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SOME REMARKABLE NEW BIRDS FROM
DYAUL ISLAND, BISMARCK ARCHIPELAGO,
WITH ZOOGEOGRAPHICAL NOTES

BY
FINN SALOMONSEN

NOONA DAN PAPERS
NO. 9



København 1964

Kommissionær: Ejnar Munksgaard

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Synopsis

The "Noona Dan Expedition" during its visit to the Bismarck Archipelago in 1962 investigated the fauna and flora of Dyaul Island, which was hitherto unexplored. The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of striking endemic forms, the description of which forms the first part of the present paper.

The second part of the paper deals with various zoogeographical problems in connection with the history of the fauna of Dyaul. The morphological differentiation of the endemic forms must have required a certain amount of time, during which the populations were isolated from those of the neighbouring islands (New Ireland and New Hanover). It is noteworthy that the Gazelle Channel, not broader than 14 km, has been broad enough to form an effective barrier. The length of the period of isolation has been roughly estimated on the basis of a comparison with the faunas of similar tropical islands (Philippine Islands, West Sumatran Islands). It is demonstrated that the populations of the main chain of islands in the Bismarck Archipelago are either identical or only slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is explained as primarily the result of a greater evolutionary rate in the Dyaul populations, but a time factor must be involved also. Evidence is given for the assumption that the main islands were mutually connected, forming one or two big islands, when Dyaul had already received its fauna.

A comparison is made between the faunas of Dyaul and of the Hibernian Islands, which latter differ from Dyaul in having a rather impoverished fauna and only slightly differentiated indigenous subspecies. In order to explain these differences an attempt is made to analyse the factors which control island colonization by birds. According to this analysis Dyaul, evidently, has greater possibilities than the Hibernian Islands for colonization by birds.

New Ireland and New Hanover form the origin of the main part of the land-bird fauna in four zoogeographically different groups of islands: (1) The Admiralty Islands and the St. Matthias Islands, (2) The Hibernian Islands, (3) The Duke of York Islands, and (4) Dyaul Island. The zoogeographical differences between these four categories of islands are due to the unequal possibilities for avian colonization and to the differences in the geological history which have been described in the present paper.

Dyaul Island in the Bismarck Archipelago was discovered in 1767 by Lieutenant PHILIPP CARTERET during the celebrated voyage of the "Swallow". CARTERET called the island Sandwich Island, and this name was used for more than a hundred years, and was the most common designation even in the German period (REICHENOW 1899, map; PARKINSON 1907, p. 251; SIEVERS 1910, p. 439). During this period, however, the name Djaul or Djaule began to appear, and this name, spelled Dyaul, is now the official designation of the island.

From a natural history point of view Dyaul is quite unexplored. When planning the itinerary of the "Noona Dan Expedition" I, therefore, included a visit to Dyaul during the contemplated investigation of the Bismarck Archipelago. The visit to Dyaul took place in the period in which I served as scientific leader of the expedition. The results of the ornithological investigation proved so interesting that I organized a second visit to the island, but this could not be arranged until I had already left the expedition.

The island of Dyaul is situated due south of the western end of New Ireland, from which island it is separated by the deep Gazelle Channel (fig. 1). The area of Dyaul is 115 sq. km, *i.e.* of the same size as Feni Islands and somewhat smaller than the Lihir group and the Tabar group north of New Ireland. It is of a longitudinal shape, the length being 30.5 km, the greatest breadth 7.1 km. It consists mainly of raised coral rock, which forms a rolling lowland, with hills reaching altitudes of usually about 50–70 meters, in one place (Mt. Bendemann) raising rather abruptly to an altitude of almost 200 meters. The coastal areas are covered with extensive coconut plantations alternating with native gardens and second growth. Further inland there are scattered patches of well developed original forest, and along the coasts there is in most places a broad zone of mangroves; in a few places beach forest is developed. The island is thinly populated; there are only about two hundred inhabitants gathered in four villages, but to this number should be added the imported New Guinea labour on a few big coconut plantations under Australian management.

The "Noona Dan" called at Lamatau Harbour, on the central part of the north coast of Dyaul, on March 1st, 1962. In the following two weeks, until March 13th, I carried out ornithological collecting and investigations with the nearby village Sumuna as camp, in the first days together with Dr. LORENZ FERDINAND, who, how-

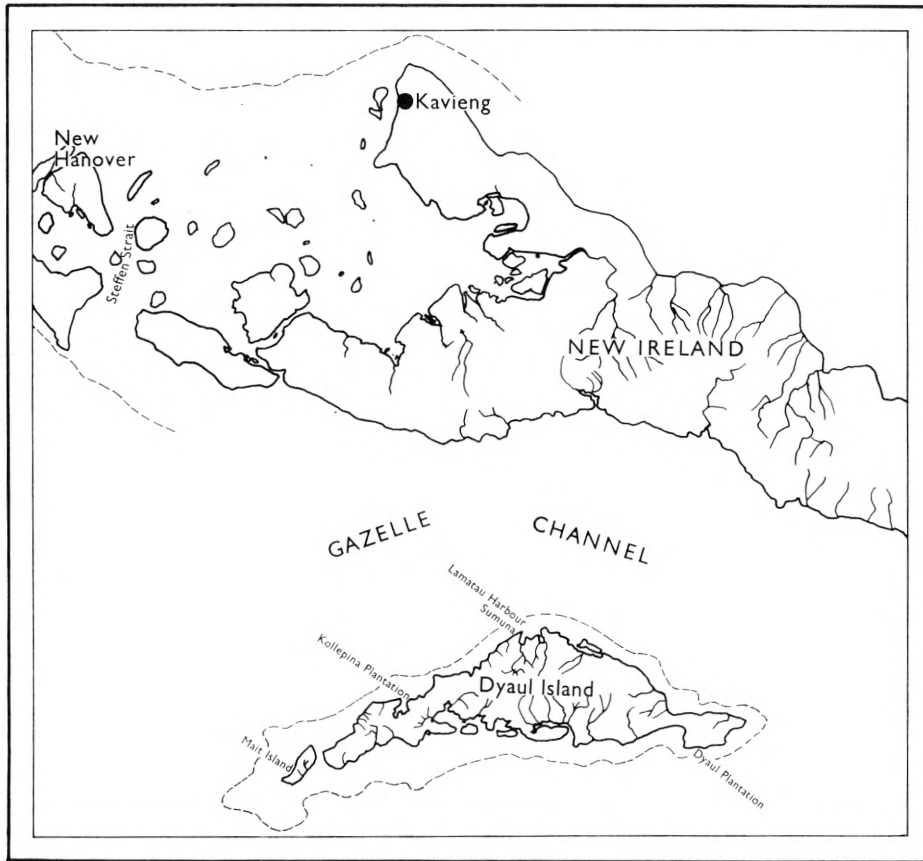


Fig. 1. The situation of Dyaul Island, giving all collecting stations of the "Noona Dan Expedition". The broken line designates the 100 meters line of depths.

ever, had to leave the expedition on March 4th, already. An excursion was made to Kollepina Plantation on the western part of the north coast, and Dr. FERDINAND made a boat trip to Mait Island, mainly with the purpose of studying sea birds. During the second visit of "Noona Dan" Mr. IB TRAP-LIND collected birds at Dyaul Plantation, at the eastern end of the island, from May 30th to June 10th 1962, while the main scientific staff of the expedition worked on Mussau Island. All the collecting stations on Dyaul are shown on the map fig. 1.

My thanks are due to Dr. DEAN AMADON, Chief-Curator of Birds, The American Museum of Natural History, New York, for sending me comparative material of *Monarcha hebetior*, *Monarcha verticalis* and *Lalage leucomela*. I am indebted, further, to SOFUS CHRISTIANSEN, M. Sc. and VIGGO HANSEN, M. Sc. for various geographical information.

Description of New Forms

The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of endemic forms which strikingly differed from their allies on New Ireland. These new forms are described below, while the main description of the bird life of Dyaul will be published elsewhere.

Dicaeum eximium phaeopygium, new subspecies

Type: ♂ ad., Sumuna, Dyaul Island, 3. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 951.

Diagnosis: Differs strikingly from the two other forms of this species (nominate *eximium* Sclater and *layardorum* Salvadori) by having the entire upper parts uniform dark brown without the contrasting bright carmine colour on rump and upper tail-coverts of the two other forms and without the rufous coloration of the head found in nominate *eximium*. The differences hold good of both sexes. In addition the females have a much longer white loreal streak, extending on to the sides of nape. The bill is distinctly longer and the wing on an average longer than in nominate *eximium*. Adult males of the three subspecies are illustrated on plate I, fig. 1.

In *phaeopygium* the entire upper parts are dark and sombre brown, but in most specimens there is a slight dull brownish red tinge on the upper tail-coverts and a slight chestnut tinge on the forehead, but not on the crown and occiput, which are of the same colour as the back and not contrastingly coloured as in nominate *eximium*. The under parts are nearest to those of *eximium*, but the grey colour of the sides of head, sides of breast and of the median longitudinal streak on abdomen is more greyish black, distinctly darker than in *eximium*, and the ear-coverts and sides of throat are uniform dark grey (in *eximium* rufous), at most with a brownish tinge on the ear-coverts; also, the red pectoral patch in the males is generally of greater extension than in *eximium*. The adult females differ from those of nominate *eximium* in the same way as the males and, in addition, in having the white loreal streak (which is absent in males), much longer, continuing above the eye onto the sides of the nape, while in *layardorum* and nominate *eximium* it stops in front of the eye.

In both sexes of nominate *eximium* the upper-side of head and nape, the sides of the throat and the ear-coverts are rufous contrasting with the mantle and back, which are olive-brown, lighter and more bright than the coloration in *phaeopygium*, while the rump and upper tail-coverts are shining carmine red. *D. e. layardorum* differs from *eximium* in having the head and back uniform dark grey, not olive-brown, and without contrastingly coloured head; the grey colour on the sides of breast is lighter than in *eximium*, and the flanks are more brightly coloured, olive-yellow rather than olive-greenish brown. The main differences between the three forms concern the upper parts and can be summarized as follows:

	<i>eximium</i>		<i>layardorum</i>		<i>phaeopygium</i>
Head	rufous	}	dark grey	}	dark brown
Back	olive-brown		dark grey		dark brown
Rump	carmine		carmine		

Measurements: The size differences between the three forms are negligible, but *phaeopygium* has a longer bill than the two other forms and apparently a slightly longer wing, at least than nominate *eximium*.

Length of Wing¹

<i>phaeopygium:</i>	13 ♂♂ ad. 53–56, one 51 (54.1);	2 ♀♀ ad. 48, 50
<i>eximium:</i>	15 ♂♂ ad. 50–53, one 55 (52.3);	3 ♀♀ ad. 48.5–50.5 (49.2)
<i>layardorum:</i>	3 ♂♂ ad. 52–55 (54.0);	1 ♀ ad. 49

Length of Bill (from Skull)

<i>phaeopygium:</i>	13 ♂♂ ad. 11–12, one 10.5 (11.4);	3 ♀♀ ad. 11–11.2 (11.1)
<i>eximium:</i>	15 ♂♂ ad. 9.8–11.2 (10.5);	3 ♀♀ ad. 10–10.8 (10.4)
<i>layardorum:</i>	3 ♂♂ ad. 10–10.8 (10.3);	1 ♀ ad. 11

The individual measurements are enumerated in table 1.

TABLE 1
Measurements of *Dicaeum eximium*
(All specimens mentioned collected by the "Noona Dan Expedition")

Wing	♂♂ ad.	♀♀ ad.	♂♂ juv.
Dyaul (<i>phaeopygium</i>)	51, 53, 53, 54, 54, 54, 54, 54, 55, 55, 55, 55, 56	48, 50, — ^a	
New Hanover (<i>eximium</i>)	52, 53	50.5	52
New Ireland (<i>eximium</i>)	50, 51, 52, 52, 52, 52, 52, 52, 53, 53, 53, 53, 55	48.5, 49	
New Britain (<i>layardorum</i>)	52, 55, 55	49	
Bill (from skull)			
Dyaul (<i>phaeopygium</i>)	10.5, 11, 11, 11.2, 11.5, 11.8, 11.8, 11.8, 12, 12, 12, 12, 12	11, 11, 11.2	
New Hanover (<i>eximium</i>)	10.5, 11	10.8	11
New Ireland (<i>eximium</i>)	9.8, 10, 10, 10, 10, 10, 10.2, 10.5, 10.8, 11, 11, 11.2, 11.2	10, 10.5	
New Britain (<i>layardorum</i>)	10, 10, 10.8	11	

^a Wings in moult, not measured.

Material: 13 ♂♂ ad., 3 ♀♀ ad.

Range: Restricted to Dyaul Island.

Remarks: The main difference between *phaeopygium* and the two other forms is the loss of the contrasting bright carmine red rump patch in *phaeopygium*. A similar

¹ All measurements given in the present paper are in mm. The figures in brackets are the means.

patch, which must be regarded as homologous to that found in *eximium*, is widespread in the genus *Dicaeum*, but its presence or absence is usually a species character, not a subspecific one, and this emphasizes the principal importance of the morphological differentiation in *phaeopygium*. A contrasting carmine rump patch is present in the Moluccan *D. vulneratum* Wallace, but not in its ally *D. erythrothorax* Lesson; it is present in the Papuan *D. geelvinkianum* A. B. Meyer, but not in the related *D. pectorale* S. Müller (which I regard as conspecific with *D. geelvinkianum* owing to the existence of intermediate forms; cf. SALOMONSEN 1960, p. 23). A contrasting carmine rump patch is present also in *D. nehrkorni* Blasius of Celebes and *D. maugei* Lesson of the Lesser Sunda Islands, but absent in the males of the closely allied *D. sanguinolentum* Temminck and Laugier (but retained in the females), and absent in both sexes of the superspecies *D. hirundinaceum* (including *D. hirundinaceum* (Shaw and Nodder), *D. celebicum* S. Müller, *D. monticolum* Sharpe and *D. ignipectus* (Blyth); cf. SALOMONSEN 1961, p. 10). Even in *D. aeneum* Pucheran of the Solomon Islands, which is related to *geelvinkianum* and *eximium*, the red rump patch has been lost, which indicates that this species and *phaeopygium* have developed in a parallel way.

While *layardorum* is restricted to New Britain nominate *eximium* is found both on New Ireland and New Hanover, and the populations inhabiting these two islands are quite indistinguishable. On a previous occasion I examined very large series from both islands (in the American Museum of Natural History, New York), but could find no differences between them. The Dyaul form is a derivative of nominate *eximium*, not of *layardorum*. The chestnut tinge on the forehead which is usually present in *phaeopygium* is a remnant of the rufous colour found on the head and nape of nominate *eximium*, but absent in *layardorum*. Also, the dark brown colour of the upper parts of *phaeopygium* is closer to the olive-brown of nominate *eximium* than to the dark grey colour of *layardorum*. Evidently, Dyaul has been colonized from New Ireland.

***Monarcha chrysomela pulcherrima*, new subspecies**

Type: ♂ ad., Sumuna, Dyaul Island, 7. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 1021.

Diagnosis: Adult males: Differ very strikingly from all subspecies of this species in having the upper parts uniform yellow without any black, in all other particulars indistinguishable from nominate *chrysomela*, except for a slightly smaller wing length.

Adult females: Nearest to nominate *chrysomela*, but differing strikingly in having much more yellow in the plumage. While nominate *chrysomela* has the upper parts and wings uniform dark greenish olive, in some specimens with a yellowish tinge on the head and rump, *pulcherrima* has the forehead and sides of head as well as the rump and upper tail-coverts bright yellow and the lesser and median wing-coverts broadly edged with yellow; the remaining upper parts are distinctly lighter than in nominate *chrysomela*, citrine green, not dark greenish olive.

Immature females¹: Differ from nominate *chrysomela* in the same way as the adult females.

Specimens of both sexes of the new form and of nominate *chrysomela* are illustrated on plate I, fig. 2.

Measurements: The wing-length is slightly smaller than in nominate *chrysomela* from New Ireland. The specimens from New Hanover appear to bridge the difference between the Dyaul and the New Ireland population. The slightly smaller wing-length of the New Hanover birds in comparison with that of the New Ireland birds is also apparent from the measurements taken by MAYR (1955, p. 32): New Hanover 5 ♂♂ 70–74 (72.3), New Ireland 8 ♂♂ 71.5–76 (73.1).

Length of Wing

pulcherrima (Dyaul): 5 ♂♂ ad. 69–71 (70.1); 3 ♀♀ ad. 71–73 (71.7)
chrysomela (New Hanover): 4 ♂♂ ad. all 72; 1 ♀ ad. 72
 — (New Ireland): 6 ♂♂ ad. 73–76 (74.2); 2 ♀♀ ad. 73, 73

Length of Bill (from Skull)

pulcherrima (Dyaul): 5 ♂♂ ad. 14–16.8 (15.6); 3 ♀♀ ad. 15–15.8 (15.4)
chrysomela (New Hanover): 6 ♂♂ ad. 15–17 (15.7); 1 ♀ ad. 15.5
 — (New Ireland): 6 ♂♂ ad. 14–16 (15.2); 2 ♀♀ ad. 16, 16

The individual measurements are enumerated in table 2.

TABLE 2
 Measurements of *Monarcha chrysomela*
 (All specimens mentioned collected by the "Noona Dan Expedition")

Wing	♂♂ ad.	♀♀ ad.	♂♂ juv.	♀♀ juv.
Dyaul (<i>pulcherrima</i>)	69, 69, 70.5, 71, 71	71, 71, 73		67, 70
New Hanover (<i>chrysomela</i>) . . .	72, 72, 72, 72, — ^a , — ^a	72	71	68
New Ireland (<i>chrysomela</i>)	73, 73, 74, 74, 75, 76	73, 73		68
Bill (from skull)				
Dyaul (<i>pulcherrima</i>)	14, 15, 16, 16, 16.8	15, 15.5, 15.8		15.6, 16
New Hannover (<i>chrysomela</i>) . . .	15, 15.2, 15.5, 15.5, 16, 17	15.5,	16	16
New Ireland (<i>chrysomela</i>)	14, 14.5, 15, 15.8, 15.8, 16	16, 16		16.5

^a Wings in moult, not measured.

Material: 5 ♂♂ ad., 3 ♀♀ ad., 2 ♀♀ juv.

Range: Restricted to Dyaul Island.

Remarks: It is noteworthy that *pulcherrima* has diverged much further than any other subspecies within the species *chrysomela*. Nominate *chrysomela* inhabits New

¹ Immature males: Not examined. In nominate *chrysomela* they are similar to the immature females, but have slightly more yellow on the upper parts.

Hanover and New Ireland. In the Bismarck Archipelago the species inhabits also the Lihir group and the Tabar group, in which areas it has developed local subspecies, *whitneyorum* Mayr and *tabarensis* Mayr, respectively. These two forms differ only inconsiderably in colour pattern from nominate *chrysomela*, the males being lighter yellow, not so orange, the females darker greenish olive on the upper parts; in addition, *whitneyorum* is distinctly larger (wing-length in ♂♂ ad. 77.5–80), while *tabarensis* is intermediate in size between *whitneyorum* and nominate *chrysomela* (MAYR 1955, p. 31). The extension of the black area on the upper parts in the males of *whitneyorum* and *tabarensis* is just as in nominate *chrysomela*. This holds good also of all the remaining forms of this species, inhabiting the New Guinea area (*kordensis*, *melanonotus*, *aurantiacus*, *praerepta* and *aruensis*; cf. MAYR 1941, p. 135), some of them having even more black on the upper parts than nominate *chrysomela*. This shows how pronounced the differences are which separate *pulcherrima* from the other subspecies of *chrysomela*. The differences between *pulcherrima* and the other subspecies in the coloration of the females are almost as striking as in that of the males.

Monarcha ateralba, new species

Type: ♂ ad., Sumuna, Dyaul Island, 2. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 923.

Description: Adult males and females: Forehead, forepart of crown, lore, feathers around eye, chin and throat black with a dull gloss, the feathers of forehead and forepart of crown scale-like and stiff and somewhat erect, a narrow transversal band across crown, ear-coverts, temporal region and sides of neck white, posterior part of crown, occiput, neck, mantle, scapulars and anterior part of back bluish black, slightly glossy, posterior part of back, rump and upper tail-coverts as well as the entire under parts below throat pure white, lesser, median and greater wing-coverts, except the outer two-three greater coverts, white, remaining parts of wing, including remiges, black, axillaries white, tail-feathers black, the three outer pairs broadly tipped with white, the apical white band being at least 20 mm broad on the two lateral pairs of tail-feathers, slightly more narrow and sometimes mixed with black on the third pair. Male and female are exactly similar in coloration, but the female is distinctly smaller than the male.

Juveniles: Forehead, forepart of crown, ear-coverts, sides of head, throat and forebreast orange rusty, lower breast, flanks and under tail-coverts lighter, tinged with pale buff, centre of abdomen almost white, upper parts dark grey, on back suffused with brownish olive, rump and upper tail-coverts white tinged with light buff, wings sepia-brown, lesser and median coverts light buff, inner greater coverts pale grey finely tinged with buff, tail-feathers blackish brown, the three outer pairs with about 20 mm broad white tips as in the adult birds.

Specimens of adult males of the new species and of its nearest relative, *M. verticalis* Sclater, are illustrated in fig. 2.

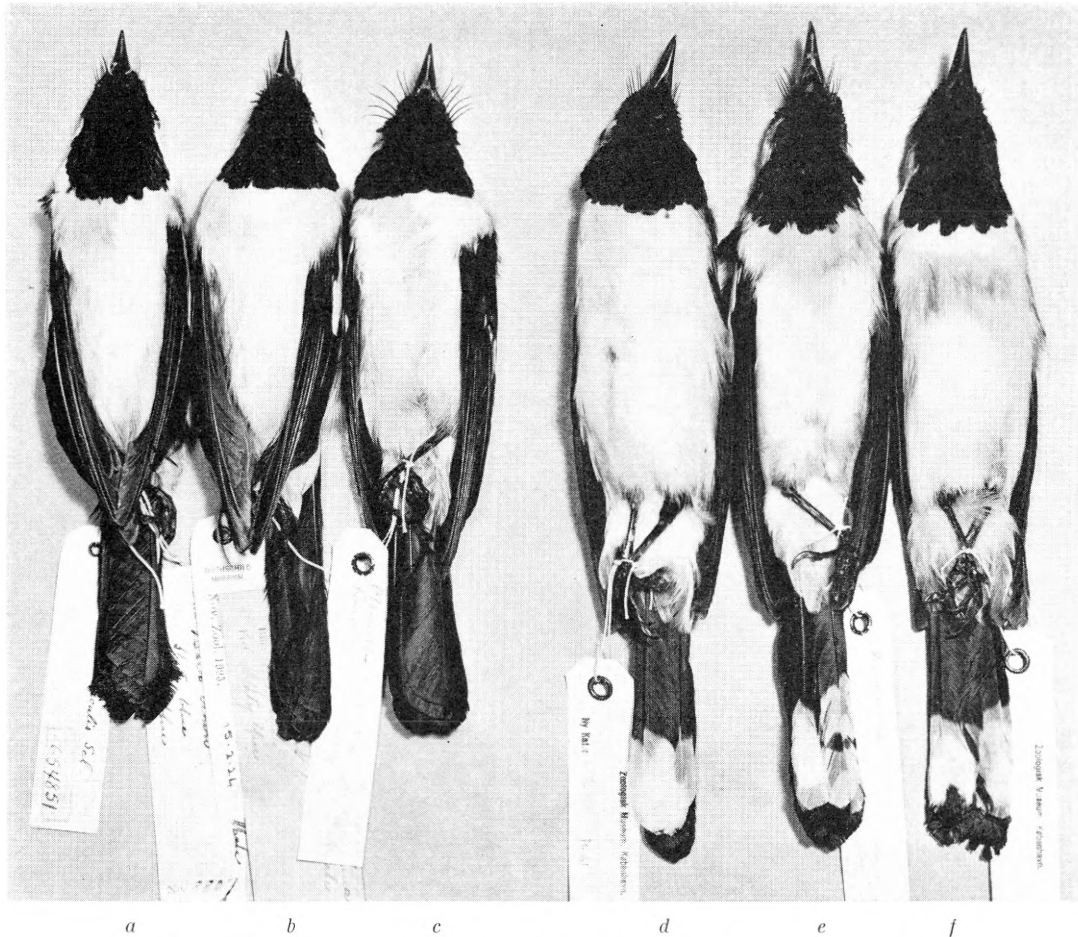


Fig. 2. Adult males of *Monarcha verticalis* (a-c) and *M. ateralba* (d-f), collected on New Ireland (a, b), New Hanover (c) and Dyaul (d, e, f); a and b belonging to the American Museum of Natural History, New York, c, d, e, and f collected by the "Noona Dan Expedition".

Measurements: A much bigger bird than *M. verticalis*, with longer wings, tail and bill, which appears from the following list of measurements.

Length of Wing

ateralba: 6 ♂♂ ad. 91-95 (93.0); 2 ♀♀ ad. 86, 90
verticalis: 5 ♂♂ ad. 83-88 (86.2); 4 ♀♀ ad. 82-85 (83.0)

Length of Tail

ateralba: 6 ♂♂ ad. 84-87 (85.0); 2 ♀♀ ad. 79, 85
verticalis: 5 ♂♂ ad. 74-79 (76.6); 4 ♀♀ ad. 71-75 (72.7)

Length of Bill (from Skull)

ateralba: 6 ♂♂ ad. 17-19 (18.0); 2 ♀♀ ad. 17.8, 18.2
verticalis: 5 ♂♂ ad. 15.5-16 (15.9); 4 ♀♀ ad. 15-16 (15.7)

The individual measurements are enumerated in table 3.

The tail is relatively slightly longer than in *M. verticalis*, constituting 91.4 percent of the wing-length, compared with 88.9 percent in *verticalis*. In addition, the graduation of the tail is stronger, the distance between the shortest (lateral) and the longest (central) tail-feathers being 13–15 mm, compared with 5–8 mm in *verticalis*.

Material: 6 ♂♂ ad., 2 ♀♀ ad., 1 ♀ juv.

Range: Restricted to Dyaul Island.

Remarks: The new species is nearest to *M. verticalis* Sclater, inhabiting Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover, but differs strikingly from this species both in coloration and in proportions. The main differences in coloration between the adult birds of the two species concerns the tail, which is uniform black in *verticalis*, and with the apical parts of the outer three pairs white in *ateralba* (cf. fig. 2). The white colour of the upper-parts is more extensive in *ateralba*, in which the lower back, the rump and all the upper tail-coverts are white, while in *verticalis* the lower back is mixed with grey, due to concealed dark feather-bases, and the longest upper tail-coverts are constantly black. In *ateralba* the two sexes are absolutely identical in coloration, but in *verticalis* there is a slight difference, the males having the lower parts of the back white with concealed grey feather-bases, whereas the females have the lower back uniform grey, sometimes mixed with white, but

TABLE 3
Measurements of *Monarcha ateralba* and *M. verticalis*
(The specimens mentioned collected by the "Noona Dan Expedition"
when not otherwise stated)

Wing	♂♂ ad.	♀♀ ad.	♀♀ juv.
<i>M. ateralba</i> (Dyaul)	91, 92, 93, 93, 94, 95	86, 90	85
<i>M. verticalis</i> (New Hanover)	86, 87	83	
— (New Ireland)	83 ^a , 88 ^a	82 ^a , 85 ^a	78, 78 ^a
— (New Britain)	87	82	
Tail			
<i>M. ateralba</i> (Dyaul)	84, 84, 84, 85, 86, 87	79, 85	82
<i>M. verticalis</i> (New Hanover)	75, 79	71	
— (New Ireland)	74 ^a , 79 ^a	73 ^a , 75 ^a	68, 73 ^a
— (New Britain)	76	72	
Bill (from skull)			
<i>M. ateralba</i> (Dyaul)	17, 17.5, 18, 18.2, 18.5, 19	17.8, 18.2	18
<i>M. verticalis</i> (New Hanover)	16, 16	16	
— (New Ireland)	15.5 ^a , 16 ^a	16 ^a , 16 ^a	15.5, — ^a , ^b
— (New Britain)	16	15	

^a Belonging to the American Museum of Natural History, New York.

^b Bill broken.

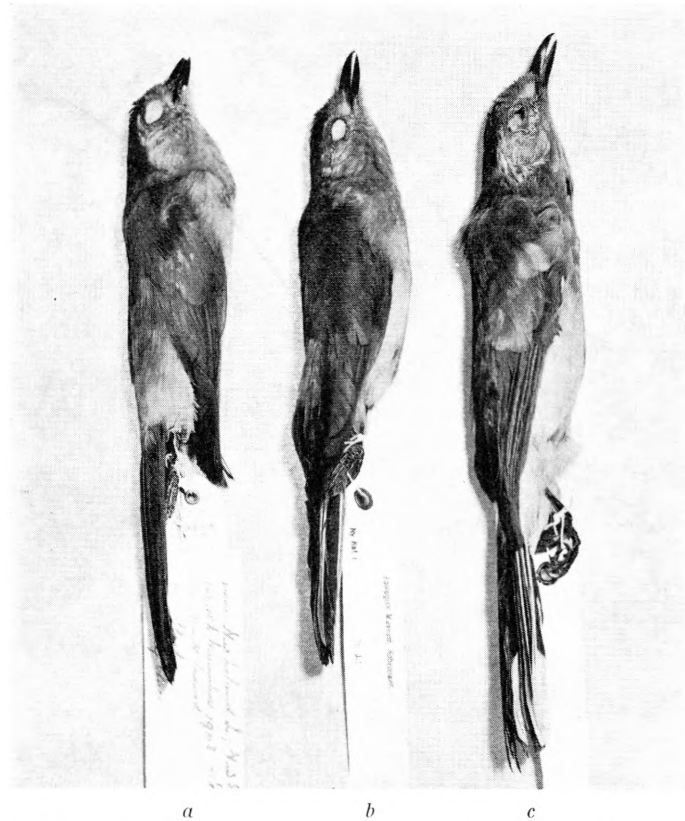


Fig. 3. Juvenile females of *Monarcha verticalis* (a, b) and *M. ateralba* (c), collected on New Ireland (a, b) and Dyaul (c); a belonging to the American Museum of Natural History, New York, b and c collected by the "Noona Dan Expedition". Note big proportions, light wing-coverts and different tail pattern in *ateralba*.

always with more grey than in the males. This sexual difference was pointed out by REICHENOW (1899, p. 85), but wrongly doubted by HARTERT (1925, p. 129).

The differences between the two species in the juvenile dress are even more striking than in the adult birds. The tail is uniform blackish brown in *verticalis*, and the apical parts white for about 20 mm on the three outer tail-feathers in *ateralba*, thus showing the same character as the adult birds. In *verticalis* the crown and nape are dark grey, the mantle, back and wing-coverts olive-brown, while in *ateralba* grey is the predominating colour and the wing-coverts are contrastingly coloured, light buff or pale grey. In *verticalis* the rump and upper tail-coverts are greyish buff and the longest tail-coverts dark slate-grey, in *ateralba* these parts are white with a buffish tinge, the longest upper tail-coverts pure white, and the light colour of the rump extending anteriorly onto the lower back. In *verticalis* the forehead, lore, eye-region, ear-coverts, sides of head and the chin are grey with or without a slight brownish tinge, in *ateralba* these parts are orange rusty, of the same colour as the throat, but strongly contrasting

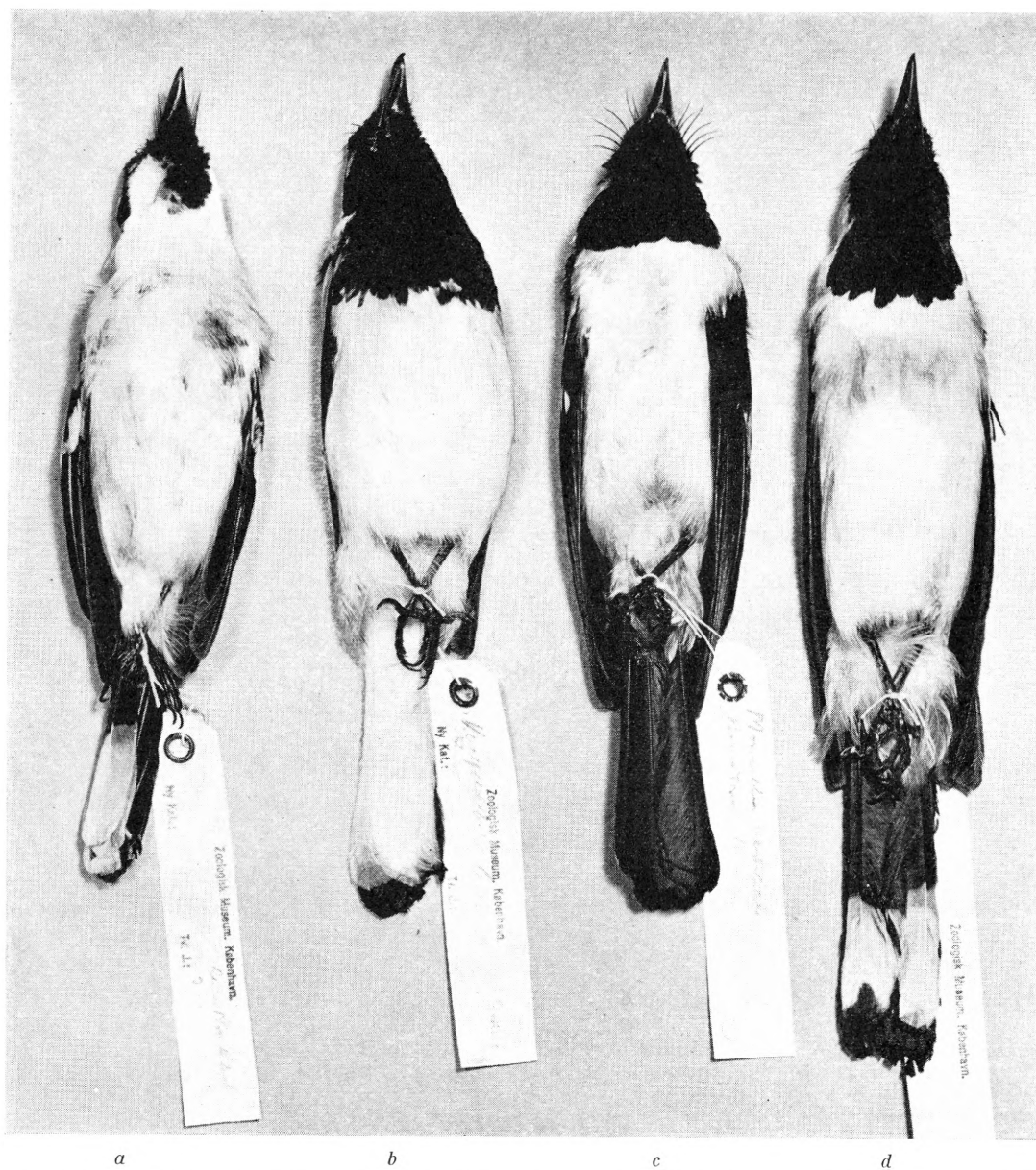


Fig. 4. Adult males of the four species belonging to the superspecies *Monarcha verticalis* inhabiting the Bismarck Archipelago; *a* *M. mencke* from Mussau in the St. Matthias Islands, *b* *M. infelix* from Manus in the Admiralty Islands, *c* *M. verticalis* from New Hanover, *d* *M. ateralba* from Dyaul; all collected by the "Noona Dan Expedition".

with the dark grey colour of the crown and nape. In *verticalis* the throat and breast are coloured buff or tawny, in *ateralba* bright orange rusty. Cf. also fig. 3 for differences between the two species in the juvenile dress.

The black-and-white Monarch Flycatchers form a complicated group, and the mutual relationship of the different species is still not settled. The division into sections or superspecies has been discussed mainly by MEISE (1929, p. 459), MAYR (1944, p. 162, and 1955, p. 25) and VAN BEMMEL (1948, p. 344). The species inhabiting the Bismarck Archipelago and the Solomon Islands can be united into a superspecies (*verticalis*). MAYR (*loc. cit.*) includes in this superspecies a number of other forms (*manadensis*, *leucura*, etc.), but this arrangement has not met with general approval.

It is not easy to decide whether *ateralba* should be regarded as a full species or a strongly differentiated subspecies of *verticalis*. The form inhabiting the Admiralty Islands (*infelix* Selater) has always been regarded as a full species. It differs, admittedly, much more from *verticalis* than does *ateralba* (cf. fig. 4), but is, on the other hand, similar to *verticalis* in proportions (wing-length of ♂♂ ad. 82–87, ♀♀ ad. 77–83, tail-length in ♂♂ ad. 69–78, in ♀♀ ad. 67–75, according to MAYR 1955, p. 29). As far as the colour pattern of the tail is concerned *ateralba* is intermediate between *verticalis* and *infelix* and approaches very much *menckei* Heinroth from Mussau, which is a very distinct species (cf. fig. 4). Even the pronounced differences between *verticalis* and *ateralba* in the colour pattern of the juvenile plumage speaks in favour of the view-point that these two taxa are best treated as full species. VAN BEMMEL (*loc. cit.*) has pointed out that the juvenile plumages in these flycatchers are often suggestive when discussing relationship. Summing up, the distinct differences in colour pattern of both adult and juvenile birds combined with the considerable differences in proportions between *verticalis* and *ateralba* make it in my opinion inadvisable to regard these two taxa as conspecific.

I have compared specimens of *verticalis* from New Hanover, New Ireland and New Britain and find them indistinguishable. This has been noticed also by MAYR (1955, p. 28), who adds: "It is rather odd that no subspecies have formed in this species, which belongs to a group elsewhere strongly inclined to geographic variation."

***Monarcha hebetior cervinicolor*, new subspecies**

Type: ♀ ad., Sumuna, Dyaul Island, 6. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 1013.

Diagnosis: Adult females: Nearest to *M. h. eichhorni* Hartert, but differ strikingly in having crown pale ash-grey, lores and frontal feathering almost whitish and somewhat contrasting, upper parts much lighter rufous, under parts white, under tail-coverts and lower abdomen tinged with light cinnamon and throat and breast suffused with light grey, but some specimens with under parts almost uniform white, primaries and secondaries blackish brown with whole outer web rufous, tertiaries uniform

rufous only with blackish shaft-streak, tail-feathers rufous, the two central pairs slightly suffused with darker brown.

Juvenile females: Differ from *eichhorni* in the same way as the adult females.

Males: Indistinguishable from *eichhorni* in coloration.

In females of *eichhorni* the crown is darker slate-grey, the lores and front of the same colour, not paler, the upper parts chestnut, very much darker and duller than in *cervinicolor*, the under parts slate-grey, lighter on abdomen and suffused with chestnut on flanks, primaries and secondaries blackish brown, with only a narrow chestnut border on outer web, tertiaries blackish brown narrowly edged with chestnut on both webs, tail-feathers blackish brown narrowly edged with fuscous chestnut.

Adult females of the new form and of *eichhorni* are illustrated on plate II, fig. 1.

Measurements: The proportions of *cervinicolor* are slightly larger than those of *eichhorni*. This holds good particularly of the tail, but is apparent also in the measurements of wing and bill. Nominate *hebetior* is in all respects a much smaller bird than the two other subspecies, the tail being particularly short.

Length of Wing

cervinicolor: 5 ♂♂ ad. 86–88 (87.4); 6 ♀♀ ad. 77–84 (80.2)

eichhorni: 4 ♂♂ ad. 83–85 (84.0); 7 ♀♀ ad. 74–81 (78.7)

hebetior: 3 ♂♂ ad. 75–77 (76.0); 1 ♀ ad. 69

Length of Tail

cervinicolor: 4 ♂♂ ad. 75–79 (77.3); 6 ♀♀ ad. 70–77 (72.7)

eichhorni: 4 ♂♂ ad. 68–75 (71.5); 7 ♀♀ ad. 61–69 (66.2)

hebetior: 3 ♂♂ ad. 59–62 (60.7)

Length of Bill (from Skull)

cervinicolor: 5 ♂♂ ad. 21–22 (21.6); 6 ♀♀ ad. 20–22 (21.0)

eichhorni: 4 ♂♂ ad. 19–22 (20.5); 7 ♀♀ ad. 19–22 (20.3)

hebetior: 3 ♂♂ ad. all 18; 1 ♀ ad. 18

The individual measurements are enumerated in table 4.

Material: 5 ♂♂ ad., 6 ♀♀ ad., 2 ♀♀ juv.

Range: Restricted to Dyaul Island.

Remarks: The most remarkable character of *cervinicolor* is the rufous colour of tail and wing, which in *eichhorni* and nominate *hebetior* are predominating blackish brown. This is noteworthy, because the closely allied species *Monarcha alecto* also has rufous wings and tail. Even in its whitish under parts with cinnamon under tail-coverts and in its bright rufous upper parts *cervinicolor* approaches or matches *alecto*. It is highly interesting that the isolated form on Mussau (nominate *hebetior*) exhibits a similar resemblance to *alecto* in the white colour of the under parts and in the brightness of the rufous upper parts, while the colour pattern of wings and tail is similar to that in *eichhorni*. On the other hand, females of nominate *hebetior* possess another *alecto* character, namely the black (not grey) crown. Evidently, nominate

hebetior and *cervinicolor* show an almost equal mixture of *alecto* and *eichhorni* characters, although perhaps the *alecto* characters are somewhat more strongly manifested in nominate *hebetior* than in *cervinicolor*.

The relation between the two closely allied species *alecto* and *hebetior* is interesting from an evolutionary point of view. *M. alecto* is a widespread species, inhabiting the Moluccas, the Papuan region and northern Australia, in the Bismarck Archipelago distributed on Umboi, New Britain, New Ireland, New Hanover, Dyaul, Tabar, Tanga, Feni, Vitu Islands and the Admiralty Islands, showing in its huge range only a slight

TABLE 4
Measurements of *Monarcha hebetior*
(The specimens mentioned collected by the "Noona Dan Expedition"
when not otherwise stated)

Wing	♂♂ ad.	♀♀ ad.	♀♀ juv.
<i>cervinicolor</i> (Dyaul)	86, 87, 88, 88, 88	77, 80, 80, 80, 80, 84	77, 77
<i>eichhorni</i> (New Hanover)	83 ^a	76, 81, 81, 81, 81	
— (New Ireland)	85 ^a	74 ^a	74 ^a
— (New Britain)	84, 84	77	
<i>hebetior</i> (Mussau)	75, 76, 77	69	67
Tail			
<i>cervinicolor</i> (Dyaul)	75, 77, 78, 79, — ^b	70, 72, 72, 72, 73, 77	66, 67
<i>eichhorni</i> (New Hanover)	69 ^a	62, 68, 68, 69, 69	
— (New Ireland)	68 ^a	61 ^a	66 ^a
— (New Britain)	74, 75	66	
<i>hebetior</i> (Mussau)	59, 61, 62	— ^c	54
Bill (from skull)			
<i>cervinicolor</i> (Dyaul)	21, 21.5, 21.5, 22, 22	20, 20.5, 21, 21, 21.5, 22	21, 21
<i>eichhorni</i> (New Hanover)	22 ^a	20, 20, 20.8, 21, 22	
— (New Ireland)	21 ^a	19 ^a	20 ^a
— (New Britain)	19, 20	19	
<i>hebetior</i> (Mussau)	18, 18, 18	18	18

^a Belonging to the American Museum of Natural History, New York.

^b Tail in growth, not measured.

^c Tail damaged, not measured.

geographical variation. *M. hebetior* is restricted to the Bismarck Archipelago, living side by side with *alecto* in New Britain, New Ireland, New Hanover (*eichhorni*) and Dyaul (*cervinicolor*), and inhabiting also Mussau (*hebetior*), where *alecto* does not occur. MAYR (1955, p. 30), who of course did not know the existence of *cervinicolor*, explained this distribution by assuming that *alecto* spread to Mussau, where it was modified and became the present *hebetior*, and that this latter form subsequently, having reached species level, reinvaded the Bismarck Islands, where it became still

more modified, developing into *eichhorni*. The distribution of the two species and the intermediate character of nominate *hebetior* made this theory very plausible. The discovery of *cervinicolor*, however, complicates the situation. It is difficult to understand why *alecto*, which according to MAYR represents an old element, has remained completely unchanged on Dyaul, while the newcomer *hebetior* was able to develop the strikingly different *cervinicolor* in a much shorter period of time. The resemblance between *cervinicolor* and *alecto* is due either to a secondary parallelism or—as in nominate *hebetior*—to an actual retainment of *alecto* characters. Whichever alternative may be the correct one I find it most probable to assume that *alecto* twice invaded the Bismarck Archipelago from New Guinea. The first colonization gave rise to the development of the species *hebetior*, which eventually occupied three separate areas (Mussau, Dyaul, and the main tier of islands), the populations of which diverged and formed the three present subspecies. The second colonization by *alecto* was much more recent and has not resulted in any morphological differentiation.

The coloration of the males in the three forms of *hebetior* is, so far I can see, practically identical, and this species represents a very clear case of heterogynism. The colour of the crown in females of nominate *hebetior* is similar to that in *alecto*, as said above, but is not identical with it. In *alecto* the crown is bright glossy bluish black, while in *hebetior* it is black with only a dull gloss, and the feathers are short and of a soft velvety texture, not scaly and not forming a rounded cap as in *alecto*. This difference is important for a characterization of the species *hebetior* as compared with *alecto*. It has been shown above that the coloration of upper parts, under parts, wings and tail in all these forms is very varying and not suitable to characterize the species. The best distinction marks between the species *hebetior* and *alecto* are the colour and feather texture of the males, which are identical in nominate *hebetior*, *eichhorni* and *cervinicolor* and clearly different from *alecto*, and the colour and feather texture of the crown in the females and immature birds, which part is dull black (nominate *hebetior*) or grey (*eichhorni*, *cervinicolor*) in *hebetior*, glossy bluish black in *alecto*.

M. h. eichhorni exhibits some slight geographical variation. MAYR (1955, p. 30) states that New Ireland females are slightly brighter rufous and paler and also slightly smaller than New Britain ones. The single female from New Britain collected by the "Noona Dan Expedition" is not so rufous on the upper parts as New Ireland and New Hanover birds, tending more towards olive-brown, and, in addition, the bill is shorter in both sexes (cf. table 4). The alleged difference in size between the New Britain and New Ireland birds is not apparent in my small series. At any rate, more material is needed to decide whether New Britain birds are separable. During my stay with the "Noona Dan Expedition" I collected a good series of females (five specimens) on New Hanover from which island females were previously unknown. They do not differ from New Ireland females in any respect.

The females of *M. alecto* living sympatrically with *M. hebetior* on many islands in the Bismarck Archipelago and belonging to the subspecies *chalybeocephala* Garnot

do not show any appreciable variation on New Britain, New Ireland, New Hanover, Dyaul and Credner Islands, in which localities the "Noona Dan Expedition" collected a number of specimens (Credner Islands being a new locality for this species). MAYR (1955, p. 30) states that New Ireland birds are paler than those from New Hanover and New Britain, but I cannot see any difference, but there is some individual variation, however. The birds from Feni Islands, which I have seen in life, but failed to collect, are stated to be slightly darker (MAYR, *loc. cit.*). The population of the Admiralty Islands, of which I have seen some specimens in the American Museum of Natural History, are much darker rufous on the upper parts than those from all the other islands in the Bismarck Archipelago and appears to form a marked subspecies. This has been noticed already by HARTERT (1930, p. 72) and by MAYR (1941 a, p. 3), who both state that the variation in this species is patchy and does not follow any geographical pattern, the New Guinea specimens, particularly those from Biak and Numfor Islands, being as dark as the Admiralty Islands birds, and that it is not possible, therefore, to separate any subspecies. I have not seen any New Guinea specimens and at present cannot add to the discussion, but the fact remains that the Admiralty Islands birds distinctly differ from those of the other islands in the Bismarck Archipelago.

***Lalage leucomela sumunae*, new subspecies**

Type: ♀ ad., Sumuna, Dyaul Island, 5. March 1962, coll. FINN SALOMONSEN, in Zoologisk Museum, Copenhagen, collector's number 989.

Diagnosis: Differs in both sexes from the forms inhabiting the main chain of islands in the Bismarck Archipelago (*falsa* Hartert, *karu* (Lesson and Garnot) and *albidior* Hartert) in having the under parts pure white, completely without rufous, in some specimens (mostly males), however, with a faint yellowish wash on the under tail-coverts; in addition, the females have the upper parts slightly darker grey. The barring on the under parts in both sexes is similar to that in *albidior* from New Hanover or is slightly paler and the bars slightly narrower. Finally, the bill is slightly longer than in all the other forms of the Bismarck Islands. The new form is more similar in coloration to the forms inhabiting the distant Lihir Island (*ottomeyeri* Stresemann) and Tabar Island (*tabarensis* Mayr), which both have white under parts just as *sumunae*, but, further, in both sexes have much more white on the wing-coverts and secondaries, while the under parts in the males of these two closely allied forms are completely unbarred, being practically pure white (cf. fig. 5), and even in the females the barring on the under parts is much more faint than in *sumunae* and the other forms of the Bismarck Archipelago. There are also other differences.

Altogether, the differences between most of the forms of the Bismarck Archipelago are more pronounced in the females than in the males, and I have, therefore, chosen a female as the type.

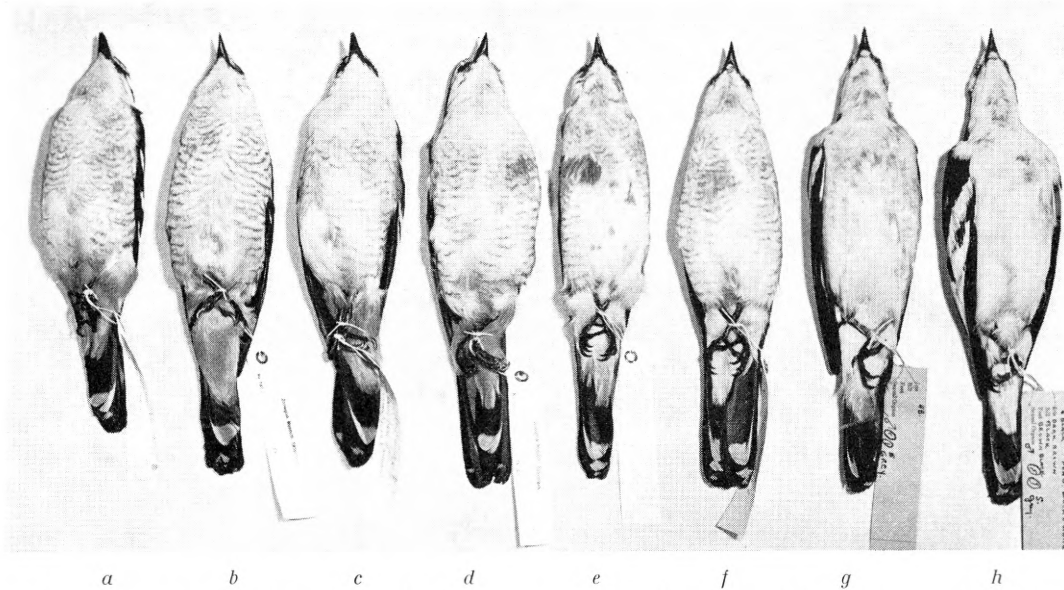


Fig. 5. Adult males of various forms of *Lalage leucomela* from the Bismarck Archipelago; *a-b karu* from New Ireland, *c-d albidior* from New Hanover, *e-f sumunae* from Dyaul, *g-h ottomeyeri* from Lihir; *a, b, c, d, e* and *f* collected by the "Noona Dan Expedition", *g* and *h* belonging to the American Museum of Natural History, New York.

Adult females of the new form and of *karu* are illustrated on plate II, fig. 2, while adult males of *karu*, *albidior*, *sumunae* and *ottomeyeri* are shown in fig. 5.

Measurements: All the forms of the Bismarck Archipelago are evidently of the same size (cf. also the measurements given by MAYR 1955, p. 9), but *sumunae* differs from all the rest by having a slightly longer bill.

Length of Wing

<i>sumunae:</i>	6 ♂♂ ad. 98–103 (99.8);	6 ♀♀ ad. 93–100 (96.5)
<i>albidior:</i>	4 ♂♂ ad. 97–102 (100.0);	2 ♀♀ ad. 96, 102
<i>karu:</i>	4 ♂♂ ad. 98–101 (99.5);	9 ♀♀ ad. 93–101 (96.1)
<i>falsa:</i>		1 ♀ ad. 97
<i>ottomeyeri:</i>	2 ♂♂ ad. 100, 102;	2 ♀♀ ad. 98, 101
<i>tabarensis:</i>	1 ♂ ad. 101;	2 ♀♀ ad. 99, 99

Length of Bill (from Skull)

<i>sumunae:</i>	6 ♂♂ ad. 16.5–18.8 (17.4);	6 ♀♀ ad. 17–18 (17.2)
<i>albidior:</i>	4 ♂♂ ad. 16–17 (16.4);	2 ♀♀ ad. 15.2, 16
<i>karu:</i>	4 ♂♂ ad. 15–17 (16.0);	9 ♀♀ ad. 15.2–16.8 (16.0)
<i>falsa:</i>		1 ♀ ad. 16
<i>ottomeyeri:</i>	2 ♂♂ ad. 16, 17;	2 ♀♀ ad. 16, 16
<i>tabarensis:</i>	1 ♂ ad. 15.5;	2 ♀♀ ad. 15, 16

The individual measurements are enumerated in table 5.

Material: 6 ♂♂ ad., 6 ♀♀ ad.

Range: Restricted to Dyaul Island.

Remarks: The "Noona Dan Expedition" collected material of the forms *falsa*, *karu*, *albidior* and *sumunae*, but failed to find the very rare *conjuncta* Rothschild and Hartert on Mussau, which is known only from the type (♂ ad.). The Tabar and Lihir groups were not visited, but material of the two indigenous forms was kindly supplied by the American Museum of Natural History, New York.

It is noteworthy that the forms inhabiting the islands both south of New Ireland (Dyaul) and north of this island (Tabar, Lihir) have, independently of each other, acquired the same character, the complete loss of rufous on the under parts. All other forms of this widespread species, including those of Australia and the Papuan region, have buffish or partly rufous under parts (MAYR and RIPLEY 1941, p. 13, map). The isolated form of Mussau (*conjuncta*) has retained the deep rufous colour of abdomen and under tail-coverts, but it differs strikingly from the other forms by the complete absence of barring on the under parts and by lacking the white superciliary streak. Evidently, *conjuncta* is a very distinct form. Compared with the peripheral forms (*sumunae*, *ottomeyeri*, *tabarensis*, *conjuncta*) the central populations (*falsa*, *karu*, *albidior*) are much less differentiated. A cline for decreasing amount of rufous on the under parts runs from New Britain (and Umboi) through New Ireland to New Hanover, and the forms with white under parts on Dyaul, Tabar and Lihir may possibly

TABLE 5
Measurements of *Lalage leucomela*
(The specimens mentioned collected by the "Noona Dan Expedition"
when not otherwise stated)

Wing	♂♂ ad.	♀♀ ad.
<i>sumunae</i> (Dyaul)	98, 98, 99, 100, 101, 103	93 ^a , 95 ^a , 95 ^a , 97, 99, 100
<i>albidior</i> (New Hanover)	97, 100, 101, 102	96, 102
<i>karu</i> (New Ireland)	98, 99, 100, 101	93 ^a , 94, 95, 96 ^a , 96, 96, 97, 97, 101
<i>falsa</i> (New Britain)		97
<i>ottomeyeri</i> (Lihir)	100 ^b , 102 ^b	98 ^b , 101 ^b
<i>tabarensis</i> (Tabar)	101 ^b	99 ^b , 99 ^b
Bill (from skull)		
<i>sumunae</i> (Dyaul)	16.5, 17, 17, 17, 18, 18.8	17, 17, 17, 17, 17, 18
<i>albidior</i> (New Hanover)	16, 16, 16.8, 17	15.2, 16
<i>karu</i> (New Ireland)	15, 16, 16, 17	15.2, 15.5, 16, 16, 16, 16, 16, 16.2, 16.8
<i>falsa</i> (New Britain)		16
<i>ottomeyeri</i> (Lihir)	16 ^b , 17 ^b	16 ^b , 16 ^b
<i>tabarensis</i> (Tabar)	15.5 ^b	15 ^b , 16 ^b

^a Wings immature.

^b Belonging to the American Museum of Natural History, New York.

be regarded as end-links of this cline. Some specimens from neighbouring islands in the main chain are indistinguishable. The darkest females from New Ireland have as much rufous on the under parts as the New Britain specimens, but these latter can be distinguished by their slightly more fuscous, not so greyish upper parts. Similarly, the lightest New Ireland females are quite indistinguishable from New Hanover females. As far as the males are concerned, the differences are still less pronounced. The extension of the rufous colour on the under parts is generally smaller in the males than in the females, and most males of *albidior* and *karu* are very similar, some even indistinguishable on this character, while the females can usually be separated. In the males of *albidior* the barring on the under parts is reduced and more indistinct than in *karu*, and the ground colour of the throat and forebreast is pure white, in *karu* washed with grey (fig. 5), but some males of *karu* are indistinguishable from *albidior* even in this character. Consequently, I consider *albidior* a rather weak, although acceptable form.

Previous notes on the geographical variation of this species in the Bismarck Archipelago have been given mainly by HARTERT (1925, p. 131), STRESEMANN (1933, p. 114), MAYR and RIPLEY (1941, p. 13) and MAYR (1955, p. 8).

Zoogeographical Remarks

The fauna of Dyaul is noteworthy in many respects. The island has a relatively rich fauna, compared with that of other islands of similar size and situation. Dyaul is not an outlying and remote island, but nevertheless it is characterized by possessing a number of striking endemic forms, which phenomenon is ordinarily characteristic of peripherally isolated faunas. The development of these endemic forms has taken place in spite of the close proximity of Dyaul to New Ireland. These facts call for some zoogeographical comments.

The morphological differentiation of the endemic forms of Dyaul must have required a certain amount of time, during which the populations were isolated from those of New Ireland. The length of this period of isolation is not easy to determine, but a rough estimate can be attempted on the basis of a comparison with other tropical island faunas which have developed under environmental conditions similar to those of the Bismarck Archipelago, *i. e.* exposed to only very slight and negligible differences in the selection pressure due to environmental factors.

The Philippine Islands offer a good example. The islands Negros, Panay and Guimaras form part of the so-called Central or Viscayan Province, a zoogeographical area characterized by many striking endemic species and subspecies. The lowland avifaunas of the said three islands are very similar, and the geographical variation within the populations of the area is very slight and restricted to a few species. The narrow straits separating the three islands are so shallow that the islands must have been broadly connected during the glacial periods. Consequently, the mutual separa-

tion and subsequent isolation of the bird populations inhabiting Negros, Panay and Guimaras, respectively, must be a recent phenomenon.

Another example is offered by the West Sumatran Islands. They are even more suitable for a comparison with Dyaul, because they are of about the same size, while the Philippine islands mentioned above are considerably bigger. Among the West Sumatran Islands Nias has a close faunal relationship with Sumatra. It is richer in species than any of the other West Sumatran Islands, but it is poor in endemisms, and the few local subspecies are usually only slightly differentiated from the Sumatran forms. Nias bears all the earmarks of being a very young island. Something similar can be said about the nearby small Batu and Banjak Islands, of which the faunal relationship with Sumatra is even closer. All these islands are situated inside the 100-fathom line, which indicates that they were connected with Sumatra until the late Tertiary and again temporarily in the glacial periods. The other small islands situated on the former Sunda Shelf, even remote ones like the Anambas Islands and the Natuna Islands, resemble Nias in possessing a fauna which is very similar to that of the mainland.

The remaining West Sumatran Islands are all situated outside the 100-fathom line. The island Enggano is a deep-sea island, which has not been in connection with Sumatra for a very long geological period, if ever. The fauna of this island is more divergent than that of any of the other West Sumatran Islands and at the same time the most impoverished. Something similar is the case of the northernmost island, Simalur, also an old oceanic island, although its faunal elements are by no means so differentiated and the fauna is much richer than that of Enggano. The Mentawi Islands possess a still richer fauna, consisting of forms that are generally closer to the Sumatran ones than those inhabiting Enggano and Simalur; cf. also SALOMONSEN 1961, p. 30.

From the description of the insular faunas given above it appears that populations which have been isolated recently, *i. e.* after the last glacial period (about 15,000 years ago) have diverged very little, if at all, while the isolates of greater age have been subject to much greater differentiation. A comparison between the populations of Dyaul and those of the West Sumatran Islands gives the result that the differentiation of the former is of the same order of magnitude as that of the Enggano populations. This indicates a comparatively great age. Dyaul, on the other hand, resembles Nias in having a relatively richer fauna.

It should here be added that, from an evolutionary point of view, it is necessary to distinguish between two fundamentally different categories of insular faunas. The first one comprises those faunas which have been isolated through a segregation of a former continuous range, such as the faunas inhabiting the above-mentioned islands on the former Sunda Shelf. The second category comprises those faunas which have been founded by colonists across the sea. The "founders" of such truly oceanic populations comprise, as a rule, very few individuals or a small flock. For genetical reasons, therefore, the morphological differentiation of the populations takes

place at a much greater rate than that in populations on islands separated from a land-mass. These differences must be carefully considered in all zoogeographical studies of island faunas.

The following notes form an attempt to elucidate some of the problems connected with the history and origin of the fauna of Dyaul, based on a comparison with that of the other islands in the Bismarck Archipelago.

Comparison with the Fauna of the Main Chain of Islands

The distribution and differentiation in the Bismarck Archipelago of the species which have developed striking endemic forms on Dyaul have been dealt with above and will be briefly summarized.

Dicaeum eximium: New Britain (*layardorum*), New Ireland and New Hanover (*eximium*), Dyaul (*phaeopygium*). The forms *eximium* and *layardorum* are rather similar and have both a bright carmine red rump, while *phaeopygium* differs strikingly from them by having the rump brownish like the back. The significance of this difference is borne out by the fact that loss of the red rump patch in other groups within the genus *Dicaeum* serves to distinguish full species (not subspecies).

Monarcha chrysomela: New Ireland and New Hanover (*chrysomela*), Tabar Island (*tabarensis*), Lihir Island (*whitneyorum*), Dyaul (*pulcherrima*). The three first forms are very similar and, furthermore, do not appreciably differ from the New Guinea forms. The Dyaul form *pulcherrima* differs strikingly from all other forms within this species by its uniform yellow upper parts in the adult males.

Monarcha verticalis superspecies: In the Bismarck Archipelago four distinct species belong to this superspecies, of which *infelix* from the Admiralty Islands and *menckei* from Mussau in the St. Matthias Islands are the most aberrant. The species *M. verticalis* is found on Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover, without showing any geographical variation. The Dyaul species *ateralba* is strikingly different from *verticalis*.

Monarcha hebetior: New Britain, Duke of York Islands, New Ireland and New Hanover (*eichhorni*), Mussau (*hebetior*), Dyaul (*cervinicolor*). Both the Dyaul and the Mussau form are strikingly different from the form inhabiting the main chain of islands and possess characters which in various ways approach those of the allied species *M. alecto*.

Lalage leucomela: Umboi, New Britain and Duke of York Islands (*falsa*), New Ireland (*karu*), New Hanover (*albidior*), Dyaul (*sumunae*), Tabar (*tabarensis*), Lihir (*ottomeyeri*), Mussau (*conjuncta*). The first three forms, inhabiting the main chain of islands, are rather similar, having in common rufous colour on the under parts; the Dyaul, Tabar and Lihir forms have white under parts, while *conjuncta* is very aberrant.

The distribution of these species in the Bismarck Archipelago has been outlined on the map fig. 6. The range given can be divided into three units:

(1) Dyaul Island (black on the map) with striking endemic forms in all five species.

(2) The range on the main chain of islands and on the island groups north-east of New Ireland, comprising *Monarcha verticalis*, *Monarcha hebetior eichhorni*, the forms of *Monarcha chrysomela* with black back, the forms of *Dicaeum eximium* with carmine red rump, and the forms of *Lalage leucomela* with rufous colour on the under parts (but including also the distinct forms with white under parts on Tabar and Lihir).

(3) The remaining distribution of the said species and superspecies in the Bismarck Archipelago, including distinct representatives of *Monarcha hebetior*, *Lalage leucomela* and the superspecies *Monarcha verticalis* (*M. menckei*) on Mussau and another distinct species of the *Monarcha verticalis* complex (*M. infelix*) in the Admiralty Islands.

It appears from the summary above that in all five species the populations of the main chain of islands (Umboi, New Britain, Duke of York Islands, New Ireland, New Hanover) are either identical or only comparatively slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is probably to be explained primarily as the result of a greater evolutionary rate in the Dyaul populations, due to their genetic history (change of genetic environment; cf. MAYR 1954, p. 175) as a consequence of their foundation through oversea crossing by a minority of individuals. This is probably not the whole truth, however. Other factors must have been active in order to develop the extraordinary characters of the Dyaul endemics. The time-factor, particularly, has been of importance. I venture to forward the theory that the main chain of islands were mutually connected, forming one or two big islands, in a period when Dyaul had already received its fauna. This land-connection would account for the similarity of the populations inhabiting the main islands. The status of the Duke of York Islands is noteworthy in this respect. This group is even smaller than Dyaul (only 60 sq. km) and situated at a similar distance from the "mainland" (both from New Ireland and New Britain). Consequently, the conditions for morphological differentiation of the local populations should be expected to be just as favourable as on Dyaul, or even more so. Nevertheless, not a single endemic form has developed on the Duke of York Islands. The possibility that an unimpeded gene flow could take place across the straits separating the Duke of York Islands from the neighbouring islands, but not across the narrow channel between Dyaul and New Ireland, is not acceptable. It must be assumed, therefore, that the Duke of York group is much younger than Dyaul, either because it emerged in a more recent period, or because it was connected with New Britain for a long time. The probability speaks for the latter alternative.

Even the island of Umboi, on which only a few weak subspecies have developed, must have been in land connection with New Britain. The islands of New Hanover and New Ireland have definitely been united in the past, at least during the glacial periods. The depths of the strait separating them is less than 30–50 meters and the

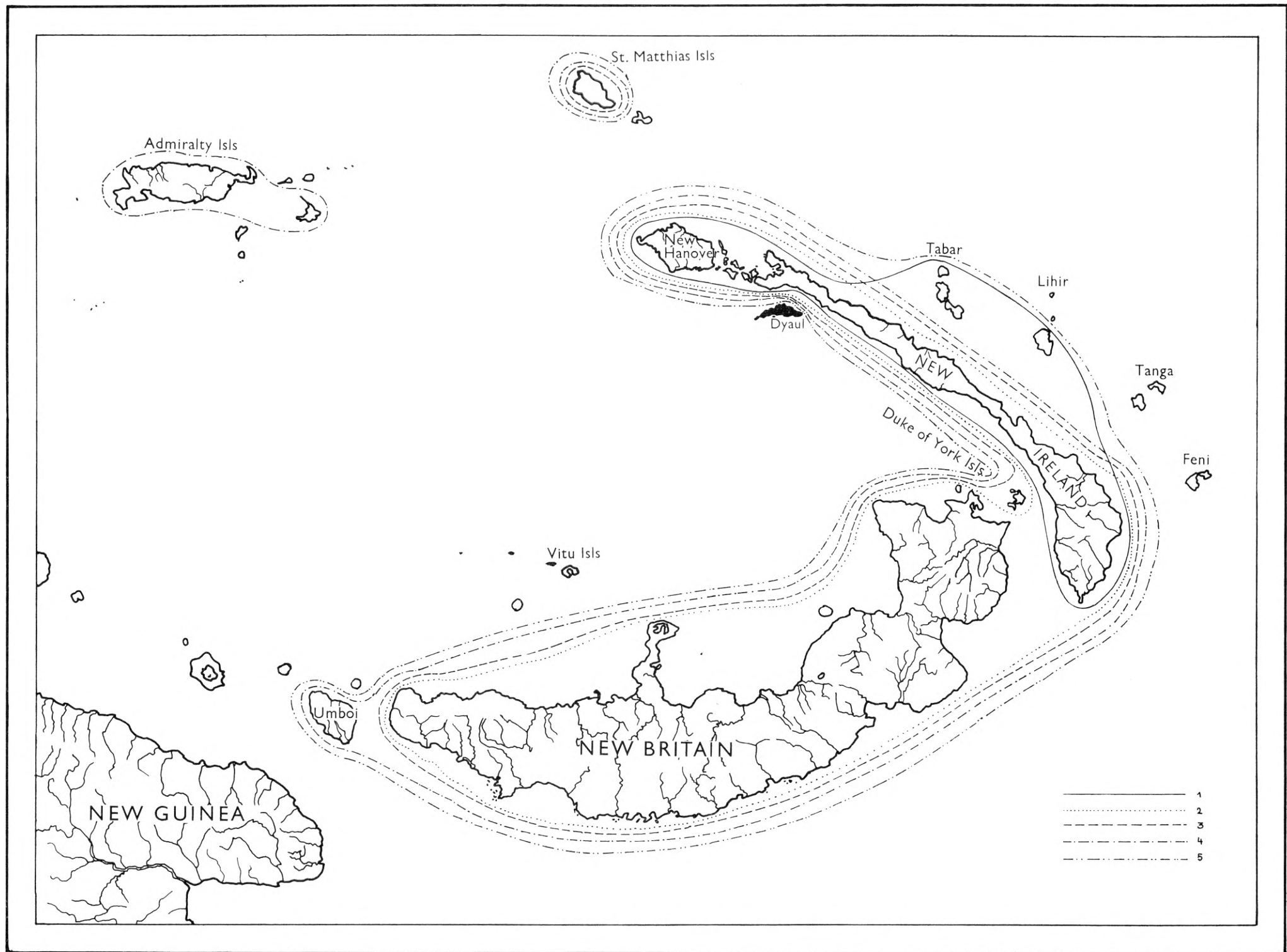


Fig. 6. The range in the Bismarck Archipelago of the five species which on Dyaul Island (black on the map) have developed strongly differentiated endemic forms; 1 *Monarcha chrysomela*, 2 *Dicaeum eximium*, 3 *Monarcha hebetior*, 4 *Monarcha verticalis* (superspecies), 5 *Lalage leucomela*.

span between them is bridged by many islands. Consequently, the bird fauna is rather similar on the two islands, most species occurring in the same or only slightly different subspecies on New Ireland and New Hanover.

The two former islands (Umboi-New Britain-Duke of York and New Ireland-New Hanover) were undoubtedly in land connection with each other originally, making the whole main chain of islands in the Bismarck Archipelago one big area. The connection between the two islands in question must, however, have been interrupted rather early in order to explain the differences in the composition of the fauna and the development of strikingly different endemic species on the two islands (*e. g.* in the genera *Micropsitta*, *Ninox*, *Dicrurus*, *Philemon*, *Myzomela*, *Lonchura*), but the faunal colonization of Dyaul must probably date almost as far back in the past.

Admittedly, there is no geological evidence for the assumption that these islands have ever been connected, but the meagre geological information does not contradict it either. I revert to this point below (p. 30).

As mentioned above, the strong differentiation of the Dyaul forms must have required a long time of isolation. It is noteworthy that the Gazelle Channel, not broader than 14 km, in spite of its extreme narrowness has been broad enough to form an effective barrier, preventing gene flow between the populations of New Ireland and Dyaul. Such a situation is extraordinary, but not unique. Even more narrow water gaps are known to separate distinct forms in the Lesser Sunda Islands, in the Western Papuan Islands and in other archipelagos. The gaps between certain islands in the Solomon Islands, which are inhabited by markedly different species belonging to the superspecies *Zosterops rendovae*, are even as narrow as 5–6 km (MAYR 1940, p. 266, and 1942, p. 227), although it appears that the narrowness of these barriers has been exaggerated (GALBRAITH and GALBRAITH 1962, p. 5). The faunal differences between New Britain, New Ireland and New Hanover, which have developed in spite of the narrowness of the water gaps separating these islands, have been emphasized by HEINROTH (1903, p. 99) and HARTERT (1924, p. 194).

Dyaul has undoubtedly received its entire avifauna from New Ireland, apart from a few species which may have immigrated from New Hanover. The morphological characters of the endemic forms on Dyaul are probably in most cases derivative, while those of the forms inhabiting the main island chain represent a more original stage.

Comparison with the Fauna of the Hibernian Islands

It appears from fig. 6 that none of the five species in question have reached the groups of Tanga and Feni and two only have reached Tabar and Lihir, namely *Monarcha chrysomela* and *Lalage leucomela*. Both these species have developed endemic forms on Tabar and Lihir, but in the case of *Monarcha chrysomela* these forms are relatively slightly differentiated, while the *Lalage leucomela* forms have diverged as much as—or even more than—the Dyaul form.

It is a remarkable phenomenon that the five species which have developed

TABLE 6
Breeding passerine species, total area and shortest distance from
New Ireland of Dyaul and the Hibernian island groups

Passerine Species	Dyaul	Tabar	Lihir	Tanga	Feni
<i>Pitta erythrogaster</i>	*	*			
<i>Hirundo tahitica</i>			*	*	
<i>Lalage leucomela</i>	*	*	*		
<i>Coracina tenuirostris</i>	*		*	*	*
<i>Cisticola exilis</i>		*	*		
<i>Rhipidura leucophrys</i>	*	*	*		
— <i>rufiventris</i>	*	*	*	*	
<i>Monarcha cinerascens</i>	*	*	*	*	*
— <i>ateralba</i>	*				
— <i>chrysomela</i>	*	*	*		
— <i>hebetior</i>	*				
— <i>alecto</i>	*	*		*	*
<i>Pachycephala pectorialis</i>	*	*	*	*	*
<i>Aplonis metallicus</i>	*	*	*	*	*
— <i>cantoroides</i>	*	*	*	*	*
<i>Corvus orru</i>	*				
<i>Dicaeum eximium</i>	*				
<i>Cinnyris sericea</i>	*	*	*		*
— <i>jugularis</i>	*	*	*	*	*
<i>Myzomela cruentata</i>	*	*			
Total number of breeding passerine species	18	14	13	9	8
Total area (in sq. km)	115	251 ^a	170	99 ^b	115 ^c
Shortest distance from New Ireland (in km)	14.4	23.0	46.8	42.5	48.2

^a Simberi 50, Tatau 96, Tabar 105.

^b Boang 22, Malendok 65, Lif 9, Tefa 3.

^c Ambitie 82, Babase 33.

strongly differentiated forms on Dyaul are so poorly represented on the Hibernian Islands¹. Altogether, these islands are much poorer in species than Dyaul. The general distribution of the bird life on these islands is unknown, because the results of the "Whitney South Sea Expedition" (the only expedition which have collected on all four island groups) have not been published, but it is possible to compare the number of passerine species breeding in the different island groups on the basis of the distributional notes published by MAYR (1955, p. 1-46). These species are enumerated in

¹ The islands northeast of New Ireland have no collective name, but in the German period they were often called the "Hibernische Inseln". This designation included not only the four island groups of Tabar, Lihir, Tanga and Feni, but even the remote St. Matthias group and the low atoll Nissan. I have in the present paper retained the name, for lack of any better, but have restricted it to the four first-mentioned island groups, which form a natural geographical unit, being of a similar appearance and structure and having, so far known, a similar geological history.

a list in table 6, which is based on MAYR (*loc. cit.*), HARTERT (1926, p. 33), MEYER (1934, p. 294) and my own investigations.

It appears from table 6 that I found 18 species of passerine birds during my stay on Dyaul, while the corresponding figures for the Hibernian Islands are: Tabar 14, Lihir 13, Tanga 9 and Feni 8. A total of 35 species of breeding passerines is known from New Ireland. Of these species, however, nine are exclusively or predominantly found in the mountains, the number of true lowland species being only 26. This shows that the number of passerine species inhabiting Dyaul rather strongly approaches that found in the lowland of New Ireland, and the same fact holds good of the non-passerines. The number of species inhabiting Dyaul is probably still slightly greater than mentioned above, because a few species (*Cisticola exilis?*, *Hirundo tahitica?*, *Lonchura sp.?*) may have escaped our notice during the rather short visit of the "Noona Dan Expedition" to the island. As far as the Hibernian Islands are concerned, it should be added that MEYER (1934, p. 299) once professed to hear the call note of *Dicaeum eximium* on Lihir, but this must be due to some mistake as this species has never been encountered on Lihir. Even more uncertain is MEYER's statement of the occurrence of a *Munia sp.* (= *Lonchura*) on Lihir, based solely on a native name, which MEYER, however, admits may also be the name of a quail. There is no evidence for the occurrence of a *Lonchura* on Lihir.

Within most species the populations of the different Hibernian Islands are very similar. When subspecifically different from the New Ireland population they are either identical on most of the Hibernian Islands or at least very similar, *i. e.* they resemble each other more closely than they resemble the New Ireland population. This may indicate that occasional inter-island crossings take place in the Hibernian Islands resulting in subsequent gene-flow, but the effects of such incidents must be negligible. All evidence, gathered from similar tropical islands, tends to show that invasions of this kind occur as a rule much too rarely to be of any consequence to the genetical constitution of the population. On the other hand, the similarity of the endemic island forms within each species makes it an obvious conclusion that the different islands have been colonized by stray immigrants from the other islands rather than by independent invasions from New Ireland. It is fair to conclude that in each species as a rule only one successful oversea crossing from New Ireland was required. Once established on one island the species managed to colonize one or more of the other Hibernian Islands. This development is not surprising, however, as it forms the normal procedure in island colonization. It is a well-known zoogeographical fact that the potentialities for colonizing small islands are greater in populations of other small islands than in those inhabiting larger land-masses, because the former are already adapted to the insular environment.

It is not easy to decide which one of the four Hibernian island groups originally received the immigrants from New Ireland; the situation differs from one species to another. There are two cases in which a species is restricted to only one island (*Myzomela cruentata*, *Pitta erythrogaster*), and this is in both cases Tabar. In the cases

in which a species is found on only two islands these are usually Tabar and Lihir. This tends to show that Tabar, and perhaps in some cases Lihir, received the colonists from New Ireland. The problem can be further illustrated by a study of the morphological differentiation of the island populations. In *Lalage leucomela*, *Pachycephala pectoralis* and *Monarcha chrysomela* the Lihir form appears to be less modified than that of Tabar, and this indicates that Lihir was first colonized. In the case of *Cinnyris sericea* the Tabar and Lihir populations belong to the same subspecies as that of New Ireland, but in the coloration of the females approach the distinct form (*eichhorni*) of Feni (MAYR 1955, p. 40). Obviously, this species crossed from New Ireland to Tabar or Lihir and then from one of these islands, subsequently, invaded Feni, but failed to colonize Tanga. In *Rhipidura rufiventris* the situation is almost the contrary; the Tanga population (*tangensis*) is less modified than that of Lihir and Tabar (*gigantea*) and probably constitutes the first colonization, but in this case Feni was not reached. In *Coracina tenuirostris* the population of Feni belongs to the New Ireland subspecies *remota*, while those of Lihir and Tanga are identical and form the endemic subspecies *ultima*. Obviously, this species colonized Feni from New Ireland and then, subsequently, spread westwards from Feni to Tanga and Lihir, but has not reached Tabar.

Taking all facts together it appears that the waves of invasions emanating from New Ireland in most cases reached Tabar or Lihir and more rarely Tanga or Feni. Altogether, the passerine fauna of the latter two islands is more impoverished than that of Tabar and Lihir, numbering only 8–9 species, compared with 13–14 in Tabar-Lihir. It is obvious that the general colonization of the islands took place *via* Tabar-Lihir, but that a number of species failed to extend their breeding range from these two islands to Tanga and Feni. It should be added, however, that the absence of a species from one of the islands does not necessarily imply that it never has occurred there; it may have bred there in a former period and was afterwards wiped out.

The situation of the Hibernian Islands on the same are parallel to New Ireland may be taken as an indication of a former connection between the islands. Nothing is known about it, however, and from a zoogeographical view-point nothing speaks in favour of it. To all appearance, the composition of the bird-fauna of the four island groups makes the impression of being the result of random dispersal across the sea in rather recent time. Any existence of a former land connection between New Ireland and the Hibernian Islands is quite out of the question.

It is noteworthy that all passerine species inhabiting the Hibernian Islands have a wide distribution, ranging well into the Papuan region or even much farther than that. Not a single species endemic to the Bismarck Archipelago have reached the islands, while three of such species (*Dicaeum eximium*, *Monarcha hebetior* and *Monarcha ateralba*) occur on Dyaul. This is rather puzzling, because the latter species constitute an older fauna element and, therefore, were able to dispose of a longer period of time in which they could make a crossing to the islands. None of these indigenous species can be considered "old relicts" with declining population size and shrinking distribu-

tion and it is not probable that they formerly extended their breeding range to the Hibernian Islands, but the widely ranging species, presumably, possess greater colonizing powers and superior competitive capacities.

The development of endemic forms on the Hibernian Islands is not particularly pronounced. Only one form has reached species level (*Accipiter eichhorni* Hartert on Feni¹) and the endemic subspecies are as a rule only comparatively slightly differentiated².

A comparison between the passerine fauna of Dyaul and that of the Hibernian Islands shows that Dyaul is characterized by its greater richness in species and by its high proportions of distinct endemic forms. In order to explain these differences between Dyaul and the Hibernian Islands it is necessary to analyse the factors which control island colonization by birds. An attempt to perform such an analysis is made below.

Factors Controlling Island Colonization

The possibilities available to an island for colonization by land birds across the sea are dependent mainly on:

- (1) The age of the island, *i. e.* the length of time in which the island could have received avian immigrants.
- (2) The size of the island.
- (3) The distance from the area from which immigrants can be expected.
- (4) The direction and strength of the prevailing winds.
- (5) Habitat characters and biotic factors.

These factors are analysed below separately in order to throw some light on the history of the avifauna of Dyaul and the Hibernian Islands.

Age: The Hibernian Islands are partly volcanic in origin and are probably younger than Dyaul (*cf.* below, p. 31). It is even possible that volcanic activity has destroyed parts of the fauna at a recent date. The relatively low age of the Hibernian Islands may account for their paucity of species and their scarcity of striking endemic forms.

Size: It appears from table 6 that all the satellite islands of New Ireland have an area of about the same order of magnitude. Tanga and Feni are practically the same size as Dyaul, while Lihir is somewhat larger and Tabar more than twice as large. Nevertheless, Dyaul has more species than Tabar and Lihir and even twice the number of that on Tanga and Feni. Consequently, the small differences in size are probably of minor importance only.

Distance: The island groups of Lihir, Tanga and Feni are situated at the same distance from New Ireland, while Tabar is at only half this distance from New Ire-

¹ By MAYR (1957, p. 2) regarded as conspecific with *Accipiter albogularis* of the Solomon Islands.

² The number of endemic subspecies restricted to only one island is 5 on Tabar, 3 on Lihir, one on Tanga and one on Feni.

land, and Dyaul is still closer. These differences may have some bearing on the number of species on the islands. There is a certain correlation between the narrowness of the separating water gap and the number of species, at least as far as Dyaul and Tabar are concerned (cf. table 6).

Wind: The southeastern trade-wind, which is the prevailing wind from May to October blows approximately parallel to the longitudinal direction of New Ireland and does not favour immigration either to Dyaul or to the Hibernian Islands. The monsoon, blowing from November to April, is mostly northern (northeastern-northwestern), and thus favourable for invasions to Dyaul from New Ireland (or from New Hanover), but very unfavourable for the Hibernian Islands.

Habitat: The physical and biotic environment of Dyaul and that of the lowland of New Ireland appear to me to be very similar. The Hibernian Islands differ from Dyaul in being much more mountainous and, if anything, this should result in a more varied environment with a greater number of ecological niches and, consequently, favour the presence of a greater number of species. This difference appears to be of no significance, as the Hibernian Islands are actually poorer in species than Dyaul.

Summing up, Dyaul has evidently greater possibilities than the Hibernian Islands for colonization by New Ireland birds. It is situated closer to New Ireland, is favoured by the direction of the wind and is probably of greater age. These facts may explain the greater richness of the fauna of Dyaul, and its greater antiquity would even satisfactorily explain the stronger development of endemic forms. The assumption concerning the difference in geological age rests on a very slender foundation, however.

Other factors than those mentioned above may have influenced the faunal history of Dyaul and made the situation more complicated. The possibility cannot be ruled out that Dyaul, contrary to the Hibernian Islands, was once in connection with New Ireland. The existence of such a former land bridge would alter the whole picture drastically. If originally being a fraction of New Ireland Dyaul would have taken over the entire lowland fauna of New Ireland, and the richness of its fauna would then be easily explained. Under such circumstances the differentiation of the endemic forms, on the other hand, would have required a much longer period of time than if Dyaul was a truly oceanic island (cf. above, p. 22). The great depth of the Gazelle Channel, amounting to about 1000 meters, is no argument against the land connection; uplifts of this magnitude actually have taken place. A few notes on the geological history are necessary.

Notes on Geology

The geology of New Ireland and its satellite islands is characterized by a violent tectonic and volcanic activity, which gave rise to drastic developments in the later periods of the Tertiary. On both New Ireland and Dyaul wide-spread andesite and tuff layers are evidence of a former very strong volcanic activity. On New Ireland there are extensive layers of oligocene limestone as well as chalk beds with foraminifera

belonging to recent species. These cannot, therefore, possibly be older than Pliocene, and are most probably from Pleistocene. Even on Dyaul scattered occurrences of tuffs with foraminifera have been found (SAPPER 1910, p. 22; SIEVERS 1910, p. 439). The chalk beds on New Ireland are found on altitudes up to 1100 meters above sea level, which shows that an enormous upheaval, amounting to at least 1500 meters, has taken place in the recent past. It is evident that the present New Ireland, New Hanover and Dyaul were formed partly by uplift, partly by volcanic extrusion. The volcanic activity, which may have been submarine, cannot be dated, but probably took place in the latest part of the Tertiary. The upheaval is so young that the emergence of the islands above the sea cannot have taken place before Pleistocene. During the latter part of the upheaval, in a period extending into the Quaternary, enormous layers of coral rock were deposited upon the older sediments, adding considerably to the area of the islands (SAPPER 1910, p. 57-60). It is very likely that in a certain period Dyaul was in land connection with New Ireland-New Hanover, but, admittedly, this theory cannot be proved at present. It is noteworthy, however, that the terraced profile of Dyaul and that of the south coast of New Ireland, closely correspond, according to verbal information by SOFUS CHRISTIANSEN, M. Sc., indicating that even during the recent upheaval the two islands are influenced in a parallel way and probably are somehow in connection with each other.

Bearing in mind that the development of the Dyaul endemics must have required a long time of isolation, it is obvious that Dyaul, if it was originally part of New Ireland, was detached from that island rather early, and at any rate earlier than the period in which New Ireland and New Hanover were separated. The great depth of the Gazelle Channel indicates that the age of Dyaul as an independent island cannot possibly be less than 100,000 years, and an estimate of 200,000 years probably comes nearer the truth, but at present this is mere guesswork.

The geological features of the four Hibernian Islands are very similar. They are characterized by a strong volcanic activity, continuing still to-day. Layers of young eruptives are mixed with raised coral beds. There are no signs of older deep sea sediments (SIEVERS 1910, p. 452). This shows that these latter, if present at all, have been completely covered by coral rocks, and this indicates, in my opinion, that the upheaval took place rather slowly and that the islands, consequently, are younger than Dyaul and New Ireland.

New Ireland-New Hanover as Centre of Origin

It has been mentioned above that New Ireland and New Hanover probably formed one island until quite recently. This double-island forms the origin of the main part of the land-bird fauna in a number of islands. These islands belong to four different zoogeographical categories:

(1) The Admiralty Islands and the St. Matthias Islands. These are outlying islands, far removed from New Ireland, characterized by a relative paucity of species and a great percentage of markedly different endemic species and subspecies, char-

acters which are typical of peripherally isolated faunas. Both island groups are inhabited by 15 species of passerine birds (but not necessarily the same species on both groups), *i. e.* only one more species than Tabar, in spite of the very much greater area of both island groups (1950 sq. km in the Admiralty Islands, compared with 251 sq. km in Tabar). There is a slight New Guinea element on the Admiralty Islands, and even on the St. Matthias Islands (*Myzomela nigrita*).

(2) The Hibernian Islands. These islands are situated much nearer to New Ireland than the St. Matthias Islands and the Admiralty Islands. They are poor in species, although relatively richer (in relation to their small area) than the said outlying islands, and the percentage of striking endemics is small. They do not possess a typically peripheral fauna, but like the islands of the first category they are oceanic, in the zoogeographical sense of the word, *i. e.* they have received their fauna across the sea; cf. MAYR 1941 b, p. 199. The islands have received faunal elements also from the Solomon Islands, most prominently on Feni, but traceable westwards to Lihir.

(3) The Duke of York Islands. Situated between New Ireland and New Britain, but closest to the latter and with the Credner Islands serving as stepping stones for invading birds. The faunal connection with New Britain is much closer than that with New Ireland; as a matter of fact, there is no proof of a New Ireland origin for any of the species found on Duke of York Islands. They are inhabited by 12 species of passerine birds, none of which have developed endemic forms. The area is somewhat smaller than that of Dyaul. It has probably been in land connection with New Britain until quite recently.

(4) Dyaul Island. This island is situated as near to New Ireland as the Duke of York Islands, but differs by having a much richer fauna (18 passerine species) and by having developed a number of striking endemic forms. The fauna of Dyaul cannot be called peripheral and, as said above, the island is possibly not even oceanic. The relationship of its bird fauna is clearly with New Ireland, but a certain influence from New Hanover is present, however, in spite of the much longer distance from that island (50 km, compared with 14 km from New Ireland). The Dyaul form (*sumunae*) of *Lalage leucomela* is obviously an offshoot of the New Hanover form (*albidior*), which latter is almost intermediate between the New Ireland form (*karu*) and *sumunae*. In the case of *Monarcha chrysomela* the populations of New Ireland and New Hanover are indistinguishable in coloration, but the population of New Hanover is intermediate in proportions between that of New Ireland and that of Dyaul. This may indicate that the Dyaul population originated from New Hanover, but the different proportions may as well express differences in adaptation to some environmental factor; at any rate, similarity in measurements may not necessarily represent any close genotypical agreement, but may be the result of parallel developments. It is more important, however, that a specimen (♂ ad.) from New Hanover tends towards the Dyaul form *pulcherrima* in coloration, having the black feathers of the upper parts supplied with broad yellow edges, producing a variegated pattern. This specimen either represents the first step towards the colour pattern of *pulcherrima*

or it constitutes a hybrid between the two forms. If the latter explanation is correct it shows that gene-flow between the populations is possible, but obviously only in exceptional cases and undoubtedly soon being subject to "swamping".

Summary

The "Noona Dan Expedition" during its visit to the Bismarck Archipelago investigated the fauna and flora of Dyaul Island, which hitherto was unexplored. The position of Dyaul, situated due south of the western end of New Ireland, is given on the map fig. 1, on which also all the collecting stations are shown. A short description of the topography and vegetation of Dyaul is given on p. 3.

The most remarkable result of the ornithological investigation of Dyaul was the discovery of a number of striking endemic forms, the description of which forms the first part of the present paper. In the following enumeration of the Dyaul endemics the principal importance of the morphological differentiation is emphasized:

Dicaeum eximium phaeopygium, new subspecies (p. 5). Differs strikingly from the two other forms of this species by the loss of the bright carmine red rump patch. A similar evolutionary step has been taken also in other groups within the genus *Dicaeum*, but then usually serves to distinguish full species (not subspecies). Adult males are illustrated on plate I, fig. 1; measurements are given in table 1.

Monarcha chrysomela pulcherrima, new subspecies (p. 7). Differs strikingly from all other forms of this species by its uniform yellow, not black, upper parts in the adult males. Both sexes are illustrated on plate I, fig. 2; measurements are given in table 2.

Monarcha ateralba, new species (p. 9). Differs from its nearest ally, *M. verticalis*, so strikingly both in proportions and coloration that it has evidently reached species level. The new species belongs to the superspecies *M. verticalis*, which is represented in the Bismarck Archipelago by four species (fig. 4). Adult males of the new species are illustrated in fig. 2, juvenile specimens in fig. 3; measurements are given in table 3.

Monarcha hebetior cervinicolor, new subspecies (p. 14). The females differ strikingly from the two other forms of this species by several characters (*e. g.* rufous, not blackish brown, tail) which approach those of the allied species *M. alecto*. Adult females are illustrated on plate II, fig. 1; measurements are given in table 4. The relation between the two closely allied species *M. hebetior* and *M. alecto* is discussed, and the theory is set forth that *alecto* twice invaded the Bismarck Archipelago from New Guinea. The first invasion gave rise to the development of *hebetior*, while the second and more recent colonization has not resulted in any morphological differentiation.

Lalage leucomela sumunae, new subspecies (p. 18). Differs from all the forms inhabiting the main chain of islands in the Bismarck Archipelago (*falsa*, *karu*, *albidior*) by having white under parts without rufous. A complete loss of rufous has taken place

also in the forms inhabiting Tabar and Lihir, but all other forms of this widespread species have buffish or partly rufous under parts. Adult females are illustrated on plate II, fig. 2, adult males of various subspecies in fig. 5; measurements are given in table 5.

The morphological differentiation of the endemic forms of Dyaul must have required a certain amount of time, during which the populations were isolated from those of New Ireland. The length of this period of isolation has been roughly estimated on the basis of a comparison with similar tropical islands (Philippine Islands, West Sumatran Islands). Attention is drawn to the fact that, from an evolutionary point of view, it is necessary to distinguish between two categories of insular faunas: (1) Those faunas which have been isolated through segregation of a formerly continuous range, and (2) those faunas which have been founded by colonists across the sea. In the latter category the morphological differentiation of the populations will take place much more rapidly than in the former category.

The distribution of the above-mentioned five species in the Bismarck Archipelago has been outlined on the map fig. 6. In all five species the populations of the main chain of islands (Umboi, New Britain, Duke of York Islands, New Ireland and New Hanover) are either identical or only slightly differentiated when compared with the striking forms on Dyaul. This phenomenon is explained as primarily the result of a greater evolutionary rate in the Dyaul populations, but a time-factor must have been involved also. Evidence is given for the assumption that the main islands were mutually connected, forming one or two big islands, when Dyaul had already received its fauna. It is noteworthy that the Gazelle Channel, not broader than 14 km, has in spite of its extreme narrowness been broad enough to form an effective barrier, preventing gene-flow between the populations of New Ireland and Dyaul.

A comparison is made between the passerine fauna of Dyaul and the island groups of Tabar, Lihir, Tanga and Feni, for which four groups the collective designation "Hibernian Islands" has been revived. None of the five species which have developed strongly differentiated forms on Dyaul have reached Tanga and Feni, and two only (*Monarcha chrysomela* and *Lalage leucomela*) have reached Tabar and Lihir; cf. fig. 6. Altogether the Hibernian Islands are poorer in species than Dyaul. It appears from table 6 that Dyaul is inhabited by 18 species of passerine birds, Tabar by 14, Lihir by 13, Tanga by 9 and Feni by 8. The corresponding figure for the lowland of New Ireland is 26. Within most species the populations of the different Hibernian Islands are very similar, *i. e.* they resemble each other more closely than they resemble the New Ireland population. This similarity makes it obvious that the different islands have been colonized by stray immigrants from the other islands rather than by independent invasions from New Ireland. In each species as a rule only one successful oversea crossing from New Ireland was required. Once established on one island the species managed to colonize one or more of the other Hibernian Islands. The waves of invasions emanating from New Ireland reached in most cases Tabar or Lihir, more rarely Tanga or Feni. A number of species which have colonized Tabar

and Lihir failed to extend their breeding range from these two islands to Tanga and Feni, which, consequently, have a more impoverished fauna than Tabar-Lihir. To all appearance, the composition of the bird-fauna of the four Hibernian Islands gives the impression of being the result of random dispersal across the sea in rather recent time, and nothing speaks in favour of the view that a land-connection ever existed between them.

All passerine species inhabiting the Hibernian Islands have a wide distribution outside the Bismarck Archipelago; not a single species endemic to the Bismarck Archipelago has reached the Hibernian Islands. The widely ranging species, therefore, presumably possess greater colonizing powers and superior competitive capacities.

While the Hibernian Islands have a rather impoverished passerine fauna and only slightly differentiated indigenous subspecies, Dyaul differs in having a greater richness in species and a high proportion of distinct endemic forms. In order to explain these differences an attempt is made to analyse the factors which control island colonization by birds. The possibilities available to an island for colonization by land birds across the sea are dependent mainly on: (1) The age of the island, (2) The size of the island, (3) The distance from the area from which immigrants can be expected, (4) The direction and strength of the prevailing winds, and (5) Habitat characters and biotic factors. The total area and the distance from New Ireland of Dyaul and the four Hibernian Islands are given in table 6. A comparison between Dyaul and the Hibernian Islands tends to show that Dyaul evidently has greater possibilities than the Hibernian Islands for colonization by New Ireland birds. It is situated closer to New Ireland, is favoured by the direction of the wind and is probably of greater age. These facts may explain the greater richness of the fauna of Dyaul, and its greater antiquity would even satisfactorily explain the stronger development of endemic forms. It is probable, however, that Dyaul, contrary to the Hibernian Islands, was once in land-connection with New Ireland. In that case Dyaul would have taken over the entire lowland fauna of New Ireland, and the richness of its fauna could then be easily explained. On the other hand, under these circumstances the differentiation of the endemic forms would have required a much longer period of time.

According to the geological features of New Ireland and its satellite islands (briefly described on p. 30–31) the present New Ireland, New Hanover and Dyaul were formed partly by uplift, partly by volcanic extrusion, which took place in the later periods of the Tertiary. The upheaval, which amounted to at least 1500 meters, extended into the Quaternary, and the emergence of the islands above the sea could not possibly have taken place before the Pleistocene. It is obvious, for zoogeographical reasons, that Dyaul, if it was originally a part of New Ireland, must have been detached from that island rather early, and at any rate earlier than the period in which New Ireland and New Hanover were separated. The age of Dyaul as an independent island is estimated to be somewhere between 100,000 and 200,000 years. It is probable that the upheaval took place more slowly in the Hibernian Islands than in Dyaul and

New Ireland and that, consequently, the Hibernian Islands are younger, but the geological evidence is insufficient for a satisfactory clarification of the question.

New Ireland and New Hanover form the origin of the main part of the land-bird fauna in four zoogeographically different groups of islands: (1) The Admiralty Islands and the St. Matthias Islands, which are outlying islands with a typically peripheral fauna (impoverished, but with a high proportion of strongly modified forms). (2) The Hibernian Islands, which just like (1) are oceanic, but differ in having only slightly differentiated endemic forms. (3) The Duke of York Islands, which are not oceanic and completely lack endemic forms. (4) Dyaul Island, which is possibly not oceanic and has a comparatively rich fauna with many strikingly modified endemic forms. The said zoogeographical differences between the four categories of islands are due to the unequal possibilities for avian colonization and to the differences in the geological history which have been described in the present paper.

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PLATES

PLATE I

Fig. 1. Adult males of the three forms of *Dicaeum eximium*; *a-b* *layardorum* from New Britain, *c-d* nominate *eximium* from New Ireland, *e-f* *phaeopygium* from Dyaul; all collected by the "Noona Dan Expedition".

Fig. 2. Adult specimens of *Monarcha chrysomela* from the Bismarck Archipelago, showing differences between nominate *chrysomela* from New Ireland (*a-b* adult males, *e* adult female) and *pulcherrima* from Dyaul (*c-d* adult males, *f* adult female); all collected by the "Noona Dan Expedition".



Fig. 1.



Fig. 2.

PLATE II

Fig. 1. Adult females of *Monarcha hebetior*, showing differences between *cervinicolor* from Dyaul (*a-c*) and *eichhorni* from New Hanover (*d, e*) and New Ireland (*f*); *a, b, c, d* and *e* collected by the "Noona Dan Expedition", *f* belonging to the American Museum of Natural History, New York.

Fig. 2. Adult females of *Lalage leucomela* from the Bismarck Archipelago, showing differences between *karu* from New Ireland (*a-d*) and *sumunae* from Dyaul (*e-h*); all collected by the "Noona Dan Expedition".

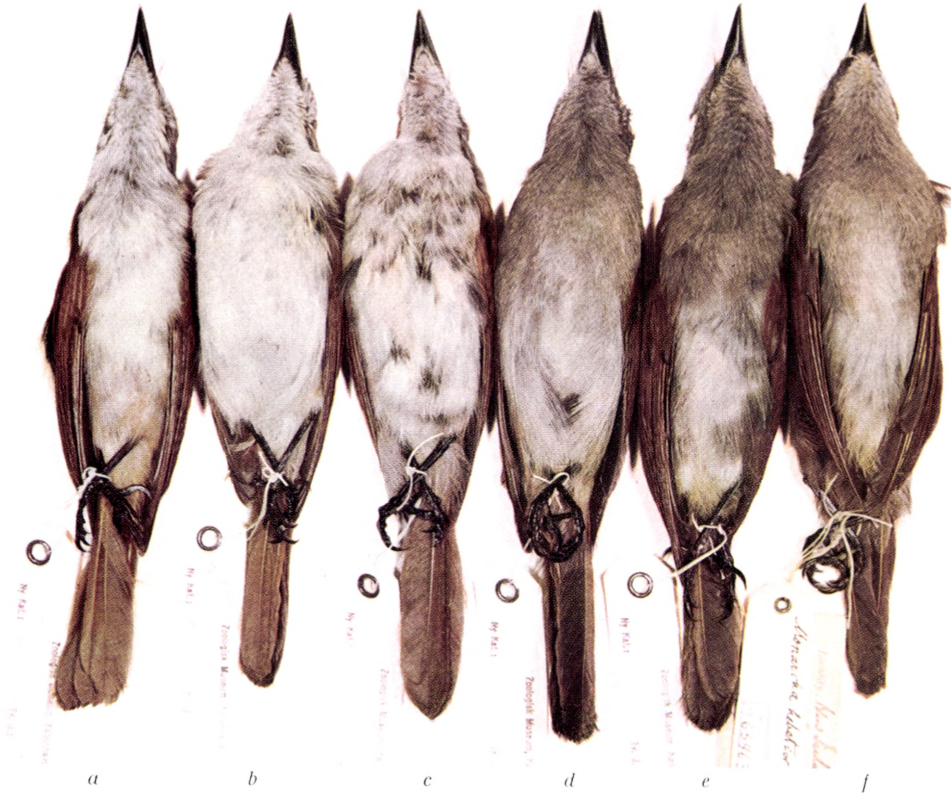


Fig. 1.



Fig. 2.

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