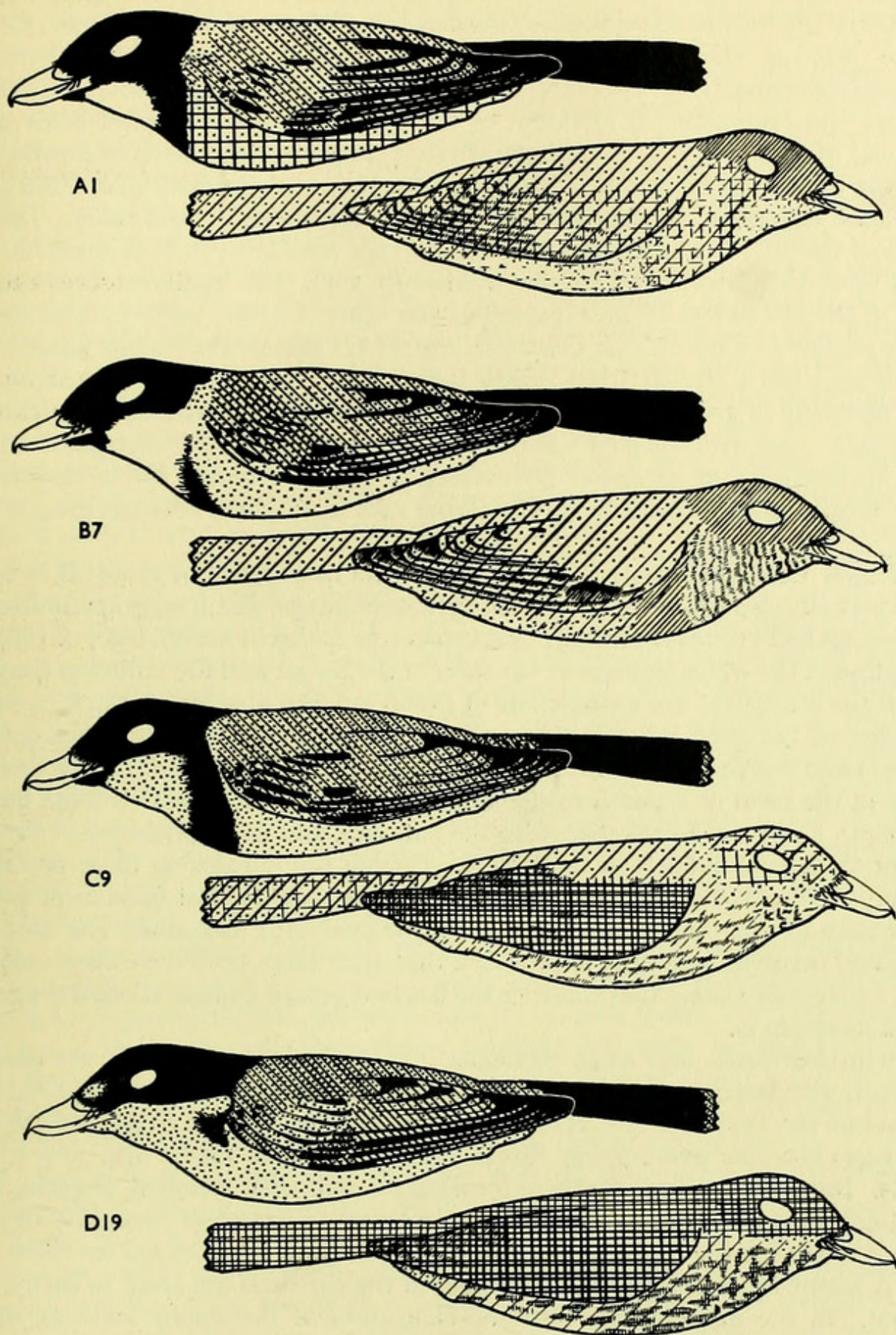
FIG. 2.—Four extreme forms of *P. pectoralis* (*schlegelii* assemblage) which intergrade with more nearly standard ones (*soror* assemblage). Sumba A1 ; Ternate B7 ; Shortland C9 ; Vanua Levu D19a.

Myiagra cervinicauda, *Myzomela nigrita tristrami* and *Dicaeum tristrami*), or increased variability (*Ptilinopus solomonensis solomonensis*, *Halcyon chloris solomonis*, *Coracina lineata makirae* and *Petroica multicolor polymorpha*) in comparison with their western representatives. These trends may result simply from the isolated peripheral position and impoverished avifauna of the island. However, several birds on San Cristobal and its outlying islands are derived from southern Melanesia rather than from the rest of the Solomons (*Ptilinopus richardsii*, *Lalage leucopygia*, *Vitia parens*, *Rhipidura fuliginosa*, *Myiagra cervinicauda* and *Myzomela cardinalis*). The variability of the male of *P. pectoralis* here suggests the possibility of hybridization, which might have disturbed the sexual dimorphism (p. 165). The Vanikoro race G38 shows some of the characters to be expected in the other putative parent : the female is rather similar to that on San Cristobal, except for its streaked white throat, while the juvenile has a streaked but yellow throat. The San Cristobal race shares with most members of group G the pale tail of the male and the melanin-free throat of the female ; and with the New Caledonian race G34 the rufous breast-patch and pale cap. In the light of extensive hybridization between unlike forms elsewhere, it seems most probable that the San Cristobal race is a hybrid between groups C and G.

The New Caledonian race G34 differs from its neighbours of group G in several systematically important characters of the male plumage, which suggest affinities with *P. schlegelii* and groups A to C of *P. pectoralis* (the *schlegelii* assemblage, p. 168). The elongation of the white feathers at the sides of the throat and the failure of the gorget to join the auriculars are reminiscent of group B. The absence of black tips in the fore-edge of the gorget (laterally) is characteristic of the whole assemblage. The rufous breast is found elsewhere only in *P. schlegelii* and group A, and on San Cristobal, and is in the form of a patch rather than a band only on New Caledonia and San Cristobal. These two forms share also the pale cap, and the suppression of the collar (except for lateral patches in the latter). Though the females on these two islands are very different, that on New Caledonia agrees with typical females of group C rather than of group G in having the belly washed with melanins. The number of characters involved makes it improbable that they have been developed independently, and it seems likely that this race too has had genetic contributions from group C as well as group G.

Two further forms, here assigned to group H, show characters which are elsewhere systematically important and confined to the *schlegelii* assemblage (see Table III). The race on the Tenimber Isles H42 has a yellow throat. That on Ndeni and the Santa Cruz islets H52 has overlapping throat feathers without black tips, and a black mantle. But in other respects these forms agree well with members of group H. It would not be justifiable (without further evidence) to deny the possibility of independent origin for these characters, and to postulate mixed ancestry for these forms also. A latent tendency towards yellowing of the throat is apparent in many forms (p. 142). In the melanic race H52 the elongation of the throat feathers and the exclusion of melanin from their tips may be significant in maintaining the conspicuousness of the throat-patch despite encroachment by black areas (as in the other melanic race C13).

The populations between Koro and the large Fijian islands (D18b & 19b–20a) are evidently hybrid (Mayr, 1932b). There is much variability—especially on Ovalau, Rambi and Kio D18b & 19c—in the degree of development of the male gorget and forehead-spots, and in the colour and streakiness of the female underparts. The average character of the populations changes progressively from Koro to the mainland of Vanua Levu (D20b to 19a), while the population on Ovalau D18b is intermediate in character between those of Koro D20b and Vitu Levu D18a. Unfortunately, my material is inadequate to demonstrate quantitatively the changes in hybrid index and in variability which are qualitatively apparent in Mayr's description.

The races on Koro and Vatu vara D20b–21 are themselves intermediate in character between the extreme Fijian forms (D18a & 19a) and members of group H, to which they are linked by the races in southern Fiji H54–56. Males on Koro and Vatu vara have yellow throats with gorgets, those in southern Fiji white throats with gorgets ; the yellow forehead reappears on Vatu vara ; while all Fijian males have the collar obscure or very narrow. Females in southern and central Fiji (D20–21 & H54–56) are all much alike—differing from those of northern Fiji in having unstreaked cinnamon underparts, and from most of those in group H in having them almost uniform from chin to vent and with scarcely any carotenoid. Blackness of the mantle (D20 & H55–56) and greyness of the wing quills (D19 & 21 & H56) are common to forms on either side of the intergroup boundary.

Group H intergrades with groups A and B also. The male on Sumba A1 has a black chin, a small throat-patch, no black tips in the fore-edge of the gorget, a rufous ventral wash and a wholly black tail. These characters are reduced or absent elsewhere in group A, the dilution being greatest in the Flores Sea A4 and least in Java A2a. Although there is a sharp change in size at the Ombai Strait (along which the boundary between groups A and H has been drawn), and the special male characters of group A do not appear east of it, the female on Timor H39 is very like that in the Flores Sea (which differs from other females of group A in having a pure white throat and pinkish belly), and there is a fairly complete series of forms leading to a typical member of group H on Buru (H39 to 41 & 44).

Males in the northern Moluccas B6–7 have black chins, long throat-feathers partly covering the gorgets, and wholly black tails ; while the females are unusual in their heavily-barred throats, pure greys and olives, olive breasts and grey auriculars. There is a perfect series of intermediates leading from these through Obi B8 and Ceram H43 to Buru H44. Although the male characters of group B do not appear there, the female in the Peleng Isles H46 is very like that on Obi B8, and the Sula Isles female H45 is intermediate between those of Peleng and Buru.

The changes involved are quite different in these three areas of intergradation. They involve oddities of pattern, as well as the quantitative changes which seem more likely to be subject to environmental selection. Only in the Lesser Sunda Isles is there a marked climatic gradient (of increasing aridity eastwards from Java to Timor) with which the progressive change in character might be correlated. But here the character-progression (from A1–2a–2b–3–4–H39) does not run parallel to that of climate. In the Moluccas the changes span only seven degrees of latitude across the equator, and in Fiji four degrees within the tropics, so that regular climatic

changes cannot be great. It seems unlikely that adaptation to environmental gradients is involved in these character-progressions, although adaptive clines might be developed in relation to subtle differences (perhaps in the fauna or flora). The geographical patterns of character-dilution suggest introgression rather than continued gene-exchange between gradually diverging populations (see Text-fig. 8). Finally, groups A, B and D seem (p. 168) to be more closely related to one another than to group H, with which they all intergrade.

There is thus no reason to believe that the intergradation in these areas is primary. The situation can be explained with the maximum economy of hypothesis in terms of a recent burst of range expansion by group H, which has come into secondary contact with diverse and anciently-isolated forms and freely interbred with them. The same thing has almost certainly happened in the western Solomons, where *dahli* E25 is a relatively very recent arrival and the hybrid population E26 is still exceedingly variable. Meise (1936) and Mayr (1942) have suggested that the *Pachycephala* on Koro D20b is of hybrid origin and has been genetically stabilized by subsequent selection. This seems much the most probable explanation for the other intermediate, though not especially variable, forms just considered.

Since the characters which distinguish groups E to H from one another are relatively slight and mainly quantitative, it is more difficult to decide whether the intergradation between these groups is primary or secondary. On the other hand there is less reason to doubt that the rather similar forms involved can interbreed, and the character-geography strongly suggests gene-flow between these groups in several areas (Text-fig. 8).

Mayr (1954a) has pointed out that, while the male in southern New Guinea E24 is like its relatives E23 and 25, the female shows (in its buffy belly with little yellow, and lack of black in the tail) dilution by characters of group F. The dilution appears to decrease into south-eastern New Guinea E26a (Rand, 1940). It is clear that gene-flow from northern Queensland F31b is involved. Mayr also suggests that the character gradient in mid-western Australia (E22d to a) is the result of gene-flow from south-western Australia F28a. The partly olive tail of the male and the reduction of carotenoid support this ; but the birds become smaller southwards instead of larger, and the female shows no sign of the pinkish underparts and barred throat characteristic of the south-western form. It seems more probable that the changes are clinal (p. 187).

In the Louisiades H47, the female shows the bright yellow underparts, white throat (though without mottling) and narrow gorget of group E, but has a very brownish mantle like those of group H, while the male has olive edges to the wing quills. This form could equally well be assigned to either of these groups. The female on Tabar H50 resembles those of group E in the same respects, as to a lesser degree does that on Manus H51. It seems reasonable to suppose that the intergradation in the Louisiades is secondary, and this might be true of the Tabar race also ; but it is most unlikely that the small and recently-arrived populations of *dahli* E25 in the Bismarcks could sufficiently swamp the presumably large population on isolated Manus. This is surely a case of convergence, as in Tonga H57.

While the male on Damar H41 is very like those of Timor and Babar H39–40

(which I suppose to have been affected by gene-flow from group A), the female is different, closely resembling that of the Sula Isles H45 (which has affinities with group B). There may perhaps have been gene-flow across the Banda Sea. But the barred throat characterizing these females is also found in Australia, and the male on Damar has grey edges to the wing quills like those of group E. If gene-flow (other than from group A) is involved here, it seems more likely that it has been across the Timor Sea from northern Australia E23.

The three forms in the Santa Cruz archipelago are remarkably different. The male on Ndeni and the islets H52 is melanic and has the throat feathers elongated, while those on Utupua H53 and Vanikoro G38 are close to the standard. Groups E to H differ mainly in the characters of the female. The Ndeni female is very near the standard, and a typical member of group H ; that on Vanikoro is quite different, most like the Snow Mountain female E27, and apparently a northern representative of group G ; while that on Utupua is intermediate between them. It is possible that this intergradation is primary, and that group H has spread west and east after its origin in the Santa Cruz, but more probably the contact was secondary.

Marks of hybridity

Knowing that hybridization is possible between very dissimilar forms of *P. pectoralis*, we have considered many forms which are intermediate, both geographically and phenotypically, between well-marked groups to be of hybrid origin, even though their variability is not exceptional. Several of these presumably hybrid forms differ from both putative parents (and from most other forms in the superspecies) by characters which are retarded in the male, or advanced in the female plumage. Partly olive (or grey) tails in the male are found in *P. soror* and the southern members of groups E, F and G ; in certain presumptive hybrids (San Cristobal C17, Timor to Damar H39–41, Louisiades H47 and Kandavu H54) ; and nowhere else. Female throats without melanic washes or mottling are found in *P. soror* and the southern members of groups E and G ; in some hybrids (Flores Sea and Salayer A4–5, San Cristobal C17, Timor and Babar H39–40, Louisiades H47 and Utupua H53) ; and nowhere else. Partly black tails in the female are found in *P. soror* and members of group E ; on San Cristobal C17 (and black shafts on Babar H40) ; and nowhere else. The presumptive hybrid females on Obi B8, Babar H40 and Utupua H53 have much brighter yellow bellies than their relatives on either side.

In other parts of the species range, the amount of black in the tails of both sexes, and the depth of carotenoid coloration, are involved in character-progressions which may be climatically determined (p. 186). But while in these clines intensity of pigmentation increases with increasing temperature and humidity, in the forms under discussion the male tail tends to be pale and the female tail and belly to be deeply-coloured. Furthermore, there is no reason to suppose that the islands in the Flores Sea, Timor, Babar, Damar, Obi, the Louisiades, San Cristobal, Utupua and Kandavu share environmental factors which distinguish them from neighbouring islands. If the apparent regularities are real, it seems most probable that they are related to the secondary intergradation which characterizes *P. pectoralis* in these areas.

These trends are not the phenotypic expression of heterosis, since the variable

hybrid populations E26, D18b & 19b–c do not show them. Possibly the tendency towards breakdown of the sexual dimorphism reflects genetic disturbances produced by hybridization, or selective changes involved in regaining a balanced genome. These might be expected sometimes to blur the distinction between the adult female and juvenile plumages, producing retarded rather than advanced characters in the female. This may be the explanation for the reversal of south-to-north changes in northern Queensland (p. 156). Many characters might be considered as advanced or retarded, and it would be dangerous to take their occurrence as evidence of hybrid origin ; but the possibility of such effects needs to be considered in assessing the systematic importance of characters, and in tracing environmental correlations.

Though these characters tend to appear together in forms of hybrid origin, the distribution of each is very erratic. The abrupt loss of black from the male tail (coinciding with a sharp increase in size, and the loss of ventral rufous) at the Ombai Strait, and its progressive reappearance eastwards here (H39 to 41) and in the Louisiades (H47a to c) suggests that this character may be dependent upon a rather precise balance between genes from each parental group. If this is true of all the " marks of hybridity ", and each has a different threshold value which depends also upon the parental genomes involved, the sporadic realization of these trends is not surprising.

Sympatry

All the forms of the *pectoralis* superspecies replace one another geographically, except in New Guinea. There *P. soror* and *P. schlegelii* represent one another altitudinally, but meet at about five thousand feet. There is no sign of intergradation between these very distinct species. They are the endemic representatives of *P. pectoralis*, and occupy the primary hill and mountain forest respectively. *P. pectoralis* itself has only been able to enter New Guinea by way of certain disturbed habitats. In the lowlands of the south and south-east E24–25a, it occupies coastal second growth, and may never come in contact with *P. soror* of the hill forest (though they are only three miles apart on Fergusson and Goodenough Islands respectively). Another race of *P. pectoralis* is known only from two river valleys on the northern slopes of the Snow Mountains E27. These valleys have been much affected by intensive native cultivation, which has stripped the forest from their floors and far up their sides. The local race of *P. pectoralis* seems to live largely in second-growth stands of *Casuarina* in the resultant grasslands, but also in the forest (Archbold, Rand & Brass, 1942). *P. schlegelii* descends a little way into the valley forest, and is found there side by side with *P. pectoralis*, with no signs of intergradation. Elsewhere in New Guinea *P. soror* is found up to the level of the valley floors, but it seems to be absent locally, and only appears in the hill forest more than a thousand feet lower.

P. soror and the mountain race of *P. pectoralis* are so much more alike than intergrading forms outside New Guinea that one would expect that they must be conspecific. But the absence of interbreeding between them can scarcely be due solely to extrinsic barriers. They have been collected within a few miles of one another (on the only expedition which has yet encountered the montane race of *P. pectoralis*)

and must surely meet on occasion. *P. pectoralis* in the Snow Mountains is separated from its relatives in southern New Guinea by over three hundred miles of primary forest. It seems possible that further investigation will show the known populations to be a few of many, small and scattered among the mountains, wherever disturbance of the forest by man, landslide, wind, flood or fire provides a shifting foothold (cf. Rand, 1941, on the origin of the grassland avifauna). In any case, *P. pectoralis* has presumably passed through the range of *P. soror* to reach the known localities in the Snow Mountains. It is not strictly true to say (Rand, 1940) that this race of *P. pectoralis* shows no closer relationship to *P. soror* than does the southern New Guinea one. Discounting the effects in southern New Guinea E24 of gene-flow from group F, most of the changes (male throat feathers grey-based, collar reduced, mantle greener, edges of wing-quills olive and broader, female with olivaceous breast, brown cap and blacker tail) are in fact in the direction of *P. soror*. But even if these differences
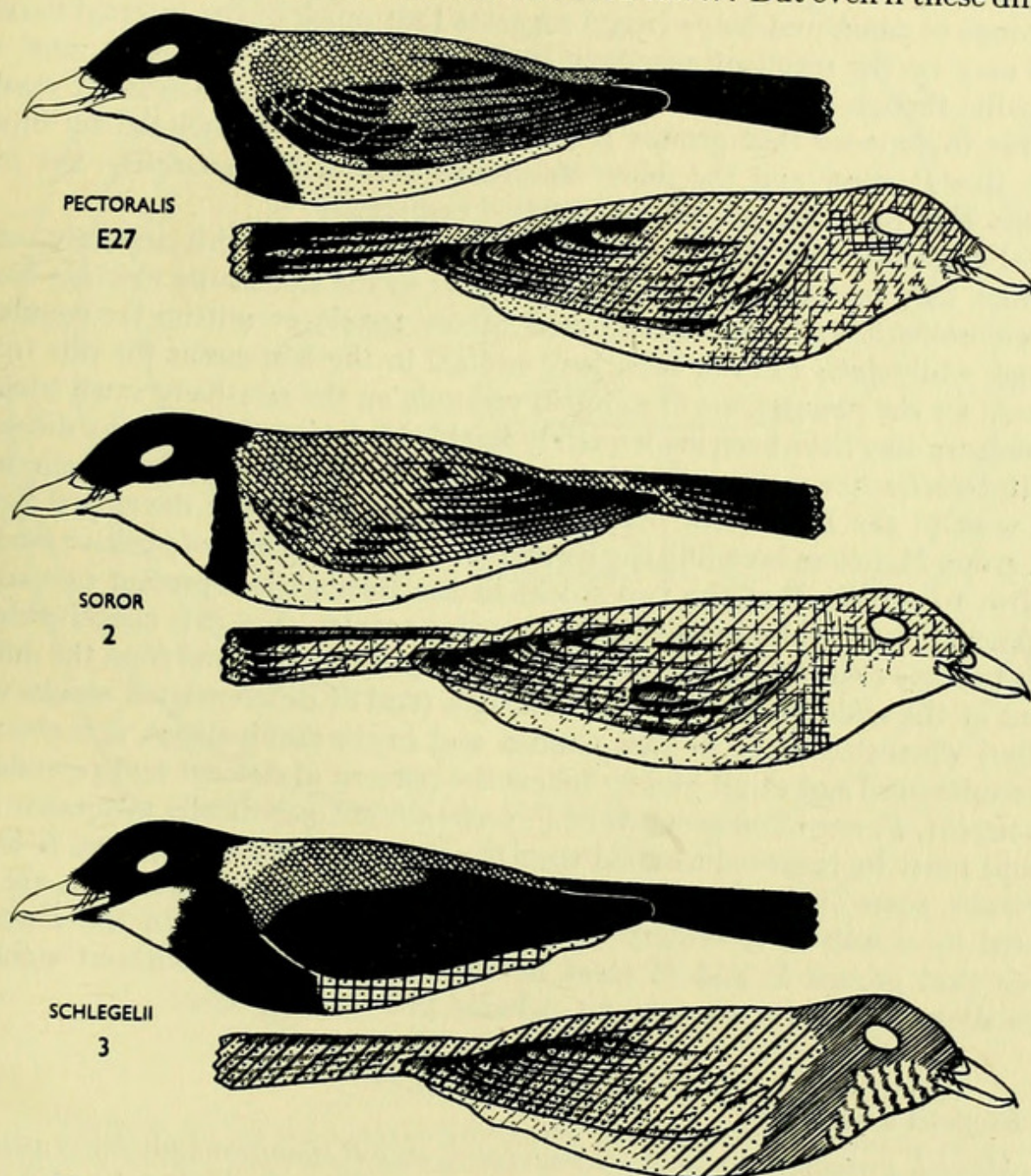
FIG. 3.—The three sympatric forms, in the Snow Mountains of New Guinea. *P. pectoralis* E27 ; *P. soror* 2a ; *P. schlegelii* 3a.

from other members of group E imply gene-flow from *P. soror*, rather than parallel adaptation to higher altitudes (p. 188), the introgression must have been slight and soon ended. The great reservoir of *soror* genes would otherwise soon swamp the small populations of *P. pectoralis* in the mountains, destroying not only the rather slight phenotypic differences but the genetic determination of habitat preference which presumably keeps the two forms apart. Although the evidence is very indirect, it seems that *P. soror* and group E of *P. pectoralis* are genetically sympatric species.

A rather similar situation arises in the Bismarcks, where *dahli* E25 occupies small islands (but also occurs at certain coastal localities on the large islands) while the endemic race H48 keeps strictly to the dense forest inland (Dahl, 1899). Probably because of this difference in habitat preference, there seems to be little interbreeding between the two forms, though Hartert (1926) records that occasional males on New Britain combine the smaller size and greener mantles of the endemic race with the greyer wings of *dahli*, and Mayr (1955) suggests that much of the internal variation of *dahli* may be the result of gene-flow from group H. The two forms must meet occasionally, though *dahli* may not normally breed on the large islands. It would be reasonable to suppose that groups E and H must be partly isolated by intrinsic barriers, like *P. soror* and the Snow Mountains race of *P. pectoralis*. Yet in the Louisiades H47 the same groups have merged completely.

Several explanations might be put forward to account for this anomaly, any or all of which may be true in part. It may be that in the Louisiades existing barriers have been broken down by hybridization (cf. Sibley, 1954*b*), permitting the populations to merge, while *dahli* has not been long enough in the Bismarcks for this to have happened. Or the populations of group H endemic on the relatively small islands of the Louisiades may have been inadequately shielded from interbreeding by differences in habitat-preference. Or after interbreeding in the Louisiades, *dahli* in the islands west of the Louisiades (E25b–c) may have secondarily developed barriers against group H, before invading the Bismarcks. In the absence of positive evidence, it is safest to assume that the two stocks in the Bismarcks represent one another geographically, and seldom meet in the breeding season. Yet it is conceivable that intrinsic barriers to interbreeding are effective here. From this, and from the different reactions of the *schlegelii* and *soror* assemblages (and of differentiated stocks within the latter) when they meet in New Guinea and in the archipelagos, it is clear that species-limits need not at all closely follow the pattern of descent and resemblance.

P. schlegelii, *P. soror* and group E of *P. pectoralis* are genetically sympatric (Cain, 1953) and must be regarded as good species. Yet the subspecies-groups A to H of *P. pectoralis*, some of them much less alike than are *P. soror* and group E, are interconnected by a web of secondary intergradation (Text-fig. 4). In the absence of evidence that groups E and H meet in the breeding season without significant interbreeding, all these groups can be included in a single species.

GROUP AFFINITIES

The *schlegelii* assemblage

P. schlegelii, groups A to D of *P. pectoralis*, and *P. flavifrons* all differ markedly from the standard patterns for the superspecies. Each is distinguished from the

others by characters which are not merely striking but stable and systematically important (as is shown by their co-variation). At first sight they seem to be independently derived from more standard forms, rather than closely related to one another. There is little in common, for example, between *P. schlegelii* and the Fijian group D (Text-figs. 3 and 2, bottom).

Yet there are important resemblances between members of this assemblage of forms. Most striking is the similarity between females of *P. schlegelii* and of *P.*
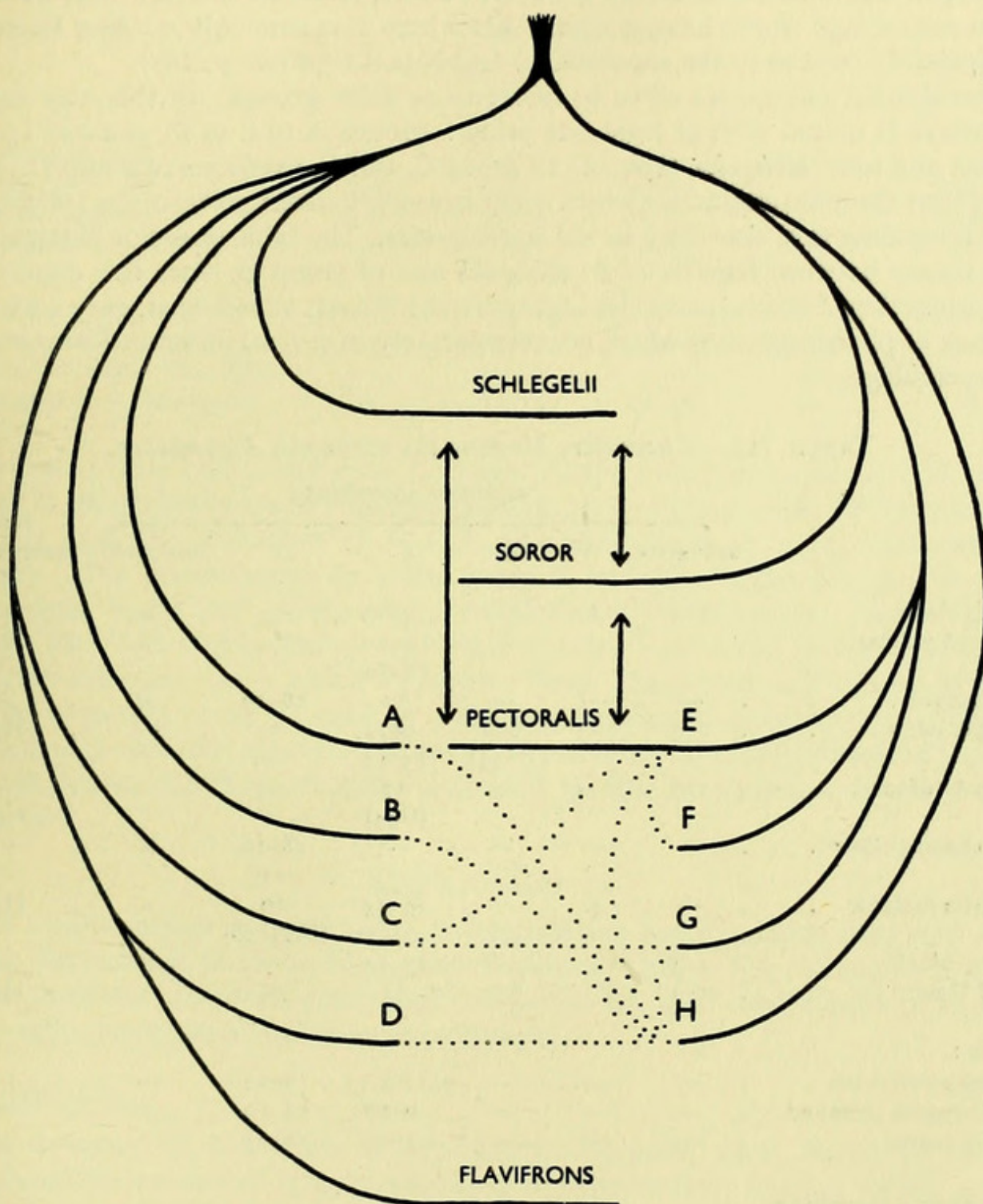
FIG. 4.—Diagram of the phylogeny suggested for the superspecies, showing secondary intergradation between subspecies-groups of *P. pectoralis* (dotted) and sympatric co-existence in New Guinea (arrows).

pectoralis in the northern Moluccas (group B). Furthermore, the males of the same forms are alike in having black chins, and throat-patches overlapping the gorgets without black tips to the feathers. These two characters of the males are shared by forms in most of the groups of the *schlegelii* assemblage. The black chin is absent from all the hybrid forms and from group D, but characterizes *P. schlegelii, P. flavifrons* and undiluted members of groups A to C. It is not found elsewhere in the superspecies (except in the black-throated race H57). The unusual structure of the gorget-edge is less affected by gene-flow, and is found in almost all the members of the assemblage which have gorgets. Elsewhere it occurs only on New Caledonia G34 (possibly related to the assemblage) and Ndeni H52 (see p. 162).

Several other characters serve to link two or more groups. In this way each of the groups is united with at least one other : groups A to C of *P. pectoralis* to one another and to *P. schlegelii*, group D to group C, and *P. flavifrons* to group D. Table III sets out the main characters which occur in more than one group of the assemblage, while remaining rare elsewhere in the superspecies. The table does not illustrate the resemblance between females of *P. schlegelii* and of group B, since this depends on the conjunction of several characters (grey-barred throat, olive breast, grey auriculars and lack of phaeomelanins) which occur separately in several different forms outside the assemblage.

TABLE III.—*Characters Uniting the* schlegelii *Assemblage.*

	schlegelii	A	B	C	D	flavifrons	soror assemblage
Male :							
Chin black	1–3	1	6–7	9–15	—	×	—
Throat yellow	—	—	—	9–17 (E26)	18–21	×	H42
No gorget	—	—	—	12	18–19	×	—
gorget edge	1–3	1–3	6–8 (H43)	9–11, 13–15	—	—	H52
breast rufous	1–3	1–4	—	17 (G34)	—	—	—
Forehead yellow	—	—	—	—	18–19, 21	×	—
Mantle melanic	—	4	—	13–14	20 (H55–56)	×	H52
Wing black	1–3	4	—	13–14	—	×	—
Tail black	1–3	1	6–7	13	—	×	H52
Female :							
Cheeks yellowish	—	—	—	9, 11 & 12	18–19	—	—
Underparts streaked	—	—	—	9–16	18–19	—	—
Wing russet	—	—	—	9–16	18–21	—	—

The **soror** assemblage

P. soror and the remaining groups of *P. pectoralis* are united negatively rather than positively, by the absence of those unusual characters which distinguish and link

together the groups and species belonging to the *schlegelii* assemblage. Since group H as a whole scarcely departs from the average characters of the whole superspecies, it can be associated with other groups only negatively. However, there are a few characters and trends which link *P. soror* with groups E to G and these with one another, and are rather rare in the *schlegelii* assemblage. These are set out in Table IV.

TABLE IV.—*Characters Uniting the* soror *Assemblage (except Subspecies-group H).*

	soror assemblage				schlegelii assemblage
Male :	soror	E	F	G	
Carotenoid pale . .	1–3	22	28–30	34, 36–38	—
Quills grey . . .	1–3	22–25	28–30	— .	D19, 21
Coverts yellow . . .	—	22–25	28–32	35 .	D18–19
Tail pale	1–3	22	28–32	34–37 .	C17
Female :					
Throat white . . .	1–3	22–27	—	34–38 .	A4–5
Throat streaked (not belly)	—	25, 27	—	38 .	—
Cap grey (not auriculars) .	—	22–25	28–33	— .	A5

Several of these characters seem to appear chiefly in higher latitudes, and may be related to the generally cooler climates encountered by these groups. Yet they are very different from the characters of *P. schlegelii*, which lives at higher altitudes than *P. soror*. The resemblances between group F and the Vanua Levuan race D19 (grey-edged wings and yellow-edged wing-coverts in the male ; barred throat, melanic belly and almost complete absence of carotenoid in the female) may be due partly to selection under cooler climates. These characters, and others which (it may be objected) could be used to erect any number of alternative assemblages, are evidently unstable, since they appear independently in widely-scattered localities and cut across the discontinuities indicated by the co-variation of more stable characters.

ARRANGEMENT

The considerations of relationship, intergradation and sympatry discussed above permit the various forms to be arranged systematically. The categories of super-species, species, subspecies-group and subspecies are used, and considerable infra-subspecific geographical variation is recognized.

The superspecies

The category of Artenkreis or superspecies (Rensch, 1928; Mayr, 1931a) was introduced for groups of strictly allopatric representatives, some of which are too unlike to be considered conspecific. Mayr pointed out that the great practical usefulness of this category might be expected to decline as the possibility of unlike representatives being conspecific became generally accepted. More recently the scope

of the superspecies has been extended to include groups of forms some of which are genetically sympatric (Cain, 1953), with their breeding ranges even overlapping slightly (Mayr and Vaurie, 1948 ; Mayr, 1949 ; and definition in Mayr, Linsley and Usinger, 1953). This extension gives the category permanent value, in expressing the relationship between forms which can never be considered conspecific yet which have barely ceased to represent one another geographically. But it removes the objective criterion which limited the use of the superspecies under the older usage, and opens the way to further extension. There is a danger of the category losing its special connotations of geographical replacement, becoming synonymous with the species-group.

Sometimes a species or superspecies is represented locally by a pair of sympatric species, so that it would be arbitrary to include one rather than the other in the superspecies, or to exclude both. Cain (1954*b*) has introduced the term " doublet " for such pairs in the *Ptilinopus purpuratus* superspecies, and this usage is helpful in indicating cases of double invasion. Where triple invasion by a single species has resulted in three representatives locally, the term " triplet " may be used. For example, *Zosterops lateralis* is represented by a doublet on Lord Howe (*Z. strenua* and *Z. l. tephropleura*), and by a triplet on Norfolk Island (*Z. albogularis*, *Z. tenuirostris* and *Z. l. norfolciensis*).

P. soror is so like many members of *P. pectoralis*, while *P. schlegelii* is so strikingly different, that the former is the obvious New Guinea representative. *P. soror* and *P. pectoralis* seem to be only genetically sympatric, without actual overlap, and might be included in one superspecies. But we have seen that, while *P. soror* is indeed the more closely related to some subspecies-groups of *P. pectoralis*, *P. schlegelii* is so to others. The two species should therefore be considered as a New Guinea doublet, like *Ptilinopus coronulatus* and *Pt. pulchellus* (Cain, 1954*b*). The local intrusion of *P. pectoralis* itself means that there is a triplet on the northern slopes of the Snow Mountains.

Species

All the remaining forms are geographical representatives. Those that intergrade must be conspecific, so that even the extreme forms on Sumba and in the northern Moluccas, Solomons and northern Fiji belong to *P. pectoralis*. Certain striking single characters have evidently arisen several times independently, and most modern systematists would agree in placing within *P. pectoralis* both the hen-feathered races on Rennell and Norfolk Island C16 & F33, and the melanic ones in the Solomons and Santa Cruz C13 & H52.

However, there are a few extreme forms (Text-fig. 5) whose status is doubtful, and can only be decided by comparing the degree of difference between them and their nearest relatives with that shown between sympatric species on the one hand, and between intergrading subspecies on the other. But in the *pectoralis* superspecies, two sympatric forms are much more alike than many intergrading ones : the relationship between visible differentiation and the establishment of barriers to interbreeding is not the same in New Guinea as in the archipelagos. The forms of doubtful status are all found on more or less isolated islands, whose avifaunas are

much poorer in species than those of New Guinea and include at most one other species of *Pachycephala* (*P. rufiventris* on New Caledonia). It is reasonable to suppose that the intergradation of unlike subspecies in the archipelagos is more relevant here than the coexistence of like species in New Guinea (p. 179).

P. flavifrons in Samoa is a derivative of the Fijian group D (Table III), but deserves the specific rank always accorded it. Group D is itself the most aberrant in *P. pectoralis*, and is probably on the borderline of ethological and genetic incompatibility with the rest of the species, while *P. flavifrons* has acquired further unusual characters —including the unique cock-feathering of its females.

Previous authors have considered the Tongan form H57 as a distinct species (*P. melanops*) because of the black throat of the male. In other ways this form is
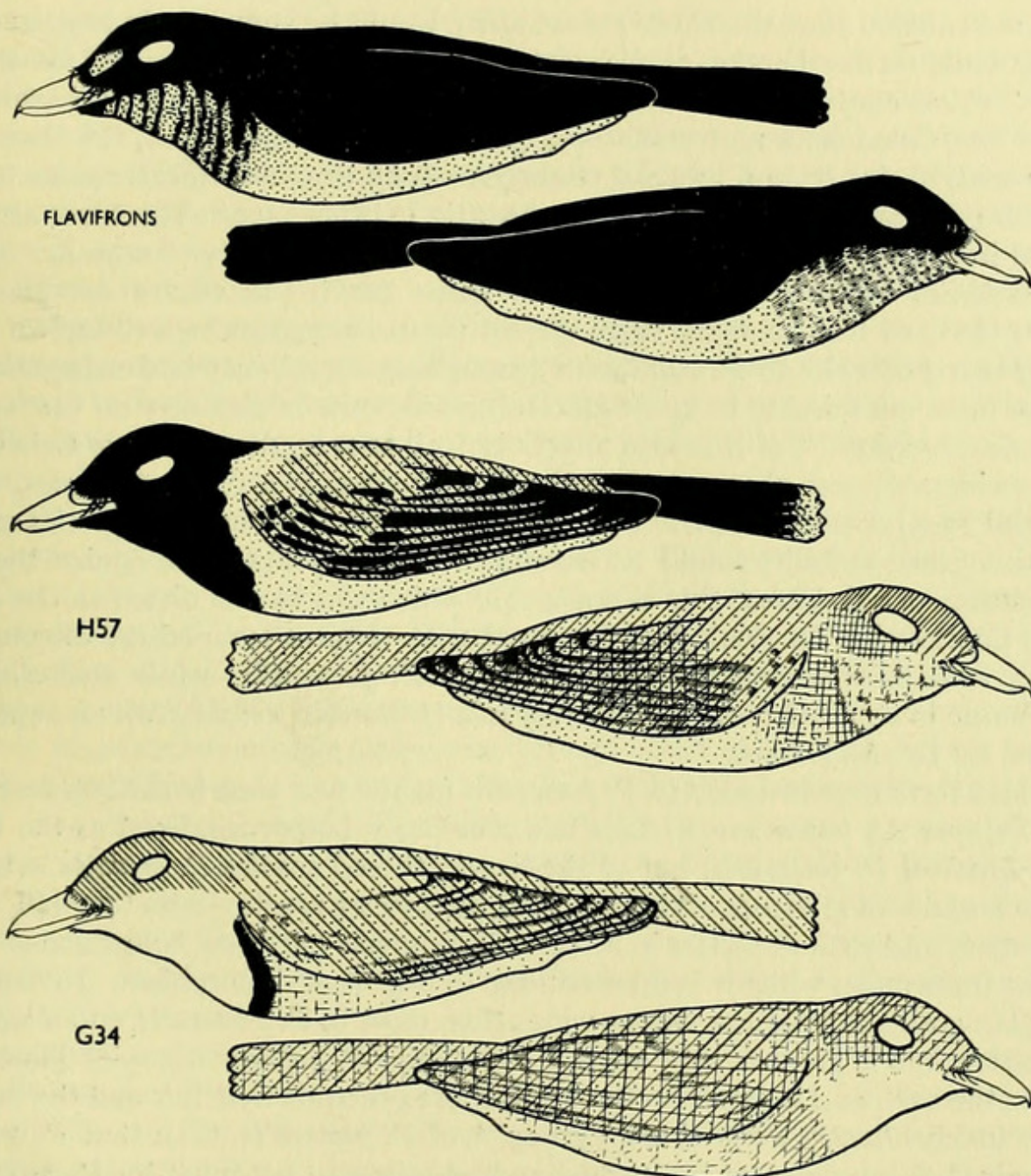
FIG. 5. Three unusual island forms. Samoa, *P. flavifrons*; Tonga, *P. p. melanops* H57; New Caledonia *P. [p.] caledonica* G34.

rather close to the standard pattern. It seems to be a member of group H, not more modified than might be expected from its isolation and the poverty of the avifauna in which it is placed. There is no reason to believe that the black throat reflects any very profound genetic change. The white throat-patch is very restricted on Sumba A1 and in *P. schlegelii*, and reduced to narrow white barring on black in individuals of the latter's close relative *P. aurea*. The mountain species *P. nudigula* and *P. implicata* (derived from the *pectoralis* superspecies) have acquired blackish throats independently. On the other hand, the black throat does alter the appearance of the male most markedly, and might therefore be of ethological importance. But so does the abolition of the gorget, and even more the total loss of the distinctive male pattern : yet there has been gene-flow between races with and without gorgets, while hen-feathered males in dimorphic races are able to find mates and breed. It is most improbable that the black throat alone would be sufficient to restrict inter-breeding while further barriers were selected for, in the event of a second invasion of Tonga. " *P. melanops* " ought therefore to be considered as a race of *P. pectoralis*.

In the New Caledonian representative G34 also the male is unusual, the female less so. The male shows several unusual characters (long throat-feathers, rufous breast-patch and pale cap), which appear independently in other races. This form has been excluded from *P. pectoralis*, even by Mayr (1945), for nomenclatural reasons. *Muscicapa caledonica* Gmelin, 1789—the valid name for it—antedates *M. pectoralis* Latham, 1801, so that merging them should mean changing the well-known name *Pachycephala pectoralis* to *P. caledonica* throughout its seventy-odd subspecies. It would be most undesirable to upset an established name in this way on the basis of a subjective decision. Yet it is also unsatisfactory to recognize the New Caledonian form, considerably less aberrant than the Fijian races, as a distinct species. Mayr (1941b and 1945) does not include *P. caledonica* in lists of the endemic species of New Caledonia. Since stability could be maintained by refusing to recognize the sub-specific status of *caledonica*, this is not a case which can be submitted to the International Commission for Zoological Nomenclature. I have avoided the dilemma by including *caledonica* among the subspecies of *P. pectoralis*, while enclosing the specific name in square brackets (*Pachycephala* [*pectoralis*] *caledonica*), an expedient suggested by Dr. A. J. Cain.

The third form here included in *P. pectoralis* for the first time is the hen-feathered one on Salayer A5 (*teysmanni*). This has previously been considered as the representative, not of *P. pectoralis*, but of the hen-feathered species *P. orpheus*, which is very like females of group A. It agrees with the former species in its long bill, black in both sexes, and with the latter in its juvenile plumage (streaked below and without rufous on the wings), while it is intermediate in degree of dimorphism. Juveniles of the Sundan group A have less rufous wings than most in *P. pectoralis*, and a nestling from Pantar A3b is greyish with ventral streaking. *P. orpheus* occupies Timor and islands to the east, and it seems on the whole more probable that this and the Salayer form are independently derived from group A of *P. pectoralis*, than that *P. orpheus* has colonized Salayer across the three-hundred-mile gap occupied by *P. pectoralis*, and there partly reversed its loss of dimorphism. If this interpretation is correct, there is no reason to separate the Salayer *Pachycephala* from *P. pectoralis*.

Subspecies-groups

There is no formal category between the species and the subspecies, and I call the eight divisions of *P. pectoralis* subspecies-groups. Zeuner (1943) has used the term in a rather different sense. The recognition of subspecies-groups permits the inclusion of well-marked geographical representatives (e.g. *Corvus corone* and *C. cornix* : cf. Huxley, 1942, 249) in a single species, while still expressing both the distinction between them and the minor subspeciation within each. There are no nomenclatural rules for such informal categories, and it is convenient here to use geographical designations rather than subspecies names for them.

Subspecies

No two populations have precisely the same distributions of genes, so that it is futile to attempt the subspecific separation of all local forms which differ statistically from the others. In avian systematics, some variant of the " seventy-five per cent rule " (see Mayr, Linsley and Usinger, 1953) is widely accepted as a lower limit for the constancy of differences between subspecies. This is a useful check on excessive splitting which should probably be retained whatever further considerations are introduced. But it does not take account of the magnitude and systematic importance of the differences. A very slight though constant difference in a single character which varies in response to climatic differences suffices to separate two forms ; while greater though rather less constant differences in several characters whose co-variation shows them to be largely independent of climate, and of systematic importance, do not. The subspecies-concept remains purely morphological, while that of the species now depends ultimately upon genetic isolation.

In parts of the range of *P. pectoralis*, the birds from almost every island can be distinguished by careful comparison of long series. This is true especially of the New Hebrides (G36–37f) and the Bismarcks (E25d–j and H48a–49). Mayr (1945) recognized six subspecies in the New Hebrides, but now considers that most of these should be combined (*in litt.*). The differences (almost entirely confined to the females) are slight, concern highly labile characters (such as the intensity of carotenoid and degree of phaeomelanization), intergrade through series of islands, and are exceeded by individual differences. The recognition of six subspecies conceals the true situation —that *P. pectoralis* is remarkably uniform throughout a great number of widely separated islands in the New Hebrides, though the population on Aneitum G36 is clearly distinguishable from the rest. I have therefore combined all the remaining populations (G37). The Erromango population G37a deserves subspecific separation according to current usage (p. 205), but those from Efate to the Banks Islands G37b–f should be combined.

Populations of groups E and H are distinguishable in series from island to island in the Bismarcks. The differences in group E are mainly in size, with populations of larger (E25b, c & d) and smaller (E25e) birds distributed apparently sporadically (cf. *Cacatua galerita triton*, Mayr, 1937). There are also slight differences in the pigmentation of the females and in the depth of carotenoid in the males. The situation is best expressed by combining the populations from south-eastern New

Guinea to Nissan E25a–k in *dahli*—though that on Fergusson E25c is on the border-line of subspecific recognition by current usage. There is little greater variation in plumage between populations of group H in the Bismarcks H48a–49, and that little is almost entirely confined to the females. There has as yet been no attempt to divide the populations from Umboi to Lavongai H48a–c, although the females can be distinguished in series (Mayr, *in litt.*). Females on Mussau and Lihir H48d–49 are more distinct—about as much so in relation to the other Bismarcks females as those on Erromango are in the New Hebrides. The Lihir form H49 is here separated subspecifically on account of its much greater size. But while that on Mussau H48d deserves separation under current usage, it is here combined with H48a–c to emphasize the homogeneity of this series of populations in contrast to those of Tabar and Manus H50–51, whose females are much more distinct.

By considering these areas of incipient subspeciation, and raising the level of difference required for separation so as to clarify the pattern of variation, we have arrived at a pragmatic standard for the subspecies of *P. pectoralis*. When this is applied elsewhere in the species range, a number of named subspecies are combined with others. This is especially true of the "small-island forms" (p. 188), of which only those on Ternate and Tidore B7 and Lihir H49 are sufficiently distinct to be separated on size alone, at this level of difference. Some of the remainder (e.g. H43b) are distinct enough for separation according to the seventy-five per cent rule, while others (e.g. A3b) are perhaps not.

The principle that minor subspecies should be combined, in order to emphasize the more important discontinuities, can be applied to variation on continents also. In Australia I have recognized only those forms considered by Mayr (1954a) to be original isolates—the subsequent expansion, intergradation and minor evolution of which have partly obscured the situation. Although the mangrove-living forms E22 in north-western Australia are known only from a few widely-separated localities, their variation is wholly of clinal type. The situation could be expressed in nomenclature as "*P. p.* cl. *bynoei-melanura-violetae*" (E22a–c–23), but it is convenient to separate the populations which show these regular changes from the more constant ones to the east E23. In *P. schlegelii* the populations of south-eastern New Guinea 3b should be combined with those of the Snow Mountains 3a, because the changes are slight in comparison with those which distinguish the Vogelkop and Cyclops Mountain races A1–2, and intergrade through central New Guinea (Mayr & Gilliard, 1954). In *P. soror*, on the other hand, there is a sharp change in the colour of the male tail in passing from the Bismarck and Saruwaged Mountains 2b to those of south-eastern New Guinea 3—relatively important in this less variable species.

The populations between Koro D20b on the one hand, and Viti Levu and Vanua Levu D18a & 19a on the other, are variable, and their hybrid indices evidently depend mainly on their distances from the parental populations. That on Taviuni D20a is only slightly affected by gene-flow from Vanua Levu, and is best included with the Koro race. Those on Ovalau D18b and Rambi and Kio D19c are also perhaps closer to the latter, but are considerably modified by gene-flow from Viti Levu and Vanua Levu respectively, and are therefore included in the subspecies of those islands. It does not seem desirable to recognize several hybrid races, differing

only in hybrid index and variability (cf. Mayr, 1932b). If this were done, consistency would demand the recognition of the constant Santa Anna population C17b as subspecifically distinct from the variable ones on San Cristobal C17a.

The subspecies numbered on Text-fig. 6, in the check-list, and in the text are delimited to make as clear as possible the pattern of isolation in the superspecies. It is not suggested that this arrangement should be generally adopted, since it does not accord with current usage, and a list of the subspecies to be recognized is therefore given on p. 205. But it does reveal the more important discontinuities which excessive splitting obscures, and the subspecies thus delimited have perhaps more biological significance, since some attempt has been made to consider discontinuity rather than mere constancy of difference (cf. Sibley, 1954a). It seems that the subspecies-concept might with advantage be modified by introducing such considerations. This would seldom require such considerable changes in the number and scope of subspecies as are necessary in the exceptionally variable species *P. pectoralis*.

EVOLUTION

Geographical speciation in New Guinea

The distribution of species and subspecies in many New Guinea birds strongly suggests that northern New Guinea was once isolated (Mayr & Gilliard, 1952), and this agrees with what is known of the tectonic history of the island (Carey, 1938). Some of the northern endemics have since spread into the Vogelkop. The pattern of variation of *P. schlegelii* and *P. soror* and the distribution of forms related to them (discussed below) suggest that they were originally geographical representatives, with the former in the Vogelkop and northern New Guinea (*P. schlegelii* 1–2) and the latter in the rest of the island (*P. soror* 2–3).

P. schlegelii has three distinct subspecies, with that of the Cyclops Mountains 2 combining characters shown by those of the Vogelkop 1 and the Snow Mountains 3 (and so perhaps ancestral to both). The Vogelkop form has invaded the Wandammen Mountains, which suggests that the species was absent from the nearer Snow Mountains at the time of colonization. There is no sharp break between the Snow Mountains 3a and the south-east 3b (though there are gradual clines), suggesting a rather recent expansion in this area. In *P. soror*, despite its greater overall homogeneity, there is a slight but definite break at this point (subspecies 2 / 3), while there is no appreciable difference between the birds of the Snow Mountains and of the north. This species has evidently colonized the northern mountains much more recently than those of the south-east. Both species have distinctly brown females in the Vogelkop, but in *P. soror* this is the only marked character of the Vogelkop race. Several birds are blacker in the Vogelkop than elsewhere in New Guinea, and this may be related to greater humidity (Cain, personal communication). If the parallel tendencies towards brownness in *Pachycephala* females here are adaptive, the changes may have been produced rather quickly. Also, isolation allows rapid change, unimpeded by gene-flow. *P. soror* may have been longer in the south-east than in the Vogelkop, despite the greater distinctiveness of the female in the latter area.

Two species in New Guinea seem to be hen-feathered derivatives of *P. schlegelii*

and *P. soror*. *P. lorentzi* is found within the geographical and altitudinal range of *P. schlegelii* in the Snow Mountains 3, and resembles the female of that species. *P. meyeri* bears the same relationship to *P. soror* in the Vogelkop 1. If these are relicts of early reciprocal invasions, their distribution tends to confirm that at one time *P. schlegelii* was absent from the Snow Mountains, and *P. soror* from the Vogelkop. Distribution and variation within *P. pectoralis* further reinforce this suggestion. Females of the Moluccan subspecies-group B, geographically near the Vogelkop, are remarkably like those of *P. schlegelii* (p. 169). Central members (subspecies-groups A to C) of the *schlegelii* assemblage are distributed towards the north of the species range, while the *soror* assemblage (especially the central groups E to G) is southerly. The early distribution of the assemblages according to this hypothesis is shown in Text-fig. 7, from which group H is omitted because its origins are obscure (p. 182).

Origin of the dichotomy

The presence of a doublet, representing locally a single more widespread species, implies double invasion. It has been suggested above that in the *pectoralis* super-species the second invasion took place within what is now New Guinea. If this is not true, the evidence suggests that *P. schlegelii* represents the endemic New Guinea stock, and that the *soror* stock arose as its geographical representative in Australia. While (outside New Guinea) the *schlegelii* assemblage is confined to islands, the *soror* assemblage occupies Australia. It must be rare for a form evolved in isolation on an archipelago, in competition with relatively few species, to compete successfully in the rich avifauna of primary forest on a continent, especially under the different physical conditions at high altitudes. But an Australian forest bird might well colonize the New Guinea hill forest. Gradual invasion across the Arafura shelf (often dry in the past) might favour the perfection of predeveloped isolating mechanisms (p. 180). The scattered and restricted subspecies-groups belonging to the *schlegelii* assemblage show a relict distribution comparable to that of the old species in the *Rhipidura rufifrons* superspecies (Mayr & Moynihan, 1946), while the *soror* assemblage occupies a wide and almost continuous range, like that of *R. rufifrons* itself, most of which has evidently been colonized comparatively recently. Patterns of intergradation in *P. pectoralis*, especially in the Banda Sea, suggest that the *soror* assemblage is still expanding (presumably as the result of selection) at the expense of the *schlegelii* assemblage. It is hard to accept the latter as a relatively recent colonist of New Guinea, in the face of competition from an entrenched *P. soror*.

Since the intergradations of group C with the *soror* assemblage are evidently secondary (p. 160), it is necessary to pass through group H in order to derive *P. soror* from proto-*schlegelii* by way of primary intergradation in the archipelagos (see Text-fig. 7, right-hand inset of Text-fig. 6, and Text-fig. 8). Of the possible sequences by which it could be derived in this way, the least improbable is *schlegelii*–B–H–G–E+F–*soror* ; but it is not convincing. The almost inescapable conclusion is that the *schlegelii* stock arose from the common ancestor in New Guinea, and the *soror*

stock either there or in Australia. This implies that *P. schlegelii* and *P. soror* are not merely terminal forms without issue, such as are produced by the double invasion of islands (e.g. *Zosterops*, p. 172 ; *Ptilinopus mercieri* and *Pt. dupetithouarsii*, Cain, 1954*b*), but represent the basal forms of their respective assemblages, geographically very near to their areas of origin.

Since the sympatric species *P. schlegelii* and *P. soror* are connected by way of secondary intergradation in *P. pectoralis*, which proves to be specifically distinct from them both, this conclusion seems to imply reticulate evolution (Text-fig. 4). The origin of a genetically isolated new species from two existing ones is a commonplace in botanical systematics, but the mechanism commonly involved (allotetraploidy) seems to be incompatible with the genetic mechanisms of sexually-reproducing animals (see Dobzhansky, 1937). There is no question of any such mechanism being involved in the *pectoralis* superspecies, since the forms of *P. pectoralis* which are in the biospecific relationship to *P. soror* (E24 & 27) are pure members of the *soror* assemblage. However, the evolution of the superspecies appears to have been reticulate at the species level only if the present status of *P. schlegelii* and *P. soror* is conventionally reflected back in time to their point of divergence. At the time when gene-flow between proto-*schlegelii* and proto-*soror* effectively ceased, permitting them to diverge in isolation, the barriers between them were probably almost entirely extrinsic ; and there is no reason to suppose that intrinsic isolating mechanisms had been perfected before they independently colonized the archipelagos and Australia. The existing mechanisms are local products of selection, and the supposition that the primary dichotomy of the superspecies took place in New Guinea does not imply that established species barriers were later broken down.

Development of isolating mechanisms

While in New Guinea the *schlegelii* and *soror* assemblages are represented by distinct biospecies, in the archipelagos they have proved capable of interbreeding freely wherever they have met. Biologically, New Guinea is strikingly distinguished from the surrounding islands by its vastly richer fauna. It is the centre of distribution of *Pachycephala*, with twelve species (cf. Mayr, 1941*a*—*P. aurea, P. lorentzi, P. meyeri, P. simplex* (with *griseiceps*), *P. hyperythra, P. modesta, P. rufiventris* (with *monacha*), *P. rufinucha, P. tenebrosa*, and the *pectoralis* superspecies). At the time when *schlegelii* and *soror* were developing intrinsic barriers against interbreeding with one another, they were probably in effective contact with most of the other nine. It may well be that the barriers were to some extent predeveloped before the two stocks met again, as a by-product of selection acting towards isolation from their sympatric congeners (especially *P. meyeri* and *P. lorentzi*). Similarly, *P. soror*'s barriers against the closely related subspecies-group E of *P. pectoralis* may have been prospectively developed, when the former came in contact with *P. schlegelii*.

In Australia, *P. pectoralis* is in effective contact with *P. simplex, P. rufiventris, P. lanioides* and *P. olivacea* (of which the first two are probably rather recent arrivals

—Mayr, 1954a). Possibly the specific distinctness of group E from *P. soror* is partly related to the development of barriers against these, and especially against the northern mangrove species *P. lanioides* and *P. simplex*.

In the archipelagos *P. pectoralis* meets with no more than one congener on any island : with *P. grisola* on Java and Bali (A2) ; with *P. nudigula* on Sumbawa and Flores (A3a) ; with *P. orpheus* on Timor and Wetar (H39) ; with *P. rufiventris* (including the *griseonota* group) on Damar, Tenimber, the Moluccas and Sula Isles, Rossel and New Caledonia (H41–45, B6–8, H47c & G34) ; with *P. simplex* on Fergusson (E25c) ; and with *P. implicata* on Bougainville and Guadalcanal (C9 & 11). Of these *P. grisola* in the lowlands, and *P. nudigula* and *P. implicata* in the mountains, are altitudinally separated from *P. pectoralis*, while *P. rufiventris* probably occupies drier habitats on the average (as in Australia) and shows altitudinal separation on Ceram and Buru (pp. 189–190). Only on Timor and Wetar is there an overlap, of long standing and without marked ecological separation, between *P. pectoralis* and a closely-related species, *P. orpheus*. On Timor and Wetar, *P. pectoralis* is large in comparison with its relatives to the west, and with sympatric *P. orpheus* ; which in turn has large representatives (*par*) on Roma, Letti and Moa, where the former does not occur. This suggests that there has been selection for size difference between the two species in the zone of overlap, as between *Sitta neumayer* and *S. tephronota* (Vaurie, 1950). It is noteworthy that in this region the intergradation between subspecies-groups of *P. pectoralis* is strongly stepped at the Ombai Strait (between subspecies-groups A and H), which suggests that gene-flow has not been as free as in the Moluccas and Fiji.

It seems therefore that the predevelopment of isolating mechanisms between the *schlegelii* and *soror* assemblages may be related to the intensity of selection against interbreeding with related species, to which the populations concerned were subject before they met. The degree to which they had developed different ecological preferences may also be relevant. It is probably more than a coincidence that group E of *P. pectoralis*, which is genetically isolated from its close relative *P. soror* in New Guinea (and to some extent from group H in the Bismarcks), is the most ecologically specialized in the superspecies (p. 190). New Guinea provides greater opportunities for altitudinal separation than any of the surrounding islands, and *P. schlegelii* and *P. soror* replace one another in this way to an extent seen in the archipelagos between *P. pectoralis* and much less closely related species.

Another factor which may have affected the reaction of the two stocks on meeting is the manner in which this took place. Within New Guinea they would at first have been opposed to one another over a broad front, and separated by the relatively unsuitable habitat of lowland forest. Invasion through this would be slight but continuous, producing rare hybrids in the lowland zone. These would be at a selective disadvantage, and at the edge of this zone there would be strong selection in favour of isolating mechanisms. Once developed these would allow the stocks to overlap, and the developed mechanisms would spread back into the populations, followed by waves of reciprocal invasion. The same would happen where group E of *P. pectoralis* met *P. soror* at the edge of its range, and the development of isolating mechanisms would finally permit the former to penetrate the range of the latter as a distinct

biospecies. In the archipelagos, on the other hand, the second colonizing wave (represented largely by group H) would have arrived over water, and its genetic representation in the population would probably be increased less by repeated invasion than by selection. In the absence of effective pre-established isolating mechanisms the new element would be incorporated in the endemic population, and no barriers could subsequently be developed.

A suggested course of events

Several alternative sequences of invasion and differentiation might be suggested, any of which could have produced the existing pattern of variation. It would not be profitable to discuss at length the pros and cons of these hypothetical alternatives, since the evidence does not seem adequate to decide between them with any finality. However, the following sequence seems to fit the facts more neatly than any alternative, and is perhaps worth putting forward for comparison with those deduced for other groups in the area (e.g. *Ptilinopus purpuratus* species-group in Ripley & Birkhead, 1942; *Halcyon chloris* species-group in Mayr, 1949; *Coracina* species-groups in Ripley, 1941, and Voous & van Marle, 1949; *Rhipidura rufifrons* species-group in Mayr & Moynihan, 1946; *Dicrurus hottentottus* superspecies in Mayr & Vaurie, 1948; *Dicaeum cruentatum-hirundinaceum* species-group in Mayr & Amadon, 1947). It is presented without qualification, for the sake of brevity.

It seems that the common stock of the superspecies arose in New Guinea (where the greatest concentration of *Pachycephala* species is to be found at present). *P. nudigula* on Sumbawa and Flores and *P. implicata* on Bougainville and Guadalcanal probably represent the relicts of an early burst of colonization westwards and eastwards respectively. The north-western and south-eastern populations in New Guinea, more or less effectively isolated from one another, diverged as subspecies. From the west and north " *schlegelii* " colonized the Lesser Sunda Isles (proving specifically distinct from *P. nudigula*), Moluccas, and Solomons (proving specifically distinct from *P. implicata*). The resulting widely-separated populations became very different from one another. Internal diversity may have been developed in groups A and B to much the same extent as is seen in group C to-day, before it was obscured by gene-flow. New Caledonia was probably colonized from the Solomons before the development of the special characters of group C, while there was a later expansion to Fiji and on to Samoa. Meanwhile the " *soror* " subspecies had colonized Australia. Because of the more humid climate and frequent emergence of the Arafura shelf during the Pleistocene, its range was probably more or less continuous. Not until the colonization of Southern Melanesia and the separation of northern and southern populations by the Recent eremiation of Australia (Browne, 1945) could the internal differentiation of the *soror* assemblage proceed far.

When the two New Guinea forms invaded one another's ranges as *P. schlegelii* and *P. soror* (their hen-feathered representatives *P. lorentzi* and *P. meyeri* having already done so), a contemporary systematist would have expressed the situation in terms of a superspecies (the *schlegelii* assemblage) overlapping in New Guinea with a polytypic species (the *soror* assemblage). Yet the assemblages fused when they

met in the archipelagos, mainly as a result of the explosive expansion of group H (black in right-hand inset, Text-fig. 6). Probably the complex palimpsest produced by new colonists interbreeding with the old, and incorporating characters proper to them, appeared first in New Caledonia at the invasion of Southern Melanesia from Australia.

The origin of group H is obscure. The most distinctive forms belonging to this group are widely separated (p. 160), and so do not help in determining the direction of expansion. Its derivation from one of the groups belonging to the *schlegelii* assemblage would imply too much reversal and convergence to be plausible. Since its common characters are very close to the standard for the whole superspecies, it may even represent a rather conservative though highly adaptable derivative of the common ancestor in New Guinea. Or the resemblance between its Banda Sea and Pacific sections may be convergent. But on the whole group H seems most likely to have arisen from the *soror* assemblage, as a stock adapted to island life, in the Banda Sea. Former island populations between Tenimber H42 and the Louisiades H47 may have become extinct during the Pleistocene fluctuations in sea-level over the Arafura shelf. Whatever its origin, the group has spread widely until its influence is apparent from Java to Tonga, and has interbred with very unlike island forms belonging to both assemblages. At this time the contemporary systematist would have regarded *P. soror* as conspecific with the whole complex of intergrading forms, and would have looked on the superspecies as analogous to a ring species—with *P. soror* and *P. schlegelii* specifically distinct in New Guinea, yet connected through series of interbreeding forms in the archipelagos. The latest major event, the escape of group E from Australia as a colonist of coastal and second-growth formations, shows that this is an oversimplification, and that morphological analogy may be misleading in the assessment of potential isolating mechanisms. Group E penetrated the range of *P. soror* as a distinct, though very similar and closely-related, species ; merged completely with its near relatives of group H in the Louisiades, yet remains more or less isolated from the same group in the Bismarcks ; and has interbred freely with the very dissimilar and phylogenetically distant group C in the Solomons.

Rate of divergence

In general, the degree of difference now to be seen between related forms (both within and between subspecies-groups) agrees reasonably well with the sequence of events suggested above, when the retarding effect of gene-flow between populations has been taken into account. The groups belonging to the *schlegelii* assemblage are much more different from one another than those of the *soror* assemblage. Group C shows the most internal differentiation of any group in the superspecies, while there is considerable variation within group A despite the levelling effect of gene-flow from group H. Group D is evidently derived from group C, and there is remarkably little difference between the populations on Viti Levu and Vanua Levu ; while *P. flavifrons*, derived from group C at second hand, shows no appreciable variation between Savaii and Upolu. The females of group B are so like those of *P. schlegelii* that the populations in the northern Moluccas may have been in genetic contact

with those of the Vogelkop long after the invasion of the Lesser Sunda Isles and Solomons, and the slightness of the geographical variation there bears out this supposition.

P. schlegelii and *P. soror* are here supposed to be New Guinea endemics of equal antiquity, and the former to have occupied a discontinuous range before their reciprocal invasions—so that its greater geographical variation is not unexpected. Similarly, the comparative uniformity of the Australian groups agrees with what is known about the rates of divergence in populations of continental and of insular range. In the characters common to most of its members, group G is little more distinct from groups E and F than they are from one another, and combines characters of each (Table IV). This suggests that southern Melanesia may have been colonized at about the time that increasing aridity effectively divided the range of *P. pectoralis* in Australia. However, there is considerable variation within group G (even when the effects of a genetic contribution from the *schlegelii* assemblage to New Caledonia have been allowed for) and the much greater uniformity of groups E and F must be attributed to their more or less continuous continental ranges. Both these groups have isolated representative populations on small islands far from Australia, but hen-feathering on Norfolk Island F33 is the only considerable change shown by these populations. The distribution of group E in New Guinea and the nearby islands strongly suggests the very recent incursion of an ecologically-specialized form, and recent colonization is the probable explanation for lack of divergence on Lord Howe F32 also.

Although there is considerable local variation within group H, widely separated forms are remarkably similar (for example, the females in the southern Moluccas, Bismarcks and Santa Cruz H43-44, 48-49 & 52-53). Apart from the effects of intergradation with other groups, the isolated sections of this group in the Banda Sea, eastern Papuan islands, Santa Cruz and Fijian archipelagos are not well differentiated from one another. It seems probable that most of the large range of this group has been colonized relatively recently, despite the wide scatter of very distinctive forms (p. 160). This conspicuous divergence of some of its members, in one or a few characters, is discussed below (p. 184).

Unexpected uniformity

In some areas there is surprisingly little geographical variation from island to island, although the distances involved are not small in comparison with those between islands occupied by strikingly different forms in other archipelagos. Where there is evidence of gene-flow between groups (as in the Banda Sea, Louisiades and Fiji), it is evident that the populations on different islands are or have been in genetic continuity, and the uniformity may be attributable to swamping. Elsewhere it may reasonably be explained in terms of colonization too recent for much subsequent diversification, as has been suggested for group H as a whole, and for the insular expansions of groups E and F.

But the slightness of the geographical variation within the New Hebrides G36-37f, in contrast to the marked differences between the forms on the different island-

groups of Southern Melanesia (G34, 35, 36 + 37, & 38), does not at first sight seem to be susceptible to either of these explanations. There is no evidence for exceptional gene-flow here (except perhaps from New Caledonia G34 to Aneitum G36), and the New Hebridean type is too distinct from its relatives for the whole archipelago to have been colonized only recently. The distances between islands in the New Hebrides are shorter than those separating them from the Loyalty Isles G35 and Vanikoro G38, but there are several gaps (e.g. from Erromango to Efate G37a/b, and from Maewo to Gaua G37e/f) comparable with those which separate very distinct forms on Guadalcanal C11, Malaita C12 and San Cristobal C17, or on New Caledonia G34 and the Loyalty Isles G35. Almost all the New Hebridean gaps are wider than those which separate the three marked races of the central Solomons C13–15.

Much of the New Hebridean avifauna shows this combination of a fairly high degree of endemism with surprisingly slight geographical variation. This might follow if geographical variation were closely related to environmental differences, and if the New Hebrides were environmentally much more uniform than the other archipelagos. But, in *Pachycephala* at least, variation does not seem to be as minutely correlated with demonstrable local differences as this theory would demand, while the New Hebrides show much more variation in climate and vegetation (from a marked dry season, with permanent grasslands, in the south to a very equable equatorial climate, with only rain forest, in the north) than do the Solomons. It seems that for a considerable part of the avifauna, genetic isolation between the islands of the New Hebrides is either imperfect or only recently established. The existing patterns of variation might result from the splitting up of an originally continuous range (by subsidence), or from an expansion into new territory (by island-building or other external changes, since several species are involved).

The geological evidence (Mawson, 1905) is that most of the New Hebridean islands except Malekula and Santo G37d have arisen since the late Pliocene, either by volcanic extrusion or by uplift. The terraced profile of parts of the central New Hebrides is very marked, and quite unlike anything seen in the eastern Solomons (Cain & Galbraith, personal observation). It is possible that geological events, and their ecological consequences, can be invoked in partial explanation of the avifaunal peculiarities of San Cristobal, including the incursion of a Southern Melanesian *Pachycephala* (Galbraith, in preparation).

Unexpected diversity

Some forms, on the other hand, are more different from their close relatives than is to be expected from the suggested sequence of events on the assumption that populations not swamped by gene-flow have diverged at approximately the same rate. The outstanding forms (i.e. A4 & 5; C12, 13, 14, 16 & 17; D21; E27; F33; H42, 52 & 57; *P. flavifrons* (an offshoot of group D), and the subspecies (1) of *P. schlegelii* and *P. soror*) occupy more or less restricted ranges, isolated at the periphery of their respective groups. The law of peripherally-isolated populations (Mayr, 1954b) is well illustrated in areas where geographical variation is less advanced : the comparatively well-marked forms in the northern Moluccas (B7), New Hebrides (G36, & G37a)

and Bismarck archipelago (H49–51, & H48d) are all peripheral. Mayr discusses the possible explanations: drift, resulting from small population size; selection, resulting from environmental differences (physical and biotic); and "genetic revolution", resulting from a small gene-pool (initially because of the smallness of the founding population, and subsequently because replenishment by gene-flow is restricted).

Because such aberrant peripherally-isolated populations often occupy relatively small islands, drift has been invoked to explain them. But few forms of *P. pectoralis* are found on tiny islets (the exception, group E, has as yet diverged little over a widely scattered range), and it is improbable that the local effective breeding populations of this common bird are sufficiently small for selection to be overcome by random fixation and elimination of genes.

The brownness of the females of both *P. schlegelii* and *P. soror* in the Vogelkop may be an adaptation to very humid conditions (p. 177), while there is evidence of the selective influence of climate on *P. pectoralis*, not only in Australia but to some extent in the archipelagos (p. 187). Certain regularities of geographical variation in different bird species suggest that the physical environment varies from island to island more than is generally supposed, and considerable local differences in climate between habitats within one island support this view (Cain, unpublished). Unfortunately, meteorological data for this region are scanty, and are probably affected less by the relatively slight changes in average climate from island to island than by the precise siting of the stations. Although differences in the physical environment cannot be ruled out, the diversity of characters involved makes it necessary to look further for the causes of differentiation in peripherally-isolated forms.

Biotic differences (especially in the avifauna) seem more promising, but are still more difficult to assess. Trends in the dimensions of forms on small islands are discussed below (p. 188), and are probably related to ecological redeployment. Most of the divergent forms occur in avifaunas which are relatively poor in species, and most of the variations in male plumage reduce the distinctiveness of the pattern. But the two features of the avifauna which are most likely to impinge on the visual properties of the pattern—the presence or absence of visual predators, and of species with similar patterns—do not provide a comprehensive explanation of the variation. Lack of visual predation might be expected to relax dorsal crypsis, and in fact two of the the three forms with black mantles are restricted to islands without known hawks (Samoa (*P. flavifrons*), and Ndeni and Santa Cruz islets H52). But both *Accipiter novaehollandiae* and *A. albogularis* are found on Vella Lavella together with the black-mantled *Pachycephala* C13, and the latter hawk may have been overlooked on Ndeni. Only in Australia and New Guinea, the Lesser Sunda Isles and New Caledonia does *P. pectoralis* overlap with other *Pachycephala* species having similar male patterns (*P. soror, P. schlegelii, P. aurea, P. rufiventris* and *P. lanioides*). The loss of the gorget on Malaita C12, for example, is not solely related to the absence of such species, since the only other *Pachycephala* in the Solomons (*P. implicata*) is restricted to the mountains of Bougainville and Guadalcanal and does not have a conspicuous pattern. But such a loss might be disadvantageous in a richer avifauna containing species of similar plumage and behaviour patterns.

Mayr (1954b) has pointed out that when an island is colonized by a few stray pairs from a large and genetically variable population, the initial representation of genes will be more or less random . The selective changes involved in regaining a coadapted genetic system will depend on the genes available, so that unpredictable differences between isolated populations arising in this way are to be expected. However, in all these populations there will be selection in favour of genes which have a favourable effect in the homozygote and are at an advantage against a more uniform genetic background, so that some regular trends may be looked for. Both these expectations are fulfilled in *P. pectoralis*. Most of the variations seem to appear entirely at random, yet the ones which strikingly affect the pattern occur only in such peripheral localities. Melanism of the mantle is confined to more or less isolated forms on rather small islands (Djampea, Kalao tua and Madu, Vella Lavella, Ganonga, Rendova and Tetipari, Ndeni and the Santa Cruz islets, Taviuni, Koro, Ngau, Ongea Levu, Fulanga and Wangava, and Upolu and Savaii). Furthermore, the traces of gene-exchange between populations separated by several miles of sea are unusually clear in *P. pectoralis*, and the rapid falling-off in gene-flow with increasing distance will obviously have important genetic effects in this species.

ADAPTATION

Character and climate

The adaptive significance of geographical variation in relation to climatic differences emerges most clearly in continental areas, exposed to regular climatic gradients and occupied by continuous populations. Irregular differences in climate, and the effects of isolation and bursts of colonization by different stocks, make it difficult to correlate character and climate in insular regions (cf. Snow, 1954). In many species of birds, clinal changes are strongly marked from north to south down the eastern coast of Australia, in relation to decreasing average temperature. In this area *P. pectoralis* presents the appearance of a series of isolates with secondary intergradation, rather than of a continuous cline (Mayr, 1954a). The Tasmanian population F29 is isolated by sea, and there seems to be a gap in the range of the species between southern Queensland F31a and the rain-forests around Cairns F31b. There is no reason to doubt that the populations from eastern Victoria to southern Queensland F30a–31a are continuous, and material from intermediate localities may show the phenotypic changes to be gradual.

We may arrange the three presumptive isolates of the east coast in a southwards series ; and since groups E and F are closely related we may perhaps add the Northern Territory isolate as a first member. If the northern Queensland populations F31b were included, they would introduce a slight reversal of the otherwise progressive changes. There has evidently been gene-flow from this region into Cape York and across the Torres Straits, and it seems possible that reciprocal flow has produced a retardation of the female characters here (p. 166). Therefore the southern Queensland form F31a instead will be taken to represent group F in the north of its range. Our series from north to south is then : (a) Northern Territory E23, (b) southern Queens-

land F31a, (c) eastern Victoria F30a, (d) Tasmania F29. In this series the following progressive (though neither smooth nor synchronous) changes are apparent :

(i) increasing wing-length (and presumably body-size) ;
(ii) increasing relative tail-length ;
(iii) decreasing absolute and relative bill-size ;
(iv) decreasing amount of solid black (in the male tail) ;
(v) decreasing concentration of carotenoid (female plumage and male tail especially).

Such a series of progressive changes might be maintained without climatic adaptation, by gene-flow from end-forms which had diverged in isolation. The characters of an intermediate population would then depend mainly on its degree of genetic isolation from each gene-source. However, changes (i), (iii) and (iv) (increasing body size, decreasing relative length of appendages and concentration of melanins) are sufficiently general among homoiothermous animals, in relation to increasing latitude, to be recognized as Bergmann's, Allen's and Gloger's ecological rules (see Huxley, 1942). Furthermore, all five of these changes are paralleled in Palaearctic titmice (*Parus* spp., Snow, 1954), in relation to decreasing temperature. It is most probable that the changes seen in *P. pectoralis* in eastern Australia are likewise adaptive. In certain other parts of the species-range parallel trends are discernible, although (as in *Parus*) there are numerous exceptions among island forms.

From the Northern Territory to midwestern Australia (E23–22a), solid black and intensity of diffuse melanin and of carotenoid decrease, but wing-length also decreases and proportions are not much affected. The small size and general pallor of these forms are paralleled in group A of the Lesser Sunda Isles, and it is noteworthy that these two areas are the driest occupied by the superspecies. In many groups of birds (Snow, 1954 ; Cain, unpublished), intensity of pigmentation falls off with decrease both in temperature and in humidity. This applies both to melanins (Gloger's rule) and to carotenoids. In arid regions the range of temperature is great, and it may be that coloration and body-size are responding to lower minimum and higher maximum temperatures respectively.

In group G, the male tail is black in the north G38, olive in the south G34–36, and olive with black subterminally in the centre of the range G37. There is a southwards decrease in the intensity of carotenoid, especially in the females, from Vanikoro G38 through the New Hebrides as a whole G36–37 (with local variation) to New Caledonia G34 ; but the Loyalty Isles race G35 is yellowest of all, and no corresponding regularities in the variation of size and proportions are apparent. Throughout the archipelagos there are such hints of climatic correlations, but the exceptions are so numerous that they cannot be relied upon. Thus at the level of the subspecies-groups within the *schlegelii* assemblage, it might be suggested that the low intensity of carotenoid in the females of groups A and D is correlated with the aridity of the Lesser Sunda Isles and the coolness of Fiji respectively ; while in the hot and moist Moluccas females of group B have intense yellow pigment. But there is as great variation in this character between adjacent islands of the Solomons (C9, 11 & 12 against 10 & 13–17), whose climates cannot be very different. Another possible climatic correlation, since both localities are rather arid, is in the appearance of a pinkish

phaeomelanic wash over breast and belly of the females in southern Australia F28 and on Timor H39. But the appearance of the character also on small islands of the Flores Sea A4, and its absence from females of group E from the most arid parts of Australia, seem to contradict this. As in Palaearctic tits, climatic correlations are merely hinted at among isolated forms.

Character and habitat

In New Guinea members of the superspecies occupy different altitudinal belts, with more or less overlap, from coastal second-growth (*P. pectoralis* E24) through hill forest (*P. soror*) and lower montane cleared land (*P. pectoralis* E27) to mountain forest (*P. schlegelii*). The three highland forms of this series agree in the olivaceous wash on the underparts of their females—found elsewhere in the superspecies only in forms derived from *P. schlegelii*. The relict species *P. nudigula* and *P. implicata* (in the mountains of the Lesser Sunda Isles and Solomons) also show this character, which thus seems to have been independently acquired about five times by members and close relatives of the *pectoralis* superspecies, in relation to life at higher altitudes. The males also of *P. nudigula* and *P. implicata* are strongly washed with olive beneath, while those of *P. soror* have an olivaceous appearance (due largely to the long grey feather bases showing through). Possibly the rufous ventral wash of male *P. schlegelii* represents a parallel adaptation to high altitudes. The small size of the white throat-patch in *P. schlegelii* and *P. soror*, the reappearance of grey bases to the white feathers in *P. pectoralis* E27, and the greying or blackening of the throat in *P. nudigula* and *P. implicata* may also be parallel responses to similar environments. All these trends are towards the blurring of the conspicuous ventral pattern (obscured also in the montane species *P. rufinucha*, *P. tenebrosa* and *P. olivacea*).

Several subspecies have been described from the Banda Sea, which inhabit small islands and closely resemble those of adjacent large islands, but which are described as being larger, with conspicuously larger bills and often with more golden-olive mantles. This is true of Lomblen, Pantar and Alor A3b compared with Sumbawa and Flores A3a ; Wetar H39b compared with Timor H39a ; Amboina H43b compared with Ceram H43a ; and Ternate and Tidore B7 compared with Morotai, Halmahera and Batjan B6. Unfortunately the series of several of these forms available to the authors of the descriptions and to me are not adequate for the statistical significance of the differences to be determined. In the Bismarck archipelago the populations on Lihir and Tabar H49–50 are conspicuously larger and larger-billed than those of the large islands H48 & 51. The same is true of *dahli* E25 in comparison with its close relatives in northern Australia E23 (the populations E25 lying between, being affected by gene-flow, are ineligible for comparison) and of the races on Lord Howe and Norfolk Islands F32–33 in comparison with the parental populations at the same latitudes in Australia F31a. All the races which are strikingly larger than their close relatives (and have correspondingly large bills) occupy small or low-lying islands : Ternate and Tidore B7, the Loyalty Isles G35, the Tenimber Isles H42, Lihir and Tabar H49 & 50, and Tonga H57. This tendency towards large size, and particularly towards large bill size, is well known among insular birds

(Murphy 1938 ; Mayr & Vaurie 1948), and may be related to redeployment of the few species on such islands among the available food niches. However, Mayr's figures (1932a, b) do not suggest any such general rule in the Solomons, Santa Cruz, New Hebrides and Fiji, for situations where closely related populations occupy neighbouring islands of different sizes.

It has already been noted that markedly divergent subspecies occur on rather isolated, and usually small, islands. Apart from the effects of isolation and the small gene-pools of founding populations, the relative paucity of species on these islands may have been an important factor in permitting the male pattern to diverge widely from the standard. For example, in group A hen-feathering occurs on Salayer A5 (about 35 resident land bird species) and melanism of the mantle on islands in the Flores Sea (about 55 species), whereas the male on Sumba A1 (about 110 species) is ventrally conspicuous and dorsally cryptic. In group C hen-feathering occurs on Rennell C16 (about 35 species) and melanism on peripheral islands of the central Solomons C13–14 (about 60 species), while the male on Guadalcanal C11 (about 95 species) is standard for the group. The male on Norfolk Island F33 (about 15 species) is hen-feathered, unlike its relatives in eastern Australia F30–31 (several hundred species). The mantle is wholly black on Ndeni and the Santa Cruz islets H52 (about 20 and 10 species respectively), and in *P. flavifrons* of Samoa (about 30 species). In Fiji the correlation with avifaunal poverty is less clear : black-mottled mantles occur on Koro, Ngau and the southern Lau archipelago D20b, H55-56 (25–30 species) and not on Viti Levu (about 50 species) ; but on two islands with apparently similar avifaunas (about 40 species), black mottling appears on Taviuni D20a but not on Vanua Levu D19a. It may be that further species remain to be discovered on Vanua Levu, a large and mountainous island, whereas Taviuni is smaller and better known. But elsewhere, too, the realization of these trends seems capricious. Although neither hen-feathering nor melanism of the mantle occur where the avifauna is rich, they are not always present where it is poor. Well-marked races which do not show these tendencies occur on the following small, low or isolated islands : Tidore and Ternate B7, Russel Islands C10c, Vatu vara D21, Lord Howe F32, Loyalty Islands G35, Aneitum G36, Vanikoro G38, Wetar, Babar, Damar and Tenimber H39b–42, Lihir, Tabar and Manus H49–51, Utupua H53, Kandavu H54 and Tonga H57.

Variation in habitat

The members of the *pectoralis* superspecies throughout its range are forest birds which forage for soft-bodied insects (and some berries) among the twigs and branches of the substage and lower canopy. Field notes are rare in the literature, but it is clear that there is considerable variation in the habitats selected by different forms. The altitudinal deployment in New Guinea has already been mentioned, and races of *P. pectoralis* are found at different altitudes on different islands.

Group A is found only above 6,500 ft. in eastern Java A2a and above 3,000 ft. on Bali A2b, but from 4,000 ft. down to sea-level on Flores A3a (Hartert, 1897 ; Stresemann, 1913 ; Meise, 1929 ; Rensch, 1931 ; Hoogerwerf, 1948). This may be related to the presence of the lowland *P. grisola* on Java and Bali, and of the mountain *P. nudigula* on Flores.

Altitudinal preferences are known to differ from island to island in the Solomons, though the details remain to be worked out. Mayr (1932a) reports the species as rare or absent in the lowlands of Bougainville and Malaita C9 & 12, though common near the coast on Choiseul C10a. Cain and Galbraith (1956) heard it occasionally in the lowland forest on Guadalcanal C11, but found it much more common in the hill forest at about 2,000 ft., and up to the lower limit of the mist forest (where it is replaced by *P. implicata*). On San Cristobal C17 I found it to be common at 2,000 ft. and down to the coast. It is recorded by Donaghho (1950) in the lowland forest on Guadalcanal, but not by Sibley (1951) in the same habitat on New Georgia C15.

The altitudinal preferences of *P. pectoralis* in the northern Moluccas and Fiji do not seem to have been recorded. *P. flavifrons* is found at 600 ft. and above on Upolu (Nicoll, 1904).

On Timor H39a, *P. pectoralis* occupies a greater vertical range than has been recorded elsewhere, from sea level to 7,500 ft. (Stein, 1936 ; Mayr, 1944c). It is absent from the lowlands (occupied by *P. rufiventris*) on Ceram H43a and Buru H44, and reaches 5,000 ft. (Stresemann, 1914a, b). Scott (1946) records it on Santo G37d as commonest in the higher forest, though frequent also in the open lowland forest. I have seen it on that island and on Efate G37b in tangled second growth near the shore, a habitat never seen to be occupied by the species on Guadalcanal and San Cristobal. In southern and eastern Australia it is found in dense and open forest (records in the *Emu*, 1902 to date), but not in the dense myrtle-beech forest of the wettest areas on Tasmania F29 (Lawrence, 1952), where *P. olivacea* is found.

The most striking specialization in habitat is found in group E. This occupies mangroves fringing the deserts of north-western Australia E22 ; mangroves, coastal forest and second growth from northern Australia to the Bismarcks and Solomons E23–26 (especially on very small islands) ; and second growth in the highlands of New Guinea E27. This specialization has allowed it to penetrate the ranges of the deep-forest forms *P. schlegelii*, *P. soror* and *P. pectoralis* H48. Although the two males E25 and H48 in the Bismarcks are similar in appearance, they differ markedly in habitat, conspicuousness and song (Dahl, 1899). As a consequence of their different habitat-preferences, members of group E must be exposed to different micro-climates from the neighbouring forest races. The special conditions in desert-fringing mangroves (presumably humid, yet subject to extremes of temperature) may explain the apparently contradictory changes of phenotype in north-western Australia E22 (p. 187).

The variability of the hybrid populations on small islands off Shortland E26 may well be maintained by selection in relation to habitat differences. These populations are separated from one parental stock (C9) by less than three miles, from the other (*dahli* E25k) by almost two hundred. The latter occupies islets such as these, which elsewhere in the Solomons have no *Pachycephala*. Presumably the hybrids are better adapted to small islands than are the pure forms of group C. A surprising feature of the hybrid sample is that the smallest males have the whitest throats (like the small *dahli*) and the largest the yellowest throats (like the large Shortland race). In isolation, genetic linkage alone could keep the recombination classes scarce in the population for a few generations only. This would imply that at the time the known

specimens were collected (1927) the hybrid populations were very young indeed, in which case they may by now have become partly stabilized. Supposing the situation to be of longer standing than this implies, the observed co-variation might be achieved by continued gene-flow from the parental stocks, or by selection in favour of the parental genotypes, or both. Recolonization by *dahli* must be almost unknown, while birds may arrive from Shortland rather frequently. In view of the failure of group C to colonize habitats such as are occupied by the hybrids, it seems probable that the *dahli* genotype is being maintained by selection, in the face of gene-flow from Shortland.

Variation in bill size

The absolute and relative length and stoutness of the bill varies greatly within the superspecies, to an extent which in many groups of birds would be considered to warrant generic separation. But the colour-patterns of the males are so clearly allied to one another that even Mathews (1930) places all these forms in a single genus. The variation shown by the bill is largely independent of the major discontinuities, and certain regularities apparent in a cursory study (pp. 186 and 188) show it to be at least partly adaptive. It is therefore relatively unimportant in the study of relationships within the group, and has not been dealt with in this paper.

Except in long series, the finer geographical variation is to some extent obscured by individual variation and the inaccuracies of measurement (especially of bill depth). The tables (p. 217) give some idea of the range in length and stoutness. Evidently very different bills (e.g. massive in Tenimber H42, slender in the Louisiades H47 and stubby in Tasmania F29) must be best adapted to taking correspondingly different food. But almost nothing is known about geographical differences in diet. The Guadalcanal race C11 takes considerably larger insects on the average than the smaller race, with a shorter and finer bill, on San Cristobal C17 (Cain & Galbraith, 1956). Dahl (1899) records that of the two stocks in the Bismarcks, *dahli* E25 (with slightly the longer bill) takes a proportion of vegetable matter, while the race on the large islands H48 does not.

CONCLUSIONS

The very different plumage patterns of the sexes provide a large number of more or less independent characters which vary in stability and systematic importance, from the " qualitative " characters which unite males of the *schlegelii* assemblage to the slight differences in pigmentation and dimensions which distinguish closely-related populations on neighbouring islands. This makes it possible to study relationships within the superspecies despite the independent origin and loss of even the most stable characters, since the local co-variation of several relatively labile characters can be of equal importance. Most of the stable characters are provided by the male pattern, and most of the more plastic ones by that of the female. The relationships suggested in this paper could not all have been arrived at by considering one sex alone, and it may not be possible to decide with any certainty the affinities of hen-feathered species such as *P. simplex, P. sulfuriventer* and *P. philippensis*. In

organisms which do not show such diversity in conventional museum material, a genetic situation of equal complexity could only be interpreted by bringing in further characters (whether of internal anatomy, cytology, genetics, biochemistry, physiology, ecology or behaviour), which are most desirable in this group also, to test the validity of conclusions based entirely on a study of skins (cf. Wilson & Brown, 1953).

The combination of great colonizing ability (implying dispersal) and divergence of neighbouring populations (implying philopatry) shown by the *P. pectoralis* super-species is remarkable, though not unprecedented. However, *P. pectoralis* is unique in having so many and so diverse forms, all of which are strictly allopatric, and between the most dissimilar of which there has been extensive gene-exchange. In this super-species hybridization and sympatry are largely independent of phylogenetic relation-ships, cutting across the division into *schlegelii* and *soror* assemblages. It seems to be impossible to predict whether or not any given pair of representatives would interbreed on coming together, by considering only their resemblance and relation-ship. Purely local adaptations to the environment, and the manner of their meeting, are perhaps important in determining the outcome (p. 179). Although at the species level we have an objective criterion, not found higher or lower in the systematic hierarchy, for the relative status of any two populations which come in contact, it may not always be possible to use this criterion quite consistently in delimiting a given species. Strictly there are no biospecies, but only biospecific relations between sympatric populations. In the *P. pectoralis* superspecies, however, the three species *P. schlegelii*, *P. soror* and *P. pectoralis* can be satisfactorily delimited—although the different relationships between groups E and H in the Louisiades and Bismarcks (p. 168) suggest that in other groups it may be necessary to draw species-limits more arbitrarily. Morphological analogy is still the only available yardstick in determining the status of isolated representatives ; but the co-existence of closely-related forms in New Guinea, and interbreeding between more distant relatives in the archipelagos, demonstrate that other factors must be taken into account. Though at present we can only speculate on the nature of these factors, we need not consider as distinct species all those geographical representatives which are more different than the most similar pair of related sympatric species. It is justifiable and expedient to admit a wider range of representative forms to a single species than is the current practice. (In accordance with this consideration the Guadalcanal representative of *Cichlornis whitneyi* Mayr has been described as a subspecies (Cain & Galbraith, 1955), although the differences between it and the form in the New Hebrides are greater than those between many sympatric pairs of warblers.)

The pattern of variation shown by the superspecies is interpreted as the result of colonizations by two stocks which diverged in New Guinea and attained biospecific relations with one another there, yet interbred freely in the surrounding archipelagos. The Lesser Sunda Isles, Moluccas and Solomons seem to have been colonized indepen-dently at an early date, from western and northern New Guinea, while the peculiar forms in northern Fiji and Samoa represent colonists from the Solomons (from which the New Caledonian race may also have received a contribution). Southern Melanesia is populated by forms which must have come from Australia at a later date (and which probably in turn colonized San Cristobal). Gaps in the range of these

groups, from the Banda Sea through the western Papuan islands and Santa Cruz to southern Fiji and Tonga, are occupied by a relatively undifferentiated stock which must have expanded relatively recently, and has formed hybrid populations with all the older groups with which it has come in contact. Finally, the stock which in northern Australia had become ecologically specialized for life in coastal and second-growth formations, has thereby been enabled to penetrate similar habitats in New Guinea and the eastern Papuan islands—sometimes merging completely with resident forms, sometimes remaining more or less isolated from them.

This distributional history accords well with the avifaunal peculiarities of the sub-regions within Australasia, exemplifying several trends. For example, *P. pectoralis* is essentially an Australasian bird—but it slightly transgresses Wallace's Line and is stopped, not by the edge of the Sunda shelf, but presumably by the moister conditions and richer avifauna of western Java. Mayr (1944a) has shown that for the avifauna as a whole the Lombok Strait is merely the most effective single barrier in the series presented by water gaps and climatic differences along the Sunda Isles route. As is true of many birds, the species is represented by a peculiar form on the Tenimber Isles. The invasion from the Cape York peninsula of the relatively dry areas of southern and south-eastern New Guinea is paralleled by several species (e.g. *Pachycephala rufiventris, Myiagra rubecula* ; and see distribution maps in Mayr, 1944b).

In the south-west Pacific the history of the species is representative for important elements of the avifauna. The Solomons are occupied by an ancient and peculiar endemic group, derived from New Guinea and showing extreme variation from island to island, whereas the Bismarcks have evidently been colonized only comparatively recently. A stock from Australia has occupied southern Melanesia and continued to San Cristobal (where the endemic form exemplifies several trends), and the New Hebrides are occupied by rather uniform populations. Both the northern Moluccas and the Solomons have well marked forms, belonging to the *schlegelii* assemblage and contrasting with those of the Banda Sea and eastern Papuan islands; but these are independently derived from *P.schlegelii* rather than directly related to one another. Faunal affinities between the two regions have been pointed out (Zeuner, 1943, 173 for *Troides* and Hale Carpenter, 1953, 149 for *Euploea* (Lepidoptera) ; Voous & van Marle, 1949, for *Coracina*), and others might be suggested (e.g. *Eos, sensu stricto,* and " *Eos* " *cardinalis* ; *Dicaeum erythrothorax* and *D. aeneum* ; *Rhipidura rufiventris cinerea-obiensis* and *Rh. cockerelli*). The authors quoted postulate a continuous island chain, broken by the northwards drift of New Guinea as recently as the Pliocene ; but the explanation put forward for *Pachycephala* may be more acceptable—common origins in New Guinea, with parallel evolution under the effects of similar climates, avifaunas and degrees of isolation.

No mention has been made of primitive characters. These can, of course, be recognized only from their occurrence and co-variation, not on *a priori* grounds. Clearly the immediate common ancestor of the superspecies was not hen-feathered but sexually dimorphic, and sexual dimorphism has been lost independently three times in *P. pectoralis* (and in the opposite way by *P. flavifrons*). Other striking characters are similarly debarred from consideration by their scattered or peripheral distribution.

It is reasonable to suppose that the proto-*schlegelii* showed the black chin and over-lapping throat-feathers which characterize members of the assemblage derived from it. But, without making unjustifiable assumptions about the possibility of independent origin or secondary loss of characters, it does not seem that anything can usefully be said about the other characters of this form, or about the common ancestor of both assemblages. Since the striking male variants from the standard pattern mostly reduce its distinctiveness, and since degenerative changes under relaxed selection probably proceed more quickly than selective enhancement of the pattern's visual properties, it is rather more likely that in any given instance the direction of evolution was away from the standard. But not even as much as this can be said of the labile female pattern.

SUMMARY

1. *Pachycephala pectoralis*, *P. soror*, *P. schlegelii* and *P. flavifrons* are considered to belong to a single superspecies, represented by a doublet in New Guinea (*P. soror* and *P. schlegelii*) with which *P. pectoralis* overlaps slightly. Standard patterns for males and females are pragmatically defined, and character-geographies of a number of the more clearly-defined variants given. Despite the independent origin and loss of characters, natural groups of subspecies can be distinguished (though not diagnosed) by considering the whole constellation of characters, weighted according to their co-variation. However, extensive secondary intergradation makes some of the boundaries between groups vague.

2. A great range of forms is connected by intergradation, and must be considered as a single species (*P. pectoralis*), although in New Guinea a pair of close relatives co-exist. It is concluded that conspecific allopatric forms may be more different than sympatric species, and *P. caledonica* of New Caledonia and *P. melanops* of Tonga are accordingly admitted to *P. pectoralis* (as is *P. " orpheus " teysmanni* of Salayer). The ability to interbreed is shown to be largely independent of relationship, and the species-limits to cut across the phylogenetic classification.

3. Current criteria for the recognition of subspecies are criticized, and a higher standard of difference applied, in a subspecies-arrangement of *P. pectoralis* designed to reveal more clearly the uniformities and discontinuities. It is not suggested, however, that this arrangement should be adopted at present, and a list of sub-species to be recognized according to current practice is provided in the appendix.

4. The distributional history of the superspecies is considered, and it is concluded that *P. soror* and *P. schlegelii* are descended from former geographical representatives within New Guinea. Near-standard subspecies of *P. pectoralis* in Australia, Southern Melanesia and elsewhere are closely related to *P. soror*, yet intergrade extensively with the peculiar endemic forms of the Lesser Sunda Isles, Moluccas, Solomons and Fiji—whose affinities are rather with *P. schlegelii*. But this view does not necessarily imply reticulate evolution, in the sense of a breakdown of established interspecific barriers.

5. As might be expected from theoretical considerations and studies on geographical variation in other animals, few correlations with climate or habitat can be detected within the insular range of *P. pectoralis*. In Australia, however, regularities are

apparent which agree with the well-established ecological rules of variation in homoiothermous animals ; and certain trends are apparent in forms which inhabit high altitudes, small islands, and islands where there are few bird species. There are in addition progressive character-changes in several insular areas, but most of these are interpreted as the result of secondary intergradation between forms of different origin. The geographical pattern of variation in these areas is consistent with the hypothesis of gene-flow, with peripherally-isolated forms shielded from its effects. It is possible that certain characters tend to appear especially in forms of hybrid origin.

CHECKLIST

Synonyms given by Mathews (1930) and Mayr (1932a, b, 1941a and 1954a) are not quoted here. A list of the subspecies to be recognized according to current practice is given on p. 205.

PACHYCEPHALA SCHLEGELII Schlegel

1 *Pachycephala schlegelii schlegelii* Schlegel.

Pachycephala Schlegelii Schlegel, 1871 (from MS von Rosenberg). Tijdschr. ned. dierk. Ver. **4**, p. 43—l'intérièur de la Nouvelle-Guinée [Arfak Mountains, according to Mayr, 1941a, 149].

Range : mountains of the Vogelkop, and Wandammen Mountains.

2 *Pachycephala schlegelii cyclopum* Hartert

Pachycephala schlegelii cyclopum Hartert, 1930. Novit. zool. **36**, p. 54—Cyclops Mountains.

Range : Cyclops Mountains.

3 *Pachycephala schlegelii obscurior* Hartert

Pachycephala schlegelii obscurior Hartert, 1896. Novit zool. **3**, p. 5—Eafa District [Owen Stanley Mts.].
Pachycephala schlegelii viridipectus Hartert & Paludan, 1936. Mitt. zool. Mus. Berlin, **21**, p. 203—Kunupi [Weyland Mts.].

Range : (a) Weyland, Nassau and Oranje Mountains (" Snow Mountains ") intergrading with (b) Saruwaged and Sepik Mountains, and mountains of south-eastern New Guinea.

PACHYCEPHALA SOROR Sclater

1 *Pachycephala soror soror* Sclater

Pachycephala soror Sclater, 1873. Proc. zool. Soc. Lond. p. 692—Atam [Hatam], Arfak Mountains.

Range : mountains of the Vogelkop.

2 *Pachycephala soror klossi* Ogilvie-Grant

> *Pachycephala soror klossi* Ogilvie-Grant, 1915. Ibis Jubilee Suppl. No. 2, p. 88—
> the Utakwa Valley.

Range : (a) mountains of northern New Guinea (Mamberano) and Weyland, Nassau and Oranje Mountains (" Snow Mountains "), intergrading with (b) Hagen, Bismarck and Saruwaged Mountains.

3 *Pachycephala soror bartoni* Ogilvie-Grant

> *Pachycephala soror bartoni* Ogilvie-Grant, 1915. Ibis Jubilee Suppl. No. 2, p. 89—
> British New Guinea [Type : Owen Stanley Range, 5,000 ft.].

Range : mountains of south-eastern New Guinea and Goodenough Island.

PACHYCEPHALA PECTORALIS (Latham)

A1 *Pachycephala pectoralis fulviventris* Hartert

> *Pachycephala fulviventris* Hartert, 1896. Bull Brit. orn. Cl. **5**, p. 47—Sumba.

Range : Sumba.

A2 *Pachycephala pectoralis javana* Hartert

> *Pachycephala pectoralis javana* Hartert, 1928. Bull. Brit. orn. Cl. **48**, p. 88—Mt.
> Ardjuino, East Java.

Range : (a) eastern Java, intergrading via (b) Bali with A3.

A3 *Pachycephala pectoralis fulvotincta* Wallace

> *Pachycephala fulvotincta* Wallace, 1863. Proc. zool. Soc. Lond. p. 492—Flores.
> *Pachycephala pectoralis jubilarii* Rensch, 1929. J. Orn. Lpz. Festschr. p. 202—Alor.

Range : (a) Sumbawa and Flores,   (b) Lomblen, Pantar and Alor.

A4 *Pachycephala pectoralis everetti* Hartert

> *Pachycephala everetti* Hartert, 1896. Novit. zool. **3**, p. 170—Insula Djampea.
> *Pachycephala pectoralis atromaculata* Meise, 1929. J. Orn. Lpz. **77**, p. 448—Kalao tua.

Range : Djampea, Kalao tua and Madu.

A5 *Pachycephala pectoralis teysmanni* Büttikofer

> *Pachycephala teysmanni* Büttikofer, 1893. Notes Leyden Mus. **15**, p. 167—Macassar,
> South Celebes [corrected to Salayer by Meyer & Wigglesworth, 1898, Birds of Celebes,
> **2**, p. 397].

Range : Salayer.

B6 *Pachycephala pectoralis mentalis* Wallace

> *Pachycephala mentalis* Wallace, 1863. Proc. zool. Soc. Lond. p. 30—Batjan et Gilolo [Type : Batchian].
> *Pachycephala pectoralis gilolonis* Kuroda, 1938. Tori. **10**, p. 114—Halmahera.

Range : Morotai, Halmahera and Batjan.

B7 *Pachycephala pectoralis tidorensis* van Bemmel

> *Pachycephala pectoralis tidorensis* van Bemmel, 1939. Treubia, **17**, p. 99—Tidore.

Range : Tidore and Ternate.

B8 *Pachycephala pectoralis obiensis* Salvadori

> *Pachycephala obiensis* Salvadori, 1878. Ann. Mus. Stor. nat. Genova, **12**, p. 330—in Obi.

Range : Obi Islands.

C9 *Pachycephala pectoralis bougainvillei* Mayr

> *Pachycephala pectoralis bougainvillei* Mayr, 1932. Amer. Mus. Novit. No. 522, p. 10 —Bougainville Island, Solomon Islands.

Range : Buka, Bougainville and Shortland.

C10 *Pachycephala pectoralis orioloides* Pucheran

> *Pachycephala orioloides* Pucheran, 1853. Voy Pôle Sud. Zool. **3**, p. 57—îles Salomon (San-Jorge).
> *Pachycephala pectoralis pavuvu* Mayr, 1932. Amer. Mus. Novit. No. 522, p. 15— Banika Island, Pavuvu or Russel group, British Solomon Islands.

Range : (a) Choiseul, (b) Ysabel, St. George and Florida Islands, (c) Russel Islands.

C11 *Pachycephala pectoralis cinnamomea* (Ramsay)

> *P.[seudorectes] cinnamomeum* Ramsay, 1879. Nature, Lond., **20**, p. 125—Guadalcana.

Range : Guadalcanal.

C12 *Pachycephala pectoralis sanfordi* Mayr

> *Pachycephala sanfordi* Mayr, 1931. Amer. Mus. Novit. No. 504, p. 22—Malaita Island, British Solomon Islands.

Range : Malaita.

C13 *Pachycephala pectoralis melanonota* Hartert

> *Pachycephala melanonota* Hartert, 1908. Bull. Brit. orn. Cl. **21**, p. 106—Vella Lavella I., Central Group of the Solomon Islands.

Range : (a) Vella Lavella, (b) Ganonga.

C14 *Pachycephala pectoralis melanoptera* Mayr

Pachycephala pectoralis melanoptera Mayr, 1932.   Amer. Mus. Novit. No. 522, p. 18 —Tetipari, central Solomon Islands.

Range : Rendova and Tetipari.

C15 *Pachycephala pectoralis centralis* Mayr

Pachycephala pectoralis centralis Mayr, 1932.   Amer. Mus. Novit. No. 522, p. 15— Vangunu Island, central Solomon Islands.

Range : Kulambangra, New Georgia, Vangunu and Gatukai.

C16 *Pachycephala pectoralis feminina* Mayr

Pachycephala feminina Mayr, 1931.   Amer. Mus. Novit. No. 486, p. 25—Rennell Island.

Range : Rennell.

C17 *Pachycephala pectoralis christophori* Tristram

Pachycephalus christophori Tristram, 1879.   Ibis, 4th ser., **3**, p. 441—Makira Harbour, San Cristoval, Solomon Islands.

Range : (a) San Cristobal, (b) Santa Anna.

D18 *Pachycephala pectoralis graeffii* Hartlaub

Pachycephala græffii Hartlaub, 1866.   Ibis, new ser., **2**, p. 172—Viti-levu.
Pachycephala (?) *optata* Hartlaub, 1866.   Ibis, new ser., **2**, p. 172—Ovalau.

Range : (a) Viti Levu and Waia, intergrading through (b) Ovalau with D20b.

D19 *Pachycephala pectoralis aurantiiventris* Seebohm

Pachycephala aurantiiventris Seebohm, 1891.   Ibis, 6th ser., **3**, p. 96—Bua in Vanua Levu.
Pachycephala pectoralis ambigua Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 16— Rambi Island, Fiji Islands.

Range : (a) Yanganga and most of Vanua Levu, intergrading via (b) Thaukandrove Peninsula and (c) Kio and Rambi with D20a.

D20 *Pachycephala pectoralis torquata* Layard

Pachycephala torquata Layard, 1875.   Proc. zool. Soc. Lond. p. 150—Taviuni.
Pachycephala pectoralis koroana Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 15— Koro Island, Fiji Islands.

Range : (a) Taviuni (intermediate between D19c and D20b) and (b) Koro.

D21 *Pachycephala pectoralis bella* Mayr

Pachycephala pectoralis bella Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 14—Vatu vara Island.

Range : Vatu vara.

E22 *Pachycephala pectoralis melanura* Gould

> *Pachycephala melanura* Gould, 1842. Proc. zool. Soc. Lond., p. 134—North coast of Australia [Derby, according to Mathews 1920, p. 229].
> *Eopsaltria hilli* Campbell, 1910. Emu, **10**, p. 168—Hecla Island, Parry Harbour, North-West Australia.
> *Pachycephala melanura bynoei* Mathews, 1918. Aust. avian Rec. **3**, p. 136—Port Hedland.

Range : (a) North West Cape to De Grey River, (b) Broome, (c) King Sound, (d) Hecla Island (off Cape Bougainville) and Napier Broome Bay—clinal series, confined to mangroves.

E23 *Pachycephala pectoralis violetae* Mathews

> *Pachycephala gutturalis violetae* Mathews, 1912. Aust. avian Rec. **1**, p. 76—West Northern Territory [Daly R., according to Mathews 1920, p. 224].

Range : coasts and offshore islands of Arnhem Land and Gulf of Carpentaria, from Daly River to Normanton.

E24 *Pachycephala pectoralis spinicauda* (Pucheran)

> *Pteruthius spinicaudus* Pucheran, 1853. Voy. Pôle Sud, Zool. **3**, p. 58—l'île Warriors [Torres Str.].
> ? *Pachycephala salomonis* Oustalet, 1877. Bull. Soc. philom. Paris, 6th ser., **12**, p. 95 —des îles Salomon [see p. 207].

Range : (? west coast of Cape York Peninsula), Cape York, islands in Torres Strait and coastal and second-growth formations in southern New Guinea from Merauke eastwards, probably intergrading with E25 near Hall Sound.

E25 *Pachycephala pectoralis dahli* Reichenow

> ? *Pachycephala innominata* Salvadori, 1881. Ornit. Pap. Mol. **2**, p. 222—in Papuasia—ins. Teste (*Ramsay*).
> *Pachycephala melanura dahli* Reichenow, 1897. Orn. Mber. **5**, p. 178—Credner-Inseln, Raluan.
> *Pachycephala pectoralis neuhausi* Stresemann, 1934. Orn. Mber. **42**, p. 24— Sinabiet [Malie].
> *Pachycephala pectoralis fergussonis* Mayr, 1936. Amer. Mus. Novit. No. 869, p. 2 —Fergusson Island, D'Entrecasteaux Archipelago.

Range : (a) ? south-eastern New Guinea, from Hall Sound to Milne Bay, (b) ? Teste Island, (c) Fergusson Island, (d) Long Island, (e) Witu Islands, (f) islands in Bungula Bay, New Britain, (g) Talele, Vatom, Duke of York and Credner (Palikuru) Islands, and shores of Blanche Bay, New Britain, (h) Nusa Island (off Kavieng, New Ireland), (j) Malie Island, Lihir group, (k) Nissan Island.

E26 *Pachycephala pectoralis whitneyi* Hartert

> *Pachycephala pectoralis whitneyi* Hartert, 1929. Amer. Mus. Novit. No. 364, p. 14 —Whitney Island [type designation and discussion attached in error to *Pachycephala implicata*].

Range : Whitney, Momalufu and Akiki Islands, east of Shortland—variable hybrid population between E25 and C9. Related populations, or pure populations of E25, may remain to be discovered elsewhere in the northern Solomons (see p. 208).

E27 *Pachycephala pectoralis balim* Rand

Pachycephala pectoralis balim Rand, 1940. Amer. Mus. Novit. No. 1072, p. 8—Balim River, altitude 1,600 meters ; Snow Mts., Netherland New Guinea.

Range : second growth in the Balim and Bele Valleys, northern slopes of Mount Wilhelmina.

F28 *Pachycephala pectoralis fuliginosa* Vigors & Horsfield

[*Pachycephala*] *fuliginosa* Vigors & Horsfield, 1827. Trans Linn. Soc. Lond. **15**, p. 241—South coast of New Holland [Port Lincoln, according to Mathews, 1920, p. 208].

Pachycephala occidentalis Ramsay, 1878. Proc. Linn. Soc. N.S.W. **2**, p. 212—Western Australia [Albany, according to Mathews, 1920, p. 209].

Range : (a) south-western Australia, west of a line through Geraldton, the Wongan Hills, Lake Grace and Esperance, (b) South Australia (Eyre and Fleurieu Peninsulas and Kangaroo Island), intergrading via (c) Victorian mallee with F30a.

F29 *Pachycephala pectoralis glaucura* Gould

Pachycephala glaucura Gould, 1845. Birds of Australia, **2**, part 18, p. 65—Van Diemen's Land and the islands in Bass's Straits.

Range : Tasmania (except the forests of the south-west) and islands in Bass Straits.

F30 *Pachycephala pectoralis pectoralis* (Latham)

Muscicapa pectoralis Latham, 1801. Index Orn. Suppl., p. 51—Nova Hollandia [Port Jackson, according to Mathews 1920, p. 208].

Pachycephala gutturalis youngi Mathews, 1912. Novit. zool. **18**, p. 313—Victoria [Lal Lal, according to Mathews 1920, p. 209].

Range : (a) Victoria east of a line from Heytsbury to Castlemaine, probably intergrading with (b) New South Wales. The range extends west of the Great Dividing Range into the Riverina district of southern New South Wales. Probably confined to eucalyptus forest, and riverine forest in savannah woodland.

F31 *Pachycephala pectoralis queenslandica* Reichenow

Pachycephala queenslandica Reichenow, 1899. Orn. Mber. **7**, p. 8—Nord Queensland [Bellenden Kerr, according to Mathews, 1920, p. 209].

Pachycephala gutturalis ashbyi Mathews, 1912. Novit. zool. **18**, p. 313—South Queensland [Blackall Ranges, according to Mathews, 1920, p. 209].

Range : (a) extreme north-eastern New South Wales (Richmond River) and southern Queensland (north to Mackay and Whitsunday Island), (b) Cairns district. Probably confined to rain forest.

F32 *Pachycephala pectoralis contempta* Hartert

> *Pachycephala contempta* Hartert, 1898.   Bull. B.O.C. **8**, p. 15—Lord Howe Island.

Range : Lord Howe.

F33 *Pachycephala pectoralis xanthoprocta* Gould

> *Pachycephala xanthoprocta* Gould, 1837.   Proc. zool. Soc. Lond., p. 149—in Novâ Cambriâ Australi, apud oram orientalem [error for Norfolk Island according to Mathews, 1928, Birds of Norfolk & Lord Howe Islands, p. 40].

Range : Norfolk Island.

G34 *Pachycephala* [*pectoralis*] *caledonica* (Gmelin)—see p. 174.

> *Muscicapa caledonica* Gmelin, 1789.   Syst. Nat. **1**, p. 944—nova Caledonia.
> *Eopsaltria variegata* Gray, 1859.   Proc. zool. Soc. Lond. part 27, p. 162—Island of Nu.
> *Pachycephala morariensis* Verreaux & des Murs, 1860.   Rev. Mag. Zool. p. 393— [le] camp de Morari [New Caledonia].

Range : New Caledonia and Isle of Pines.

G35 *Pachycephala pectoralis littayei* Layard

> *Pachycephala Littayei* Layard, 1878. Ann. Mag. nat. Hist. 5th ser., **1**, p. 375— Lifu, New Caledonia [!].

Range : Lifu and Uvea, Loyalty Islands.

G36 *Pachycephala pectoralis cucullata* (Gray)

> *Eopsaltria cucullata* Gray, 1859.   Cat. Birds Trop. Is. Pacific, p. 21—New Hebrides (Aneitum).

Range : Aneitum.

G37 *Pachycephala pectoralis chlorura* Gray

> *Pachycephala chlorurus* Gray, 1859.   Cat. Birds Trop. Is. Pacific, p. 20—New Hebrides (Erromango, Aneiteum) [restricted to Erromango by Mayr, 1932*b*, p. 3].
> *Pachycephala intacta* Sharpe, 1900.   Ibis, 7th ser., **6**, p. 343—Sandwich Bay, Mallicollo.
> *Pachycephala pectoralis brunneipectus* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 4 —Epi Island.
> *Pachycephala pectoralis banksiana* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 6 —Vanua Lava, Banks Islands.
> *Pachycephala pectoralis efatensis* Mayr, 1938.   Amer. Mus. Novit. No. 986, p. 2— Efate Island, New Hebrides.

Range : New Hebrides and Banks Islands, north of Tanna : (a) Erromango, (b) Efate and Nguna, (c) Mai, Tongariki, Epi, Lopevi, Pauuma and Ambrym, (d) Malekula, Malo, Espiritu Santo, and Dolphin Island, intergrading through (e) Omba, Raga and Maewo with (f) Gaua, Vanua Lava and Ureparapara.

G38 *Pachycephala pectoralis vanikorensis* Oustalet

P[achycephala] vanikorensis Oustalet, 1877.   Bull. Soc. philom. Paris, 6th ser., **12**, p. 95—l'île Vanikoro.

Range : Vanikoro.

H39 *Pachycephala pectoralis calliope* Bonaparte

Pachycephala calliope Bonaparte, 1850.   Conspic. Gen. Av. **1**, p. 328—Timor.
Pachycephala melanura arthuri Hartert, 1906.   Novit. zool. **13**, p. 299—Wetter.

Range : (a) Timor and Samau, (b) Wetar.

H40 *Pachycephala pectoralis sharpei* Meyer

Pachycephala Sharpei Meyer, 1884.   S.B. Isis Dresden, Jahr 1884, Abhandl., p. 36—ins. Babbar.

Range : Babar.

H41 *Pachycephala pectoralis dammeriana* Hartert

Pachycephala melanura dammeriana Hartert, 1900.   Novit. zool. **7**, p. 17—Dammer Island.

Range : Damar.

H42 *Pachycephala pectoralis fuscoflava* Sclater

Pachycephala fuscoflava Sclater, 1883.   Proc. zool. Soc. Lond. p. 198—Larat, ins. Tenimberensem.

Range : Tenimber Islands.

H43 *Pachycephala pectoralis macrorhyncha* Strickland

Pachycephala macrorhyncha Strickland, 1849. Contr. Orn. (Jardine), p. 91—Amboina.
Pachycephala macrorhyncha alfurorum Stresemann, 1914.   Novit. Zool. **21**, p. 132—Gunung Sofia (Mittel-Seran).

Range : (a) Ceram, (b) Amboina.

H44 *Pachycephala pectoralis buruensis* Hartert

Pachycephala melanura buruensis Hartert, 1899. Bull. Brit. orn. Cl. **8**, p. 32—Buru.

Range : Buru.

H45 *Pachycephala pectoralis clio* Wallace

Pachycephala clio Wallace, 1862.   Proc. zool. Soc. Lond., p. 341—Sula and Buru [restricted to the Sula Islands by Hartert, 1899.   Bull. Brit. orn. Cl. **8**, p. 33].

Range : Sula Islands.

H46 *Pachycephala pectoralis pelengensis* Neumann

Pachycephala melanura pelengensis Neumann, 1941. Zoöl. Meded. **23**, p. 112—Peleng.

Range : Peleng and Banggai Islands.

H47 *Pachycephala pectoralis collaris* Ramsay

Pachycephala collaris Ramsay, 1878. Proc. Linn. Soc. N.S.W. **3**, p. 74—Courtance Island, South-East coast, New Guinea ; *tom. cit.*, p. 281—Teste Island [see p. 206].
Pachycephala rosseliana Hartert, 1898. Bull. Brit. orn. Cl., **8**, p. 8—Rossel Island.
Pachycephala pectoralis misimae Rothschild & Hartert, 1918. Novit. zool. **25**, p. 311—St. Aignan or Misima Island.

Range : (a) Conflict, Begum and Egum groups (and Coutance or Teste Islands?), intergrading through (b) Misima and the Deboyne group with (c) Rossel.

H48 *Pachycephala pectoralis citreogaster* Ramsay

? *Saxicola merula* Lesson, 1828. Voy. Coquille (Duperry) Zool. **1**, pt. 2, p. 662—la Nouvelle-Irlande, aux environs du Port Praslin [see p. 209].
Pachycephala citreogaster Ramsay, 1876. Proc. Linn. Soc. N.S.W. **1** p, 66—New Britain and adjacent islands.
Pachycephala pectoralis sexuvaria Rothschild & Hartert, 1924. Bull. Brit. orn. Cl. **44**, p. 50—St. Matthias Island (Mussau).

Range : (a) Umboi and New Britain, (b) New Ireland and Feni, (c) Lavongai, (d) Mussau.

H49 *Pachycephala pectoralis ottomeyeri* Stresemann

Pachycephala pectoralis ottomeyeri Stresemann, 1933. Orn. Mber. **41**, p. 116—Komat auf Lihir.

Range : Lihir Island.

H50 *Pachycephala pectoralis tabarensis* Mayr

Pachycephala pectoralis tabarensis Mayr, 1955. Amer. Mus. Novit., No. 1707, p. 35—Tabar Island, Tabar group.

Range : Tabar Island.

H51 *Pachycephala pectoralis goodsoni* Rothschild & Hartert

Pachycephala pectoralis goodsoni Rothschild & Hartert, 1914. Novit. zool. **21**, p. 296—Manus.

Range : Manus.

H52 *Pachycephala pectoralis ornata* Mayr

> *Pachycephala pectoralis ornata* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 8—Santa Cruz [Ndeni], Santa Cruz Islands.
> [*Pachycephala*] *atrata* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 10—*nomen nudum* [used by Mayr in MS.].

Range : (a) Ndeni, (b) Reef, Duff and Swallow groups.

H53 *Pachycephala pectoralis utupuae* Mayr

> *Pachycephala pectoralis utupuae* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 8—Utupua, Santa Cruz Islands.

Range : Utupua.

H54 *Pachycephala pectoralis kandavensis* Ramsay

> *Pachycephala kandavensis* Ramsay, 1876.   Proc. Linn. Soc. N.S.W. **1**, p. 65—" Kandavu ".

Range : Kandavu group and Mbengha.

H55 *Pachycephala pectoralis vitiensis* Gray

> *Pachycephala vitiensis* Gray, 1859.   Cat. Birds Trop. Is. Pacific, p. 20—Feejee Islands (Island of Ngau).

Range : Ngau.

H56 *Pachycephala pectoralis lauana* Mayr

> *Pachycephala pectoralis lauana* Mayr, 1932.   Amer. Mus. Novit. No. 531, p. 12—Ongea Levu Island, Lau Archipelago, Fiji Islands.

Range : Ongea Levu, Fulanga and Wangava, southern Lau Archipelago.

H57 *Pachycephala pectoralis melanops* (Pucheran)

> *Eopsaltria melanops* Pucheran, 1853.   Voy. Pôle Sud., Zool. **3**, p. 56—Vavao.

Range : Vavau group and Late, Tonga.

PACHYCEPHALA FLAVIFRONS (Peale)

> *Eopsaltria flavifrons* Peale, 1848.   U.S. Explor. Exped. Birds (subsequently withdrawn), p. 96—Upolu.

Range : Upolu and Savai, Samoa.

Subspecies to be recognised according to current usage

Subspecies which are distinguished from one another by measurements alone, and which are near the borderline of subspecific distinctness under the seventy-five percent rule, are bracketed together and the junior name indicated by an asterisk.

Pachycephala schlegelii :
  1 *schlegelii*
  2 *cyclopum*
  3 *obscurior*

Pachycephala soror :
  1 *soror*
  2 *klossi*
  3 *bartoni*

Pachycephala pectoralis :
  A1 *fulviventris*
  A2 *javana*
  { A3a *fulvotincta*
  { A3b *jubilarii**
  A4 *everetti*
  A5 *teysmanni*
  B6 *mentalis*
  B7 *tidorensis*
  B8 *obiensis*
  C9 *bougainvillei*
  C10a–b *orioloides*
  C10c *pavuvu*
  C11 *cinnamomea*
  C12 *sanfordi*
  C13 *melanonota*
  C14 *melanoptera*
  C15 *centralis*
  C16 *feminina*
  C17 *christophori*
  D18a *graeffii*
  D18b *optata*
  D19 *aurantiiventris*
  D20a *torquata*
  D20b *koroana*
  D21 *bella*
  E22a *bynoei*
  E22b–c *melanura*
  E22d *hilli*
  E23 *violetae*
  E24 *spinicauda*

  { E25c *fergussonis**
  { E25d–j *dahli*
  E26 *whitneyi*
  E27 *balim*
  F28a *occidentalis*
  F28b–c *fuliginosa*
  F29 *glaucura*
  F30a *youngi*
  F30b *pectoralis*
  F31a *ashbyi*
  F31b *queenslandica*
  F32 *contempta*
  F33 *xanthoprocta*
  G34 *caledonica*
  G35 *littayei*
  G36 *cucullata*
  G37a *chlorura*
  G37b–f *intacta*
  G38 *vanikorensis*
  H39a *calliope*
  H39b *arthuri*
  H40 *sharpei*
  H41 *dammeriana*
  H42 *fuscoflava*
  { H43a *alfurorum**
  { H43b *macrorhyncha*
  H44 *buruensis*
  H45 *clio*
  H46 *pelengensis*
  H47a–b *collaris*
  H47c *rosseliana*
  H48a–c *citreogaster*
  H48d *sexuvaria*
  H49 *ottomeyeri*
  H50 *tabarensis*
  H51 *goodsoni*
  H52 *ornata*
  H53 *utupuae*
  H54 *kandavensis*
  H55 *vitiensis*
  H56 *lauana*
  H57 *melanops*

NOTES

Pachycephala schlegelii viridipectus Hartert & Paludan (3b)

The differences between *viridipectus* and *obscurior* 3a are too slight for subspecific separation (cf. Mayr, *in litt.*), besides which they intergrade smoothly (Mayr & Gilliard, 1954).

Pachycephala pectoralis jubilarii Rensch (A3b)

From a study of A.M.N.H. material, Mayr (*in litt.*) concludes that the size difference between *jubilarii* and *fulvotincta* A3a is sufficient for subspecific separation.

Pachycephala pectoralis atromaculata Meise (= A4)

Mayr (*in litt.*) finds no difference in colour between *atromaculata* and *everetti*, and my few measurements suggest no size difference adequate for separation.

Pachycephala pectoralis gilolonis Kuroda (= B6).

Mayr (*in litt.*) finds no difference between *gilolonis* and *mentalis*.

Pachycephala pectoralis ambigua Mayr (D19c)

The undesirability of recognizing two variable hybrid subspecies (*ambigua* and *torquata* D20a) between *aurantiiventris* D19a and *koroana* D20b has been discussed (p. 176). Since *ambigua* intergrades smoothly with *aurantiiventris* it seems best to combine them, although the end populations are very distinct.

Female of **bynoei** (E22a)

There are four females from Cossack in the White Collection of the National Museum of Victoria. Although no comparative material of *melanura* E22c was available, these appeared to agree well with the female of that form. The desirability of a comparative description has been pointed out to the Museum authorities.

Intergradation of **spinicauda** (E24) with **dahli** (E25)

A single female from Dalena, Hall Sound (A.M.N.H. Reg. No. 329999) differs from typical *spinicauda* females, and approaches those of *dahli*, in having the underparts much yellower and less ochraceous (cf. Rand, 1940).

The subspecies on Teste Island

Ramsay (1878a, 74) described *Pachycephala collaris* (H47a) from Cou(r)tance Island, off the coast of south-eastern New Guinea. Later (1878b, 281) he recorded *P. melanura* (= *spinicauda* E24) on Coutance, and gave the locality of *collaris* (without further comment) as Teste Island, off the extreme south-eastern tip of New Guinea. He further described from Teste a form which Salvadori later (1881, 222) named *P. innominata* (? E25b) from this description. The single specimen is described as having an ashy-grey tail and slaty-black occiput, and the yellow collar " intercepted on the head and neck ".

The type of *collaris* and the female described by Ramsay are in the British Museum (Natural History), Reg. Nos. 95.12.24.2 & 4 respectively. Neither bears a field label, but both are reputedly from Coutance. Two males (B.M.(N.H.) Nos. 78.10.19.5 & 6) bear field labels giving their locality as Teste, and No 6 is recorded as collected

by G. W. Baiston Ingham, one of the collectors mentioned by Ramsay (1878b, 241). These specimens agree well with males of *spinicauda, fergussonis* and *dahli* E24 & 25c–k.

There are no further specimens of *P. pectoralis* from Teste or Coutance Islands in the B.M.(N.H.), the A.M.N.H., or the Australian Museum. It seems most probable that both are inhabited by black-tailed forms of group E., and that the lost type of *innominata* was a specimen moulting into adult plumage. Conceivably Ramsay's notorious unreliability over localities extends in this instance to the description, and " ashy-grey " should refer to the wings. *P. innominata* Salvadori must be considered unidentifiable. The type locality of *collaris* remains to be determined. For the present it seems best to accept the evidence of the original description, and the label of the type, giving the locality as Coutance.

Pachycephala pectoralis fergussonis Mayr (E25c)

The two known specimens of *fergussonis* are distinctly larger than typical *dahli*, and slightly deeper yellow beneath. However, *dahli* from Long Island E25d (and Teste E25b ?) approach them in size. In view of the geographical variation in size within *dahli*, and the slightness of the colour difference, it is best to submerge *fergussonis* in *dahli* until females are available for comparison (cf. Mayr, *in litt.*).

Pachycephala salomonis Oustalet. (? = E24)

The locality of the single (male) specimen was given (Oustalet 1877, 95) as the Solomon Islands, although d'Urville's " Voyage au Pôle Sud " in the " *Astrolabe* " and " *Zélée* " did not stop there. From an examination of the type by Professor Berlioz, Mayr (1932a, 21) concluded that *salomonis* is a synonym of *dahli* Reichenow, 1897 (E25), but that (owing to the unreliability of the locality and the heterogynism of closely related races) it must be considered unidentifiable. Comparison of the type with males of *dahli, spinicauda* and *citreogaster*, kindly undertaken by Professor Berlioz, confirms that it is inseparable from those of the *violetae-spinicauda-dahli* aggregate E23–25, and quite different from *citreogaster* H48. Mayr (1955, 34, and *in litt.*) supposes the type to have been collected at Port Praslin, New Ireland, and the name therefore to be a synonym of *citreogaster*. This error springs from that (Mayr, 1932a) of supposing that the type was collected on D'Urville's earlier " Voyage de *l'Astrolabe*", which called at Port Praslin.

Even if the locality of *salomonis* were known, the principle of conservation (Copenhagen Decisions, 1953, 25) would debar the use of the name, since it seems not to have been used since its publication. From the itinerary of the voyage it seems most probable that the type was collected at Port Essington (*violetae* E23) or the Torres Strait (*spinicauda* E24), where the vessels actually called ; though it might have been brought by canoe from Teste Island or Nissan (*dahli* E25), or even from somewhere in the northern Solomons (cf. *whitneyi* E26 ?). In the circumstances, *P. salomonis* must be considered unidentifiable.

White-throated **Pachycephala** *in the Solomons*

Besides the hybrid race *whitneyi* E26 on small islands west of Shortland, there are indications that other populations related to *dahli* E25 may remain to be discovered in the northern Solomons. Hartert (1926, 46) records a specimen from Munia, south-west of Fauro in the Bougainville Strait. A male (B.M.(N.H.) Reg. No. 36.4.20.14) collected on or near Buka (Moyne-Chaplin, 22nd December, 1935) agrees well with *dahli* and with white-throated males of *whitneyi*, except that it has a small black chin-spot.

Pachycephala pectoralis brunneipectus, banksiana and **efatensis** Mayr (G37c, f & b)

Though separable in long series of females from different islands, all the populations from Efate to the Banks Islands G37b–f should be combined in *intacta* Sharpe (cf. Mayr, *in litt.*).

Pachycephala macrorhyncha alfurorum Stresemann (H43a)

The size difference between *alfurorum* and *macrorhyncha* H43b seems to be sufficient for subspecific separation (Mayr, *in litt.*), as my measurements tend to confirm.

Pachycephala collaris Ramsay (H47a)

In view of the uncertainty about the type locality of *collaris* (p. 206), Professor Mayr has suggested that a redescription of the original specimens may be useful.

The following descriptions must be read in conjunction with those of the standard patterns (p. 138). Colours are cited according to the code of Villalobos-Dominguez & Villalobos (1947). The type was compared with two males of *misimae* H47b from Misima (B.M.(N.H.) Nos. 99.5.20.6 & 7) and one of *rosseliana* H47c (1917.11. 21.1); Ramsay's female with two of *misimae* from Misima (99.5.17.43 and 99.5.20.5). Unfortunately, they were not critically compared with a male of *collaris* from East Island, nor a female of *rosseliana*, both borrowed from the American Museum of Natural History.

ADULT MALE.   Type (B.M.(N.H.) Reg. No. 1895.12.24.2).

Throat-feathers with little or no grey at bases (as *misimae* and *rosseliana*).

Underparts about OOY/OY.17.12° : *misimae* similar, *rosseliana* a little more golden, towards OOY.

Underside of tail a little more olivaceous, less fuscous, than in *rosseliana*, *misimae* intermediate.

Collar somewhat washed with brownish-olive on hind-neck : in *rosseliana*, much narrower and quite olivaceous on hind-neck, *misimae* intermediate.

Mid-back about YYO.5.12° : *rosseliana* darker and greener, about YYO/Y.3.12°, *misimae* paler and slightly greener, about YYO(Y).7.12°.

Edges of remiges (worn) greyer, edges of upper wing-coverts yellower, centres of wing-feathers paler than in *rosseliana*—*misimae* agrees with *collaris*.

Tail (only 5 rectrices remain) yellowish olive, central rectrices without black ; remainder with vague brown patches (somewhat broken up into transverse bars) subterminally on inner webs ; shafts brown, paling basally. In *misimae* central rectrices have vague brownish barring ; remainder have blackish brown patches occupying most of the inner webs ; shafts darker brown. In *rosseliana*, central rectrices are dark olive with long blackish patches along the shafts on the inner webs ; remainder are brownish black with dull olive edges (widest towards the bases of the outer webs) ; shafts black, becoming dark brown basally,

In *rosseliana* only, the rump, upper tail-coverts and tail are somewhat washed with brown.

ADULT FEMALE. (95.12.24.4).
Throat white with brownish fringing (as in *misimae*).

Gorget narrow, pale and vaguely-defined, vinous grey in colour (about SO.16.2°) as in 99.5.20.5 of *misimae* ; in 99.5.17.43 it is wider, deeper, more sharply defined beneath and browner (about OOS.12.4°).

Underparts rich yellow, about OY.17.12° on mid-belly, with lower breast and flanks somewhat olivaceous to brownish ; 99.5.17.43 agrees ; 99.5.20.5 is much paler, about OY.18.10° on mid-belly.

Upperparts very brown, as in 99.5.17.43 (crown about OOS.6.5°, mid-back about o.4.12°) ; 99.5.20.5 is much less brown, with crown greyer (about OOS.5.3°) and mantle greener (about YYO.4.10°).

Edges of wing-feathers slightly greyer, less rufous, than in *misimae*.

Tail intermediate between 99.5.17.43 (browner) and 99.5.20.5 (greener).

Pachycephala pectoralis misimae Rothschild & Hartert (H47b)

Although it shows signs of gene-flow from *rosseliana* H47c, this form is nearest to *collaris* H47a, with which it should be combined (cf. Mayr, *in litt.*).

Saxicola merula Lesson (? = H48b)

The locality of the type, a juvenile, was given by Lesson as Port Praslin, on the south-east coast of New Ireland. This would make the name the senior synonym of *citreogaster*, though the principle of conservation would require its suppression. But many specimens brought back by French expeditions of the late eighteenth and early nineteenth centuries are wrongly localized, and several species recorded from Port Praslin do not in fact occur in the Bismarcks (Mayr, *in litt.*). Salvadori (1881, 219) questioned the locality, pointing out the resemblance of the type to juveniles of *macrorhyncha* (Amboina H43b). Juveniles of *citreogaster* and *macrorhyncha* probably cannot be separated with certainty, and Mayr, who has examined the type, considers it to be unidentifiable.

which it forms a part, and has been a constant source of advice. Professor Ernst Mayr has greatly encouraged me in the study of a group on which he is the authority, and liberally made me free of his knowledge and experience : my indebtedness to his published and unpublished work will be evident throughout the text of this paper. Dr. Dean Amadon has been to great trouble to answer a list of queries from the material in the American Museum of Natural History. Professor Jean Berlioz has been most helpful in comparing the type of *Pachycephala salomonis*, and discussing the nomenclatural problem. Dr. Allen Keast has unsuccessfully sought the type of *Pachycephala innominata* in the Australian Museum. Dr. Cain, Professor Mayr, Mr. R. E. Moreau and Dr. H. W. Parker have read drafts of this paper at various stages, and made invaluable criticisms and suggestions. Mr. H. O. Ricketts has carefully checked the final draft, detecting many lapses and obscurities, and helped me in proof-reading. Mr. R. J. Drumm, O.B.E., has greatly helped in seeing the paper through the press. Both the British Museum (Natural History) and the American Museum of Natural History have allowed me to borrow many specimens. The paper was prepared between 1952 and 1955, at the Department of Zoology and Comparative Anatomy, University of Oxford, under Professor A. C. Hardy, F.R.S. Working facilities were also granted at the Edward Grey Institute of Field Ornithology by Dr. David Lack, F.R.S., and at the Bird Room of the British Museum (Natural History) by Mr. J. D. Macdonald. Professor Hardy and the Department of Scientific and Industrial Research gave financial assistance during the preparation of the paper, and field work in the Solomons was financially supported by the Percy Sladen Trustees and the Parliamentary Grants Committee of the Royal Society.

MEASUREMENTS

In addition to my own measurements, Professor Mayr has most kindly put at my disposal most of those taken by himself (for Mayr, 1931b, c; 1932a, b; 1936, 1938, 1941a, 1944c and 1955) and by Mrs. Kate Jennings (for Mayr, 1954a). Several specimens were measured both by Mayr or Jennings and by myself, while I measured many others twice. The distributions of the discrepancies (between Mayr's and Jennings' and my own first measurements on the one hand, and my definitive series on the other) indicate to what extent these results are comparable or repeatable.

Wing :	self$_2$—Mayr	mean	− 0·07 mm.,	s.d.	± 1·20 mm.	(27 measurements)			
	self$_2$—Jennings	,,	− 0·18 ,,	,,	± 0·95 ,,	(14	,,	)	
	self$_2$—self$_1$	,,	+ 0·40 ,,	,,	± 0·24 ,,	(148	,,	)	
Tail :	self$_2$—Mayr	,,	+ 0·25 ,,	,,	± 0·98 ,,	(26	,,	)	
	self$_2$—Jennings	,,	+ 0·08 ,,	,,	± 2·11 ,,	(15	,,	)	
	self$_2$—self$_1$	,,	− 0·41 ,,	,,	± 0·51 ,,	(148	,,	)	

Although several individual discrepancies exceed 2 mm., the mean discrepancies are small. However, several of the standard deviations differ to a high degree of significance (by the variance-ratio test), and it seems unwise to combine Mayr's and Jennings' series with my own. I have inserted them at the appropriate points in the table, prefixed by M or J respectively. Asterisks indicate measurements in my series which appear also in Mayr's or Jennings'. Since weight determinations are not subject to the same personal bias, I have combined our series for C17a. Weights

for C11 were taken by Cain and myself, the remainder by the Whitney Expedition of the American Museum of Natural History.

Series of five measurements or less are given in full, with replications indicated in parenthesis—e.g. 76, 78·5, 80(2), 81·5. Longer series are summarized in the form *mean ± standard deviation (number in series)*—e.g. 86·8 ± 2·10 (13).

Recognizably distinct populations are distinguished in the tables by their ciphers, and by subspecies names (not all of which are admitted on p. 205) where appropriate. Weights and wing and tail lengths are given separately for adult males and females. The sexing of Mayr's specimens, those of the O.U.(D.Z.) Solomons Expedition (C11 & 17a), and the hen-feathered series C16 and F33 have been accepted for this purpose. However, much of the remaining material is not sexed, and some determinations are questionable. Therefore only specimens showing feathers belonging to the adult male plumage have been taken as adult males ; and only those sexed as females and showing female plumage, without male or juvenile feathers, as adult females.

In the few forms of which I had adequate series of males, females and juveniles, reliably sexed, there was little indication of significant and constant differences between sex and age groups, in the measurements of bills and tarsi (values for C17a are analysed on p. 218). I have therefore risked the introduction of some bias, in order to have longer series, by combining the measurements of all specimens except nestlings. Mayr's raw data contain very few individual measurements of bills and none of tarsi, and I have not repeated the indications of size range published in the papers cited.

Weight in grams

My measurements taken to the nearest 0·5 gm., with a long-scale spring balance (Gibb balance), calibrated in the field.

		Males		Females
C10a *orioloides*	. .	49·9 ± 2·62 (17)	.	42, 44, 50
C11 *cinnamomea*	. .	51·5 ± 2·24 (19)	.	44·9 ± 1·81 (8)
C12 *sanfordi*	. .	51·3 ± 2·25 (18)	.	49·5 ± 2·00 (19)
C17a *christophori*	. .	33·5 ± 2·96 (45)	.	32·1 ± 2·36 (20)
C17b ,,	. .	34, 35 (2)	.	—
E25k *dahli*	. .	29·0 ± 1·69 (8)	.	27, 28, 29

Wing and tail lengths, in millimetres (pp. 212–216)

My wing lengths taken to nearest 0·5 mm., from wing-bend to tip of longest primary (of left wing wherever possible), with wing pressed flat.

My tail lengths taken to nearest 0·5 mm., from tip of longer central quill to insertion of central quills in common sheath.

Tarsus and culmen lengths, and bill depth, in millimetres (pp. 217–219)

My tarsus lengths taken to nearest 0·5 mm., along outer side of tarsus, from groove of intertarsal joint to eminence near plantar angle of hind toe.

My culmen lengths taken to nearest 0·5 mm., chordwise, from tip to angle of culmen with skull.

My bill depths taken to nearest 0·5 mm., perpendicular to tomium at hind edge of nostril, from culmen to lower edge of mandible (bill fully closed).

	Wing		Tail	
	Male	Female	Male	Female
P. schlegelii				
1 schlegelii	84·5	80·5	59·5	60·5
2 cyclopum	90	88	69	—
3a viridipectus	84·5 ± 2·67 (12)	82, 84	61·7 ± 1·71 (10)	60·5, 63·5
3b obscurior	86·9 ± 2·12 (13)	82, 83, 86	65·7 ± 2·19 (13)	59·5, 67
P. soror				
1 soror	90, 92	82, 82·5, 88·5	66	63, 64, 65
2 klossi	90·3 ± 1·76 (9)	87, 87·5	60·2 ± 1·61 (10)	58
3 bartoni	87·4 ± 1·66 (11)	86·2 ± 1·71 (7)	60·9 ± 2·44 (11)	61·8 ± 2·38 (7)
P. pectoralis				
A1 fulviventris	82, 83, 86	80, 82, 82·5, 84, 87	58, 61, 62	59, 61, 62
(M)	84·5 ± 1·67 (10)	83·4 ± 1·96 (8)	59, 60, 61, 64	—
A2a javana	84·5	83	—	64
A3a fulvotincta	76, 78·5, 80 (2), 81·5	78·5 (2)	57, 57·5, 58 (3)	—
A3b jubilarii	79·5, 80·5, 81·5	81·5	59·5, 60, 62	63
A4 everetti	81 (2), 81·5, 83	77·5	61, 63·5, 64, 67·5	62·5
A5 teysmanni	75·5	73·5	60·5	55
B6 mentalis	88, 90, 90·5, 92, 94	83, 89·5, 90, 90·5	61·5, 64 (2), 64·5, 65·5	63, 63·5, 65, 65·5
B7 tidorensis	97·5, 99, 99·5 (2)	93·5, 94	71, 72, 75	66·5, 72·5
	99·3 ± 0·21 (6)[1]	—	70 (3), 71·5, 74[1]	—
B8 obiensis	95, 95·5, 97 (2)	97	68, 69, 69·5, 74·5	70
C9 bougainvillei	97·5 (2)	96, 100·5	69·5, 72·5	71·5, 73
C10a orioloides (M)	103·2 ± 2·31 (25)	98·6 ± 1·85 (12)	72·9 ± 2·42 (24)	69, 72
	100	96·5	72	69·5
C10b „ (M)	102·9 ± 1·98 (26)	98·6 ± 1·85 (12)	71·8 ± 1·85 (25)	69·8 ± 2·30 (13)
	104	—	73	—
(M)	106·3 ± 2·76 (15)	99·1 ± 3·36 (9)	74·8 ± 2·54 (13)	69·6 ± 2·96 (9)

[1] Wrongly or inadequately localized specimens, separated from *mentalis* (type (♂) : wing 90·5, tail 64) on measurements.

		Wing		Tail	
		Male	Female	Male	Female
C10c *pavuvu*		107·5	99	74	68
C11 *cinnamomea*	M	105·9 ± 1·35 (13)	100·8 ± 1·14 (13)	71·5 ± 1·45 (14)	67·9 ± 1·44 (12)
		103·5 ± 1·77 (17)	98·5 ± 2·81 (11)	76·2 ± 1·64 (16)	74·6 ± 2·19 (12)
C12 *sanfordi*	M	105·4 ± 2·01 (19)	100·0 ± 2·61 (7)	77·9 ± 1·94 (19)	74·0 ± 1·63 (7)
		104*	100*	75*	73·5*
	M	103·3 ± 2·20 (17)	99·7 ± 1·59 (18)	75·4 ± 1·62 (12)	72·9 ± 1·63 (16)
C13a *melanonota*		99	103	68	68
	M	98·0 ± 2·08 (7)	96 (3), 98	66 (2), 68, 69, 72	68 (2), 69
C13b "	M	98·4 ± 2·24 (14)	93	69·9 ± 2·40 (14)	68
C14 *melanoptera*		104*	100·5*	69·5*	71·5*
	M	105·3 ± 2·12 (25)	97, 98, 99, 101	74·0 ± 2·55 (26)	68, 69, 72 (2)
C15 *centralis*		95·5*	—	68·5*	—
	M	95·7 ± 2·39 (64)	92·3 ± 2·06 (18)	68·9 ± 2·30 (59)	66·9 ± 1·93 (18)
C16 *feminina*		85, 86·5, 93·5*	84·5*, 85	54·5, 60·5, 63*	53·5*, 54·5
	M	86·3 ± 2·85 (15)	84·8 ± 2·78 (7)	55·9 ± 2·83 (15)	54·4 ± 2·07 (7)
C17a *christophori*		85·9 ± 2·23 (41)	84·5 ± 2·32 (18)	59·6 ± 1·87 (35)	60·1 ± 1·95 (11)
	M	87·8 ± 0·83 (12)	86·1 ± 1·95 (7)	60·2 ± 2·58 (10)	59·4 ± 1·52 (7)
C17b "	M	88·5 ± 1·05 (6)	85·7 ± 1·67 (8)	58·7 ± 1·03 (6)	56·8 ± 1·58 (8)
D18a *graeffi*		91, 94, 95·5, 97·5	90·5	65·5, 68·5, 69, 73	65
	M	95·0 ± 2·29 (20)	92·75 ± 1·36 (8)	67·1 ± 2·08 (20)	65·2 ± 1·58 (8)
D18b *optata*		92·2 ± 2·45 (6)	90·5	65·5 ± 2·44 (6)	65
	M	92·7 ± 0·52 (6)	92, 93	67·0 ± 2·10 (6)	63, 64, 66
D19a *aurantiiventris*		88*, 90·5, 91·5, 93*	87	66, 68, 69·5*	66
	M	91·3 ± 1·70 (13)	86 (2), 87	66·2 ± 1·94 (16)	63, 64
D19b/c *ambigua*		92·5*	92·5*	67*	69·5*
	M	92·2 ± 1·92 (9)[2]	90·9 ± 0·90 (7)[2]	66·4 ± 1·50 (8)[2]	65·7 ± 1·51 (6)[2]
D20a *torquata*		93·6 ± 1·79 (10)	90, 91·5, 92, 93	65·3 ± 2·32 (8)	64, 64·5, 66·5 (2)
	M	95·6 ± 1·51 (10)	91·9 ± 1·36 (8)	67·1 ± 2·08 (10)	65·3 ± 1·58 (8)
D20b *koroana*		93·5*	91·5*	66*	67·5*
D21 *bella*	M	94·7 ± 1·98 (7)	91 (2), 92, 93, 94	68·6 ± 1·40 (7)	66·3 ± 1·22 (6)
	M	94	91, 92	61	62, 66
E22a *bynoei*	J	81, 85	—	64	—

[2] " Every specimen molting " (Mayr, MS).

		Wing		Tail	
		Male	Female	Male	Female
E22b melanura	J	80*, 81*, 84*	—	59*, 61·5*, 62·5*	—
		79·5, 80, 80·5, 81·5, 82	78, 82	59, 59·5, 60, 60·5, 62	59, 65
E22c "		82	79·5*	61·5	62*
E22d hilli	J	80·5 ± 1·37 (15)	78·6 ± 2·21 (7)	60·7 ± 1·83 (13)	60·1 ± 1·59 (7)
		84·5*	82*	66*	63*
E23 violetae	J	84	83	64	65
		85·5*, 86*	84*, 85*	68*	64 (2)*
E24 spinicauda	J	84·3 ± 1·60 (12)	82·4 ± 1·57 (9)	63·5 ± 2·02 (11)	61·3 ± 1·33 (10)
		87·1 ± 2·54 (6)	87·5*	63·5 ± 1·93 (7)	67*
E25a cf. dahli	J/M	(85·5, 88·5)*		(64, 65·5, 68)*	
		87·4 ± 2·13 (7)	88	66·2 ± 1·30 (10)	66·5
E25b "innominata"	M	91	91	69	66·5
E25c fergussonis	M	92·5, 93		69 (2)	
		96*		72·5*	
E25d dahli	M	94·5, 96	90	70·5, 74·5	66
E25e "		93	83	69	67·5
E25g "		86, 87		64, 64·5	63 (2), 64, 64·5
E25j "		90·5, 92 (2), 92·5	89, 89·5, 91	63·5, 65, 66, 67	63·5
E25k "	M	—		—	
		91·5 ± 2·00 (8)	89, 89·5	65·9 ± 1·20 (6)	65, 67
		92*, 95*	88 (2), 89	65*, 66·5*, 69*	64 (3)
E26 whitneyi	M		90*, 90·5*		65*
		95·7 ± 4·00 (8)	90·8 ± 2·63 (9)	66·7 ± 3·20 (8)	66·1 ± 0·99 (8)
E27 balim		88	—	68	—
E28a occidentalis	J	98·0 ± 2·10 (12)	91, 94·5, 95	76·9 ± 1·43 (8)	75, 75·5, 78
E28b fuliginosa	J	96·7 ± 2·43 (25)	93·0 ± 1·68 (15)	75·5 ± 2·44 (25)	75·0 ± 2·13 (16)
		95, 98 (3)	92·5*, 99·5	75·5 (2), 78, 79	75·5*, 80
E28c "	J	97·1 ± 1·73 (12)	94·6 ± 1·40 (8)	75·4 ± 1·43 (11)	73·2 ± 1·39 (9)
		94, 95, 97 (2), 98	90·5, 95, 96·5, 97	73, 75·5, 76·5, 77·5, 77, 78	70·5, 71, 77, 79
F29 glaucura	J	103·0 ± 2·02 (6)	99, 101	83·7 ± 2·28 (6)	78, 79
		101·2 ± 1·20 (9)	100·4 ± 2·34 (7)	80·0 ± 1·61 (7)	80·8 ± 3·08 (6)

	Wing Male	Wing Female	Tail Male	Tail Female
F30a youngi	101·5, 102 (2), 102·5	95·5, 97	79·5, 80, 80·5, 81	75, 77
F30b pectoralis }U	99·3 ± 1·95 (17)	95·1 ± 1·91 (7)	76·5 ± 2·00 (18)	73·8 ± 2·39 (16)
	95·3 ± 2·64 (6)	96·5	73·4 ± 2·88 (6)	74
	96·8 ± 2·00 (15)	95·2 ± 2·87 (11)	73·7 ± 2·50 (15)	74·5 ± 2·77 (11)
F31a ashbyi }U	87·5, 90, 95, 96·5	92	70, 71·5, 74·5 (2)	71
	93·2 ± 3·20 (10)	87·5 ± 3·39 (15)	72·5 ± 2·94 (8)	70·8 ± 2·89 (16)
F31b queenslandica }U	88, 90, 92, 94·5	88*	62·5, 64·5, 67·5, 70·5	67*
F32 contempta	90·3 ± 2·10 (26)	88·2 ± 0·99 (6)	66·6 ± 2·95 (26)	61, 64, 64·5, 65, 66
F33 xanthoprocta	93·1 ± 2·39 (8)	86, 90·5	74·1 ± 1·58 (8)	72, 73
	95·9 ± 2·16 (6)	90·5, 92·5, 93, 94·5, 96·5	74·7 ± 1·94 (6)	75·8 ± 1·40 (6)
G34 caledonica	82·4 ± 2·48 (6)	81·5, 83·5, 85, 87	65, 66·5, 67, 67·5	64·5, 65·5, 66·5, 70·5
G35 littayei	100·5, 101, 101·5	97	71·5, 73	70·5
G36 cucullata	86, 87, 87·5, 89	82, 84	63, 64, 64·5, 66·5	70·5
G37a chlorura	88·5, 90	96·5	66 (2)	58, 62·5
G37b efatensis	85·5, 87 (2), 87·5	—	63, 64, 64·5, 66·5	—
G37c brunneipectus }M	—	86·5*	—	65*
G37d intacta }M	86·9 ± 1·28 (17)	86·0 ± 1·66 (9)	65·2 ± 2·13 (18)	65·4 ± 1·43 (9)
	84·2 ± 1·62 (9)	82·5	62·6 ± 2·95 (10)	61·5
G37e cf. banksiana }M	86·0 ± 1·99 (23)	83·8 ± 1·97 (23)	63·7 ± 2·06 (21)	61·1 ± 1·86 (22)
	—	86·5*	—	66*
G37f banksiana }M	87·2 ± 1·36 (12)	84·5 ± 1·92 (6)	64·9 ± 1·49 (17)	63·3 ± 1·60 (7)
	87·5	87·5*	64·5	64*
G38 vanikorensis }M	86·4 ± 1·51 (7)	84·7 ± 1·50 (15)	62·9 ± 0·99 (8)	60·8 ± 1·83 (15)
	83*	84*	60*	58*
H39a calliope }M	85·7 ± 0·58 (16)	82·9 ± 0·99 (10)	60·4 ± 1·22 (14)	59·0 ± 1·18 (11)
	84, 87·5, 88·5, 89	88	65, 68 (2), 70·5	69·5
H39b arthuri	90·1 ± 1·83 (11)	87·5, 92·5	68·4 ± 2·42 (10)	67
H40 sharpei	91	89	71	72·5
	90	88, 90·5	64·5	66·5
H41 dammeriana	91	83	—	71·5

Species		Wing Male	Wing Female	Tail Male	Tail Female
H42 fuscoflava		109·5	101·5, 103	79·5	71·5
H43a alfurorum		89·5, 90·5, 92, 93, 94	89·5	62, 65, 67, 67·5, 68	66
H43b macrorhyncha		95·9 ± 1·32 (9)	88·5, 90·5 (3), 92	68·6 ± 1·06 (9)	65 (2), 66, 66·5, 68
H44 buruensis		92·6 ± 1·79 (9)	87·7 ± 2·52 (7)	67·6 ± 1·99 (9)	65·4 ± 2·12 (7)
H45 clio		89·7 ± 2·49 (6)	85, 86	66, 66·5, 68·5, 69·5 (2)	66·5
H47a collaris		94, 96·5*	92	65·5, 68·5*	63
	M	94·7 ± 2·16 (6)		65 (2), 67, 68, 70	—
H47b misimae		93, 94	90·5, 92	64·5, 65	63, 65·5
	M	93·3 ± 1·98 (7)		65·6 ± 1·62 (7)	
H47c rosseliana		96·5	90	66·5	—
	M	95·0 ± 1·26 (6)		65·8 ± 0·98 (6)	—
H48a citreogaster		92	87	64·5	65·5
H48b ,,		85·1 ± 1·85 (7)	81·5, 83·5	60·9 ± 2·07 (7)	57, 59·5
H48c ,,		87·5, 90	84·5	62	62·5
H48d sexuvaria		85	87	59	62·5
H49 ottomeyeri		104		73·5	—
H50 tabarensis	M	99·1 ± 1·88 (7)	91, 94	70·1 ± 0·99 (7)	
H51 goodsoni		91·5	88	65	67, 68·5
		98*		69*	61·5
H52a ornata	M	95·7 ± 1·16 (10)	91·6 ± 1·76 (13)	66·8 ± 1·56 (9)	64·0 ± 1·71 (12)
H52b ,,	M	95·0 ± 5·15 (41)	90·2 ± 1·91 (25)	64·5 ± 2·33 (42)	62·4 ± 1·83 (23)
H53 utupuae		88·5, 91, 93*	88*	62, 63·5, 65·5*	63·5*
	M	92·4 ± 1·26 (13)	89·1 ± 0·83 (11)	64·5 ± 1·37 (11)	62·1 ± 1·45 (10)
H54 kandavensis		90 (2), 92	85·5, 91	60, 65, 67·5	61, 62, 63
	M	89·4 ± 2·37 (16)	87·0 ± 1·04 (11)	66·1 ± 1·18 (15)	64·5 ± 0·93 (11)
H55 vitiensis		90*, 90·5	—	60·5, 62·5*	—
	M	91·1 ± 1·45 (9)	88·1 ± 1·17 (9)	61·6 ± 1·94 (9)	59·3 ± 0·95 (7)
H56 lauana		97*		69*	—
	M	96·7 ± 1·93 (21)	93·2 ± 1·52 (16)	66·3 ± 2·32 (20)	64·7 ± 1·54 (15)
H57 melanops		101·8 ± 2·22 (8)	95	70·1 ± 2·28 (8)	67·5
	M	103·6 ± 1·26 (19)	97·0 ± 1·28 (12)	70·7 ± 1·48 (19)	67·7 ± 0·49 (12)
P. flavifrons		86·0 ± 2·15 (14)	81·5, 83·5, 84·5, 86	58·1 ± 1·82 (12)	56, 57, 58, 61
	M	87·5 ± 1·53 (20)	83·6 ± 1·09 (18)	59·4 ± 2·22 (19)	56·8 ± 1·58 (20)

	Tarsus	Culmen	Bill depth
P. schlegelii			
1 schlegelii	23 (2)	—	5, 6
2 cyclopum	23·5 (2)	17 (2)	5·5
3a viridipectus	23·9 ± 0·79 (18)	15·6 ± 0·59 (17)	5·4 ± 0·38 (17)
3b obscurior	23·9 ± 0·65 (20)	16·0 ± 0·46 (20)	5·3 ± 0·15 (15)
P. soror			
1 soror	22·4 ± 0·38 (6)	16·5, 17	5·7 ± 0·42 (6)
2 klossi	22·1 ± 0·56 (20)	17·2 ± 0·38 (13)	5·9 ± 0·49 (17)
3 bartoni	22·2 ± 0·68 (22)	17·1 ± 0·61 (21)	5·5 ± 0·46 (21)
P. pectoralis			
A1 fulviventris	21·7 ± 0·87 (9)	18·7 ± 0·87 (9)	6·5 ± 0·53 (8,
A2a javana	19, 20, 20·5	16·5, 17, 18	5·5, 6
A3a fulvotincta	20·5 ± 0·96 (12)	18·0 ± 0·80 (12)	6·4 ± 0·48 (7)
A3b jubilarii	20·5, 21, 21·5 (2), 22·5	18 (3), 18·5, 19	5·5, 6 (3), 6·5
A4 everetti	22·4 ± 1·02 (6)	20·4 ± 0·74 (6)	6 (2), 6·5, 7 (2)
A5 teysmanni	21, 22	18, 19	5·5, 6
B6 mentalis	21·8 ± 0·67 (15)	19·4 ± 0·82 (15)	6·5 ± 0·56 (9)
B7 tidorensis	23·5 ± 0·55 (6), 23·5 (2), 24 (3)[1]	20·9 ± 0·38 (7), 21·2 ± 0·42 (6)[1]	7·3 ± 0·24 (6), 7·1 ± 0·38 (6)[1]
B8 obiensis	23·0 ± 0·64 (7)	22·1 ± 0·56 (7)	6·9 ± 0·30 (7)
C9 bougainvillei	25 (2), 25·5, 26	22·5 (2), 23, 23·5	7, 7·5, 8, 8·5
(M)	—	23·0 ± 0·95 (6)	—
C10a orioloides	23, 25 (2)	22, 23	7·5, 8·5 (2)
C10b ,,	25	24·5	9
C10c pavuvu	24·5, 26·5	23, 24	8, 9
C11 cinnamomea	24·7 ± 0·88 (37)	22·7 ± 0·87 (35)	8·1 ± 0·38 (33)
C12 sanfordi	25, 26	22, 23	8 (2)
C13a melanonota	24·5 (2)	25	8, 8·5
C14 melanoptera	24·5, 26	23 (2)	8, 8·5
C15 centralis	24·5 (2)	24, 24·5	8, 8·5
C16 feminina	26·5 ± 0·98 (7)	22·7 ± 0·87 (7)	6·7 ± 0·26 (6)

[1] Wrongly or inadequately localized specimens, separated from *mentalis* (type (♂) : tarsus 21·5, culmen 19·5, bill depth 7) on measurements.

	Tarsus	Culmen	Bill depth
C17a *christophori* ♂ ad.	24·8 ± 0·78 (93)	20·8 ± 0·67 (82)	6·8 ± 0·39 (70)
,, ♀ ad.	24·7 ± 0·85 (44)	20·9 ± 0·63 (39)	6·8 ± 0·30 (35)
,, ♂ II phase	25·1 ± 0·58 (20)	20·8 ± 0·52 (18)	6·8 ± 0·47 (14)
,, ♂/♀ I phase	25·0 ± 0·72 (10)	20·7 ± 0·56 (9)	6·6 ± 0·42 (8)
D18a *graeffi*	24·7 ± 0·77 (15)	20·8 ± 1·04 (13)	6·8 ± 0·52 (11)
D18b *optata*	26, 27 (2), 27·5 (2)	18·5, 19, 20 (3)	6, 6·5 (2), 7
D19a *aurantiiventris*	26·5 ± 0·50 (9)	19·0 ± 0·61 (9)	6·4 ± 0·32 (8)
D19c *ambigua*	23, 24·5, 25 (2), 26	18, 18·5, 19 (2), 20	6·5 (3), 7 (2)
D20a *torquata*	24·5, 25·5 (2)	18, 19·5 (2)	7
D20b *koroana*	27·0 ± 0·78 (16)	19·3 ± 0·85 (15)	6·4 ± 0·49 (13)
E22a *bynoei*	25·5, 27	19, 20	6·5
E22b *melanura*	24	20	5
E22c ,,	23, 23·5 (2)	18·5 (3)	5·5, 6, 6·5
E22d *hilli*	22·5 (2), 23 (3)	18 (5)	5 (2), 5·5 (2), 6
E23 *violetae*	22, 23·5	18, 18·5	5·5
E24 *spinicauda*	21·5, 22·5, 23·5, 24	18, 19 (3), 19·5	6 (4)
E25a cf. *dahli*	23·0 ± 0·81 (12)	19·6 ± 0·75 (10)	5·9 ± 0·54 (11)
E25b "*innominata*"	23·5	—	—
E25c *fergussonis*	24·5 (2)	20, 20·5	6, 6·5
E25d *dahli*	24·5	19·5	6·5
E25e ,,	23·5, 24	19, 19·5	6·5 (2)
E25g ,,	22·5, 23, 24	18·5, 20	5·5, 6·5, 7·5
E25j ,,	23·7 ± 0·97 (9)	19·6 ± 0·32 (8)	6·0 ± 0·25 (9)
E25k ,,	22·5 (2)	20·5 (2)	6·5, 7·5
E26 *whitneyi*	23·5, 24·5	19·5, 21	6·5 (2)
{ M	24·7 ± 1·75 (6)	(19·5, 20·5, 21, 21·5, 22)*	6·5 (2), 7·5
E27 *balim*	—	20·1 ± 1·06 (15)	6, 7
	24, 25	18·5 (2)	
F28a *occidentalis*	22·4 ± 0·78 (24)	16·6 ± 0·71 (22)	5·3 ± 0·32 (24)
F28b *fuliginosa*	21·7 ± 0·68 (6)	16·3 ± 0·82 (6)	5·5, 5·5 (2), 6 (2)
F29 *glaucura*	22·9 ± 0·69 (8)	15·7 ± 0·91 (9)	5·7 ± 0·57 (9)
F30a *youngi*	21·9 ± 0·79 (8)	16·9 ± 0·48 (7)	5·4 ± 0·32 (8)
F30b *pectoralis*	21·6 ± 0·61 (10)	17·2 ± 0·85 (8)	5·4 ± 0·35 (8)
F31a *ashbyi*	22·3 ± 1·49 (8)	17·2 ± 1·60 (8)	5·6 ± 0·45 (7)
F31b *queenslandica*	21·7 ± 0·98 (6)	17·2 ± 0·61 (6)	5·7 ± 0·41 (6)
F32 *contempta*	22·5 ± 0·68 (14)	18·6 ± 0·59 (14)	5·8 ± 0·45 (12)

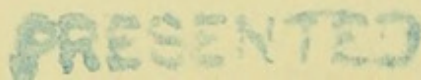|	Tarsus	Culmen	Bill depth
F33 xanthoprocta	25·4 ± 0·54 (20)	19·5 ± 0·46 (20)	6·3 ± 0·38 (19)
G34 caledonica	24·2 ± 1·17 (11)	18·5 ± 0·76 (11)	5·1 ± 0·46 (10)
G35 littayei	26 (2), 27 (2), 28·5	23, 24, 24·5 (3)	7·5 (2), 8 (2), 8·5
G36 cucullata	25·6 ± 0·49 (6)	19·7 ± 0·27 (6)	5·6 ± 0·38 (6)
G37a chlorura	24·5, 25·5	19, 19·5 (2)	6 (2), 7
G37b efatensis	24·7 ± 0·98 (6)	19·2 ± 0·61 (6)	6·1 ± 0·38 (6)
G37c brunneipectus	24·5	20	6
G37d intacta	24·5 ± 0·69 (13)	19·5 ± 0·78 (13)	6·2 ± 0·32 (13)
G37e cf. banksiana	25	20	—
G37f banksiana	25, 26	20	7
G38 vanikorensis	23·5, 24·5 (2), 25·5	19, 19·5 (2), 20	5, 6 (2)
H39a calliope	24·0 ± 0·87 (9)	21·0 ± 0·61 (9)	6·9 ± 0·52 (8)
H39b arthuri	23·5, 24	22·5 (2)	7, 7·5
H40 sharpei	25, 25·5, 26	21, 22, 23	7 (2), 7·5
H41 dammeriana	25 (2)	22·5, 23	7, 8
H42 fuscoflava	26, 28, 28·5, 29·5	24 (2), 24·5, 26	8·5 (2)
H43a alfurorum	22·9 ± 0·83 (8)	19·9 ± 0·64 (8)	6·6 ± 0·34 (7)
H43b macrorhyncha	22·7 ± 1·14 (19)	20·1 ± 0·75 (18)	6·5 ± 0·50 (17)
H44 buruensis	23·4 ± 0·81 (25)	19·1 ± 0·55 (25)	6·1 ± 0·31 (23)
H45 clio	22·3 ± 0·22 (11)	19·4 ± 1·03 (9)	6·6 ± 0·44 (11)
H47a collaris	24·5 (2), 25	22·5, 23	6·5 (2), 7·5
H47b misimae	23·5, 24·5, 25, 25·5	23 (2), 23·5, 24	6, 6·5, 7·5
H47c rosseliana	24·5, 25	23, 25	6·5
H48a citreogaster	22·5, 23	18·5, 19	6·5, 7
H48b ,,	22·3 ± 0·62 (9)	19·0 ± 0·71 (8)	6·2 ± 0·61 (9)
H48c ,,	20·5, 22·5, 23	18·5, 19, 20	6, 6·5, 7
H48d sexuaria	24, 24·5	19·5, 20	6·5 (2)
H49 ottomeyeri	25·5 (2)	22·5, 24	7, 7·5
H51 goodsoni	22, 23	20·5 (2)	6·5, 7·5
H52a ornata	26, 26·5	21	7·5 (2)
H53 utupuae	25, 25·5, 26·5 (2)	20, 20·5, 21 (2)	6, 6·5, 7, 7·5
H54 kandavensis	25·9 ± 1·02 (8)	18·4 ± 0·86 (8)	6·3 ± 0·46 (8)
H55 vitiensis	24, 25·5	18·5, 19	6, 7
H56 lauana	25, 26	20	6·5
H57 melanops	26·4 ± 0·85 (11)	20·7 ± 0·67 (9)	7·0 ± 0·50 (11)
P. flavifrons	24·5 ± 0·71 (26)	18·8 ± 0·78 (27)	6·1 ± 0·42 (24)

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