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Notes on Flowerpeckers (Aves, Dicaeidae) 4. *Dicaeum igniferum* and its Derivatives

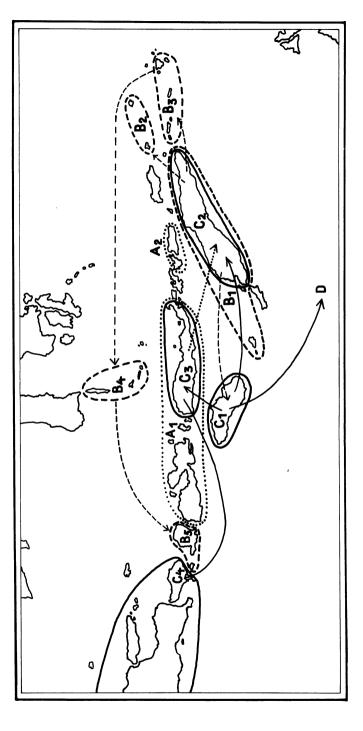
By FINN SALOMONSEN¹

In the third note on flowerpeckers (Salomonsen, 1960, Amer. Mus. Novitates, no. 2016, pp. 17-19) the relationship between the two "key species" Dicaeum nehrkorni and Dicaeum igniferum and a number of allied species was discussed. It was pointed out that Dicaeum igniferum had given rise to two lines of radiation, with subsequent formation of species. The first resulted in the development of the species D. cruentatum and D. trochileum; the second, in that of D. maugei and the superspecies D. hirundinaceum. These species, which constitute the most advanced group within the genus Dicaeum, form the subject of the present paper.

Dicaeum igniferum

This and the following six species belong to group 2 defined in the above-mentioned paper (Salomonsen, *loc. cit.*). Its members are characterized mainly by the glossy or iridescent upper parts and the distinct, rather complicated color pattern on the under parts of the males. This pattern includes a carmine or scarlet patch of varying extent on the middle parts of the throat and fore breast, usually continuing right to the base of the mandible, and surrounded by black, which covers the sides of the throat and breast and usually forms a transverse band below the red patch. Down the middle of the lower breast and the abdomen runs a longitudinal narrow black streak, frontally attached to the transverse black band. The remaining parts of the under side are generally

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cretum). Dashed line: D. maugei (B1, maugei; B2, romae; B3, salvadorii; B4, splendidum; B5, neglectum). Solid line: D. sanguinolentum (G1, unlhelminae; C2, hanieli; C3, rhodopygiale; C4, sanguinolentum). Arrows indicate the probable routes of dispersal and are marked with the same form of line (dotted, dashed, and solid, respectively) as the contour of the range of the corresponding species. The arrow Fig.1. The distribution of Dicaeum igniferum and its allies in the Lesser Sunda Islands. Dotted line: D. igniferum (A1, igniferum; A2, leading to D indicates the colonization of Australia, with subsequent separation of D. hirundinaceum.

whitish, yellowish, or buffy; in *igniferum* they are white. In the females this color pattern is completely lacking, the under parts being almost uniform whitish or yellowish.

Obviously the scarlet patch on the throat and fore breast is homologous with the red pectoral patch in the superspecies *D. erythrothorax*, while the black longitudinal band on the abdomen is homologous with the corresponding one in *D. nehrkorni*. The connection between that species and *D. igniferum* has already been discussed (Salomonsen, *loc. cit.*). *Dicaeum igniferum* resembles *nehrkorni* in having the crown and the rump red, but differs in having the red color of the crown extending over the neck and mantle and, in addition, in having a stronger and more violet gloss on the back. In the females the red color on the upper parts as well as the gloss is much duller than in the males.

When Wallace (1863, Proc. Zool. Soc. London, p. 494) described D. igniferum, he said that it resembled D. cruentatum on the upper parts and D. mackloti (= D. maugei) on the under parts. This is quite correct, and is interesting, furthermore, because, as already mentioned, two evolutionary lines emanate from D. igniferum, one leading to D. cruentatum, the other to D. maugei.

Dicaeum igniferum inhabits Sumbawa, Flores, Pantar, and Alor in the Lesser Sunda Islands. It is found in the lowlands, where it frequents open deciduous forests and shrubs, in Sumbawa also in the midmountain zone to an altitude of about 800 meters. There are two slightly different subspecies.

Dicaeum igniferum igniferum Wallace, 1863

Type Locality: Flores.

The nominate form inhabits the islands of Sumbawa and Flores.

Dicaeum igniferum cretum Rensch, 1929

Type Locality: Alor.

 53.5, 54; Flores, 50, 50, 51, 51, 52, 52.5, 53; Alor, 54, 54; Pantar, 53, 53 mm. Females: Sumbawa, 48, 49, 49, 49; Flores, 49, 49; Alor, 50.5, 51 mm. The difference is trifling indeed, and I am not very keen on accepting such weakly established forms. However, for the moment I recognize *cretum*, pending more material from Alor and Pantar.

Dicaeum maugei

This species, inhabiting a number of islands in the Lesser Sunda Islands, is clearly an offshoot of *D. igniferum*. The two species are very similar, *maugei* differing from *igniferum* only in having lost the red color on the crown, neck, and mantle, which are glossy violet, as is the back, while the rump is red (in both sexes) as in *igniferum*.

Among the subspecies of *D. maugei*, those inhabiting Timor (nominate maugei) and Roma and Damar (romae) are nearest igniferum in color pattern and proportions, only the bill is distinctly shorter, heavier, and more blunt. The length of the bill (measured from skull) is 13 mm. in igniferum and 11–12 mm. in nominate maugei, while the height is 3 mm. in igniferum and 4 mm. in maugei. Consequently, it is most likely that nominate maugei is the least-modified population and is the nearest relative of igniferum.

From Timor maugei emigrated to various smaller islands and became adapted to the conditions on such small islands as Roma, Damar, Babar, and Moa. Such adaptation enabled it to colonize other small remote islands, such as Saleyer and Djampea, and finally Lombok and nearby Nusa Penida. In this way its distribution became patchy and almost encircled that of igniferum, but the two species remained allopatric. The distribution and probable routes of colonization are shown in figure 1.

Dicaeum maugei inhabits edges of rain forests, open and deciduous forests and second growth, and is most common in the lowlands, but ascends high in the mountains. It has been recorded at altitudes up to 1200 meters in Timor and to 2000 meters in Lombok.

The geographical variation has been discussed mainly by Hartert (1896, Novitates Zool., vol. 3, p. 167; 1897, *ibid.*, vol. 4, p. 264; 1906, *ibid.*, vol. 13, p. 300) and Hellmayr (1916, Novitates Zool., vol. 23, p. 103). The latter author has shown that *Dicaeum Maugei* Lesson, 1830, should replace *D. Mackloti* S. Müller, 1843.

Dicaeum maugei maugei Lesson, 1830

Type Locality: Timor.

The nominate form inhabits Timor and the islands of Sawu and

Semau. Good series have been examined in the American Museum of Natural History and the British Museum (Natural History).

Dicaeum maugei romae Hartert, 1906

Type Locality: Roma Island.

Differs from nominate maugei only in being slightly larger, the wing in males measuring 57-59 mm., compared with 53-58 mm. in maugei. Inhabits the islands of Roma and Damar. Hartert's original series, including the type, in the American Museum of Natural History has been examined.

Dicaeum maugei salvadorii A. B. Meyer, 1884

Type Locality: Babar Island.

This form, which inhabits the islands of Babar and Moa, is of the same body size and bill form as *romae*, but differs distinctly in almost or completely lacking the black transverse band below the red throat patch, with the effect that the red color directly adjoins the white lower breast. Small series in the American Museum of Natural History and in the British Museum (Natural History) have been examined.

Dicaeum maugei splendidum Büttikofer, 1893

Type Locality: Saleyer Island.

The color pattern of the under parts is similar to that in salvadorii, but the red throat patch is lighter, more vermilion. In addition, the proportions are distinctly smaller, the wing length in males being 53–54 mm., compared with 56–58 mm. in salvadorii. Also, the bill is shorter, measuring only 11 mm., compared with 12 mm. in salvadorii. The similarity to salvadorii indicates that splendidum is derived from that form and not from romae or nominate maugei. It inhabits the islands of Saleyer and Djampea. A small series in the American Museum of Natural History and a single bird in the British Museum (Natural History) have been examined.

Dicaeum maugei neglectum Hartert, 1897

Type Locality: Lombok.

Similar to nominate maugei and romae in coloration, but differing in having the red color of throat and rump distinctly more intense, scarlet, not carmine, the transverse black band below the red throat decidedly broader, and the bill longer and more slender, measuring 13 mm., compared with 11-12 mm. in maugei. The proportions are small, as in splendidum, the wing of adult males measuring 52-56 (average 54.0) mm.

This form inhabits Lombok and the adjacent small island of Nusa Penida. The birds from this latter island have been separated by Neumann (1942, Zool. Meded. Leiden, vol. 23, p. 112) as D. maugei mariae, based on its alleged smaller measurements. Neumann gives the wing length in males of mariae as 51, 51.5 mm., compared with 53–55 mm. in eight males of neglectum from Lombok. Meise (1941, Jour. Ornith., vol. 89, p. 364) gives the measurements of the same two males of mariae as 52, 53 mm., comparing them with 53–55 mm. in Lombok males. I have examined a male from Lombok with a wing length of only 52 mm. and do not find any reason for the subspecific separation of the Nusa Penida birds.

Small series of specimens from Lombok in the American Museum of Natural History and the British Museum (Natural History), but none from Nusa Penida, have been examined by me.

Dicaeum sanguinolentum

This is the third species belonging to group 2 (cf. p. 1, above) and restricted to the Lesser Sunda Islands (and Java). It differs from D. maugei only in having lost the red color of the rump in the male, which is retained in the female. This phenomenon is peculiar, because in all other species belonging to this section of the genus Dicaeum the red color of the rump is not a sex-linked character, but either absent or present in both sexes. As far as the males are concerned, the evolutionary trend for gradual loss of red color marks, leading from igniferum via maugei to sanguinolentum, is exactly the same as the trend nehrkorni-vulneratum-erythrothorax and geelvinkianum-eximium-aeneum, although the latter case is not quite parallel.

Among the subspecies of sanguinolentum the Sumba form, D. s. wilhelminae, is evidently nearest maugei, being particularly close to nominate maugei in Timor. This latter is virtually identical in coloration with D. s. wilhelminae, apart from the fact that wilhelminae has lost the red color on the rump in the male and has a still brighter violet gloss on the upper parts and darker gray flanks. The bill is still shorter and thicker than in nominate maugei, being only 10 mm. long, but 5 mm. high.

The close relationship between D. m. maugei and D. s. wilhelminae has been stressed by Hartert (1897, Novitates Zool., vol. 4, p. 264), who was inclined to regard wilhelminae as conspecific with maugei, and by Mayr (1944, Bull. Amer. Mus. Nat. Hist., vol. 83, p. 143), who treated wilhelminae as a full species, because "it is impossible to decide, without a revision of the whole genus, whether wilhelminae is closer to maugei or

to sanguinolentum." Subsequently, however, Mayr and Amadon (1947, Amer. Mus. Novitates, no. 1360, p. 26) connected wilhelminae with the sanguinolentum group, a view with which I agree. The similarity between nominate maugei and wilhelminae indicates that the latter is an offshoot of maugei and that Sumba was colonized from Timor. Another alternative is that wilhelminae originated from the Lombok form D. maugei neglectum, but this latter is farther removed from wilhelminae than D. m. maugei, both in the coloration and in the form of the bill.

Dicaeum sanguinolentum wilhelminae has possessed considerable colonizing powers, which enabled it to undertake a number of successful interisland crossings. First, it has recolonized Timor, which now is inhabited by the distinct D. s. hanieli, living side by side with D. m. maugei. Second, it established itself on Flores, where D. igniferum was already present. The Flores form subsequently invaded Bali and Java, jumping across the interjacent islands of Sumbawa and Lombok. Finally, D. s. wilhelminae crossed the Timor Sea and settled in Australia, where it gave rise to D. hirundinaceum. This hypothesis is, at any rate, the most likely, as hirundinaceum is more similar to wilhelminae than it is to any other form. Mayr and Amadon (loc. cit.) are in favor of the theory that hirundinaceum is a derivative of wilhelminae.

The successful extension of range of wilhelminae may be partly due to the fact that in places where other closely allied species were already present (Flores, Timor) it became a mountain bird, frequenting the rain forests, while in Sumba it occurs in the deciduous forests down to sea level. Even in Bali and Java it is predominantly a mountain bird.

The preference for mountain habitats presents, however, a weakness in the whole argument, because new invaders on islands as a rule become lowland birds, while the old inhabitants retire to the mountains. Further, it invites the criticism that the morphological differences between the forms of sanguinolentum are much more pronounced than between those of maugei, a fact that also tends to indicate that sanguinolentum is the older species. Finally, sanguinolentum has the widest distribution, ranging from Java to Timor. The conclusion that sanguinolentum is an old relict mountain species, with a discontinuous distribution, and maugei a younger derivative is not easy to repudiate. However, this postulated development upsets the whole system, leaves unexplained the similarity between nehrkorni and igniferum (which is a close relative of maugei), demands an evolutionary trend exactly opposite to that in the superspecies D. erythrothorax, places the origin of the Lesser Sunda Islands species in Australia (D. hirundinaceum), and poses a number of other intricate problems. The discrepancy is, however, only apparent. Part of the difficulty, at least, may be overcome by assuming that the development took place as follows: At the end of the Tertiary D. igniferum inhabited Flores; D. maugei (a derivative of igniferum), Timor; and D. sanguinolentum (a derivative of maugei), Sumba. Subsequently sanguinolentum recolonized Timor, invaded Flores, and probably even crossed to Australia at an early date. As, in this period, Sumbawa and Lombok were mostly submerged, the Flores population colonized Bali

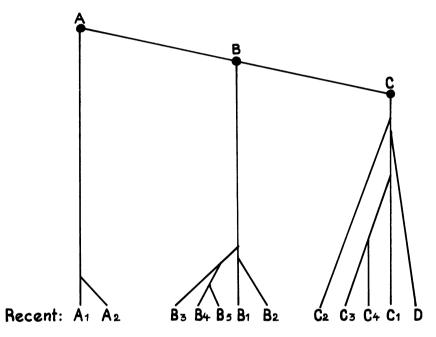


Fig. 2. Diagrammatic phylogeny of *Dicaeum igniferum* and its allies. The symbols are those used in figure 1. The length of the phylogenetic lines gives a rough measure of the time factor.

and Java directly across the sea, which accounts for the long history of the sanguinolentum group and its comparatively extensive distribution. Much more recently, after the upheaval of Sumbawa, Lombok, and other islands, D. igniferum and D. maugei began a colonization of the surrounding islands, igniferum occupying the islands adjacent to Flores, while maugei became adapted to smaller islands and to long voyages across the sea. The colonization of the available small islands probably took place in competition with other allied species, which in the same period were in the process of range expansion. Dicaeum maugei, there-

fore, was capable of colonizing only the nearest islands, while the more remote ones were occupied by *D. hirundinaceum*, *D. celebicum*, and *D. vulneratum* (fig. 3). Such is, of course, merely a brief outline of the evolutionary history. Volcanic activity, submergences, and upheavals in the Lesser Sunda Islands have most certainly contributed to make the history even more complicated.

The puzzling distribution of the closely allied species igniferum, maugei, and sanguinolentum is shown in figure 1. The most probable routes of colonization, necessary to explain the evolutionary trends discussed above, are indicated in the figure by arrows. With the use of the same symbols as in figure 1, the most probable phylogenetic lines are shown in figure 2, in which the length of the lines gives a rough measure of the time factor.

Dicaeum sanguinolentum wilhelminae Büttikofer, 1892

Type Locality: Sumba.

Abdomen and sides of breast pale grayish white, as in D. m. maugei. Even the remaining color pattern of the under parts in the male is quite similar to that of nominate maugei, only the flanks being darker, more slaty gray. The bill is heavier and thicker than in nominate maugei, as mentioned.

This is the form of Sumba Island. A long series in the American Museum of Natural History has been examined.

Dicaeum sanguinolentum hanieli Hellmayr, 1912

Type Locality: Timor.

Differs strikingly from D. s. wilhelminae in the color pattern of the under parts in the male. The red area on the throat is reduced to a small patch on the lower throat, and the black markings are reduced to a narrow transverse band below the red patch, the remaining under parts being white, with a pale yellowish tinge, as is true of the flanks also. The bill is strong and short as in wilhelminae, but perhaps on an average not quite so heavy. This is a very distinct form. It inhabits Timor. I have examined two adult males in the American Museum of Natural History.

Dicaeum sanguinolentum rhodopygiale Rensch, 1928

Type Locality: Flores.

Very similar to nominate sanguinolentum, but the under tail coverts in the males are orange-pink, not buff. Rensch (1928, Ornith. Monatsber., vol. 36, p. 80) states that, in addition, this form is larger than sanguinolentum, and gives the wing length in his two adult males as 50, 52 mm.,

compared with 47-49 mm. in a series from Java. I have examined only one male of *rhodopygiale* (in the American Museum of Natural History), which had a wing length of 51 mm., while a series of nominate *sanguinolentum* measured 48-51 (average 49.2) mm., which tends to show that the size difference is negligible. This form is restricted to Flores.

Dicaeum sanguinolentum sanguinolentum Temminck and Laugier, 1829

Type Locality: Java.

Differs from wilhelminae in having the abdomen and the sides of the breast buffy, not grayish white, the flanks black, not slaty gray, the blackish transverse band below the red throat absent, the black longitudinal streak on the lower breast and abdomen narrower and shorter, and the bill much thinner and more attenuated, being only 3 mm. high at the base, compared with 5 mm. in wilhelminae. This distinct form inhabits Java and Bali. I have examined a series from both islands in the American Museum of Natural History.

Robinson and Kloss (1923, Jour. Federated Malay States Mus., vol. 11, p. 57) separated the East Javan birds as D. s. ablutum, stating that the females had no red color on the rump. Bartels and Stresemann (1929, Treubia, vol. 11, p. 142) questioned such separation, and it was subsequently discussed by Chasen (1940, Treubia, vol. 17, p. 264), Mayr and Amadon (1947, Amer. Mus. Novitates, no. 1360, p. 26), and Voous (1948, Limosa, vol. 21, p. 99). It appears that the females of the alleged new form have the rump red, as do those of all other subspecies of sanguinolentum. I have examined the type in the British Museum (Natural History). It is undoubtedly a male in the immature plumage (in which the rump is never red), wrongly sexed as a female. A topotypical adult male is exactly similar to typical sanguinolentum from West Java.

Dicaeum hirundinaceum

The five species sanguinolentum, hirundinaceum, celebicum, monticolum, and ignipectus are closely allied and together form a superspecies. In this assemblage D. hirundinaceum is characterized by having bright red under tail coverts (in both sexes), while the other four species have them whitish, or at most lemon-yellow. A tendency to attain reddish under tail coverts is noticeable, however, in D. sanguinolentum rhodopygiale.

While in *D. sanguinolentum* the females have bright red on the rump, this character has been lost in the four other species within this superspecies. In *celebicum*, *monticolum*, and *ignipectus* the rump in the females is of exactly the same color as the remaining upper parts, but in *D. hirundinaceum* it is still dull maroon, contrasting with the back, although with varying intensity, being most pronounced in the subspecies *fulgidum*

and virtually not visible in nominate hirundinaceum.

Dicaeum hirundinaceum is clearly an offshoot of D. sanguinolentum. Nominate hirundinaceum is very similar to D. s. wilhelminae in the color pattern of the under parts, the gloss of the upper parts, and the structure of the bill, which is almost as thick and stout as in wilhelminae. Apart from possessing red under tail coverts, nominate hirundinaceum differs from wilhelminae mainly in having longer and much more pointed wings and in having the red color of the throat in the males more extended and darker, sanguineous, not bright carmine. There are four strikingly different subspecies.

Dicaeum hirundinaceum hirundinaceum (Shaw and Nodder), 1792

Type Locality: New South Wales, Australia.

This is the well-known Mistletoe-Bird of Australia. It is found virtually in all parts of the Australian continent, but in spite of such an enormous range it does not vary significantly. It has strong nomadic tendencies, and in search of its favorite food plant, the mistletoe, it carries out long and sustained flights, in which it is aided by its long and pointed, almost swallow-like, wings. It has consequently much reduced possibilities for developing any geographical variation. There is a slight cline for increasing size running from the northern tropical zone to the southern subtropical one, but the differences in size between the populations are inconsiderable and do not justify separation of subspecies. I have measured a total of 32 males [the American Museum of Natural History, 21 specimens; British Museum (Natural History), nine; Naturhistoriska Riksmuseet, Stockholm, twol from Cape York Peninsula, northern Queensland (south to Cairns), and they had a wing length of 57-64 (average 60.0) mm. A total of 20 males [the American Museum of Natural History, 15 specimens; British Museum (Natural History), five] from southern New South Wales, Victoria, and South Australia had a wing length of 61-66 (average 63.7) mm. These measurements agree well with those given by Keast (1958, Emu, vol. 58, p. 196). The populations of which the wing lengths are given above constitute the end links of the cline, but they display in their measurements, nevertheless, a considerable overlap.

Mathews (1912, Novitates Zool., vol. 18 [1911], p. 387) has described two subspecies from Australia, tormenti (type locality, northwest Australia) and yorki (type locality, Cape York), of which the types are in the American Museum of Natural History, where I have examined them. Both these names must be synonymized with nominate hirundinaceum.

Dicaeum hirundinaceum hirundinaceum has not reached Tasmania but is

found in the islands in the Torres Strait, and it once straggled to the Gulf of Papua, southeastern New Guinea, according to Iredale (1957, Birds of New Guinea, vol. 2, p. 173).

Dicaeum hirundinaceum ignicolle G. R. Gray, 1858

Type Locality: Aru Islands.

Differs from nominate hirundinaceum in having the flanks and the sides of the breast and abdomen dull olive grayish green, and the center of the lower breast and abdomen yellowish; in hirundinaceum the flanks are dark gray and the lower breast and the abdomen whitish. In addition, the proportions are smaller, the wing length in males being 51–53 mm., the wings are much more rounded, and the bill is slightly more slender. The females have a faint maroon tinge on the rump. This very distinct form inhabits the Aru Islands. I have examined small series in the American Museum of Natural History and in the British Museum (Natural History), including the type.

Dicaeum hirundinaceum keiense Salvadori, 1875

Type Locality: Kei Islands.

Differs strikingly from the preceding subspecies in having the throat, breast, and under tail coverts pink, not bright red, the pink color extending down onto the lower breast, which is whitish in hirundinaceum and yellowish in ignicolle. The flanks are paler grayish green than those of ignicolle, the longitudinal blackish streak on the abdomen is reduced and paler, more brownish gray, and the upper parts are paler violet-blue. In addition, the proportions are slightly larger than those of ignicolle, the wing length in males being 55–56 mm., but the bill is similar to that of ignicolle. The females have distinctly more maroon on the rump than those of ignicolle.

This is another very distinct island form. It is found on the Kei Islands and the adjacent small island groups Tajandu and Watubela. I have examined a few specimens in the American Museum of Natural History and two adult males in the Zoological Museum, Copenhagen.

Dicaeum hirundinaceum fulgidum Sclater, 1883

Type Locality: Tenimber Islands.

The entire under parts are pale rosy, paler than in keiense, only the sides of the abdomen having some grayish green color. The wing length in males is 53-55 mm.; the bill does not differ from that of keiense. The females have the rump dark maroon, strongly contrasting with the back. This is the most divergent subspecies of hirundinaceum. It is restricted to the Tenimber (= Tanimbar) Islands. I have examined a good series from

Larat Island in the American Museum of Natural History, and the type specimen (from the same island) in the British Museum (Natural History).

Dicaeum celebicum

Dicaeum hirundinaceum, celebicum, monticolum, and ignipectus show a very strong affinity, and it is a matter of taste whether these four birds should be considered full species, as they are in the present paper, or regarded as conspecific, as has been done by other students. An obvious evolutionary line runs in the direction hirundinaceum-celebicum-monticolum-ignibectus, which is apparent both in the morphological characters and in the range pattern. A good example of this evolutionary development is the trend in the bill structure, from the robust bill of nominate hirundinaceum through the intermediate stage in the northern island forms of hirundinaceum to the more slender form in celebicum, monticolum, and ignipectus, in which the bills are virtually identical. Further, one notes the occurrence of the dark olive grayish green color on the flanks and the sides of the breast and of the abdomen. This "clay color" is not present in any of the species in the Lesser Sunda Islands (igniferum, maugei, and sanguinolentum), but occurs in the island forms of D. hirundinaceum (secondarily reduced in fulgidum), reappears in celebicum, is most pronounced in the subspecies sulaense, and becomes predominant in monticolum and ignipectus, species in which it is the only color found. Finally, we observe the gradual change in the gloss of the upper parts, which in celebicum does not differ essentially from that of hirundinaceum, while monticolum is virtually intermediate in this respect between celebicum and the very divergent ignipectus. This will suffice, but other points could be added.

Another fact that speaks in favor of the described evolutionary line is the different magnitude of the geographical variation within each of the four species in question. *Dicaeum hirundinaceum*, which, according to the theory, is the most ancient of the four species, has developed the most extravagant forms (such as *fulgidum*). In *celebicum* the geographical variation is still rather striking, while in *ignipectus* it is comparatively slight, the general color pattern, which is found throughout its range, being subject to minor alterations only. This tends to show that *ignipectus* is the youngest of the species in question. *Dicaeum monticolum* is monotypic.

Mayr and Amadon (1947, Amer. Mus. Novitates, no. 1360, p. 28) are inclined to think that *celebicum* is closely allied to *sanguinolentum* and that it is directly derived from that species by a colonization of Celebes and adjoining islands from the Lesser Sunda Islands. I do not agree with this view, because it implies that two important non-adaptive characters, viz.,

the loss of red on the rump of the females and the development of "clay color" on the sides of the under parts, must have evolved independently in *celebicum* and *hirundinaceum*, which is very unlikely.

The most probable explanation of the development within this group of species follows. Sometime in the late Pleistocene, when the Sahul Shelf was partly dry land, *D. hirundinaceum* colonized the islands, where the populations eventually became the subspecies *ignicolle*, *keiense*, and *ful-*

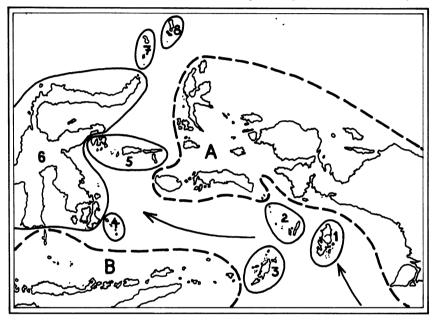


Fig. 3. The route of colonization by Dicaeum hirundinaceum-celebicum, indicated by arrows: 1, ignicolle; 2, keiense; 3, fulgidum; 4, kühni; 5, sulaense; 6, celebicum; 7, sanghirense; 8, talautense. Only those island groups have been occupied that are situated between the areas inhabited by the superspecies Dicaeum erythrothorax (dashed line, A) and by Dicaeum maugei (dashed line, B), respectively.

gidum. There it became adapted to island conditions, which involved also a capability for colonizing islands across the sea. Two related species possessed a similar faculty, although to a much lesser degree, namely, D. maugei and D. vulneratum. In this period the Moluccas and the Papuan region were inhabited by the superspecies D. erythrothorax, and the Lesser Sunda Islands by D. maugei and other species, but the island groups in the broad corridor between these areas were uninhabited by flower-peckers. These islands, therefore, could be subject to colonization by en-

terprising species, and D. hirundinaceum-celebicum succeeded in occupying most of the island groups in the Celebes region, although probably in competition with D. vulneratum and D. maugei. From the Kei Islands hirundinaceum penetrated as far as the Watubela Islands, but vulneratum blocked its way at the Gorong Islands. In the race for the islands south of Celebes maugei succeeded in occupying Saleyer, celebicum the Tukangbesi Islands. In figure 3 the final arrangement of the species is shown, with the hirundinaceum-celebicum group sandwiched between maugei and the superspecies erythrothorax. Only in the big island of Celebes could two species (nehrkorni, belonging to the superspecies erythrothorax, and celebicum) live side by side.

The range expansion of hirundinaceum must have taken place with some speed and at an early date, before the most striking characters of the Tenimber and the Kei subspecies had been manifested in the genotype. It is understandable, therefore, that some of the subspecies of celebicum, such as kühni and, particularly, sanghirense, still seem surprisingly similar to nominate hirundinaceum and even to D. sanguinolentum wilhelminae.

The further expansion, from the Celebes region to Borneo and the Philippines, involves the shifting of habitat from small islands to mountain forests. This is not a unique phenomenon, however, but is paralleled in many other species, of which *Turdus poliocephalus* forms an especially striking example. The montane-insular type of distribution in tropical birds has recently been discussed by Braestrup (1956, The natural history of Rennell Island, vol. 1, p. 140).

As stated above, the two island and lowland species (hirundinaceum and celebicum) and the two mountain species (monticolum and ignipectus) could all very well be regarded as conspecific. The reason for not doing so in this paper is the fact that from a morphological point of view each forms a well-defined unit. The main characters of the celebicum group are the white or whitish under tail coverts (red in hirundinaceum, yellow in monticolum and ignipectus), the uniform grayish brown upper parts of the females, and the dark bluish violet gloss on the upper parts of the males; this last character is common to celebicum and hirundinaceum. The bill is thinner and more slender than in hirundinaceum. All the subspecies are rather distinct.

Dicaeum celebicum kühni Hartert, 1903

Type Locality: Tukangbesi Islands.

The male is colored principally like that of D. sanguinolentum wilhelminae, but the flanks are grayish olive and the blackish longitudinal streak along the middle of the abdomen is lighter and less well defined. The wing length in males is 52-53 mm. It is restricted to the Tukangbesi

Islands. A small series in the American Museum of Natural History, including the type, has been examined.

Dicaeum celebicum sulaense Sharpe, 1884

Type Locality: Sula Islands.

In the male the sides of the under parts and the flanks are dark olive grayish green, of exactly the same color as in *D. hirundinaceum keiense*, and the longitudinal streak on the abdomen is grayish, not black, and rather thin and ill defined, which is also a character of *keiense*. The upper parts are slightly more lilac-blue than those of *kühni*, not so bluish black. The wing length in males is 51–54 mm. This form inhabits the Sula and the Banguey Islands. The populations of the two island groups are quite similar. A series of six males in the American Museum of Natural History and the type specimen in the British Museum (Natural History) have been examined.

Dicaeum celebicum celebicum S. Müller, 1843

Type Locality: Celebes.

Compared with kühni and sulaense, the flanks are darker, grayish black with an olive tinge, the middle parts of the abdomen and the under tail coverts are tinged with light creamy yellow, not grayish white, and the upper parts are dull amethystine, a color type that is unique in the whole group but is approached by sulaense. The proportions are smaller; the wing length in males is 47–50 mm.

This form inhabits Celebes, including the islands of Muna and Buton. It frequents gardens and orchards, open land with plantations, second growth and edges of forests, from sea level to an altitude of at most 1000 meters. A long series in the American Museum of Natural History has been examined.

Dicaeum celebicum sanghirense Salvadori, 1876

Type Locality: Sangihe Islands.

The under parts in the male are very near those of the male of *D. sanguinolentum wilhelminae*, having pure gray flanks, but the upper parts are more ink-blue, not so bluish purple. The wing length in males is 50–54 mm. This form is restricted to the Sangihe Islands. I have examined two males in the American Museum of Natural History (from Siao Island) and one male in the Zoological Museum, Copenhagen (from Great Sangihe Island).

Dicaeum celebicum talautense Meyer and Wiglesworth, 1895

Type Locality: Talaut Islands.

The under parts below the red throat patch are almost uniform dark grayish black, the white color being virtually absent. The gloss of the upper parts is of the same shade as in *sulaense*. The wing length in males is 51–56 mm. This distinct form inhabits the Talaut Islands. Specimens from Lirung Island and Karakelong Island are identical. A good series in the American Museum of Natural History has been examined.

Dicaeum monticolum Sharpe, 1887

Type Locality: Mt. Kinabalu, Borneo.

The male has "clay-colored" flanks, similar to those in *D. celebicum sulaense*, but the light areas of the under parts (the middle of the lower breast and of the abdomen and the under tail coverts) are lemon-yellow, not white. In this way monticolum has a color pattern on the under parts very similar to that of ignipectus. The upper parts are glossy bluish, with a tendency towards greenish, clearly nearest such forms of celebicum as sanghirense, but with a distinct approach to the steel-green color of ignipectus. The bill is very similar to that of celebicum, but slightly finer and more attenuated. The wing length in males is 47–54 mm.; a long series has been measured.

The female differs strikingly from that of celebicum, hirundinaceum, and the allied species inhabiting the Lesser Sunda Islands. Whereas in all these species the upper parts of the females are grayish, they are green in monticolum. In D. celebicum talautense, however, there is a marked greenish tinge on the rump. Just as in the male, the color of the upper parts in the female indicates the transition from celebicum to ignipectus. The similarity of the male to that of sulaense, as regards the clay-colored flanks, has been emphasized by Harrisson and Hartley (1934, Bull. Brit. Ornith. Club, vol. 54, p. 159), who regard these two forms as conspecific.

From a taxonomic point of view D. monticolum has been treated very differently. Chasen (1935, Bull. Raffles Mus., no. 11, p. 269) unites it with sanguinolentum and ignipectus, Mayr and Amadon (1947, Amer. Mus. Novitates, no. 1360, p. 28) unite it with celebicum, while Delacour (1946, Zoologica, vol. 31, p. 4) regards it as a full species. Dicaeum monticolum forms the connecting link between celebicum and ignipectus, and, being a mountain form, it could best be united with ignipectus, which is also a mountain bird. I prefer to retain monticolum as a full species, thus following Delacour, because both celebicum and ignipectus constitute units of closely allied forms, as mentioned above, and, as monticolum is almost a perfect intermediate between these two species, it also is better kept as a full species.

Harrisson and Hartley (loc. cit.) have separated the population of Mt. Dulit as zita, which, in a lengthy description, is stated to differ from monticolum in having grayish green, not dull green, flanks, less dark and more

glossy blue upper parts, smaller and less bright scarlet throat patch, and thinner and slightly longer bill. Chasen (loc. cit.) has already questioned the validity of zita, and, having examined the type specimen and the entire original material, in the British Museum (Natural History), of this alleged subspecies, I cannot recognize it. The type specimen is very slightly colder grayish green on the flanks, and paler, not so warm yellow, on the abdomen, but the remaining seven males are virtually identical with topotypical monticolum. The bill of the Mt. Dulit specimens appears to be on an average slightly longer, but the other points of difference mentioned in the description I am unable to see. The measurements of the two populations (based on eight males and four females from Mt. Dulit and eight males and three females from Mt. Kinabalu) are: wing length, Mt. Dulit, males 47–53 mm., females 45–48 mm.; Mt. Kinabalu, males 48–54 mm., females 42–47 mm.; bill length (from skull) in males, Mt. Dulit 12–14 mm., Mt. Kinabalu 11–13, usually 12, mm.

Dicaeum monticolum is restricted to the mountains of Borneo from Mt. Kinabalu to the upper Kapuas Mountains, where it frequents the mossy forest above an altitude of 1200 meters, but is exceptionally recorded as far down as 800 meters.

Dicaeum ignipectus

In the males of the Philippine races the coloration of the under parts is very similar to that of *D. monticolum*, while the upper parts are iridescent steel-green. In the females the upper parts, likewise, have a steel-green gloss, although not so bright as in the males; in the northern races the upper parts in the females are dull green, exactly as in *monticolum*.

The similarity between monticolum and ignipectus implies that the former has colonized the Philippines from Borneo. An emigration from Borneo to the Philippines, or vice versa, is quite an ordinary phenomenon in birds, both in lowland and in mountain species. Among the latter, Rhinomyias gularis, Sitta frontalis, Orthotomus cucullatus, Muscicapa westermanni, and Muscicapa hyperythra offer good examples.

While emphasizing that the Philippine races in the ventral color pattern are similar to monticolum, Mayr and Amadon (1947, Amer. Mus. Novitates, no. 1360, p. 28) stress that the Malayan and Sumatran races resemble D. sanguinolentum ventrally. On the accompanying map (p. 25) they indicate ignipectus as a derivative of sanguinolentum and give the direction of emigration as from Java through the southeastern Asiatic continent to the Philippines, where ignipectus abruptly faces monticolum and celebicum. This is just the opposite of my own view. In my opinion there is no question about the close relationship between ignipectus and monticolum, of which the latter represents the connecting link between celebi-

cum and ignipectus. The Sumatran race of ignipectus (beccarii), on the other hand, is the most divergent among all the subspecies of ignipectus and, at the same time, is widely different from sanguinolentum. It shares with the latter the buffy color of the abdomen and the sides of the breast, but the males differ strikingly by the steel-green gloss on the upper parts and the loss of the carmine throat patch, and the females by the greenish upper parts and the loss of the red rump. It is very unlikely, therefore, that there is a direct connection between sanguinolentum and ignipectus.

Robinson and Kloss (1918, Jour. Federated Malay States Mus., vol. 8, p. 248) state that beccarii belongs to a group that includes also ignipectus, sanguinolentum, and pygmaeum. The inclusion of this last-named species is noteworthy, because there is a close resemblance between beccarii and D. pygmaeum davao; the latter resembles a miniature edition of the former (cf. Salomonsen, 1960, Amer. Mus. Novitates, no. 2016, p. 13). Any present attempt to explain this resemblance must be guesswork. The suggestion that a colonization has taken place from Sumatra across the seas to the Philippines is too farfetched indeed.

Dicaeum ignipectus in its huge range is everywhere an inhabitant of mountain forests, in most places not occurring lower than altitudes of 1000–1200 meters, but its altitudinal range varies geographically according to climatic conditions. In China it undertakes regular movements to the lowlands in winter and may occasionally even breed there.

Dicaeum ignipectus apo Hartert, 1904

Type Locality: Mt. Apo, Mindanao.

Until quite recently, this form was known only from the type locality, but in Mearns's unpublished diaries (kept in the United States National Museum, Washington, where I studied them) it is noted that he met it on Mt. Malindang, Misamis Occidental Province, although he did not collect it. During the Danish Philippine expedition 1951–1952 we found it commonly on Mt. Katanglad, Bukidnon Province, at altitudes of 1200-1300 meters and, further, secured a single specimen in the Diuata Mountains, Agusan Province, at an altitude of about 1300 meters. Probably it occurs on all high mountains in Mindanao. Recently, Rabor (1952, Auk, vol. 69, p. 257) has recorded it from Negros, where two males were collected on Cuernos de Negros Mountains at an altitude of 1200 meters. Rabor states that there is no difference in plumage between the Negros and Mindanao birds, but that the wings of the Negros birds are shorter, measuring 52, 53 mm., compared with 56 mm. in a male from Mt. Apo. In a subsequent paper Riley and Rabor (1956, Condor, vol. 58, p. 290) give the wing length of the same two Negros males as 53.0, 53.5 mm. I have measured nine males from Mindanao (seven in the Zoological Museum, Copenhagen, and two in the American Museum of Natural History), which had a wing length of 52–56 (average 53.7) mm.

Dicaeum ignipectus bonga Hartert, 1904

Type Locality: Samar.

Very similar to apo, but smaller, the wing length being 48 mm. in the type specimen (male), which is the only specimen known. It is restricted to Samar. I have examined the type specimen, which is in the American Museum of Natural History.

Dicaeum ignipectus luzoniense Ogilvie-Grant, 1894

Type Locality: Luzon.

Differs from apo and bonga in having the sides of the head in males slategray, not black, the abdomen and the under tail coverts paler yellowish, and the flanks grayish brown, less tinged with olive. The wing length in males is 50-55 (average 52.8) mm. It inhabits the mountains of northern Luzon. A series in the American Museum of Natural History and a few specimens (including the type) in the British Museum (Natural History) have been examined.

Dicaeum ignipectus formosum Ogilvie-Grant, 1912

Type Locality: Formosa.

The males are very near *D. i. apo* in coloration, with the sides of the head black, but the under parts are distinctly darker buff. The females differ from those of the three preceding subspecies in having dull green upper parts without gloss and darker under parts. The wing length in six males [two specimens in the American Museum of Natural History, two in the British Museum (Natural History), and two in Naturhistoriska Riksmuseet, Stockholm] is 49–53 (average 50.8) mm., which is about the same as in nominate *ignipectus*. This form is restricted to Formosa (Taiwan), where it frequents the temperate forests between 600 meters and 1500 meters, in the fall and winter descending to 300 meters, according to Hachisuka and Udagawa (1951, Quart. Jour. Taiwan Mus., vol. 4, nos. 1–2, p. 21). However, the type specimen, collected on Mt. Arizan, was secured at an altitude of 1800 meters (Ogilvie-Grant, 1912, Ibis, ser. 9, vol. 6, p. 653).

Dicaeum ignipectus ignipectus (Blyth), 1843

Type Locality: Nepal and Bhutan.

Similar to formosum, but the males differ in having broad buff edges to the glossy feathers of the upper parts and to those of the sides of the

head (most pronounced in the fresh plumage), a stronger buffy tinge on the under parts, and a smaller red throat patch, which is restricted to the lower throat, while the upper throat is buffy. The females are similar to those of formosum, but have more olive-green, not so bright green, upper parts and much darker under parts. The color of the upper parts resembles that in the females of D. monticolum, but these latter have grayish white, not buffy, under parts. The wing length in males is 48–52 (average 50.2) mm.

This form is widely distributed in the mountains of east Asia. Its range covers the Himalava, at altitudes between about 1500 meters (exceptionally down to 600 meters) and 3000 meters, from about Kangra in northern Puniab eastward to northeastern Assam, the Khasi Hills, Naga Hills, Manipur, Lushai Hills, Burma south to about latitude 16° N. (Mt. Mulavit, Taok Plateau), northernmost Siam (Chiang Mai region), Tonkin, Laos, and Annam south to the Langbian Plateau, in the areas south of the Himalaya occurring at altitudes between 1000 meters and 2600 meters, locally varying and exceptionally down to 750 meters; further, ranging into southern China, where it is found in southern and western Yunnan (at altitudes up to 3300 meters), southeastern Sikang, southern Szechwan, north to about Kwanhsien, southern Hupeh, north to the Yangtze River (Hing-shan [= Hsienshan], Ichang), all of Kwangsi, southeastern Kweichow, all of Kwangtung, southern and central Fukien, north to about Minhow (= Foochow). There are very few breeding records from the lowlands of southeastern China, but D. ignipectus is a common winter bird there, in the period November to April, obviously originating from the mountains.

There is very little variation in the enormous series of nominate ignipectus that I have examined. In some males, however, the upper parts are more bluish, not steel-green, and, at the same time the throat patch is paler carmine and slightly smaller. Specimens of this appearance have been examined from Ichang (upper Yangtze Valley), western Szechwan, Fukien, Kwangtung, and the Langbian Plateau (southern Annam). Styan (1893, Ibis, p. 470) named such specimens D. cyanonotum. I have examined his type (from Ichang) and his entire material in the British Museum (Natural History). There has been some discussion about this form, summarized by La Touche (1930, Handbook of the birds of eastern China, vol. 1, p. 468), but, as mentioned above, it is an individual variety. Riley (1938, Bull. U. S. Natl. Mus., vol. 172, p. 514) has recorded this variant in his Chinese and Annamese material.

Koelz (1954, Contrib. Inst. Reg. Explor., vol. 1, p. 21) separated the birds from the Lushai Hills, Assam, as *pulchellum*, stating that they were darker. I cannot see any differences between Nepal, Assam, and Burma

birds, although I have not examined specimens from the Lushai Hills. Vaurie (1959, The birds of the Palearctic fauna; Order Passeriformes, p. 554) states that *pulchellum* averages a little more richly colored above and below, but that the differences are slight and not constant.

My study of nominate *ignipectus* has been based mainly on the very large series in the British Museum (Natural History). (For the description of a supposed hybrid between this form and *Dicaeum cruentatum*, see below.)

Dicaeum ignipectus dolichorhynchum Deignan, 1938

Type Locality: Trang, peninsular Siam.

Very similar to nominate *ignipectus*, but the bill is longer, more attenuated, and straighter. In addition, the carmine throat patch is slightly smaller and paler, the buff color of the under parts slightly paler, and the greenish gloss on the upper parts brighter, but these color differences are not constant. The bill of six males [three in the American Museum of Natural History, three in the British Museum (Natural History)] measure (from skull) 11.5–13.0 (average 12.0) mm., compared with 10.0–11.0 (average 10.5) mm. in 10 males of nominate *ignipectus*.

This form is restricted to the mountains of southern peninsular Siam and the Malay States, from Trang and Phatthalung (= Padalung) south to southern Selangor and northern Pahang, recorded at altitudes of between 900 meters and 1600 meters. Small series in the American Museum of Natural History and the British Museum (Natural History) have been examined.

Dicaeum ignipectus cambodianum Delacour and Jabouille, 1928

Type Locality: Cambodia.

The male differs strikingly from that of all previously mentioned forms of this species in the total absence of the red throat patch. The throat is pale buff like the sides of the breast, the abdomen, and the under tail coverts. In addition, the black patch on the sides of the chest and the black longitudinal streak on the abdomen are somewhat reduced. In the coloration of both the upper parts and the under parts this form bears a strong resemblance to Dicaeum pygmaeum davao. Contrary to nominate ignipectus, this form is probably a rare bird. Only two specimens are known, the type in the British Museum (Natural History), where I have examined it, collected at Le Bokor in the mountains Chaîne de l'Eléphant, Cambodia, at an altitude of 900 meters, and a male collected at the mountain Kao Kuap, near Krat (altitude unknown). The latter specimen was described as Dicaeum umbratile by Riley (1930, Proc. Biol. Soc. Washington, vol. 43, p. 191), but the au-

thor has subsequently rightly relegated this name to the synonymy of cambodianum (Riley, 1938, Bull. U. S. Natl. Mus., vol. 172, p. 515). The female is unknown.

Dicaeum ignipectus beccarii Robinson and Kloss, 1916

Type Locality: Korinchi, Sumatra.

Similar to cambodianum in all particulars, differing only in having the under parts darker buff, more rusty, and the bill perhaps slightly shorter. The bill of three males [two in the American Museum of Natural History, one in the British Museum (Natural History)] measures (from skull) 10-11 (average 10.7) mm., compared with 12 mm. in the type specimen of cambodianum. The wing length is 48-50 mm., which is only slightly less than in nominate ignipectus. The female has a slight gloss on the green upper parts, approaching the coloration of the Philippine subspecies.

This form inhabits the mountains of northern Sumatra (Korinchi, Atjeh, Brastagi), where it has been recorded at altitudes of between 900 meters and 1100 meters. Dicaeum van heysti Robinson and Kloss (1918, Jour. Federated Malay States Mus., vol. 7, p. 239) is an immature male of this form, which was soon realized by the describers (Robinson and Kloss, 1918, ibid., vol. 8, p. 248). I have examined four specimens in the American Museum of Natural History, including the type of D. van heysti, and one specimen in the British Museum (Natural History).

Dicaeum cruentatum

This species, in which the males have the whole upper parts red, with black feather bases, is undoubtedly a rather close relative to the "key species" D. igniferum and D. nehrkorni, which in their coloration approach cruentatum; it represents a higher evolutionary stage and may be a derivative of either of them. The red upper parts tend to show relationship with igniferum, but the under parts, on the other hand, differ considerably from those in igniferum. The characteristic color pattern of the under side in igniferum and its relatives (maugei and the superspecies hirundinaceum) is described above. It differs widely from that of cruentatum, in which the under parts are light, whitish or buffy, with the sides of the head and breast black or slate-colored, strongly contrasting with the light median parts. Therefore, the relationship with igniferum may, after all, not be particularly close. It is noteworthy that in D. cruentatum sumatranum the entire throat and the flanks are uniform smoky gray, resembling the condition in D. nehrkorni, which indicates a close connection between cruentatum and nehrkorni, although the color pattern of sumatranum is not primitive, but a secondary acquisition (see below).

The females of *D. cruentatum* have warm brown upper parts, with a bright carmine rump. This color pattern is found also in the species *maugei*, *sanguinolentum*, *trochileum*, *nehrkorni*, and *vulneratum*, which no doubt indicates relationship.

Dicaeum cruentatum and the group of other advanced species within the genus Dicaeum are allopatric, except in two places: Borneo, where cruentatum lives side by side with trochileum; and the lowlands of southeastern China, where it is found with ignipectus. In both areas cruentatum is apparently able to produce hybrids with the species with which it coexists. A supposed hybrid between cruentatum and trochileum from Borneo has been described by Voous and Van Bemmel (1949, Treubia, vol. 20, p. 35). A supposed hybrid between cruentatum and ignipectus, a male from Kwang Lung, Fukien, collected in November, 1898, by C. B. Rickett [No. 1905.12.24.202 in the British Museum (Natural History)], has hitherto not been described but is of particular interest, because its color pattern throws light on the probable origin of these species. The upper parts in this specimen are mixed red and metallic blue in the entire area where cruentatum is red, but there is a distinct red "cap" covering the crown, just as in D. nehrkorni and D. igniferum. There is a large red patch on the lower throat, just as in ignificatus, but even the feathers of the upper throat and chin have red tips, which make these areas mottled red, in this way approaching the pattern of the Philippine races of ignipectus and of the species belonging to the superspecies hirundinaceum and the species allied to them that inhabit the Lesser Sunda Islands. The breast and the abdomen are pale buff (without any black markings) and the flanks gravish green. The shade of the color on the flanks as well as that on the breast and abdomen is intermediate between the coloration of the corresponding parts in ignipectus and that of the same areas in cruentatum. The plumage of this supposed hybrid thus shows an equal mixture of ignipectus and cruentatum characters and at the same time exhibits two characters (red "cap" and red upper throat) that are not found in any of the parental species but that may date back to previous phylogenetic stages.

Dicaeum cruentatum is a very common and well-known lowland bird, frequenting cultivated areas, village and town gardens and orchards, open country with isolated trees, bamboo groves and light secondary forests and plantations, and occasionally mangroves. In Assam and Burma, however, it is partial to evergreen forests and generally does not occur elsewhere. It is found from sea level to altitudes of between 800 meters and 1200 meters, varying locally.

Dicaeum cruentatum cruentatum (Linnaeus), 1758

Type Locality: Bengal.

This form has a wide distribution on the Asiatic mainland. It is found from eastern Nepal, Assam, Bengal (except west) and Chittagong, through all of Burma, Indochina, Siam, and the Malay States, northward into southeastern China, where it ranges through Kwangtung and Fukien, and has been recorded also from Kwangsi (Yung, 1930, Bull. Dept. Biol., College Sci., Sun Yatsen Univ., Canton, no. 5, p. 23). It also inhabits the island of Hainan. Older records from Yunnan and Formosa have never been verified and are probably erroneous. In the Malay States it is found on all the small coastal islands, including Tioman. A sight record of this species from the Rhio Archipelago probably involves individuals pertaining to this subspecies (cf. Chasen, 1935, Bull. Raffles Mus., no. 11, p. 268).

There is some slight geographical variation within this subspecies, but it is too insignificant to give rise to separation of further subspecies. This view strongly contrasts with that held by the most recent reviewers (Mayr and Amadon, 1947, Amer. Mus. Novitates, no. 1360, p. 22), who recognize no fewer than five subspecies from continental Asia, including Hainan. Still, in Sharpe's review of the flowerpeckers (1909, Hand-list of the genera and species of birds, vol. 5, p. 21), only one continental form was recognized, but in the next year Hartert (1910, Novitates Zool., vol. 17, p. 243) separated ignitum (Malay Peninsula) and coccineum (southern China) from nominate cruentatum (Bengal), although on very slender grounds. A few years later the Siamese population was separated as siamense Kloss, 1918, and the Hainan one as hainanum Hachisuka, 1926. The validity of all these forms has been repeatedly discussed, but the evidence of the authorities is conflicting, and it is not worth while to give any details. The most important contributions to the discussion have been made by Hartert (loc. cit.), Robinson (1915, Ibis, ser. 10, vol. 3, p. 755), Kloss (1918, Ibis, ser. 10, vol. 6, p. 216), Robinson and Kloss (1919, Ibis, ser. 11, vol. 1, p. 624; 1924, Jour. Nat. Hist. Soc. Siam, vol. 5, no. 3, p. 389), Riley (1938, Bull. U. S. Natl. Mus., vol. 172, p. 513), Ticehurst (1941, Ibis, ser. 14, vol. 5, p. 182), Deignan (1945, Bull. U. S. Natl. Mus., vol. 186, p. 546), De Schauensee (1946, Proc. Acad. Nat. Sci. Philadelphia, vol. 98, p. 120), and Junge and Kooiman (1951, Zool. Verhandel., no. 15, p. 37).

The following notes on the geographical variation are based mainly on a study of the extremely rich and quite unequaled material in the British Museum (Natural History), but the collections in the American Museum of Natural History, Naturhistoriska Riksmuseet, Stockholm,

TABLE 1
Wing Measurements (in Millimeters) of Adult Males of Dicaeum cruentatum cruentatum

	Number of Specimens Measured	Range	Average
Kwangtung, Fukien	10	49–54	51.7
Hainan	9	49-53	50.1
Assam, Bengal	16	48-52	49.8
Burma, Siam, Annam	22	47-52	49.3
Malay States	20	46-49,	47.9
	one 51		

and Zoological Museum, Copenhagen, have also been utilized.

The variation in the continental populations, including those of Hainan, involves a slight clinal decrease in body size from north to south and differences in the intensity of the blackish color on the sides of the face, neck, and breast, of the gloss on the wings in the males, and of the light color on the under parts in both sexes, all these differences even being clinal and very trifling.

The geographical variation in body size appears from table 1, which gives the wing length of adult males.

It is, in my opinion, not possible to separate any subspecies on the basis of these differences in size. Even the two end links in the extremely shallow cline cannot be completely separated from each other; 20 per cent of the birds from the Malay States are indistinguishable from the south China birds, while of the latter 10 per cent cannot be separated from the Malayan ones. It is noteworthy that, although the Chinese population is usually recognized as a separate subspecies based on its superior size, no authority has ever published series of comparative measurements.

The Chinese population has a slightly longer bill than the more southern birds. The length of the bill, measured from the skull, in eight adult males from Kwangtung and Fukien is 12.0–13.5 (average 12.6) mm., compared with 11.0–12.0 (average 11.4) mm. in seven adult males from Burma and Siam. The birds from Malaya and those from Nepal and Bengal do not differ in bill length from those of Burma and Siam. The Hainan population is similar in this respect to the continental Chinese birds; the bill of five males measures 12.0–13.0 (average 12.4) mm. Even in bill length there is a considerable overlap; 50 per cent of the Chinese birds and 28 per cent of the Siamese birds cannot be distinguished on bill length. If anyone, nevertheless, felt inclined to sepa-

rate the Chinese birds on the basis of the slight difference in the length of wing and bill, the name *erythronotos* (Latham), 1790, must be applied, *coccineum* being preoccupied. The plumage coloration of the Chinese birds in both sexes is virtually identical with that in Burmese ones.

As far as the geographical variation in coloration is concerned, the following points are of interest. The males inhabiting the areas from Nepal to Bengal and the Chin Hills have the upper parts a shade darker scarlet than do those of the other populations, in which the upper parts are more vermilion. This difference is, however, very slight and not constant. The outer edges of the wing coverts and remiges in the males of all the northern populations are glossy bluish or bluish green, but there is a tendency towards more purplish or violet gloss in the birds inhabiting peninsular Siam and the Malay States, but at least half of the population of the latter regions cannot be distinguished on this character. There is also a slight variation in the dark color on the sides of the face, of the neck, and of the breast, which in birds from southern China, Hainan, Burma, Siam, and Indochina is slaty grayish black, while it is dull black in birds from Nepal, Assam, Bengal, and the Malay States. Even this difference is a tendency only, and a large percentage of birds cannot be referred to the right group on the basis of this character, and many specimens are intermediate. Finally, there is a slight geographical variation in the buffy tinge on the under parts. This is darkest in birds from Nepal and Assam and apparently is as dark in Hainan birds. The populations of Bengal and the Chin Hills are slightly paler and grade into the stage held by the birds of the central parts of Burma, which have usually somewhat paler, occasionally almost whitish, under parts. The south China birds are similar to Burma birds in this respect. The populations of Annam, Siam, and Tenasserim tend to be slightly darker, grading into the darker buffy color of the Malay States populations, which, however, are not quite so dark as the Nepal-Assam birds. The variation in this character is slight, often difficult to discover, even in the long series that have been available to me, and, further, appears to be patchy and irregular. A very shallow cline extends from Burma and China to the Malay States, as was the case with the body size.

In summary, none of the characters which are apt to vary geographically in the continental populations, and no combinations of them, is usable for the separation of subspecies; the variation is too slight and takes the form of shallow clines or has a mosaic pattern.

Dicaeum cruentatum sumatranum Cabanis, 1878

Type Locality: Sumatra.

This form, which inhabits Sumatra, differs strikingly from nominate cruentatum in having the upper parts lighter red, with the black bases of the feathers more extensive, the forehead black (red in cruentatum), the wing coverts and the remiges with a duller and more greenish, not so strong bluish, gloss, and the entire throat and the sides of the breast and flanks uniform smoky gray, while in cruentatum these parts are blackish, with the median parts of the throat and chin whitish, sharply contrasting. In addition, the proportions are smaller, the wing length in males being 43–46 mm.

This is a very distinct form. The gray throat and flanks are strongly reminiscent of the coloration in *D. nehrkorni*, one of the "key species," which bridges the differences between the superspecies *D. erythrothorax*, *D. igniferum* and its allies, and *D. cruentatum*. The collections in the American Museum of Natural History and the British Museum (Natural History) have been examined.

Dicaeum cruentatum niasense De Schauensee and Ripley, 1939

Type Locality: Nias Island.

Very similar to sumatranum and differing only in having a slightly stouter and longer bill and on an average longer wings. The wing length in two males is 46, 46 mm. Ripley (1944, Bull. Mus. Comp. Zoöl., vol. 94, p. 412) gives the wing length of one male as 48 mm. According to the describers (De Schauensee and Ripley, 1939, Proc. Acad. Nat. Sci. Philadelphia, vol. 91, p. 410) niasense, apart from its stouter bill, is characterized by having the wing coverts more purplish blue and the under parts darker gray than in sumatranum, but I cannot see these differences.

This form, which is restricted to Nias Island, is so similar to sumatranum that it possibly cannot be separated from it. Its final status must be decided on the basis of more material than at present available. I have examined only one male in the American Museum of Natural History and one male and one female kindly lent me by Dr. G. C. A. Junge, Leiden Museum.

Dicaeum cruentatum batuense Richmond, 1912

Type Locality: Pini Island, Batu Islands.

Similar to sumatranum, but the center of chin, throat, and chest are white, with a light buffy tinge, contrasting with the smoky gray color of the lateral areas, a color pattern that is principally identical with that in nominate cruentatum. In all other particulars this form is like sumatranum, including the smoky gray (not black) sides of head and breast and the black forehead. The proportions are practically the same

as those of *sumatranum*. Four males from Sipora have a wing length of 43, 43.5, 44, 48 mm., one female has a wing length of 43 mm. (Chasen and Kloss, 1926, Ibis, ser. 12, vol. 2, p. 300); five other males from Sipora measure 44.5–49 (average 45.8) mm. (Riley, 1929, Proc. U. S. Natl. Mus., vol. 75, art. 4, p. 40), and two further males from Sipora measure 45.5, 45.5 mm. (Ripley, 1944, Bull. Mus. Comp. Zoöl., vol. 94, p. 412). The type specimen, a male, from Pini Island, has a wing length of 45.5 mm., according to Riley (*loc. cit.*).

This form inhabits Pini Island in the Batu Islands and Sipora and South Pagi Island in the Mentawi Islands. It has never been recorded on any other islands than those mentioned above, not even on the large island of Siberut, which has been visited by many expeditions, and no doubt it is absent from the other islands in the Batu and Mentawi groups. This patchy range of an ordinarily common lowland bird strongly indicates a relict distribution.

I have not examined any material of this form, which, however, has been well described by various students.

Dicaeum cruentatum simalurense, new subspecies

Type: Rijksmuseum van Natuurlijke Historie, Leiden, No. 6651; adult male; Sinabang, Simeulue (= Simalur) Island; February 9, 1913; collectors, E. Jacobson and W. C. van Heurn.

Similar to batuense, but with distinctly larger proportions. In addition, the upper parts are darker red, more scarlet, and the gloss on the wing coverts is stronger and more bluish. These color differences, which distinguish simalurense from batuense, niasense, and sumatranum, are common to simalurense and nominate cruentatum. The wing length of two males is 50, 51 mm., of one female 47 mm., compared with 43–49 (average 45.3) mm. in 12 males and 43 mm. in one female of batuense.

This form inhabits Simalur Island, where it is not very common, according to Junge (1936, Temminckia, vol. 1, p. 74). Thanks to the courtesy of Dr. G. C. A. Junge, Leiden Museum, I was able to examine the three above-mentioned specimens of *simalurense*, the only ones known.

It is noteworthy that, while the Nias birds (niasense) are extremely similar to the Sumatran ones, the populations inhabiting the islands both north of it (Simalur) and south of it (Mentawi Islands) represent a distinct type sharply differing in coloration from sumatranum and strongly resembling the distant nominate cruentatum. In this way D. cruentatum contributes to an understanding of the highly interesting zoogeography of the West Sumatran Islands, a fascinating subject needing further study. Although all the islands are situated almost at the same distance from the "mainland," Sumatra, the faunal history of

each island is very different. The situation may be briefly summarized as follows. The southernmost island, Enggano, is a deep-sea island, which has not been in connection with Sumatra for a very long geological period. The fauna of this island is more divergent than any of the other West Sumatran Islands and at the same time the most impoverished. Similar is the case of the northernmost island, Simalur, also an

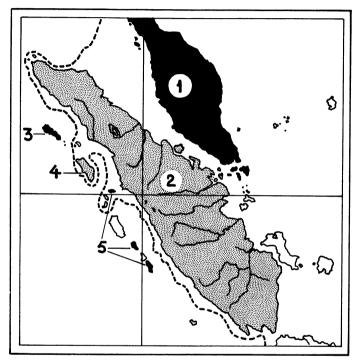


Fig. 4. The distribution of *Dicaeum cruentatum* in the Sumatra region: 1, cruentatum; 2, sumatranum; 3, simalurense; 4, niasense; 5, batuense. The areas inhabited by forms with uniform gray throat are shaded; those inhabited by forms with black-and-white throat are black. The dashed line designates the 100-fathom line.

old deep-sea island, although its fauna is by no means so differentiated and is much richer than that of Enggano. The Mentawi Islands possess a still richer fauna consisting of forms that generally are closer to the Sumatran ones than those inhabiting Enggano and Simalur. The island of Nias, situated south of Simalur, has a very close faunal relationship with Sumatra. It is not only richer in species than any of the other West Sumatran Islands, but it is poor in endemisms, and the number

of species in which the local population belongs to the same subspecies as that of Sumatra is much higher than in the other islands. 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.

The zoogeography in the Sumatra region of other groups of vertebrates than birds does not essentially differ from the description above, which has been based mainly on land birds. De Beaufort (1926, Zoögeographie van den Indischen Archipel, Haarlem) has reached similar conclusions, based on the distribution of reptiles and fresh-water fishes.

Geology bears out the results based on the faunal distribution. It appears from figure 4 that Nias and the small neighboring island groups, contrary to the other West Sumatran 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 peculiar distribution of D. cruentatum, as shown in figure 4, may serve as an illustration of the faunal history of the West Sumatran Islands. The entire Sunda-Land, including the West Sumatran Islands, must originally have been inhabited by a single form, which probably was nearest the present simalurense. The continental birds, which spread north as far as Nepal and south China, deviated in acquiring a red (not black) forehead and black (not grav) flanks and sides of the head and breast. The Mentawi Islands were situated much nearer Nias and Sumatra than was Simalur and probably were even in connection with Sumatra in certain periods. The Mentawi population of cruentatum, but not that of Simalur, was able, therefore, to follow the Nias-Sumatra birds in the next evolutionary step, the acquisition of vermilion, instead of scarlet, upper parts and more greenish gloss on the wing coverts. This may have taken place in one of the earlier glacial periods. When in one of the last glacial periods the populations of Nias and Sumatra developed the striking character of sumatranum (gray throat), the isolated populations of Simalur and the Mentawi Islands remained unaffected, retaining the ancient cruentatum-like characters.

The fact that Pini Island in the Batu Islands, which, as is Nias, is situated inside the 100-fathom curve, is inhabited by batuense and not by niasense, as would be expected, must be due to a secondary rather recent colonization from the Mentawi Islands. Even the patchy, relict distribution of cruentatum in the West Sumatran Islands, as well as its apparent rarity in most of the islands, is a secondary phenomenon, strikingly contrasting with the situation in the Greater Sunda Islands

and the Asiatic mainland, where D. cruentatum is a very common bird.

Voous and Van Marle (1949, Bijd. Dierk., vol. 28, p. 514) have described an almost parallel development in *Coracina striata*. In this species the forms inhabiting Enggano and Simalur are "presumed to be relicts of the older inhabitants of the Sunda Land," while the subspecies inhabiting the interjacent islands are very close to the Sumatran one.

Dicaeum cruentatum nigrimentum Salvadori, 1874

Type Locality: Borneo.

This form is similar to nominate cruentatum, but the chin is black and the flanks are darker grayish olive; the black on the sides of the breast is generally of greater extent. In some specimens the entire throat is black, and the greater part of the remaining under parts as well, leaving only the median parts of the breast and abdomen and the under tail coverts light buff-colored. Such specimens have received the name pryeri Sharpe, 1881. Some specimens of the normal nigrimentum phase show tendencies towards the pryeri phase, and a few specimens are intermediate. This variation constitutes a case of dimorphism and does not represent any geographical trend, as pointed out already by Moulton (1914, Jour. Straits Branch Roy. Asiatic Soc., vol. 67, p. 172) and Chasen and Kloss (1930, Bull. Raffles Mus., no. 4, p. 110). According to the collections of the American Museum of Natural History and of those of the British Museum (Natural History), examined by me, there are at least three times as many specimens of the nigrimentum as of the pryeri phase. The proportions of nigrimentum are similar to those of the Malay States population of nominate cruentatum. The wing length of seven males is 46-48 (average 47.7) mm.

This form inhabits Borneo, including its coastal islands. According to Chasen and Kloss (1933, Treubia, vol. 14, p. 163), *D. cruentatum* occurs on the Karimata Islands, but the material from this locality did not permit subspecific identification. For geographical reasons I include the Karimata birds in *nigrimentum*.

Dicaeum hosii Sharpe, 1897, is a synonym of nigrimentum. I have examined the type in the British Museum (Natural History); it is intermediate in coloration between the typical nigrimentum phase and the pryeri phase. It was stated to come from Celebes, which is obviously erroneous, as has been pointed out by a number of students, most recently by Stresemann (1940, Jour. Ornith., vol. 88, p. 53).

Dicaeum trochileum

This species, although evidently closely related to D. cruentatum, differs considerably. Not only the entire upper parts but the whole head

and throat are bright orange-red in the males, and the dark bases of the feathers are much shorter and lighter, more grayish, than in *cruentatum*. The females belong to the same color type as those of *D. cruentatum* and allied species, having light under parts and brownish upper parts with bright red rump.

Formerly this species was known under the name D. flammeum Sparrman, 1789, but Stresemann (1923, Ornith. Monatsber., vol. 31, p. 41) has drawn attention to the fact that Sparrman's Certhia trochilea has page priority over his Motacilla flammea, both names designating the same species. It had been pointed out previously by Sundevall (1857-1858, K. Svenska Vetensk. Akad. Handl., new ser., vol. 2, no. 3, p. 13) that the specimen on which Sparrman's illustration of Certhia trochilea was based was in the Stockholm collection and was a young female of Dicaeum rubrocanum (Temminck), 1824, from Java. This latter name is another designation for this species. The designation trochileum has during the last 30 years gained general acknowledgment and has, therefore, also been preferred here, in spite of the fact that page priority is not accepted in present zoological nomenclature (cf. 1953, Copenhagen Decisions on Zoological Nomenclature, p. 67). If neither Sundevall nor Stresemann can be recognized as first reviser, on account of the rigid claims now required, I take action presently as the first reviser, expressly selecting Certhia trochilea to the exclusion of Motacilla flammea. This selection is in accordance with the recommendation given by the Copenhagen Colloquium (cf. quotation above).

Dicaeum trochileum is a lowland species, rarely occurring at higher altitudes than 200 meters, frequenting cultivated areas, gardens, and similar habitats, apparently not differing generally from D. cruentatum in habitat selection.

Dicaeum trochileum trochileum (Sparrman), 1789

Type Locality: Java.

The nominate form inhabits Java, Madura, Bali, the lowlands of southeastern Borneo, Bangka (De Schauensee, 1958, Proc. Acad. Nat. Sci. Philadelphia, vol. 110, p. 294), and the island groups Karimundjowo (Chasen and Kloss, 1933, Treubia, vol. 14, p. 171), Bawean (Oberholser, 1917, Proc. U. S. Natl. Mus., vol. 52, p. 198), and Kangean (Hartert, 1902, Novitates Zool., vol. 9, p. 438). The birds from all these localities are apparently identical. I have examined the series in the American Museum of Natural History and the British Museum (Natural History), including birds from Java, Bali, and the Kangean Islands. (See text above for a discussion of a hybrid between this form and D. cruentatum nigrimentum from Borneo.)

Dicaeum trochileum stresemanni Rensch, 1928

Type Locality: Lombok.

Very similar to nominate trochileum, but the males differ in having the red color brighter, tending towards vermilion, not so orange-red, and the under parts, particularly the flanks, paler, not so dark smoky gray. In the females the under parts are slightly paler. In addition, the bill is slightly shorter; the length of bill, measured from the skull, is 11.0 mm. in one male (the type specimen), compared with 11.5–14 (average 12.5) mm. in six males from Java.

This very slightly differentiated subspecies is restricted to Lombok. Thanks to the courtesy of Prof. Erwin Stresemann, I have been able to examine one male (the type) and one female, belonging to the Zoological Museum, Berlin.

TYPE SPECIMENS EXAMINED

Dicaeum igniferum Wallace, 1863 = D. igniferum igniferum. In the British Museum (Natural History).

Dicaeum igniferum cretum Rensch, 1929 = D. i. cretum. In the Zoological Museum, Berlin.

Dicaeum mackloti romae Hartert, 1906 = D. maugei romae. In the American Museum of Natural History.

Dicaeum neglectum Hartert, 1897 = D. maugei neglectum. In the American Museum of Natural History.

Dicaeum sanguinolentum ablutum Robinson and Kloss, 1923 = D. sanguinolentum sanguinolentum. In the British Museum (Natural History).

Dicaeum hirundinaceum tormenti Mathews, 1912 = D. hirundinaceum hirundinaceum. In the American Museum of Natural History.

Dicaeum hirundinaceum yorki Mathews, 1912 = D. hirundinaceum hirundinaceum. In the American Museum of Natural History.

Dicaeum ignicolle G. R. Gray, 1858 = D. hirundinaceum ignicolle. In the British Museum (Natural History).

Dicaeum fulgidum Sclater, 1883 = D. hirundinaceum fulgidum. In the British Museum (Natural History).

Dicaeum kühni Hartert, 1903 = D. celebicum kühni. In the American Museum of Natural History.

Dicaeum sulaense Sharpe, 1884 = D. celebicum sulaense. In the British Museum (Natural History).

Dicaeum sulaense zita Harrisson and Hartley, 1934 = D. monticolum. In the British Museum (Natural History).

Dicaeum apo Hartert, 1904 = D. ignipectus apo. In the American Museum of Natural History.

Dicaeum bonga Hartert, 1904 = D. ignipectus bonga. In the American Museum of Natural History.

Dicaeum luzoniense Ogilvie-Grant, 1894 = D. ignipectus luzoniense. In the British Museum (Natural History).

Dicaeum formosum Ogilvie-Grant, 1912 = D. ignipectus formosum. In the British Museum (Natural History).

Myzanthe ignipectus Blyth, 1843 = Dicaeum ignipectus ignipectus. In the British Museum (Natural History).

Dicaeum beccarii cambodianum Delacour and Jabouille, 1928 = D. ignipectus cambodianum. In the British Museum (Natural History).

Dicaeum van heysti Robinson and Kloss, 1918 = D. ignipectus beccarii. In the American Museum of Natural History.

Dicaeum cruentatum hainanum Hachisuka, 1926 = D. cruentatum cruentatum. In the British Museum (Natural History).

Dicaeum cruentatum simalurense Salomonsen, 1961 = D. c. simalurense. In Rijksmuseum van Natuurlijke Historie, Leiden.

Dicaeum pryeri Sharpe, 1881 = D. cruentatum nigrimentum. In the British Museum (Natural History).

Dicaeum hosii Sharpe, 1897 = D. cruentatum nigrimentum. In the British Museum (Natural History).

Dicaeum trochileum stresemanni Rensch, 1928 = D. t. stresemanni. In the Zoological Museum, Berlin.