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NOTES ON THE GENUS LALAGE BOIE

By Ernst Mayr and S. Dillon Ripley

This genus is an important member of the Polynesian avifauna, even though it is absent from eastern Polynesia and from Micronesia. In the central Polynesian Islands, however, and in southern Melanesia, it is found not only on the big islands. but also on many of the outlying small islands in numerous well-defined races. The last treatment of the genus, that by Mathews in the "Syst. Av. Austr." (1930), pp. 546-548, is very unsatisfactory, because it fails to reveal the true relationships of the many described forms. It became necessary during the study of the Polynesian material to go beyond the borders of this zoogeographical district and to include in our work a cursory study of the Papuan, Australian, and Malayan forms. As the work proceeded it became clear, on the one hand, that a great many of our conclusions were at variance with the currently accepted views on the relationships of the species of this genus and, on the other hand. that the genus presented unusually favorable material for the elucidation of speciation phenomena and of the zoogeographical history of the area. It was, therefore, decided by us to devote more space to the extralimital forms and to the general discussion than has been customary in the preceding papers of this series.

GENERIC CHARACTERIZATION

It is usually difficult to define Passerine genera by morphological characters. In the family Campephagidae this is particu-

larly true, as can be seen by looking at the characters used in the "Cat. Birds Brit. Mus." (vol. 4, pp. 7–8), to identify the various genera. Still, a typical Lalage, such as nigra, tricolor, leucomela, or maculosa, is recognizable at a glance. The difficulty is rather where to draw the line between Lalage and the genera related to it.

According to the Cat. Birds (loc. cit.), Edolisoma differs from Lalage by having the culmen as long as the tarsus; Lalage has it shorter than the tarsus. This, unfortunately, is not correct. In Edolisoma, as well as in Lalage, the culmen is generally shorter than the tarsus. In fact, so far as we could determine, there are no clear-cut characters available to separate the two genera. However, it is possible to define the genus Lalage by a combination of morphological and color characters as follows:

Lalage comprises a number of small Campephagidae with rather short and slender bills and without lipochroms and special skin and feather structures; sexual dimorphism is usually well developed; the tail is medium long (70–95 per cent of the wing); there are generally prominent white wing-bars, a light rump, and often a white superciliary; the upper parts are brownish, gray, or black; the under parts are white with or without dark bars and a buffy or rufous wash.

On the basis of this definition the genus would include in addition to the nigra, aurea, and leucopygia groups (as defined below) the Philippine species melanoleuca, a discussion of which is beyond the scope of the present paper. The species fimbriata, sykesi, melaschista, and melanoptera, however, are not covered by the above-given definition, and it will be better to refer them to the genus Volvocivora.

¹ Previous papers in this series comprise American Museum Novitates, Nos. 115, 124, 149, 322, 337, 350, 356, 364, 365, 370, 419, 469, 486, 488, 489, 502, 504, 516, 520, 522, 531, 590, 609, 628, 651, 665, 666, 709, 714, 820, 828, 912, 915, 933, 939, 947, 977, 986, 1006, 1007, 1056, 1057, and 1091.

Whether or not there are good characters by which to separate *Volvocivora* from *Edolisoma* must be shown by further studies.

Several species have at one time or another been included erroneously within the genus Lalage. Among these are Turdus pacificus Gmelin, discussed at a later point in the text, and Volvocivora insperata Finsch included in the genus *Lalage* in the "Cat. Birds," vol. 4, p. 103, and other reference books. This species is a geographical representative of Edolisoma tenuirostre as pointed out by Mayr (Ornith. Monatsber.. 1939, p. 126). Other species listed in the Cat. Birds as Lalage, but no longer considered to belong to that genus, are: banksiana Gray (= Neolalage), rufiventer(=Coquus typicus), newtoni (=Coquusnewtoni), and monacha (= Edolisoma tenuirostre monachum).

GENERIC SYNONYMS

Lalage Boie, 1826, Isis, col. 973.—Type (by monotypy): Turdus orientalis Gmelin = Turdus niger Forster.

Erucivora Swainson, 1832, Faun. Bor.-Amer. Birds, p. 483.—Type (by original designation): Turdus orientalis Gmelin.

Symmorphus GOULD, 1838, Synops. Birds Austr., pt. IV, App., p. 3.—Type (by monotypy): Symmorphus leucopygus Gould.

Pseudolalage Blyth, 1861, Journ. As. Soc. Ben., XXX, p. 97.—Type (by monotypy):

Lalage melanoleuca Blyth.

Diaphoropterus Oberholser, 1899, Proc. Acad. Phila., p. 214.—Type (by original designation): Symmorphus leucopygus Gould, new name for Symmorphus Gould, 1838, not Wesmaël, 1833, Mon. Odyn. Belg.

Karua Mathews, 1913, Austral. Av. Rec., II, p. 59.—Type (by original designation): Campephaga leucomela Vigors and Horsfield.

Perissolalage OBERHOLSER, 1917, Proc. U. S. Nat. Mus., 54, p. 182.—Type (by monotypy): Perissolalage chalepa Oberholser.

Oscarornis Mathews, 1928, Novit. Zool., 34, p. 372.—Type (by original designation): Lalage sharpei Rothschild.

Of the listed names one (Symmorphus) is preoccupied, while another (Erucivora) is a strict synonym (identical genotype) of an older name. The others deserve some discussion:

The genus Neolalage Mathews, 1928, included among the Campephagidae in Mathews' Check-List (Syst. Avium Austr., II, 1, p. 551), has been proved by Mayr

(Amer. Mus. Novitates, 1933, No. 665) to belong to the Muscicapidae. Diaphoropterus will be discussed on a later page, as will Oscarornis. The genus Karua was established by Mathews on the basis of a smaller bill and different wing formation (Mathews, loc. cit.). It was also stated that in the male breeding plumage there is no white wing-bar. Comparison of specimens in the American Museum's collection does not bear out these differences. The bill is not smaller, the wing formula is not appreciably different, and no specimens were seen lacking the white wing-bar. It is obvious, on the other hand, that the species of "Karua" are closely related to the aurea group. Their size and proportions are similar and there are no color patterns that can be looked upon as fundamentally different.

Pseudolalage Blyth, based on Lalage melanoleuca, has been rejected with good reason by all recent authors and, therefore, requires no further discussion. It was based on supposed differences in the structure of the feathers of the rump. The generic diagnosis of Perissolalage Oberholser (Proc. U. S. Nat. Mus., 1917, vol. 54, p. 182) gives the specific characters of Lalage sueurii as compared to Lalage nigra, but none of the differences between these two closely related species are of generic importance.

The genus *Campochaera* (type *sloetii*) is probably a specialized offshoot of the ancestral *Lalage* stock.

Synopsis of the Species of Lalage

In view of the many conflicting statements of the recently published lists of the genus (Mathews, Chasen, etc.), and in view of the different conclusions at which we have arrived in many instances, it will greatly facilitate the understanding of the subsequent discussions if we preface them by a short outline of the classification of the species and subspecies of this genus.

Lalage nigra group

1.—Lalage nigra

(a) davisoni Kloss.

RANGE.—Nicobars.

(b) nigra Forster, with brunnescens Baker, 1923 (Selangor), and empheris Oberholser, 1912 (Nias), as synonyms.

RANGE.—Malay Peninsula, Sumatra, Nias, western Java and Karimon-Java Islands.

(c) chilensis Meyen with schisticeps Neumann, 1919, and mitifica Bangs, 1922, as synonyms.

Range.—Borneo (and islands), Philippines.

(d) leucopygialis Walden, 1872.

Range.—Celebes, Peling, Banggai, Sula Isls.

2.—Lalage sueurii

(a) sueurii Vieillot, 1818—synonyms timoriensis Müller, 1843, riedeli Meyer, 1884 (Kisser I.), celebensis Meyer, 1884 (Celebes), chalepa Oberholser, 1917 (Solombo Besar).

RANGE.—Western Java, Lesser Sunda Isls. from Bali to Timor, south Celebes (Makassar), islands of Flores Sea.

(b) tricolor Swainson, 1825.

RANGE.—Northern Australia (for a more detailed treatment see Mayr, 1940, Emu, 40, pp. 111-115).

Lalage leucopyga group

Lalage leucopyga Gould, 1838 (see p. 15)

RANGE.—Islands east of Australia from Norfolk I. north to San Cristobal, eastern Solomon Islands.

Lalage aurea group

Lalage aurea Temminck, Dec., 1825
 RANGE.—Northern Moluccas (Batjan,
 Ternate, Halmahera and Morotai).
 Lalage atrovirens

(a) moesta Sclater, 1883—Tenimber. RANGE.—Tenimber Isls.

(b) atrovirens Gray, 1862—Misol.

Range.—Western Papuan Islands (Misol, Salawati), western New Guinea (Vogelkop), and northern New Guinea from Geelvink Bay eastward to Astrolabe Bay and the Ramu River.

(c) leucoptera Schlegel, 1871—Biak. RANGE.—Biak I., Geelvink Bay.

3.—Lalage leucomela Vigors and Horsfield

(a-c) leucomela Vigors and Horsfield (before Feb. 17, 1827) (+ subsp.) (treated

in detail in Emu, 40 (1940), p. 115-117), and following races of the Papuan region: keyensis (Key Isls.), polygrammica (Aru Isls., south and east New Guinea), obscurior (D'Entrecasteaux Arch.), trobriandi (Trobriand Isls.), pallescens (Louisiade Arch.), falsa (Rook, New Britain, Duke of York), karu (New Ireland), ottomeyeri (Lihir), albidior (New Hanover), and conjuncta (St. Matthias I.).

4.—Lalage maculosa (see below)

5.—Lalage sharpei (see below)

HISTORY OF THE GENUS Lalage

An examination of the genus Lalage, as a whole, brings us to the conclusion that the origin of the genus must be looked for somewhere within the borders of the Oriental region. After having spread to the Papuan region the genus split up into several groups of which the nigra, aurea, and leucopyga groups have remained largely representative until the present time. Only in Australia and in the central New Hebrides are there cases of overlapping between members of these different groups. In each case the name given by us to the group has been taken from the first named species. There are various species in the nigra and aurea groups, each of which is, however, more closely related to the rest of the group than to any outside species.

nigra group

The two species making up this group, nigra and sueurii, differ from any of the species of the aurea group by the following characters:

Male.—The rump patch is more prominent, larger and better differentiated from the back. There is no real indication of barring on the white (sometimes grayish) of the under parts. There is no tendency to a rufous or buffy coloration on the under parts. The wing is characterized by heavy white edging to the wing-coverts, extending through the lesser wing-coverts in one species, whereas the aurea group has this character rather less pronounced and the feathers of the outer greater wing-coverts are tipped, never edged, with white.

FEMALE.—Differs from that of the aurea group by the coloration of the rump which is shaded differently from the back rather than being somewhat abrupt and patchy; upper tail-coverts only indistinctly barred and tipped; under parts much more finely barred when

barring occurs.

It has been customary to divide the nigra group into three species: nigra (with davisoni, nigra, chilensis, and sueurii), leucopygialis, and tricolor. Our researches indicate that there are only two groups: nigra (with davisoni, chilensis, and leucopygialis) and sueurii (with tricolor). These two groups are very similar and would probably be united into one species if they were strictly representative. It has been found, however, that the two species occur together in the Makassar district of southwestern Celebes without any signs of hybridization. The only other place where the two species meet is central Java, but, unfortunately, nothing is known about their relations in that region. Do they intergrade imperceptibly, do they hybridize, do they represent each other ecologically, or do they live side by side like good species? These are some of the questions that the field ornithologists in Java should study.

The superspecies nigra broke, apparently rather early in the Pleistocene, into a western (Malaysian) and an eastern group which must have been separated for a considerable period. The fact that the two neighboring races of the two groups (nigra nigra and sueurii sueurii) are the most similar, indicates that the separation occurred a considerable time after subspeciation within the groups had already started. It is probable that no birds of these species occurred on Java for a good part of the Pleistocene and that this is the reason for the decided gap in the characters.

If we compare the forms of the two species which now occur in central Java in immediately neighboring districts, we find that *sueurii* differs from *nigra* as follows:

Bill longer and more slender, culmen straighter; tail longer, wing more pointed; second primary longer than sixth (in *nigra* generally shorter than sixth); first primary very much shorter.

Adult male: Under parts pure white, not washed with gray; superciliary much less pronounced, often almost absent; gloss of upper parts (in fresh plumage) greenish, not bluish; bend of wing and lesser wing-coverts white, not black; greater upper wing-coverts white on both webs; much less white on tip of tail-feathers, white on central tail-feathers a narrow margin surrounding the entire feather, not a well-defined

tip; pale rump region reaching much higher up on the back.

Adult female: Showing much stronger sexual dimorphism, being much more rufous brown above and having the pale edges of wing-feathers and wing-coverts strongly washed with buff, not white; barring of breast and flanks very indistinct.

The majority of the points by which nigra nigra is characterized are also found in the other races of this species. important in connection with leucopygialis (Celebes). Stresemann in his recent treatise on the birds of Celebes states (1940, Journ. f. Ornith., 88, p. 127) that leucopygialis is a well-defined, isolated species of doubtful relationship and point of origin. It seems to us that he has been led astray by some of the specializations (white rump, black cap of female) which this species has evolved during a long period of isolation on Celebes. On the other hand, it has all the basic specific characters of nigra and what is still more important, it is linked up with nigra nigra by the exactly intermediate chilensis from the Philippines. It is now clear that leucopygialis has reached the Celebes Archipelago via the Philippine Islands, and has evolved there into the final step of the cline nigra-chilensis-leucopygialis.

L. sueurii was presumably isolated on the Lesser Sunda Islands, from where it spread into Australia and developed into the very similar form tricolor. At a fairly recent date it entered a rather aggressive period of colonization and settled in eastern Java, on some of the islands of the Java Sea, and in the southern peninsula of Celebes where it now lives side by side with leucopygialis.

aurea group

This group divides into five species, aurea, atrovirens, leucomela, maculosa, and sharpei, ranging from Halmahera to Samca. Certain characters set off this group from either of the others.

Male.—The rump patch is more reduced than in either of the other groups and the upper tail-coverts are more prominently barred and tipped. The white area on the wings is smaller and on the outer greater wing-coverts occurs in tips rather than in edging. There is a tendency for a rufous coloration to appear in the under parts in contrast to the buffy coloration of some

members of the other groups. Barring, when it occurs, is coarse and plentiful, particularly in the females. The tail tends to average shorter; the relative tail-length varies from 64 to 85 per cent of the wing-length, while in the *nigra* group it varies from 77 to 85, and in the *leucopyga* group from 83 to 97.

The species aurea is sharply differentiated from the other species of the group by solid rufous under parts. Disregarding this character, however, it is at once seen that in size, shape, and in the rest of its coloration it is closely related to atrovirens. L. atrovirens which occupies northern and western New Guinea lacks the rufous under parts; it has two races on two neighboring groups of islands (moesta and leucoptera).

The representative species in southern and eastern New Guinea is (karu =)leucomela, which, like aurea, has a good deal of rufous on the under parts. In one race (conjuncta) this rufous coloration is carried over the whole of the belly and vent making it appear at first closest to aurea, but further examination reveals that *conjuncta* is merely the last step in a discontinuous cline of races of leucomela extending up through the Bismarck Archipelago. The species has also settled in Northern Territory (Australia) arriving there via Aru and Kei Islands, and in eastern Australia via south New Guinea and Cape York. In the east it is found as far as the Louisiade Archipelago.

Lalage maculosa

To the east of the Louisiades there is a considerable gap in the range of the aurea group. It is completely absent from the Solomon Islands, but is found again in the central New Hebrides and Santa Cruz Islands and reaches from there eastward as far as Samoa. The two species, maculosa and sharpei, which are found in this area, are most closely related to one another but both are obviously eastern descendants of the aurea group.

It is probable that the original stock of maculosa-sharpei came directly from the New Guinea area, because the aurea group is absent from the Solomon Islands, and there are only slightly differentiated "recent" forms in the Bismarck Archipelago, the Louisiades, and in Australia. The two

New Guinea species atrovirens and leucomela are strictly representative, and it is impossible to decide which is closer to maculosa.

The first islands to be settled were evidently the large islands of the Fiji group and of Samoa (Upolu, Savaii). This assumption is not only in harmony with our general knowledge of the settlement of Polynesian Islands (Mayr, 1941), but it is confirmed by the high degree of specialization reached by the Samoan species sharpei. This development was retrogressive (see below), while, on the other hand, the maculosa and vanikorensis groups split off the Fijian woodi assemblage and developed unbarred plumages in the male and sometimes even in the female. Eventually, a second wave (maculosa) reached Samoa (via Tonga Isls.), but did not hybridize with sharpei, because the latter had already differentiated too far and had lost sexual affinity. There are now two good species of Lalage on Upolu and Savaii, but, unfortunately, nothing is known about their ecology. Judging by the analogy of similar cases one would expect that the earlier settler (sharpei) is more a forest and mountain bird and the recent settler (maculosa) more a bird of the open country in the lowlands.

Widespread (though never quite universal) characters of the forms of maculosa are: small degree of sexual dimorphism, in connection with a rather masculine female plumage; reduced barring of the under parts, particularly in the males; pronounced white pattern on wing, head (superciliary, etc.), and back; lack of buffy wash on under parts, at least in the males; heavy bill and short tail.

The eastern maculosa forms

The maculosa group is found on Samoa, the Tonga Islands, eastern Fiji (Lau Archipelago), and some of the isolated islands (Niue, Futuna, Keppel, and Boscawen). It is characterized by the reduction or absence of the barring of the under parts.

Lalage maculosa maculosa (Peale)

Colluricincia maculosa Peale, 1848, U. S. Expl. Exped., Birds, p. 81.—Samoa and Fiji;

restricted to Upolu, Samoa, by Wetmore, Ibis, 1925, p. 847.

Subspecific Characters (Adult Male).-Above glossy black, crown occasionally lightly streaked with white; the feathers of the back occasionally faintly tipped with white; rump gray, the feathers with a buffy white terminal and a blackish subterminal bar; upper tailcoverts more blackish; lores and a superciliary stripe white; a black streak from the base of the bill through the eye joining the nape; under parts white with a faint buffy wash, more pronounced on the chest, sides of throat and flanks; wings black, inner median wing-coverts white with a black shaft streak, greater, outer median, and some of the lesser wing-coverts edged or tipped with white or tawny white: tail black. central tail-feathers lightly tipped, the outer tailfeathers broadly tipped with white (12-16 mm.).1

FIRST-YEAR MALE (Immature Plumage).—Crown and back blackish brown, the crown streaked with tawny brown or white, the feathers of the back sometimes lightly tipped with tawny; rump buffy gray; lores and a superciliary stripe white to buffy white; under parts white tinted with buff on the chest and flanks; the sides of the neck, breast, and flanks with irregular black vermiculation; wings dark brown, wing-coverts, secondaries, and primary coverts edged with white or tawny white; alula with a pale tip; tail dark brown with white tips; tail-feathers more pointed.

JUVENILE MALE (Nestling Plumage).—Above blackish, the feathers of the crown and back tipped with buffy white; rump grayish buff; below white; wing and tail as in the first-year male; basal half of the lower mandible yellowish.

ADULT FEMALE.—Variable, sometimes more like adult, sometimes more like first-year male. Crown and back rusty to glossy black, the crown sometimes streaked, sometimes tipped with buff; the feathers of the back tipped with whitish buff; rump feathers gray edged with buffy white; lores and a superciliary stripe whitish; below white with a faint buffy wash and some irregular black vermiculations on the sides of throat, breast, and flanks; wings and tail as in the adult male.

The first-year female is indistinguishable from the first-year male.

Tarsus 24-26 mm.; relative tail-length 70-74 per cent of wing-length.

Upolu $6 \circlearrowleft ad.$ $3 \circlearrowleft ad.$	Wing 94–98 (96.5) 93–95 (94.5)	TAIL 67-69 (67.8) 64-69 (67.2)
Savaii 5 ♂ ad. 8 ♀ ad.	93.5–98 (96.2) 93–97.5 (95.5)	63.5-72 (67.9) 63-69 (66)

RANGE.—Upolu and Savaii Isls., Samoa. Wetmore, 1925, Ibis, p. 848, makes

Lalage sharpei Rothschild a synonym of maculosa, although in reality the two names refer to two different species of Lalage occurring in Samoa.

Lalage maculosa whitmeei Sharpe

Lalage whitmeei Sharpe, 1878, Mittheil. K. Zool. Mus. Dresden, I, p. 371.—Savage I.

SUBSPECIFIC CHARACTERS (Adult Male).— Similar to maculosa, but differing in the darker color of the rump which is gray with black tips; upper tail-coverts with white tips; crown black; a broad white superciliary not joining the white area on the sides of the neck.

IMMATURE FEMALE.—Back black; upper tail-coverts with buffy terminal bars and black sub-terminals; feathers of crown narrowly edged with brown; slightly barred on flanks and sides of breast; superciliary very broad.—White on tail about 22 mm.

Wing, ♂ 99, ♀ 98.

This description is based on two specimens in the Mus. Comp. Zoöl. at Cambridge.

RANGE.—Savage (Niue) I.

Lalage maculosa futunae, new subspecies

Type.—No. 251607, Amer. Mus. Nat. Hist.; ♂ ad.; Futuna I.; May 7, 1925, J. G. Correia.

SUBSPECIFIC CHARACTERS.—Similar to maculosa, but slightly smaller; rump darker, the feathers of the same color as the back but edged with white; post-ocular streak narrower; more white on upper wing-coverts; bill slightly longer (15, 15.5 as against 13–14.5). The amount of white on the outermost tail-feathers measures about the same (12, 13.5).

From the Tonga race, to which it seems less closely related, these birds differ by being smaller and by having no indication of a nuchal collar or white tips on the feathers of the back. The rump also is much darker and the amount of white on the tail more restricted. Tarsus 23, 25; relative tail-length 70, 73 per cent of wing-length.

	Wing	TAIL
$2 o^{-1} ad$	91, 94	67, 66

RANGE.—Futuna I., Horne Isls.

Although there are only two specimens in the Whitney Collection they are so clearly distinct from specimens of the other races, that it seems justified to describe them as new.

Lalage maculosa keppeli, new subspecies

Type.—No. 250637, Amer. Mus. Nat. Hist.; of ad.; Keppel I.; Aug. 25, 1925; J. G. Correia-Bubselfic Characters.—Similar to maculosa but slightly farger; feathers of back from nape to rump broadly tipped with white, the

¹ Measured along the shaft of the inner web of outermost tail-feather.

nape largely white, forming a poorly defined nuchal collar; feathers of the upper back with broad white spots on the outer web; rump paler gray, white superciliary stripe wider and continuing down to join the whitish collar; tail more broadly tipped with white (16-21). Tarsus 24-27 mm.; relative tail-length 69-72 per cent of wing-length.

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	Wing	TAIL
\mathbf{Keppel}		
$5 \circlearrowleft ad.$	98-100 (99)	67-70 (68.5)
5 ♀ ad.	96-99.5 (98)	65-71 (68)
Boscawen		
$7 \circlearrowleft ad.$	96-103.5 (100)	68-74.5 (71)
2 9 ad.	95, 98	63, 68

RANGE.—Keppel (Niuatobutabu) I. and Boscawen (Tafahi) I. Six of the males from Boscawen have very dirty, stained breast feathers.

Lalage maculosa vauana, new subspecies

Type.—No. 250614, Amer. Mus. Nat. Hist.; ♂ ad.; Vavau I., Tonga Isls.; Aug. 11, 1925; R. H. Beck.

Subspecific Characters.—Similar to maculosa but slightly larger; crown with white streaklets; white on the sides of the neck extended dorsally to form the beginning of a nuchal collar, occasional feathers on the back faintly tipped with white; rump more gray; more white on tailfeathers (15–18). From whitmeei this bird differs in the color of the rump as it does also from futunae, a somewhat smaller race. From keppeli it differs in having an incomplete collar, slightly less white on the tail and by not having the broad white tips to the feathers on the back.

The adult female resembles the female of maculosa but with more pronounced streaklets on the crown; more white on the sides of the neck; rump purer gray, less buffy. Tarsus 25.5-27.5; relative tail-length 67-72 per cent of wing-length.

	Wing	TAIL
Ovaka		
1 9 ad.	92	
Vavau		
9 ♂ ad.	94.5-101 (97.2)	64-70.5 (67.7)
1 Q ad.	91	66
Kapa		
$1 \circ$ ad.	93.5	65
Euakapa		
$1 \circ^{\!\scriptscriptstyle T} \operatorname{ad}.$	95.5	63
Late		
1 ♀ ad.	96	62

RANGE.—Ovaka, Vavau, Kapa, Euakapa, and Late (Vavau group), Tonga Isls.

Lalage maculosa tabuensis, new subspecies

Type.—No. 250568, Amer. Mus. Nat. Hist.; ♂ ad.; Tongatabu I., Tonga Isls.; July 6, 1925; J. G. Correia.

Subspecific Characters.—Differs from vauana in the more pronounced nuchal collar and the greater amount of white edging on the feathers of the back. Many of the feathers of the uppermost back have a narrow hidden white longitudinal streak alongside the shaft on the outer web. From keppeli it differs by having the edging and particularly the hidden longitudinal streaks much less pronounced; less white on tail (15–18.5).

The adult female of tabuensis has much more brownish upper parts as well as a more pronounced white collar and edging to the feathers of the back than vauana. From keppeli it differs in the same way as the male, also by having the crown and back much browner, less blackish. Tarsus 25–27.5; relative tail-length 68–71 per cent of wing-length.

		Wing	TAIL
Tongatabu	1 ♂ ad.	98	68.5
Eua	2 ad.	96, 101.5	64, 68
Kelefesia	$3 \circlearrowleft ad.$	98.5-99	67.5 - 69
	1 ♀ ad.	95	67.5
Namuka	$1 \supset ad.$	96	67.5
Mango	$1 \supset ad$.	99	70
	1 9 ad.	95	66
Tofua	$2 \nearrow ad.$	94.5,99	64, 67
	$2 \ Q \ ad.$	92, 94	60, 65
Kao	1 \(\text{ad.} \)	93	60
Fotuhaa	$1 \circlearrowleft ad.$	96.5	64
Tongua	1 ♂ ad.	96	66
Uanukuhahaki	$3 \circlearrowleft ad.$	95 - 97.5	65-67
	1 9 ad.	96.5	64
Oua	$2 \circlearrowleft ad.$	97.5,98	65, 68
Uoleva	$2 \circlearrowleft ad.$	98, 99	67, 70
	1 ad.	95.5	63.5
Foa	$2 \nearrow ad.$	94, 98	67, 70
	1 9 ad.	91	63

RANGE.—Tonga Isls., except Vavau group; Tongatabu Eua and (subspecies) Kelefesia, Tonumeia, Telekitonga, Mango, Namuka, Tofua, Kao, Fotuhaa, Haafeva, Tongua, Uanukuhahaki, Oua, Uoleva, Lefuka, and Foa.

Although we have included the population of the central Tonga Isls., the Haapai group, within the range of *tabuensis*, these birds differ slightly by having somewhat more white on the tips of the feathers of the back. It does not seem to us that the difference is pronounced enough to justify separation.

Mathews (Syst. Av. Austr., II, p. 548), in a footnote, has pointed out that Turdus pacificus Gmelin is not applicable to any Lalage. It is apparent from Gmelin's description (Syst. Nat., I, pt. 2, 1789, p. 813) that his bird must have been much darker below and lacking any white on the

TAIL.

lores, wings or rump. It is most likely that Gmelin's pacificus refers in reality to Clytorhynchus heinei (Finsch and Hartlaub), but as the type is no longer in existence, as inquiries at the British and Vienna museums have revealed, the exact identity of pacificus can never be proved, and it seems best to discard this name as unidentifiable.

Lalage maculosa nesophila, new subspecies

Type.—No. 251463, Amer. Mus. Nat. Hist.; ♂ ad.; Ongea Levu I., Fiji Isls.; July 30, 1924; R. H. Beck.

Subspecific Characters.—Most similar to keppeli, but differs by having much less prominent white tips to the feathers of the back and a less well-defined nuchal collar; white on tail somewhat reduced (12–18.5) as against (16–21). Under parts slightly more washed with buff. The female differs from that of keppeli by having a decidedly more brownish cast to the feathers of the upper parts.

Similar to tabuensis but more prominent streaklets on crown and averaging more white on the tips of the feathers of the back; white streaks on the feathers of the upper back much more pronounced; less white on tail; buffy wash on lower parts more distinct. Tarsus 25–26.5; relative tail- ength 65–73 per cent of winglength.

Range.—Lau Archipelago (Ono Ilau, Turtle, Ongea Levu, Fulanga, Yangasa Cluster, Marambo, Kambara, Wangava, Tavunasithi, Namuka Ilau, Mothe, Olorua, Oneata, Aiwa, Lakemba, Matuku, Vatu Vara, and Yathata), Fjii Isls.

Birds from the three islands (Matuku, Vatu Vara, and Yathata) closest to the main Fijian islands show a slight tendency toward *woodi* in their smaller size, somewhat more rusty, less glossy color of the back, and reduced collar.

The barred maculosa forms

Lalage maculosa woodi Wetmore

Lalage woodi Wetmore, 1925, Ibis, p. 845, Pl. xxvi.—Taveuni I., Fiji.

Subspecific Characters.—Similar to maculosa but smaller; crown (in some specimens) with white streaklets; feathers of the upper back with a partly concealed white spot, broader on the outer web; feathers of back and scapulars black, lightly tipped with buffy white; white on wing-coverts somewhat reduced; white tips on outermost tail-feathers somewhat smaller (10–14). Under parts white with a buffy tint; extensive black V-shaped barring on the feathers of the cheeks, sides of the neck, flanks, and in some specimens across the breast and upper abdomen. The feathers of the posterior end of

Wing

		WING	1 A11,
Ono Ilau	$1 \oslash ad.$	96.5	69
	$2 \ Q \ ad.$	97, 97.5	65, 70
Turtle (Vatoa)	$3 \nearrow ad$.	98-99.5	67-70
	$3 \ Q \ ad.$	96-99	67-69
Ongea Levu	$5 \circ \!\!\! ^{\scriptscriptstyle 7} \mathrm{ad}.$	96.5-99 (97.6)	65-69 (66.8)
_	$2 \ \ $ ad.	95, 95	63, 64
Fulanga	$6 \nearrow ad.$	96-99.5 (97.5)	64-69 (65.5)
_	$2 \ Q \ ad.$	92, 94.5	64, 63.5
Yangasa Cluster	$1 \ Q \ ad.$	92.5	64
Marambo	$1 \nearrow ad$.	97	69
	$1 \ Q \ ad.$	96.5	65
Kambara	1 \(\text{ad.} \)	93	65
Wangava	$1 \ Q \ ad.$	95	66
Tavunasithi	$4 0 \mathbf{ad}.$	95-100 (97.2)	63-67 (64.4)
	1 ♀ ad.	94	64
Namuka Ilau	$4 \circ \hspace{-0.5em} \operatorname{ad}.$	97-99 (98.2)	68-72 (69.5)
	$4 \ Q \ ad.$	94-99 (96.8)	66, 68
Mothe	$4 \nearrow ad.$	94-98 (96.1)	68-71 (69.5)
Olorua	$1 \sigma \text{ad}.$	98.5	69
	$2 \ Q \ ad.$	95.5, 97.5	66
Oneata	$3 \circlearrowleft \mathrm{ad}$.	95-100 (97.9)	66-70 (67.6)
	1 ♀ ad.	94.5	65
Matuku	$3 \circlearrowleft ad.$	94-97 (95.6)	64.5-66 (65.3)
ver to the	$3 \ $ Q ad.	91.5-95 (93.3)	65-68 (66.2)
Vatu Vara	$4 \supset ad$.	93-98 (94.9)	60-67 (63.7)
	$2 \ Q \ ad.$	92,94	62,64
Yathata	$2 \circlearrowleft \operatorname{ad}.$	94,95	66,64.5

the superciliary stripe are barred and, in some specimens, this pattern is carried down to join the barred neck feathers.

From nesophila this bird differs by its smaller size, no indication of a collar, and by having less pronounced tips on the feathers of the back; rump darker and more buffy; less white on tail; extensive barring on under parts.

The female differs by the same characters as the male. Tarsus 23–25; relative tail-length 68– 72 per cent of wing-length.

	Wing	TAIL
Ngamea		
5 ♂ ad.	93-95.5 (94.1)	63-65 (63.8)
Taveuni		
$3 \circlearrowleft \mathrm{ad}.$	90.5-94 (92.9)	60-64 (61.8)
$2 \ Q \ ad.$	90, 95	58, 61
Kio (Kioa)		
$5 \circlearrowleft ad.$	85-91 (87.8)	59-65 (61.8)
$1 \ \circ ad.$	86.5	61
Vanua Levu		
$4 0 \mathbf{ad}.$	85.5 - 92.5 (88.6)	62, 63.5
$6 \ $ ad.	85-87.5 (86)	58-61 (59.6)

Range.—Eastern group of the main Fiji Isls. (Ngamea, Taveuni, Kioa, and Vanua Levu).

The populations from the northeastern Fijian islands represent a continuous cline from Ngamea to Vanua Levu (and continued by the Ovalau race) involving the following characters: decrease of size, increase of brown on the back, and increase of buff color and barring on the under parts. In order to show the trend of variation more clearly a description of the different populations follows:

NGAMEA.—Largest; very dark above with gray rump and reduced tips on back feathers; limited amount of barring on sides of neck and breast; faint buffy wash on breast and flanks. Birds from Ngamea as might be expected are closest in general appearance to nesophila.

TAVEUNI.—Typical woodi.

Kioa.—Two of five adult males have a good deal of brown on the back, particularly in the scapular area (due to wear). All have slightly more buff on the rump and three have rather heavy barring below.

Vanua Levu.—There is some evidence for believing that there are two populations on this island. December birds (from Thakandrove Peninsula) are close to typical woodi, while two February birds (Western Vanua Levu) have more brown on the back, buffy gray rumps and a heavy buffy wash on the sides of the neck; under parts rather heavily barred.

The populations on the following islands, although still belonging to the same cline, are too distinct to be included with woodi.

There is a graded series of populations, as stated above, with the Ngamea birds forming the eastern extreme and the Ovalau birds the western one. Where the line is to be drawn, is largely a matter of opinion, but we believe that it is best to include Vanua Levu with the Taveuni race, and the small islands off Vanua Levu with the Ovalau race.

Lalage maculosa mixta, new subspecies

Type.—No. 251543, Amer. Mus. Nat. Hist.; of ad.; Ovalau I.; Oct. 22, 1924; Mrs. Correia.

Subspecific Characters.—Similar to woodi but slightly smaller; back rusty brownish black; rump darker, more buffy; buffy wash more pronounced on sides of neck and under parts; barring somewhat more extensive and carried right across the chest; same amount of white on tail (10–14.5).

The female differs from that of woodi by being somewhat more brownish on the upper parts; tips on the feathers of the back somewhat more buffy producing less of a contrasted or barred effect. Other characters differ as in the male. Tarsus 23–24.5; relative tail-length 69–72 per cent of wing-length.

	Wing	TAIL
Mathuata		
$2 \supset ad$.	81.5,88	61,64
$4 \ Q \ ad.$	82 - 86.5	60, 61
Yendua (Yandua)		
1 ♀ ad.	88	61
Ovalau		
$4 \supset ad$.	86.5-89 (87.8)	62-65 (63.3)
$1 \ Q \ ad.$	87	59
Matathoni		
$1 \supset ad.$	87	60
Yasawa		
$1 \supset ad$.	89	61.5

Range.—Ovalau and (subsp.?) Mathuata, Yandua, Naviti, Matathoni Levu, and Yasawa Isls., central and northern Fijian group.

In the Whitney Collection, there are specimens from several of the smaller islands which apparently belong to this race, but show a tendency toward *woodi* in some characters:

Mathuata.—One adult male shows somewhat more black on the back and rather less barring on the lower parts than Ovalau birds.

NAVITI.—An immature male is very blackish above but otherwise agrees well.

MATATHONI.—An adult male is rather less buffy below and with more reduced barring than typical Ovalau birds.

YASAWA.—An adult male is slightly more blackish on the upper parts.

Lalage maculosa pumila Neumann

Lalage nigra pumila Neumann, 1927, Ornith. Monatsb., XXXV, p. 19.—Viti Levu, Fiji Isls.

Subspecific Characters.—Similar to woodi but slightly smaller; upper parts suffused with rusty brown, the back especially being very dark brown; rump tawny gray; under parts slightly more buffy and much more heavily barred.

From *mixta* this race differs by being much browner, less blackish, on the back, and by having the rump more suffused with tawny; white on tail somewhat more reduced (9-13). Tarsus 22.5-24.5; relative tail-length 67-72 per cent of wing-length.

Wing Tail
Viti Levu

5 ♂ ad. 84–90 (87.3) 58–65 (60.7)
7 ♀ ad. 83–92 (86.4) 55–62 (59.3)

RANGE.—Viti Levu I., Fiji Isls.

Lalage maculosa soror, new subspecies

Type.—No. 251552; Amer. Mus. Nat. Hist.; of ad.; Kandavu I.; Nov. 10, 1924; R. H. Beck. Subspecific Characters.—Similar to pumila, but with much less barring on the feathers of the under parts and more white on the tips of the outermost tail-feathers (13–16.5 as against 9–13). Tarsus 25–25.5; relative tail-length 70–75 per cent of wing-length.

	Wing	TAIL
Kandavu $5 \circlearrowleft ad.$ 3 \circ ad.	87-92 (88.2) 87-91 (89.1)	60-65 (61.9) 58-62 (59.8)

RANGE.—Kandavu I., Fiji Isls.

This race seems to be notable by having a well-contrasted black cap and nape and dark brown back. Although a similar condition exists in *pumila*, the line of demarcation is not as clearly defined. The five adult males in the Whitney Collection are in slightly worn plumage, but not worn enough to warrant the supposition that the black-capped plumage is a composite of a freshly molted crown and a worn back.

Lalage maculosa rotumae Neumann

Lalage nigra rotumae NEUMANN, 1927, Ornith. Monatsb., XXXV, p. 19.—Rotuma I.

Subspecific Characters.—Similar to maculosa but smaller; feathers of the upper back with hidden buffy white spots; rump black with buffy tips to the feathers; under parts with a good deal of barring on the sides of the neck, breast, and flanks; a very pronounced bright tawny wash on throat, breast, and sides of neck; wing with a more tawny less white edging to the feathers; white on tail about the same (11–15).

From woodi, to which it seems to be most

closely related, rotumae differs by being larger and by having a much more tawny coloration on the tips of the feathers of back and rump, on wing-coverts, and on the under parts. The female differs as the male. Tarsus 23-24.5; relative tail-length 71-74 per cent of wing-length.

	Wing	TAIL
Rotuma		
$12 \circlearrowleft \mathrm{ad}.$	91-97 (94.2)	63.5-70 (68.6)
9 ♀ ad.	90.5-99.5 (94.7)	62.5-68 (65.3)

Range.—Rotumah I. (north of the Fiji group).

This very distinct race comes closest of all the outlying island populations to woodi, while at the same time showing a trend toward maculosa in the larger size and very dark, lightly barred upper parts.

The maculosa forms of Southern Melanesia

West of the Fijian islands, this species is confined to the three larger islands of the Santa Cruz group (Vanikoro, Utupua, and Santa Cruz), and to a few of the larger islands of the New Hebrides (Espiritu Santo, Malo, Pauuma, Epi, and Efate). No specimens were secured by the Whitney expedition from the other groups of islands in the area. The population from these islands shows an interesting combination of characters. The males have the general coloration of blue-black upper parts and very indistinct, nearly absent, barring below of the maculosa group, while the females have the dull brown coloration on the upper parts and a tendency toward barring below, as found in the females of the woodi group.

Lalage maculosa vanikorensis, new subspecies

Type.—No. 214203, Amer. Mus. Nat. Hist.; & ad.; Vanikoro I., Santa Cruz group; Sept. 24, 1926; R. H. Beck.

SUBSPECIFIC CHARACTERS.—Adult male. Similar to vauana but smaller throughout; streaklets on crown more pronounced; no trace of a collar; gray on the rump much reduced; shaft-streaks on white lesser and median wing-coverts less pronounced, white on tail about the same (14–18); under parts with faint fragmentary barring on the sides of the neck and flanks.

The adult female resembles the female of pumila rather closely but differs by being smaller, paler brown on the crown with tawny streaklets and with a suffusion of gray in the rump; barring on the under parts very much reduced. Tarsus

22-23; relative tail-length 73, 75 per cent of wing-length.

	Wing	TAIL
Vanikoro 4 ♂ ad.	83-87 (85.3)	63-67 (64.5)
5 9 ad.	83-86 (84.2)	59-64 (62.1)

Range.—Vanikoro I., Santa Cruz group.

Lalage maculosa melanopygia, new subspecies

TYPE.—No. 214207, Amer. Mus. Nat. Hist.; 3 ad.; Utupua I., Santa Cruz group; Sept. 28, 1926; J. G. Correia.

SUBSPECIFIC CHARACTERS.—Similar to vanikorensis but upper parts more uniform black; streaklets and barring on crown and back nearly absent; rump black with faint white tips; tail with equal amount of white (12.5–18).

The female differs from the female of vanikorensis as the male, the general tone of the upper parts being somewhat darker; rump rather blackish. Tarsus 22, 22.5; relative tail-length 74, 76 per cent of wing-length.

	Wing	TAIL
Utupua		
$2 \nearrow ad.$	85, 87	65, 65
1 ♀ ad.	84	65

RANGE.—Utupua I., Santa Cruz group. Two immature birds are not quite as dark as the adult female, but differ from the female of *vanikorensis* by being slightly darker on the upper parts, particularly the rump.

Lalage maculosa subspecies

	Wing	TAIL
Santa Cruz		
$2 \circ$ ad.	89.5,90.5	65, 66
1 ♂ imm.	89.5	67

Range.—Santa Cruz (Ndeni) I., Santa Cruz group.

These three specimens although close to *melanopygia* are larger with much paler rumps. It seems best to postpone the naming of this apparently undescribed form until more material is available.

Lalage maculosa modesta, new subspecies

Type.—No. 212836, Amer. Mus. Nat. Hist.; ♂ ad.; Pauuma I., New Hebrides Isls.; Aug. 12, 1926; R. H. Beck.

SUBSPECIFIC CHARACTERS.—Similar to vanikorensis but larger; rump more gray; under parts with a greater tendency to barring on the sides of the neck and breast; a distinct buffy wash, more pronounced on the breast; white on tail about the same (12-17).

The female differs from the female of vanikorensis by being larger; the upper parts more tawny and somewhat paler, particularly on the rump. From pumila this bird differs by having the upper parts, particularly the rump, paler, and by lacking the barring on the under parts. Tarsus 24, 24; relative tail-length 75–79 per cent of wing-length.

	Wing	TAIL
Pauuma		
$1 \ \mathbf{\sigma} \ \mathrm{ad}.$	90	68
4 \(\text{ad.} \)	87-90.5 (88.5)	66-70 (67.8)
$\mathbf{E}\mathbf{p}\mathbf{i}$, ,
$2 \circ \overline{} ad.$	89, 91	65,72
1 φ ad.	95	72
Espiritu Santo		
$1 \circ 7 \text{ ad.}$	88	63
Malo		
$1 \circ$ ad.	86	68

Range.—Northern and Central New Hebrides (Espiritu Santo, Malo, Pauuma, and Epi).

Two specimens from Espiritu Santo and Malo are less barred on the under parts and slightly smaller than Pauuma and Epi birds, but a larger series is needed to confirm this difference.

Lalage maculosa ultima, new subspecies

Type.—No. 212834, Amer. Mus. Nat. Hist.; \circlearrowleft ad.; Efate I., New Hebrides Isls.; July 21, 1926; R. H. Beck.

Subspecific Characters.—Similar to modesta but larger; streaklets on crown and barring on back more pronounced; gray area on rump more extensive and more uniform; under parts pure white with virtually no trace of a buffy wash; white on sides of neck more extended dorsally.

The female differs from the female of *modesta* by averaging somewhat larger and by being paler above with a very pronounced pale grayish rump; white on tail about the same (14.5-17.5). Tarsus 23, 23.5; relative tail-length 73, 74 per cent of wing-length.

	Wing	TAIL
Efate		
$2 \sigma \operatorname{ad}.$	95, 96	70, 70.5
$3 \ Q \ ad.$	91-94.5 (92.6)	70-74 (71.7)

RANGE.—Efate I., Central New Hebrides.

The male of the Efate race is remarkably close in general coloration and size to the male of *tabuensis*, the only appreciable difference being the very uniform gray appearance of the rump. The female, on

the other hand, is quite distinctive and differs appreciably from all other races of maculosa.

Lalage sharpei

This species is apparently most closely related to Lalage maculosa pumila from which it differs by being much smaller, by having no sexual dimorphism, the plumage of both sexes being of a characteristically juvenile type, and by having a white, not brown iris. Both sexes have a yellow bill and lack the prominent white wing patch. For this reason Mathews separated sharpei from Lalage and placed it in the genus Oscarornis (1928, Novit. Zool., XXXIV, p. 372). Although these plumage differences are very great, it is apparent that the pattern of the plumage is arranged precisely in the same way as in the woodi group, that in fact sharpei is an offshoot of the original Lalage maculosa population in the Fiji islands which has evolved in a retrogressive manner, and changed to such a degree that it did not produce hybrids with the succeeding wave of immigrants to Samoa, the maculosa group.

Lalage sharpei sharpei Rothschild

Lalage sharpei Rothschild, 1900, Bull. Brit. Orn. Club, X, p. XI, Upolu Island, Samoa Group.

Subspecific Characters.—Upper parts hair brown, shafts of the feathers slightly darker; rump darker, nearly olive-brown; wings blackish brown with pale edges; tail colored as back with very faint buff tips; outermost tail-feathers with poorly defined whitish tips (13–16.5); under parts white with a buffy wash and irregular dark brown barring on sides of neck, across breast, and flanks. "Tris white, bill yellow, feet brownish brown." Tarsus 22.5–23.5; relative tail-length 64–68 per cent of wing-length.

	Wing	TAIL
Upolu		
$5 \supset ad$.	79-86 (82.4)	55.5,56
$1 \ Q \ ad.$	81	54

Range.—Upolu I., Samoan group.

It is interesting to note that this species has a much more rounded wing than *maculosa* or *leucopyga*, the sixth primary being nearly as long if not as long as the second.

Lalage sharpei tenebrosa, new subspecies

Type.—No. 206142, Amer. Mus. Nat. Hist.; ♂ ad.; Savaii I., Samoa Group; May 23, 1924; R. H. Beck.

Subspecific Characters.—Similar to sharpei but much darker; upper parts dark olive-brown (Bistre of Ridgway); rump sepia; wings very dark blackish brown; tail as the back; ear-coverts and sides of hind-neck much darker, almost blackish in some individuals; under parts white with a buffy or tawny wash on sides of neck, on the breast and, extensively, on the flanks; barring on the under parts much heavier; extent of whitish on tail somewhat greater (14–19). Tarsus 22, 23; relative tail-length 68–72 per cent of wing-length.

	Wing	TAIL
Savaii		
4 ♂ ad.	78-83 (80.7)	55-60(57.1)
5 ♀ ad.	78-85 (80.6)	54-57 5 (55.8)

Range.—Savaii I., Samoa group.

CHARACTER GEOGRAPHY IN THE AUREA GROUP

Geneticists are becoming increasingly interested in the geographical distribution of certain genes within the geographical range of wild species and about the possible history of the point of origin of the mutation and its subsequent spread. Nothing is known about the genetics of *Lalage*, but there is, of course, no doubt that the various characters, used by the taxonomist, have a genetic basis. A discussion of the geographical distribution of these characters is, therefore, of general interest.

Most of the variable characters in the *Lalage aurea* group are such as vary in a similar manner in many other genera of the Campephagidae. Such characters are:

1.—General size. 2.—Proportions (as relative length of tail and bill). 3.—Degree of barring on upper and under parts. 4.—Presence and size of white marks in otherwise black regions of the body (superciliary, scapulars, upper wing-coverts, tips of tail-feathers). 5.—Color of rump. 6.—Presence and degree of buff or rufous color of under parts. 7.—Color (brown, gray, or black) of upper parts (in both sexes). 8.—Degree of sexual dimorphism, etc.

In regard to most of the characters just listed there are different potentialities within the genus. Often these latent potentialities are realized in different parts of the range, as is neatly demonstrated on the map (Fig. 1). Most of the mentioned

characters vary rather independently and it would, therefore, be a mistake to base a classification on only one of them. The barring has been lost independently at least five times in the Lalage aurea group (atrovirens, yorki, ottomeyeri, conjuncta, maculosa), and it would, therefore, be quite

an artificial arrangement to group the unbarred birds together as opposed to the barred ones. The same could be said of any other character. A more detailed analysis of some of the characters permits the following conclusions (see also tabulation):

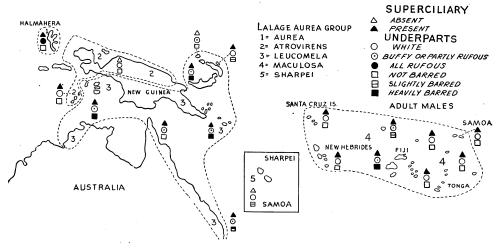


Fig. 1. Geographical variation of three (of a total of about fifteen) taxonomically important characters of the *Lalage aurea* group. A double invasion, first by *sharpei*, later by *maculosa*, has taken place on Samoa.

INDEPENDENT VARIATION OF FOUR CHARACTERS IN Lalage Buff or

$Lalage~({\it o}^{\! 7})$	Barring of under parts	rufous of under parts	Super- ciliary	Rump
aurea—Halmahera		+++	+	Black
moesta—Tenimber			+	Black, white tips
atrovirens-North New				
Guinea				White tips
polygrammica—E. and S.				
New Guinea	++	+	+	Gray, white tips
pallescens—E. Louisiades	+	+	+	Grayish black, white tips
conjuncta-St. Matthias		++		Mostly white
leucomela—E. Australia	+	+	+	Gray
vanikorensis—Santa Cruz	trace		+	Blackish gray,
				pale tips
ultima—New Hebrides	·		+	Gray
pumila—Viti Levu, Fiji	++	+	+	Brown
woodi-Taveuni, Fiji	+		+	Dark gray
keppeli—Keppel			+	Gray, white tips
maculosa—Samoa			+	Black, white tips
sharpei—Samoa	++	+		Brown

(a) Barring.—Completely absent in the species aurea (σ and φ) and atrovirens (σ only). Pronounced in most forms of the species leucomela, but much reduced in yorki, pallescens and albidior (σ only) and absent in ottomeyeri and conjuncta. In maculosa it is noticeable only in the woodi group, but is more or less obsolete in the maculosa and vanikorensis groups. It is rather strong in sharpei.

(b) SUPERCILIARY.—Is present in all forms except atrovirens (of north New Guinea), leucoptera (Biak), conjuncta (St. Matthias), and

sharpei (Samoa).

(c) Phaeomelanin on Under Parts.—Strongest in aurea, and present in all forms of leucomela, except ottomeyeri, though often restricted to the under tail-coverts or to a slight wash of the under parts. Barely indicated in some forms of maculosa, absent in most of them and in all the forms of atrovirens.

(d) White on Tail.—Least in aurea, conjuncta, and atrovirens (4-7 mm.) and most in the maculosa forms, particularly keppeli (20 mm.). L. leucomela is intermediate (10-15 mm.).

(e) Size.—The smallest species is *sharpei* (81 mm.), the largest form is, naturally, the subtropical *leucomela* (E. Australia) (104 mm.).

(f) THE RELATIVE TAIL-LENGTH.—The tail is shortest in the smallest species: sharpei (68%), and longest in the largest form: leucomela (86%). Allometric growth is, therefore, clearly involved, although no strict correlation exists. In general the species maculosa has a short tail (69-73%), the aurea-atrovirens group a medium sized tail (76-82%), and the species leucomela a long tail (80-86%), although there are forms of about comparable size in each group.

(g) Degree of Sexual Dimorphism.—There is considerable geographical variation within each one of the three groups: aurea-atrovirens, leucomela, and maculosa-sharpei. The primitive type is probably represented by leucomela with pronounced sexual dimorphism and with the female wearing a "juvenile" or truly feminine plumage, which is strongly barred underneath and grayish or brownish above. In atrovirens the male acquires a strongly masculine plumage (without barring below), but the female is still barred; in aurea the female loses the barring and becomes very similar to the male, except for the gray upper parts. The same process, to a lesser extent, occurs within leucomela, but the barring is always present in the females, even where it is reduced or absent in the males (see under a). The female of conjuncta is still unknown, but can be expected to be barred. Particularly interesting conditions are found in maculosa. The Fijian group (pumila, etc.) represents the primitive condition with slight sexual dimorphism, but male plumage of a rather feminine type (barred below, considerable brown above). Two lines of development branched off from this basic stock, a retrogressive branch, turning into sharpei, which lost its sexual dimorphism in connection with the acquisition by male and female of a similar "juvenile" plumage, and a progressive branch, culminating in maculosa, keppeli, etc., with very masculine males (glossy black above, no barring below) and only slight sexual dimorphism, because the females have acquired a masculine plumage (rather blackish above and nearly without all the barring below). L. m. vanikorensis (etc.) represents a somewhat intermediate condition, the males have already reached a highly masculine plumage, but the females still retain a rather feminine dress, with the result that these forms show a strong sexual dimorphism.

The unique interest of L. sharpei (Samoa) lies in the fact that it can be demonstrated that its primitive plumage is a secondary development. The species fits the requirements of the palaeontologist's rule that "primitive" species should be found on the borders of the range of the genus, but in this case the "primitive" species has not been "forced out" by its more progressive congeners, rather it has "deteriorated" in its isolation.

Other forms of the aurea-group are culmination points of specialization processes, for example, aurea with its complete loss of barring in male and female, and the deep rufous tawny wash of the under parts, otherwise unique in the genus, although approached by conjuncta. Another such specialized peak is L. m. keppeli with its strong albinisation factor. This form not only has the broadest white tail-tips and the broadest white superciliary, but it has white patterns also in a number of body regions which are free of white in the other forms and species of Lalage: There is a white collar across the hind-neck, the feathers of the back have broad white margins, the scapulars have broad white concealed spots, the white superciliaries merge into a white forehead and connect with the white on the sides of the neck, etc. To a lesser degree a similar albinisation is apparent in some of the neighboring forms (nesophila, tabuensis, etc.). It is important to point out that it does not occur anywhere else in the range of the genus Lalage.

In conclusion we might mention some of the potentialities of Campephagidae which are not realized in the genus *Lalage*. For this we only have to point to the closely related genus *Campochaera* (type, *sloetii*; range, New Guinea). This genus differs from *Lalage*: (a) by the presence of yellow lipochrome above and below, (b) a black throat pattern, and (c) by elongated and pointed tail-feathers.

leucopyga group

Lalage leucopyga

This group (with the single species leucopyga) apparently branched off from its ancestral stock at a very early date, and it is, therefore, impossible to trace its exact relationship. In some characters, such as the white pattern on the wing-coverts, it seems to approach L. sueurii tricolor. other characters (coloration of rump, shape of bill, sexual dimorphism), it seems to be closer to the aurea- group (atrovirens, etc.). The fact that L. sueurii tricolor seems to be a rather recent immigrant in Australia and that most of the endemic element of southern Melanesia seem to be of Papuan origin. makes it very likely that leucopyga is more closely related to the aurea assemblage than to L. s. tricolor.

In comparison with the other species of the genus the leucopyga group has softer, more downy plumage, lacks barring of the under parts (even in the female dress), has usually a pronounced buffy wash on the under parts and, in general, has more white on the greater upper wing-coverts. In its long isolation on the islands of southern Melanesia, it developed some rather unusual structural peculiarities. The tail is rather long in most forms of this species, up to 97 per cent of the wing-length. basal part of the shafts of the rump feathers is rather soft, not stiffened as in most Lalage. These characteristics were considered a sufficient excuse by Gould to erect a new genus Symmorphus (= Diaphoropterus Oberh.). In our opinion there is no justification for keeping leucopyga in a separate genus. Its coloration indicates its close relationship with the other species of Lalage, and both relative tail-length and lack of stiffness in the rump-feathers are nothing more than specific characters.

Lalage leucopyga leucopyga (Gould)

Symmorphus leucopygus Gould, 1838, Synops. Birds Austr., pt. IV, App., p. 3.—"New South Wales," in error for Norfolk I.

ADULT MALE (Normal Plumage).—Crown and

back glossy black, rump white, strongly tinged with buff; under parts white, strongly washed with buff, particularly on breast and flanks; an indistinct white spot on lores; wing black, secondaries and inner primaries narrowly bordered with white; almost all of the lesser, all median, and the inner greater upper wing-coverts white; upper tail-coverts gray; two central pairs of tail-feathers all black, others broadly tipped with white; extent of white on outermost tail-feather is 26–29 mm.¹

ADULT MALE (Retarded Plumage).—Similar to immature plumage, but alula all dark brown, and wing and tail-feathers broad as in adult. Occasionally a few glossy black feathers are interspersed among the feathers of the crown and back, particularly the crown. Of a series of 28 adult males from Norfolk I., 10 are in the retarded plumage.

IMMATURE MALE (First Year).—Crown and back dark blackish brown; rump white, heavily suffused with buff; under parts white, strongly washed with buff (somewhat more buffy than the adult); lores white; wing dark brown, secondaries and inner primaries narrowly bordered with pale tawny to white, alula tipped with white, lesser and median wing-coverts strongly washed with tawny; inner greater upper wing-coverts buffy white. Two central pairs of tail-feathers brown narrowly tipped with white, others brown tipped as in the adult. The wing and tail-feathers are rather narrower than the adult, and the basal half of the brown mandible is usually pale yellowish.

NESTLING (Juvenile Plumage).—Above dark brown, the feathers of the crown and back widely banded with buffish white; rump white, tinted with buff; below white, the chest tinted with buff, some of the feathers of the throat and chest faintly streaked with brown; wings and tail as in the immature.

ADULT FEMALE.—As the immature, except for the adult character of the wing and tail-feathers and the solid color of the alula. Indistinguishable from the adult male in retarded plumage.

Tarsus 24.5 mm.; length of tail 92-95 per cent of wing-length.

o⁷, ♀ ad.—Wing, 87-93; tail, 83-88

RANGE.—Norfolk I.

Lalage leucopyga montrosieri Verreaux et des Murs

Lalage montrosieri Verreaux et des Murs, 1860, Rev. et Mag. de Zool., p. 431.—New Caledonia (fig. Sarasin, Pl. 11, fig. 9).

Muscicapa naevia GMELIN, 1789, Syst. Nat., I, pt. II, p. 994, preoccupied by Muscicapa naevia Boddaert, 1783, p. 34.

SUBSPECIFIC CHARACTERS.—Similar to leucopyga, but smaller; rump almost pure grayish white, only faintly tinted with buff; below white, lightly washed with buff; amount of

¹ Measured on inner web along shaft.

white on lores variable, but tends to be much more reduced than in the typical race; less white on upper wing-coverts; two central pairs of tail-feathers black, narrowly edged and tipped with white; the outer tail-feathers with broad white tips; the outermost tail-feathers about half white (14–25 mm.).

The female and retarded male plumages are like those of *leucopyga*, but less suffused with buff on the rump and below.

Tarsus 22–24; relative tail-length 94–95 per cent of wing-length.

	$\mathbf{W}_{\mathbf{ING}}$	TAIL
8 ♂ ad.	85-90.5 (88)	81-84 (83)
7 ♀ ad.	83-87.5 (86)	79-83 (81)

Range.—New Caledonia.

Only one specimen (No. 564513, in the American Museum's collection collected on Cut Panie, Aug. 25, 1914) appears to be a male in retarded plumage. The tail though molting is adult in character as are the wings. The retarded plumage seems to be much rarer in this form than in the Norfolk Island race.

Lalage leucopyga simillima (Sarasin)

Diaphoropterus naevius simillimus Sarasin, 1913, "Vög. Neu Caled. Loyalty Ins.," p. 28, Pl. 11, fig. 10.—Loyalty Isls.

SUBSPECIFIC CHARACTERS.—Similar to montrosieri but slightly smaller, with a shorter tail and with less white on tail (11.5-19 mm.). The white area on the wing-coverts is more restricted. Below, the buffy wash seems to be confined to the breast in the male. The rump is almost pure white or grayish white.

The female of *simillima* differs from the female of *montrosieri* in the much darker, almost blackish brown, color of the upper parts, which is continuous throughout and does not become paler at the forehead as in the New Caledonia and Norfolk Island birds.

Tarsus 21-22; relative tail-length 84-91 per cent of wing-length.

	WING	TAIL
Maré		
$1 \supset ad.$	82	72.5
$1 \ Q \ ad.$	87	78.5
Lifu		
$5 \nearrow ad$.	84-87 (86)	70-78 (75)
4 \(\text{ad.}	83-88 (85)	71-79 (75)
Uvea		
$6 \nearrow ad$.	82-88 (85)	75-80 (77)
$2 \ \circ ad.$	82, 83	74,77

Range.—Loyalty Islands and (subsp.) southern New Hebrides (Erromango, Tanna, Aneiteum).

In the American Museum series there are no males in retarded plumage for this or any of the following races.

The Loyalty Islands' population is actually intermediate between the populations of the southern New Hebrides and New Caledonia, and it is unfortunate that it was named instead of the New Hebrides bird. There is too much overlap between the two populations to separate the New Hebrides bird, but it seems worth while to record the differences. The general size is larger:

	Wing	TAIL
Erromango		
σ ad.	85-91	80 – 82.5
φ ad.	85	76
Tanna		
$ooledel{ad}$ ad.	89	77 - 82
♀ ad.	81	
Aniwa		
otin ad.	91	78
φ ad.	84 - 85	76
Aneiteum		
ooledare ad.	85-86	76-81.5
φ ad.	84	

New Hebrides birds thus measure, wing, ♂ ad. 85–91, against 82–88, tail 75–82.5, against 70–80. The white on the tail is still more reduced 11.5–17, against 14–19 in birds from the Loyalties. The rump is less whitish, in fact in 4 of the males it is almost pure gray. There is less white in the upper wing-coverts.

No differences could be found between specimens from the four mentioned islands.

Lalage leucopyga albiloris, new subspecies

Type.—No. 212817, Amer. Mus. Nat. Hist.; ♂ ad.; Efate I., New Hebrides; July 2, 1926; R. H. Beck.

Subspecific Characters.—Similar to simillima, but slightly smaller; rump more grayish; the lores are more or less white which in a good many individuals is carried on over the eye to form a pronounced superciliary stripe; median wing-coverts white, others largely black; white area on outer tail-feathers about the same (13– 17.5).

The female agrees with the female of simillima, except that the lores are more prominently white and that there is in many examples a pronounced superciliary streak; rump more grayish; below slightly less tinged with buffy.

Tarsus 2 of ad. 23-24; relative tail-length 93-97 per cent of wing-length.

	Wing	TAIL
Efate		
$1 \supset ad$.	82	76
Mai		
$1 \supset ad$.	86	78
$5 \ Q \ ad.$	82-84	73.5 – 77
Tongoa		
$1 \stackrel{\frown}{\circ} \text{ad.}$	85.5	80
$1 \ \circ ad.$	83	74
Lopevi		
$2 \circlearrowleft ad.$	84,86	81
$3 \ Q \ ad.$	78 - 82	72.5 – 78.5
Malekula		
$7 \triangleleft ad.$	81-87	76 - 84
$1 \ \circ ad.$	79.5	74
Malo		
$1 \circlearrowleft ad.$	86	78
$3 \ Q \ ad.$	80-85.5	72 - 78
Espiritu Santo		
$1 \supset ad$.	82.5	75
$1 \ Q \ ad.$	81	75

Range.—Central and northern New Hebrides: Efate, Lelepa, Mai, Tongoa, Epi, Lopevi, Pauuma, Ambrim, Malekula, Malo, and Espiritu Santo Isls.

The characters of this race are most pronounced on Efate I. Birds from the other islands show a distinct approach toward the following race by having the superciliary stripe less developed or absent. Individual specimens from the more northerly islands cannot be identified with certainty, but the series from these islands agree better with albiloris than with the Banks Islands race.

Lalage leucopyga deficiens, new subspecies

Type.—No. 216109, Amer. Mus. Nat. Hist.; ♂ ad.; Lo I., Torres Isls.; Nov. 5, 1926; R. H. Beck.

Subspecific Characters.—Similar to albiloris, but with less white on tail (8–16) and lacking any pronounced superciliary stripe; lores sometimes with an indication of white. Similar to simillima but with a somewhat longer tail in proportion to the wing, and a longer tarsus; rump grayer; white on wing-coverts much more restricted; much less white on tail. From affinis this race differs by the color of the rump which is grayish instead of white, and by having a great deal less white on the wing-coverts and more white on the tail. Tarsus 24–25; relative taillength 91–94 per cent of wing-length.

	Wing	TAIL
Mera Lava		
$2 \circlearrowleft \mathrm{ad}.$	85.5, 87	77, 81
$1 \ Q \ ad.$	83	75

Gaua		
$2 \ \colon{3}{c}$ ad.	81,83	75, 76
$3 \ $ Q ad.	81-85	71-77
Vanu Lava		
$1 \circlearrowleft \mathrm{ad}.$	81	76
Valua		
$2 \circlearrowleft \operatorname{ad}.$	83.5,84.5	76,78.5
$2 \ Q \ ad.$	80.5,81	71,74
Bligh		
$1 \supset ad.$	81	71
L_0		
$5 \supset ad$.	79 - 85	71-77
$2 \ \circ ad.$	81,82	73, 75.5

Range.—Torres and Banks Isls.

Of a series of 32 specimens in the American Museum's collection of *deficiens*, 4 ad. φ have a well-defined loral spot, while 8 other birds (3 imm. σ , 3 ad. φ , and 2 imm. φ) show the merest trace of white.

Lalage leucopyga affinis (Tristram)

Symmorphus (Lalage) affinis Tristram, 1879. Ibis, p. 440.—Makira Harbour, San Cristoval I,

Subspecific Characters.—Differs from all the other races of leucopyga by having the smallest amount of white in the tail (1-4); the white on the rump is purer than in montrosieri or simillima and very much brighter than in albiloris or deficiens. There is no trace of a superciliary stripe. The amount of white on the wing is variable but about equal to albiloris and deficiens.

The brown on the upper parts of the adult female is paler than in any of the other races particularly on the forehead which in some cases is shaded with tawny-olive. Tarsus 23–25; relative tail-length: 83–88 per cent of winglength.

	Wing	TAIL
San Cristobal		
$7 ^{\circ} \mathcal{A} $ ad.	83-88	70-76
$9 \ \circ ad.$	83-87	70-74
Ugi		
$1 \supset ad.$	90	75
1 Ω ad.	86	76

Range.—San Cristobal and Ugi, Solomon Isls.

A single male from Ugi is larger than any of the birds from San Cristobal, but a larger series is needed to confirm this difference.

It may be interesting to say a few words about the characters which in this species are subject to geographical variation: general size, body proportions (relative size of tarsus and tail), color of the rump (buffy, whitish, gray), amount of white on

tip of lateral tail-feathers and on upper wing-coverts, presence or absence of white loral spot and superciliary, amount of buffy wash on under parts, presence or absence of a retarded male plumage, color of upper parts in female (pale or blackish brown), etc. These ten characters have been used in the description given above of the geographical variation within this species. It is unknown whether or not there are any differences between the races in regard to habits and ecological requirements.