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A REVIEW OF THE DICAIEIDAE

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INTRODUCTION

The last comprehensive revision of the entire family of flowerpeckers (Dicaeidae) was published in 1885 (Sharpe). Not only have numerous new species and subspecies been described during the past 60 years, but the whole concept of the species has been revolutionized since then. A general review of the family is therefore urgently needed. Recent work by Mayr (1941) on the New Guinea flowerpeckers, by Mayr (1945) and by Delacour and Mayr (1946) on the flowerpeckers of the Philippines, by Delacour (1946, 1947) on the flowerpeckers of Malaysia, and by Hindwood and Mayr (1946) on the genus *Pardalotus* has cleared up some of the taxonomic difficulties in this family. Others, particu-

larly the puzzling relationship of certain species in the Lesser Sunda Islands, are discussed in the present paper. Finally, the attempt has been made to form some general conclusions on the evolutionary history of this family.

Original quotations and full synonymies are not given since they are easily available in various ornithological lists and handbooks. However, when possible, reference has been made to the habits and the ecology of the various species. The senior author has had field experience with various species of Dicaeidae in New Guinea and the Solomon Islands, and the junior author in the Philippines. All the illustrations are by Alexander Seidel.

THE FAMILY DICAIEIDAE

This family of seven genera and 54 species (in about 40 superspecies) of passerine birds is restricted to the Oriental and Australian regions. Flowerpeckers are birds of small or, rarely, medium size, frequently of bright and varied colors. The plumage is often glossy but only rarely metallic. Some have bristles around the gape and nostrils, and hair-like plumes on the nape and occasionally on the flanks. They are without wattles or bare areas of skin on the head, and only one aberrant

species (*Paramythia*) is crested. The edges of the bill are frequently serrated. The tenth (outer) primary is visible, though small, in the primitive genera and vestigial in the others. The legs are short; the toes and claws stout; the tarsus is either scutellated or almost booted; the nostrils are partly covered by an operculum. The more typical genera *Anaimos* and *Dicaeum* which contain 41 of the 54 species feed about flowers on nectar and insects (hence their name flowerpeckers), and the bill is

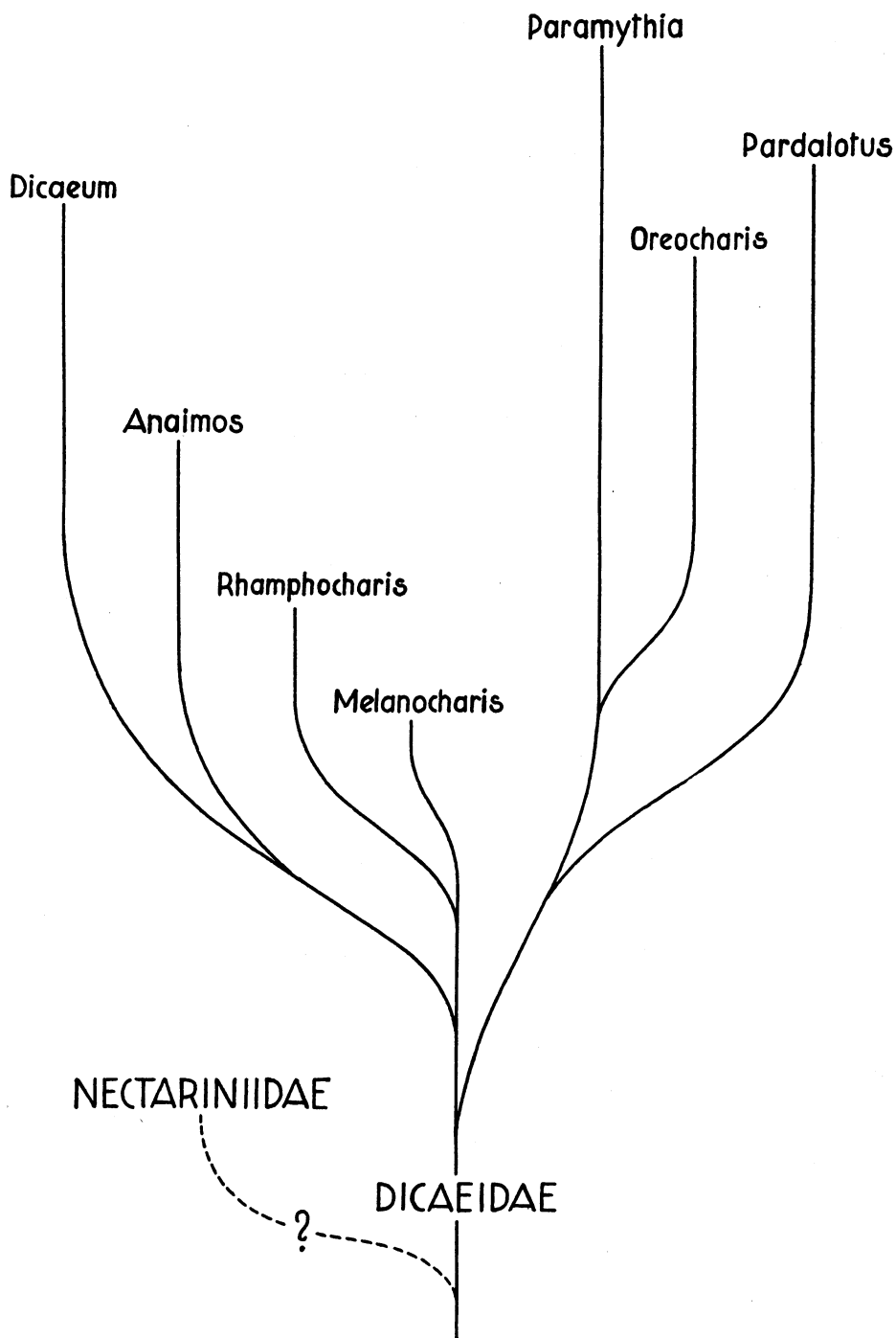


Fig. 1. Diagrammatic phylogeny of the genera of Dicaeidae.

sometimes decurved and the tongue tubular in correlation with these habits. These two genera also feed much on the berries of parasitic mistletoes. The other

genera are rather diverse in habits, as pointed out in the following section.

The supposed phylogeny of the genera is given in figure 1.

POSITION OF FAMILY

Three families, the Meliphagidae (Australian honeyeaters), Nectariniidae (sunbirds), and Zosteropidae (white-eyes), are often thought to be related to the Dicaeidae, but the evidence is rather slight. All four families (at least in some genera) take nec-

tar and small insects from flowers. The Nectariniidae and Zosteropidae are well represented in the Old World tropics both in Ethiopian and Oriental regions and have a few stragglers in the Australian region, especially the Zosteropidae which have undergone considerable evolution in Poly-

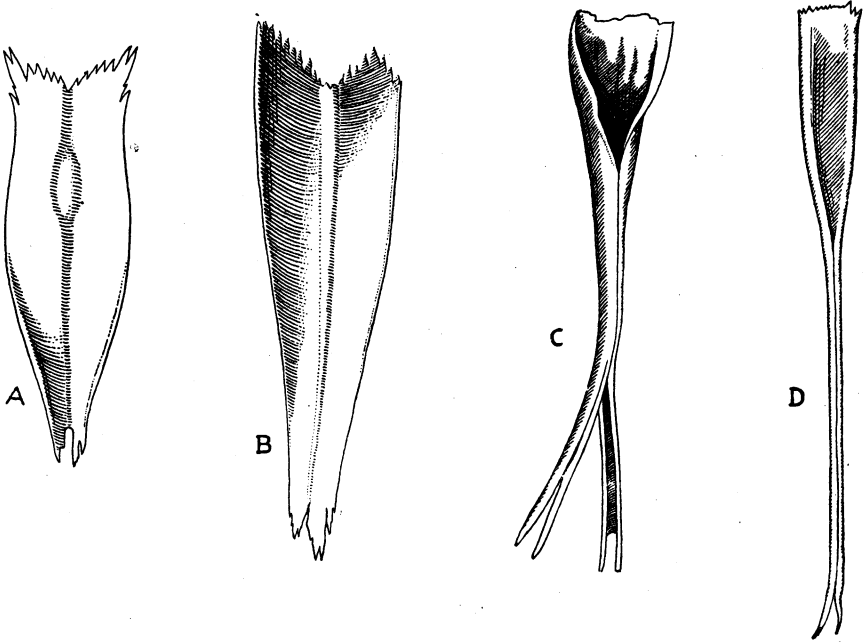


Fig. 2. Tongues of three flowerpeckers (A-C) and a sunbird (D). A. *Melanocharis versteri*, $\times 5\frac{1}{2}$. B. *Paramythia montium*, $\times 5\frac{1}{2}$. C. *Dicaeum trigonostigma* (after Gadow). D. *Nectarinia* (*Leptocoma*) sp. (after Gardner).

tar and small insects from flowers. The tongue and bill are variously modified for this habit, especially in the honeyeaters and sunbirds, less so in some flowerpeckers and white-eyes. The tenth (outer) primary is always evident in the Meliphagidae and Nectariniidae, present or absent in the Dicaeidae from genus to genus, and always absent (vestigial) in the Zosteropidae. The Meliphagidae are typical of the Australian region, extending even to Hawaii but barely reaching Bali and Celebes. The

nesia and the Solomon Islands. The Dicaeidae seem to have been originally Papuan, but reached the East Indies and Philippines early, where many species have evolved. The Nectariniidae may well represent an offshoot of stock similar to *Dicaeum*. In both, the nest is a specialized pensile bag with side entrance which, together with other resemblances, is probably significant (see also Delacour, 1944).

We have examined the tongues of two specimens of *Paramythia* (fig. 2). The

tongue is triangular, somewhat concave dorsally and with a small notch at the tip. Ventrally there is a vaguely indicated depression or line extending back from the split at the tip. In two specimens of *Melanocharis* the tongue is similar but perhaps slightly more split at the tip (fig. 2). The tongue of these two genera is of a generalized type, in keeping with their frugivorous habits. In the two species *Dicaeum hirundinaceum* and *D. concolor* examined by us the notch at the end of the tongue is deeper, and each of the two tips resulting is semitubular. In *D. trigonostigma*, as figured by Gadow and reproduced in our figure 2, each of the two tips is slightly split to form "four equally-sized semitubular projections without the slightest indication of laciniated or frayed-out margins. . . ." (Gadow, p. 235). Gadow represents the edges of the tongue behind the split tip as meeting dorsally to form a tube. In the two species we examined only a semitube is indicated, but perhaps in life the edges are brought together, forming a complete tube.

Gardner (1925, p. 26) wrote as follows: "The Dicaeidae have small tongues that are flat posteriorly but at about the middle become abruptly narrower and begin to curl into a semitube which is deeply cleft at the tip, the margins of which are smooth, forming two slender semitubular tips. This is found in *Dicaeum cruentatum*, *D. sanguinolentum*, *D. flammeum*, and *D. celebicum* [and according to our findings in *D. hirundinaceum* and *D. concolor*]. In *Acmonorhynchus* [= *Dicaeum*] *aureolimbatius* the same holds true except that the edges of each tube show a slight notching, with an attempt at the production of four tips, while in *Prionochilus* [= *Anaimos*] these notches have deepened to actual splitting with the formation of four semitubular fringeless projections." Gardner mentions Gadow's description of *D. trigonostigma* as representing another type of modification.

In summary, the tongues of *Dicaeum* and *Anaimos* are modified in a characteristic way for sucking nectar, and at the same time resemble the simpler tongues of the fruit-eating flowerpeckers from which

they could readily have evolved. The tongues of *Melanocharis* and *Paramythia* do not differ significantly from those of many passerine birds. The tongue seems to be of little taxonomic value except in genera or families where it is much specialized.

Two or three types of tongues occur in the Nectariniidae (Delacour, 1944). In one type, found in *Nectarinia* and other genera, the basic pattern is similar to that of *Dicaeum hirundinaceum* (or similar species), but the tongue is greatly elongated, very thin, and much rolled so that not only the tip but most of the tongue is conspicuously tubular. The tip is split as in *Dicaeum*, with two tubular projections. We see no reasons why the tongue of sunbirds could not represent a greater modification of the type found in *Dicaeum*. A tongue of *Nectarinia* figured by Gardner is similar to one we have examined and is reproduced in figure 2.

In the Meliphagidae the tongue is very brush-like at the tip and split into four distinct tips and hence considerably different from that of any genus of Dicaeidae. Some New Guinea genera of meliphagids resemble *Melanocharis*, but in view of their difference in habits, this is probably parallelism.

Gadow considered the dorsal feather tract of *Dicaeum* very similar to that of the swallows (Hirundinidae), but the families can scarcely be closely related in view of the many great differences between them.

The purse-shaped nests of *Dicaeum* are quite similar to those of the penduline titmice (*Remiz*). Delacour (1944, p. 19) has suggested that *Cephalopyrrus flammeiceps* of southeastern Asia may provide a link between *Remiz* and *Dicaeum*. *Cephalopyrrus*, which is usually placed with the titmice, nests in holes in trees. The females are very similar to those of *Remiz*. It will require further anatomical and life history studies to determine whether *Remiz* is really related to *Dicaeum*, or merely builds a similar nest. It is also a moot question whether *Remiz* is closely related to the true titmice (*Parus*).

Sharpe (1885, p. 2) associated the waxwings (Bombycillidae) with the Dicaeidae.

Despite some morphological similarities, these families differ considerably in habits and distribution. The relationship of the Bombycillidae to the Neotropical Ptilogonatidae is more certain, and has led Stresemann to unite these families. It is conceivable but unlikely that the Bombycillidae provide a northern link between the Ptilogonatidae and Dicaetidae. The similarity to the Hirundinidae emphasized by Gadow is of equally doubtful significance.

A few genera have been erroneously or doubtfully allied with the Dicaetidae. The Hawaiian Drepanidae are now considered to be of American derivation. Two

African genera, *Pholidornis* and *Parmoptila*, placed by Sharpe with the Dicaetidae, have been considered by Chapin to be aberrant Ploceidae and by Bates (and more recently Delacour) perhaps to comprise, along with another monotypic genus, *Hylia*, a separate family. We have examined all three and agree with Chapin and Bates that they have nothing to do with the Dicaetidae.

From the above it is only too apparent that much anatomical work is needed before the relationships of the Dicaetidae to other families is placed on a sound basis.

DISTRIBUTION OF THE DICAETIDAE

New Guinea and the Philippine Islands are the home of the greatest number of species. In the east the family extends as far as the Solomon Islands, in the south to Australia and Tasmania, in the west and north to south China and northwest India.

The number of genera and species of Dicaetidae in selected areas is as follows. Some species occur in several of the areas listed.

Ceylon: *Dicaeum*, 3
 Southern India: *Dicaeum*, 3
 Eastern and northern India, northern Burma: *Dicaeum*, 7
 Malay Peninsula: *Anaimos*, 3; *Dicaeum*, 6
 Borneo: *Anaimos*, 4; *Dicaeum*, 6
 Palawan: *Anaimos*, 1; *Dicaeum*, 2
 Luzon and Mindanao: *Anaimos*, 1; *Dicaeum*, 8
 Celebes: *Dicaeum*, 3
 Timor: *Dicaeum*, 3
 Flores: *Dicaeum*, 4
 Australia: *Dicaeum*, 1; *Pardalotus*, 6
 Tasmania: *Pardalotus*, 3
 New Guinea: *Melanocharis*, 5; *Rhamphocharis*, 1; *Oreocharis*, 1; *Paramythia*, 1; *Dicaeum*, 1 (superspecies)
 Solomon Islands: *Dicaeum*, 1 (superspecies)

The generic distribution may be further summarized as follows: In Australia and Tasmania there is one aberrant genus (*Pardalotus*) containing seven species and *Dicaeum* with one species which is a recent immigrant from the Lesser Sunda Islands. In New Guinea there are two primitive genera (*Melanocharis* and *Rhamphocharis*) containing six species and two specialized, monotypic genera (*Oreocharis*, *Para-*

mythia). The latter two resemble *Pardalotus* in some respects but are more like *Melanocharis* in habits. One superspecies of the wide-ranging *Dicaeum* has also reached New Guinea via the Moluccas and extended through New Guinea to the Bismarck Archipelago and Solomon Islands. In the Philippines, East Indies, and Malay Peninsula there are two closely related genera, *Anaimos* and *Dicaeum*, each containing a number of species. *Anaimos* seems to be more primitive and has fewer species. In tropical Asia only *Dicaeum* is known (except in the Malay Peninsula). The family does not occur beyond India and south China.

These distributional facts contain some clues as to the place and time of origin of the family. The general distribution pattern, as well as the prevalence both of primitive and of specialized genera and species on New Guinea, makes it seem probable that the family was originally a Papuan group. From here the family spread south, producing the *Pardalotus* group in Australia, and west into the Malay Archipelago, giving rise to *Anaimos* and *Dicaeum*.

It is difficult to decide when the Asiatic mainland was reached. The family is fairly well represented in the humid tropical and subtropical parts of the Indo-Chinese countries (Malay Peninsula, Burma, Indo-China), but is drastically reduced in abundance in the more arid parts of India. It

has not spread as far as the Palearctic, Africa, or Madagascar. Although the pronounced aridity of northwest India and Arabia is a comparatively recent phenomenon, it is an open question whether the Dicaeidae arrived so recently in India that they have had no opportunity to spread

into Africa or whether there was always an environmental barrier between Africa and Asia impervious to flowerpeckers. Arid zones obviously are a considerable obstacle to flowerpeckers, as indicated by the poor representation of the family in Australia, adjacent to New Guinea with its rich fauna.

PLUMAGE AND SEXUAL DIMORPHISM

In the primitive genera *Melanocharis* and *Rhamphocharis*, the prevailing coloration of the females is greenish olive. Usually the males are more or less glossed with bluish black above, and they may even (in *Melanocharis versteri*) have a metallic luster. Males of *M. striativentris* are olive green like the females. In *Rhamphocharis* the male is only slightly glossed; the female is brownish spotted above and below with white and thus very different in appearance. This spotting is perhaps foreshadowed in the obscure ventral streaking of *M. striativentris*. In most species of these two genera the tail is spotted with white; otherwise the pattern is very simple.

The coloration varies greatly in the numerous species of *Dicaeum* and *Anaimos*. *D. bicolor* is whitish below and bluish black above, thus resembling some species of *Melanocharis* (e.g., *nigra*). This resemblance is probably indicative of relationship. Females of *Dicaeum* are usually simply colored, often brownish olive above and yellowish green below, even in the more brightly colored species of the genus. In a few species such as *D. concolor*, *D. erythrorhynchos*, and *D. tristrami* the males as well as the females are dull colored, but in some of these, especially *tristrami*, there is little doubt that secondary simplification in coloration has taken place. A few species of *Dicaeum* and *Anaimos* are streaked ventrally, but the degree of streaking varies greatly even among the races of one species (*agile*). In many species bright patches of red or orange feathers occur on the crown, breast, rump, or back, and in one species (*D. annae*) there is a peculiar half-concealed patch of orange feathers on the lower back.

The back in the males is usually dark and more or less glossy. In some species the

blackish coloration has extended around to the underparts. In the brightly colored *D. papuense-haematostictum* superspecies of the Philippines, the female has acquired the bright coloration of the male.

In *Melanocharis versteri* and *longicauda* and in *Rhamphocharis* there are white spots on the tail feathers. It is a moot question whether these are homologous with those occurring in three species of *Dicaeum* (*vincens*, *melanoxanthum*, and *agile*), as in *Dicaeum* the spots are nearer the tips of the feathers. These marks are among many indicating that *melanoxanthum* and *vincens* are related; *agile*, on the other hand, is a rather aberrant species. Small round white spots occur on the tail feathers of some species of *Pardalotus*, but again it is uncertain whether they indicate relationship with other flowerpeckers or are merely associated with the extensive spotting characteristic of the pattern in this genus. Such spots on the tail do not occur in *Anaimos*, *Oreocharis*, or *Paramythia*.

There is little in the coloration of the aberrant *Oreocharis* to suggest the more typical genera of flowerpeckers, although the black head and throat may imply distant relationship to such forms as *Anaimos thoracicus*. *Paramythia* is still more specialized but with unmistakable resemblances to *Oreocharis*. Yellow is conspicuous in the remaining genus, *Pardalotus*, and probably indicates distant affinity with *Oreocharis* and more remotely with the *Anaimos-Dicaeum* group. The white spots on the outer webs of the secondaries in some of the species of *Pardalotus* are especially suggestive of *Oreocharis*. Various combinations of spots and streakings are distinctive of *Pardalotus*, though one species (*quadragnetus*) has reverted to a somewhat simpler pattern.

In *Oreocharis* the females are much simpler in coloration than males and not greatly dissimilar to those of some species of *Melanocharis* and *Dicaeum*. In *Paramythia* and some species of *Pardalotus* females have acquired the brighter coloration of the males.

TENTH PRIMARY

The tenth primary is evident, though reduced, in *Melanocharis* and *Rhamphocharis*, two genera which, on the basis of other characters as well as this, are probably primitive. A few species of typical flower-peckers have an evident tenth primary. These we have segregated in *Anaimos*, leaving the others in a presumably slightly more advanced genus, *Dicaeum*. While there is no doubt that the six species of *Anaimos*, with the doubtful exception of *olivaceus*, belong to a natural group, the

generic separation on this basis is less convincing in *Dicaeum*. Thus the peculiar *D. annae* looks like *Anaimos*, but the tenth primary is vestigial, so it must be left in *Dicaeum*. The same seems to be true of *D. anthonyi* (the only species in the family not examined). On the other hand, in *D. melanoxanthum* the tenth primary is visible, though smaller than in *Anaimos*. This species is obviously close to *D. vincens*, and we have left it in *Dicaeum*.

The tenth primary is vestigial in *Oreocharis*, *Paramythia*, and *Pardalotus*; these are specialized and rather aberrant genera in other respects. It is somewhat surprising that the four endemic frugivorous New Guinea genera, *Melanocharis* and *Rhamphocharis* on the one side and *Oreocharis* and *Paramythia* on the other, should be so different as regards the tenth primary and most other characters.

HABITS AND ADAPTATIONS

Rand (1942, p. 511) wrote of *Melanocharis nigra unicolor*, "this species was usually found solitary, low in the substage and undergrowth, but once at the 1,200-meter Camp I found numbers of them feeding on fruits high in a forest tree." He also notes that *Melanocharis longicauda* frequents both undergrowth and tall fruit trees. Of *Melanocharis versteri meeki* he adds: "This flowerpecker fed in the substage and commonly in low second growth. It was usually alone, and an active bird with quick movements. Three stomachs examined contained fruit."

Rand (1937, p. 239) found *Oreocharis* usually in parties of up to 20 or more in the lower fruit trees of the New Guinea forest. Sixteen stomachs contained only fruit of several varieties. Usually the fruit had been swallowed whole. The related *Paramythia*, as observed by Rand (p. 241), is also a fruit eater.

Diamond birds (*Pardalotus*) are almost entirely insectivorous. They seek food among twigs and foliage, actively and with a variety of postures similar to those of titmice. Hill (1911, p. 283), however, states

that *P. melanocephalus uropygialis* hunts insects in the flowers of a *Grevillea* and eucalypts, becoming smeared with honey and pollen about the throat and forehead while doing so. This is suggestive of the habits of some species of *Dicaeum*.

Chasen (1939, p. 403) summarized the habits of the species of *Dicaeum* as follows: "Usually they are seen alone; tiny, fat, but very active little birds, darting across the path from one tall flowering bush to another with a sharp *chit-chit-chit*, a sound like two pebbles being tapped together, but often they congregate at the tops of very tall flowering trees and then, through binoculars, the busy birds can be seen flitting like a swarm of hymenoptera about the blossoms on the exposed surface of the forest's canopy. . . . I have known cases in which natives employed for insect-catching in the Botanic Gardens, Singapore, have taken the tiny species of *Dicaeum* in their butterfly nets. They eat small spiders, insects and small berries and are especially fond of the berries of plants allied to the mistletoe. There is a marked partiality for the glutinous fruit of *Loranthus*. Epiphytic plants of tall trees seem to attract

flowerpeckers. The nectar of flowers is also taken as food."

Ali (1931) has made a special study of the role of flowerpeckers in India in fertilizing mistletoes (*Loranthus*) and in spreading their seeds. The flowers of *Loranthus longiflorus* are entirely dependent on nectar feeding birds for fertilization, but sunbirds are much more important in this than flowerpeckers. During the season when they are available, *Loranthus* berries form the principal food of *Dicaeum erythrorhynchos*; at other times it takes the berries of *Phyllanthus*, *Lantana*, and *Viscum* (another mistletoe), and occasionally small spiders. "While on a clump [of mistletoe] the bird hops restlessly from bunch to bunch uttering an almost incessant *chik, chik, chik* which is occasionally varied by a series of twittering notes which might be termed its song. Each berry is first tested between the mandibles; if ripe it is plucked and swallowed, broad end (i.e. where the stalk attaches) first. After it has bolted down three or four berries, one after another the bird retires to the extremity of some bare branch at the top of the host on an adjoining tree and sits quiet for a few moments with the feathers partly fluffed out. . . presently one of the viscous seeds is excreted." The seeds adhere to the branches, thus spreading the parasite. In a later publication Ali (1936 p. 778) mentions finding as many as 27 *Loranthus* berries in the intestines of *Dicaeum erythrorhynchos*.

Although *D. erythrorhynchos* rarely strips the fleshy outer covering from the berries without swallowing them, this method is usual in the thicker-billed *D. agile*. "The berry is plucked and invariably revolved between the mandibles which being thicker and stouter, appear better adapted to this method of eating. The flesh is soon detached and the seed wiped on to a neighboring twig" (Ali, 1931, pp. 148-149). In a later publication Ali and Abdulali (1938, p. 160) wrote of the habits of *Dicaeum a. agile*: "Its food consists largely of the berries of the tree parasites, *Loranthus* and *Viscum*. . . . Other berries such as those of *Lantana camara* and *Bridelia retusa* are also greedily taken, as

well as Peepal and Banyan figs. *Bombax* and *Erythrina* flowers are regularly resorted to for the nectar, and spiders likewise form part [of] the dietary. It utters *chik, chik* as it restlessly hops about the foliage. . . . While thus engaged, it spreads out its stumpy square little tail and screws it nervously edgewise from side to side." Lawrence and Littlejohns (1916) wrote of *Dicaeum hirundinaceum*, ". . . the ripe berry [*Loranthus*] was taken crosswise in the bird's bill, and the soft case split in halves by pressure. The free portion of the case was then dropped, leaving the white berry protruding from the half still attached to the branch. By pressure of this remaining half between the mandibles the seed was forced out sufficiently to allow of its being easily taken in the bill." Nestlings were fed insects when small but before they left the nest were receiving chieftly mistletoe berries. This flowerpecker also eats other types of berries, such as wild cherries. Insects are secured both from flowers and by search among foliage. This species is very restless and usually stays in the tree tops.

W. K. Dammerman (quoted by Chasen, 1939, p. 404, without a reference) wrote: "Bartels found in Java the glutinous seeds of these parasitic plants [*Loranthus*] only in the intestinal tract of the bird, the large seeds being unable to enter the very small stomach, which is found always filled with minute spiders, the chief food of the birds."

Porsch (1929) in his exhaustive study of flower-visiting birds and associated flowers, devotes 15 pages to the Dicaeidae, which is, so far as the birds are concerned, a compilation. *Dicaeum concolor sollicitans* has been found with its head smeared with nectar and pollen. Porsch found references to at least five species of *Dicaeum* visiting flowers. The following genera of plants are mentioned: *Loranthus*, *Elytranthe*, *Bauhinia*, *Bombax*.

The habits of the species of *Anaimos* are similar to those of *Dicaeum* so far as known.

FEEDING ADAPTATIONS (INTESTINAL TRACT)

Desselberger (1931) distinguishes two functional categories of intestines among

the Dicaeidae: a more primitive one, exemplified by *Melanocharis*, and a more specialized one, as found in *Dicaeum*.

The intestines of *Melanocharis* are short and wide, a condition typical for fruit-eating birds. The stomach consists of a small, glandular proventriculus and a well-developed muscular gizzard. The stomach of *Paramythia* is considerably larger, but

species consists exclusively of fruit. The anatomy of the related, also frugivorous genus, *Oreocharis*, is unknown.

Desselberger studied several species of *Dicaeum*. He found that the muscular stomach (gizzard) has become a blind sac or diverticulum with a sphincter at its opening. By this means berries (*Loranthus* and others) are shunted directly from

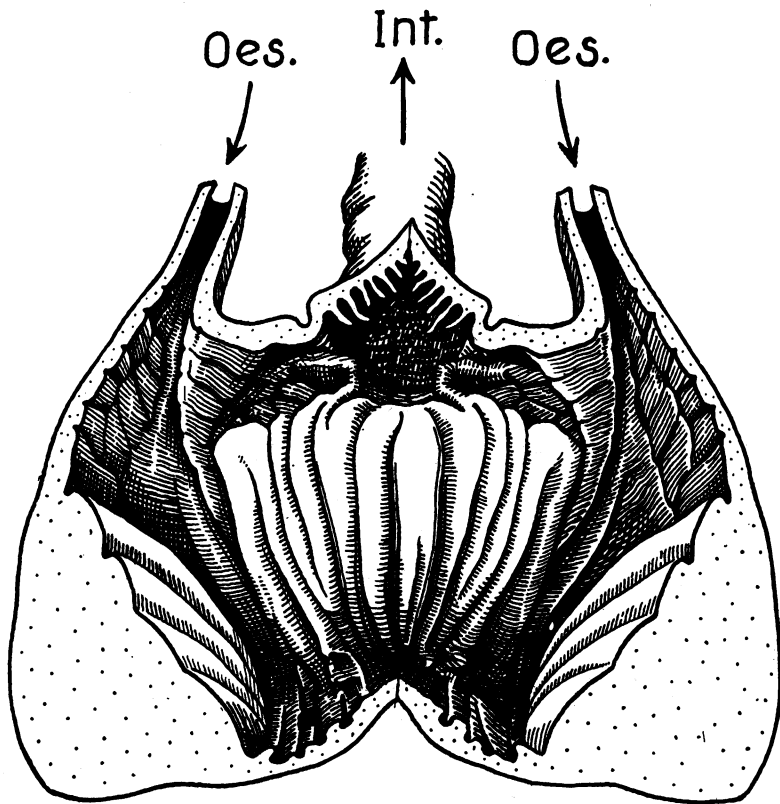


Fig. 3. Stomach of *Paramythia* cut open. Abbreviations: Oes., esophagus; int., entrance to the intestines. One of the two horny pads was cut when the stomach was opened.

it is not clear in the examined specimen (Archbold-Rand collection) whether or not the lower end of the esophagus is modified to a proventriculus; it does not appear so. The gizzard is very muscular, with two well-defined pads (fig. 3). The pylorus, which is near the esophageal entrance of the stomach, leads into a wide intestine, the mucous wall of which is modified into innumerable villae. The food of this

the esophagus to the intestine without entering the gizzard. Insects and spiders, on the other hand, enter the gizzard where they are comminuted and the digestible components are removed. This specialization permits large numbers of *Loranthus* berries to pass rapidly through the intestine, where the presumably slight amount of nutriment in their gelatinous capsules is removed. It also avoids the

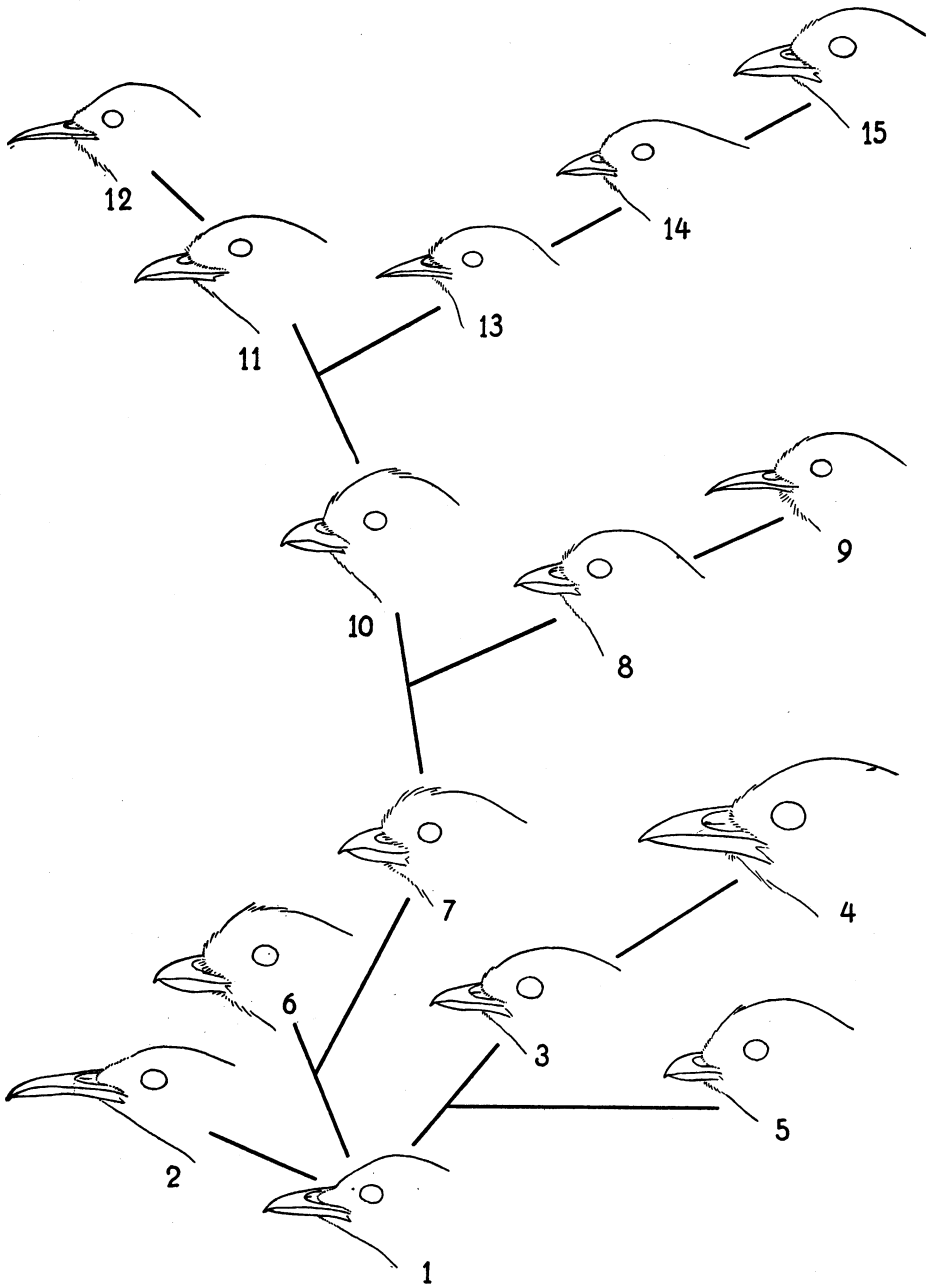


Fig. 4. Rapid evolutionary change of bill shape in the Dicaeidae. 1. *Melanocharis nigra*. 2. *Rhamphocharis*. 3. *Oreocharis*. 4. *Paramythia*. 5. *Pardalotus melanocephalus*. 6. *Anaimos olivaceus*. 7. *Dicaeum agile*. 8. *D. aureolimbatum*. 9. *D. nigrilore*. 10. *D. bicolor*. 11. *D. papuense*. 12. *D. retrocinctum*. 13. *D. nehrkorni*. 14. *D. eximium*. 15. *D. tristrami*. Compare particularly the closely related forms 1 and 2, 8 and 9, 11 and 12, and 13 to 15.

laxative effect on other food that these berries would have if held in the gizzard. Since chitinous parts are not found in the intestines, it appears that they are regurgitated as pellets. This elimination protects the mucous villae of the intestines from injury by sharp-edged chitinous particles. The intestinal tract of *Dicaeum tristrami* studied by us is exactly like that of the other species described and figured by Desselberger. One examined stomach contained 15 spiders, 14 of which were Argiopidae, and one a salticid. The intestines contained remains of berries with very minute seeds (we counted more than 90).

In the tanagers (Thraupidae) of the genus *Tangara* (*Euphonia*), which are thought to feed almost entirely on mistletoe berries of *Phoradendron* and related genera, a different and greater specialization has led to a vestigial condition of the gizzard as a section of the intestinal tract (Steinbacher, 1935).

In *Dicaeum* and *Anaimos* the tongues are, in varying degrees, tubular as in other birds in which nectar is an important item of the diet, as described above.

BILL

In the four fruit-eating genera of New Guinea, the bill is unspecialized, slightly curved, and rather broad basally. In *Rhamphocharis* it is moderately attenuated, but we do not know if this is adaptive.

The bill in *Pardalotus* is stout, arched, and short. Probably it is adapted for digging nesting burrows or enlarging cavities in trees. In feeding, the bill of *Pardalotus* is utilized for taking small insects, their larvae and eggs much in the manner of various titmice, vireos, or other insectivorous birds that have comparatively short, heavy bills.

In the genera *Anaimos* and *Dicaeum* the variations in the bill are greater and often quite puzzling either from a functional or phylogenetic point of view. In some species the bill is very stout and short, scarcely if at all decurved. In others the bill is rather thin and decurved, approaching the condition found in more typically nectar-eating birds such as sunbirds. We

might postulate a gradual adaptation of the heavier bill of fruit- and insect-eating ancestors to permit greater utilization of nectar. This seems to be, in general, true, but there have been frequent reversals of this trend, and both types occur in closely related species. *D. tristrami*, with a heavy, finch-like bill, is a geographical representative of and derived from species in which the bill is thinner. *D. nigrilore* is thin billed but undoubtedly closely related to the heavy-billed *D. aureolimbatus*. In the *papuense-retrocinctum* group of the Philippines there is considerable variation within a superspecies (fig. 4).

It is possible that some but not all of these variations among species of *Dicaeum* may be eventually proved to be correlated with specific differences in food habits. The variation is undoubtedly correlated with the fact that both the seeds of mistletoe and also tiny insects and nectar from flowers are important foods in this genus. Utilization of the bill for opening the pods of *Loranthus* and (at least in *D. agile*) for stripping the gelatinous capsule from the seeds may favor a heavier type of bill. Desselberger, however, found that the alimentary system of the stout-billed *D. aureolimbatus* is modified for the passage of *Loranthus* seeds, so we cannot assume that the stout-billed species are those in which seeds are not swallowed. Apparently consumption of nectar and tiny insects found in blossoms favors a thin, decurved bill (and tubular tongue). On the other hand, utilization of mistletoe berries is probably easier for birds with a stout bill. We may suppose that now one and now the other of these two factors has dominated in the evolution of the various species of the genus, leading to the great variation that exists from species to species. So far as the family as a whole is concerned, the thin, nectar-sucking type of bill and tubular tongue must be considered the more specialized. This type is exclusive in the possibly related specialized sunbirds (Nectariniidae) which feed on nectar and tiny insects but not berries.

The bills of the tanagers (*Tangara*) that feed on mistletoe berries are quite

similar to those of the thick-billed species of *Dicaeum*.

NESTS

The nest of *Dicaeum cruentatum*, which is typical for the genus, has been described by Baker (1934, p. 237) as follows: "They seem to be invariably made of the beautifully soft seed-down of the Simul-tree (*Bombax malabarica*), very little compressed or felted but kept in shape and position by a few shreds of grass, fungoid mycelae or by very fine hair-like roots. The nest is egg-shaped and the materials, other than the down, are used to work round the twig from which the nest is pendent, and from this they are brought down and round the nest itself, a few of the longer strands coming under the nest and up again on the far side. Round the rim of the entrance, which is rather large and at the upper side of the nest, a few grasses are twisted, making it firm enough to withstand the constant passing in and out of the parent bird. Here, too, as on the outside of the nest, cobwebs and silk are sometimes used to strengthen its structure. The lining is of the same cotton-seed down and quite soft when first put in, but soon becoming more or less felted when the eggs are laid and the birds begin to sit."

A nest of *Dicaeum eximium* from New Britain, which we have examined, is coarser in construction, being made of fine grass ornamented on the outside with pieces of dead leaves. The nest of *Dicaeum vincens* (for a photograph see Lushington, 1940) has "a pronounced hood over the somewhat large entrance." One nest of this species was 75 feet and another 125 feet high in *Dipterocarpus* trees. The nest of *Dicaeum agile* is unusually finely woven and elastic so that it will regain its shape after being rolled up.

A nest of *Anaimos percussus ignicapillus* from Borneo was similar to those of *Dicaeum* (Baker, 1934, p. 249). Coomans de Ruiter (1936) has published a photograph and description of a nest of *Anaimos xanthopygius*. It was only about a meter above the ground but well protected and concealed by large leaves. The walls

were thick so that the chamber scarcely accommodated the two young.

Diamond birds (*Pardalotus*) nest in holes in trees or in banks in burrows which they often dig themselves. They even dig nesting burrows in level sandy ground. They build elaborate nests inside these hollows which are often more or less domed but sometimes cup-shaped. These nesting habits are aberrant, but such birds as the House Sparrow (*Passer domesticus*) or Common Mynah (*Acridotheres tristis*) show that the transition from hole nests to domed nests in the open, or vice versa, is easily effected, sometimes even locally within a species.

The aberrant *Paramythia* builds a bulky, cup-shaped nest among the twigs of thick bushes (Rand, 1942, p. 513). The nests of the other New Guinea fruit-eating genera are unknown.

EGGS

The eggs of *Anaimos percussus* (the only species of the genus for which we have information) are whitish and unspotted, and the same is true of the majority of species of *Dicaeum*. *D. agile* and *D. papuense haematostictum* are known to lay spotted eggs. These species are not closely related. Nevertheless, when the color of the eggs of all species of *Dicaeum* is known it may give some clues to the affinities of the species. It would be interesting to know if *D. bicolor* and *D. anthonyi*, which seem distantly related to *papuense*, lay spotted eggs. Most forms of *Dicaeum*, so far as known, lay two or three eggs. Nests of *D. trigonostigma* in the Malay Peninsula contained but one nestling (Chasen, 1939, p. 407). *Dicaeum concolor* raises two broods (Whistler, 1934, p. 285), and the same has been inferred for other species. The species of *Pardalotus* also lay whitish unspotted eggs, the clutch varying from two to five according to species. *Paramythia* lays one egg which is white spotted with brown (Rand, 1942).

NESTING HABITS

In *Dicaeum vincens* the female builds the nest and incubates; the male helps feed the young (Lushington, 1940). Chand-

ler (1912, p. 132) found that in *Dicaeum hirundinaceum* only the female works on the nest. The male sometimes accompanies her while gathering nesting material, and the male utters a distinctive note in the vicinity of the nest. Both sexes feed the young, at first insects, later mistletoe berries. The male drives other males from the vicinity of the nest (Lawrence and Littlejohns, 1916).

In *Pardalotus* both sexes participate in digging the nest tunnel and probably in building the nest. The male is also said to aid in incubating as well as in caring for the young (Chandler, 1910). Diamond birds are said to be somewhat colonial at times in suitable nesting banks. Roberts (1937), however, noted that the male of a pair of *P. ornatus* feeding young in a hole in a bank repeatedly drove away another pardalote that was hunting a nest site in other holes in the bank.

In *Paramythia* it was observed that only the female incubates, but the male accompanies her when off the nest and aids in feeding the young (Rand, 1942).

VOICE

Typical flowerpeckers have a variety of rather sharp, almost metallic call notes. *D. hirundinaceum* also has a sweet song and a variety of twittering notes. We noticed that *Dicaeum ignipectus luzoniense* has a rather loud warbled song, and the same is probably true of many species of the genus. Pardalotes (*Pardalotus*) have rather monotonous unmusical call notes and also a trill, but little in the way of song. Rand (1937) wrote that the calls of *Paramythia* are low and short but mentions no song. Individuals of *Oreocharis*, when flying in a flock, call a sparrow-like *chip-chip*.

GENERA AND SPECIES OF DICAIDAE

The type species of genera are given in parentheses following the name of the describer of the genus. In general, we have not attempted to revise subspecies, and where we have listed them, it is primarily to indicate to what species we believe various forms should be allocated.

MELANOCHARIS P. L. SCLATER (*NIGRA*)

SYNONYMS: *Neneba* De Vis (*striativentris*); *Pristorhamphus* Finsch (*versteri*); *Urocharis* Salvadori (*longicauda*).

DIAGNOSIS: Tenth primary well developed, the exposed portion being 15 mm. or more in length and almost half the

indistinctly streaked (*striativentris*); upperparts olive green or blue black, often glossy or even metallic (*versteri*); rectrices often with white marks. Edges of bill well serrated. Bill rather short and heavy; culmen moderately decurved. Tarsus with only one or two scutes near base in front, thus almost booted (specimens of *M. versteri* in fluid).

This genus includes the most primitive flowerpeckers. Sexual dimorphism is well developed in several species, with the males more brightly colored but the females larger. Data on the latter point, as given by Mayr (1931, pp. 668-670), are:

SPECIES	WEIGHT (GMS.)		WING (MM.)	
	♂	♀	♂	♀
<i>Melanocharis nigra bicolor</i>	13, 14	15, 15.5, 17	67, 67.5	66, 68, 68.5
<i>Melanocharis longicauda captata</i>	13-15 (13.9)	14-16 (15.4)	64-67 (65.9)	64-67 (65.5)
<i>Melanocharis versteri maculiceps</i>	12.5-15.5 (14.0)	16.5-20 (18.5)	59-64 (61.8)	66-71 (69)

length of the ninth. Tail relatively long, varying from about 75 per cent (*nigra*) to 140 per cent (*versteri*) of the wing length. Color pattern simple: underparts ranging from grayish white through various shades of yellowish or greenish brown, sometimes

The data for *captata* and *maculiceps* are based on series of about six of each sex. The figures for *Melanocharis striativentris* indicate no sexual size dimorphism.

The genus *Urocharis* has not been recognized by recent authors. Mayr (1931,

p. 668, footnote) gave reasons for uniting *Pristorhamphus* with *Melanocharis*. At that time he retained the genus *Neneba* for *striativentris* because of its somewhat different proportions and body build, but we now feel it is best to associate this species with its close relatives in the genus *Melanocharis*.

The five species here included in *Melanocharis* comprise a monophyletic group whose species intergrade in all variable characters. The total range of variation is not greater than that often included by recent workers within the limits of a single genus. While *Melanocharis* is in most respects primitive, some of the species are the only ones in the family with metallic plumage.

INCLUDED SPECIES: 1, *arfakiana*; 2, *nigra*; 3, *longicauda*; 4, *versteri*; 5, *striativentris*. All the species are restricted to New Guinea. Their ranges and subspecies are given by Mayr (1941). *Melanocharis arfakiana*, the plainest colored and perhaps most primitive species of the genus, is known from only two specimens collected almost at the opposite ends of New Guinea.

RHAMPHOCHARIS SALVADORI (CRASSIROSTRIS)

DIAGNOSIS: Closely related to *Melanocharis* but bill elongated and rather thin (culmen about 18 mm. as against 12 mm. in the larger species of *Melanocharis*). Male above olive green with a very slight gloss and below gray. Female brown spotted with white. Female very noticeably larger than male (wing in male 66 mm., in female 73 mm.). The larger size and different coloration of the female are remarkable. The male is not unlike some of the simpler species of *Melanocharis* in color. The single species of this genus is restricted to the mountains of New Guinea. *Rhamphocharis* and *Melanocharis* comprise a rather old and primitive section of the Dicaeidae, which is surprisingly absent from tropical north Australia.

SPECIES: 1, *crassirostris*.

ANAIMOS REICHENBACH (THORACICUS)

SYNONYM: *Charitociris* Oberholser (*percussus*). The name *Prionochilus* formerly used for this genus is preoccupied in the insects.

DIAGNOSIS: *Anaimos* has a relatively large tenth primary and serrated bill, as do the two preceding genera. It differs from *Melanocharis* and *Rhamphocharis* as follows: tail much shorter (about 30 mm., 50–60 per cent of wing); general size much smaller (total length about 80–90 mm. against 105–107 mm.); color pattern more varied, usually with some red and yellow in plumage; no white in tail; axillaries and under wing coverts snow white; females not larger than males; tongue more or less tubular.

Anaimos is very closely related to *Dicaeum*, the only constant difference being the noticeable tenth primary of *Anaimos*. The bill in the latter is heavier than in all but a few species of *Dicaeum*, and has a more or less characteristic shape. The crown patch and white malar stripe of *Anaimos* (except *olivaceus*) are rare in *Dicaeum*, but occur in a few species. So far as known the two genera are identical in nidification and habits.

Anaimos is, with the doubtful exception of *A. olivaceus*, a closely knit, natural group. The genus is in some respects primitive, as indicated by the large tenth primary and the heavy bill. In coloration, habits, and nidification it belongs with the more specialized flowerpeckers. The six species are confined to Malaysia and the Philippines and have apparently originated in this area.

The suggested interrelationships of the species of *Anaimos* and *Dicaeum* are indicated diagrammatically in figure 5.

SPECIES: 1. *A. olivaceus*. This Philippine species is the simplest of the genus in coloration and the only one without a crown patch and without any bright colors. It has neither a malar stripe nor a rump patch. There are two races, *olivaceus* and *parsoni*.

2. *A. maculatus*. This is the only species that is streaked ventrally. It resembles *olivaceus* to some extent in coloration but has a crown patch, which links it with the following species. It occurs in peninsular Siam, Malaya, Sumatra, Borneo, and some of the nearby smaller islands (four races).

3. *A. percussus*. This species is slaty

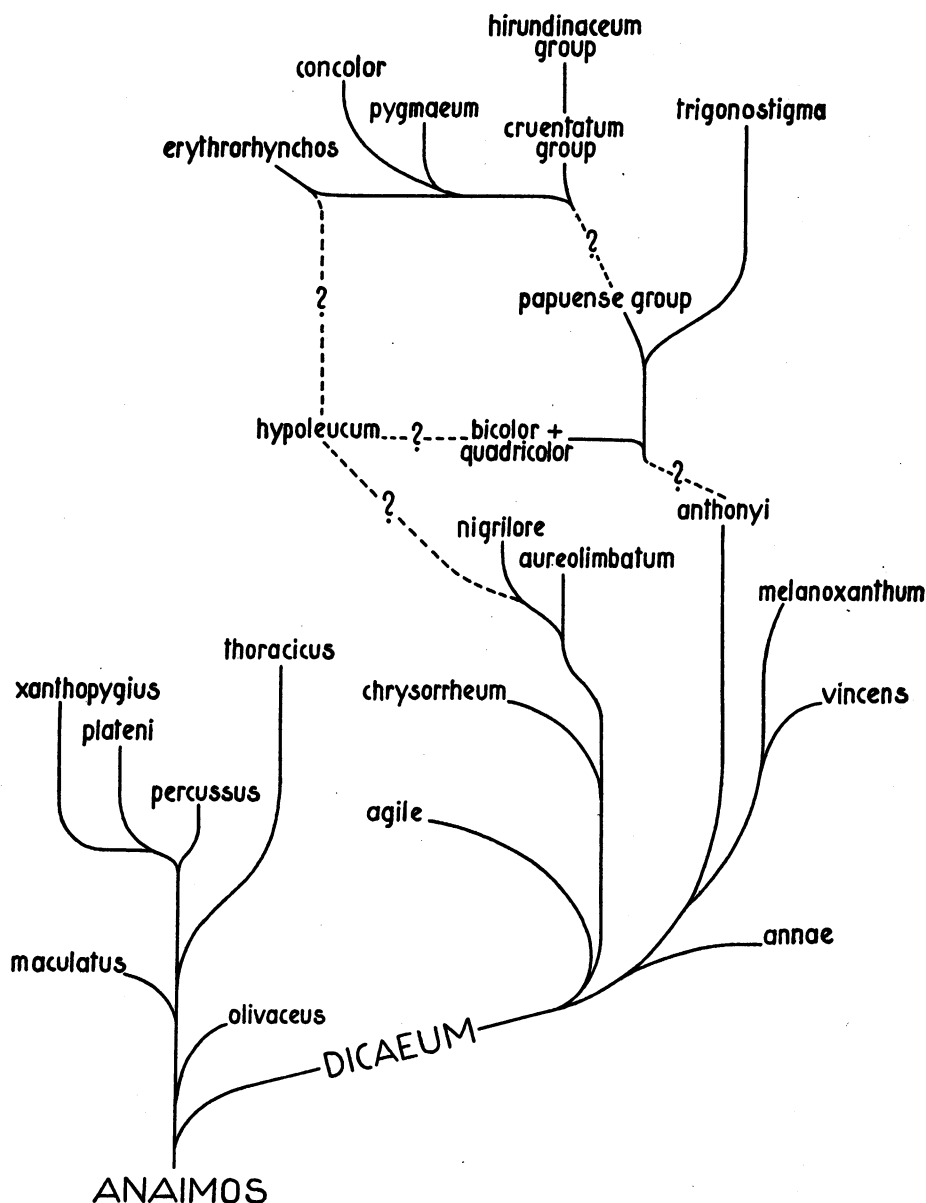


Fig. 5. Diagrammatic phylogeny of the species of *Anaimos* and *Dicaeum*.

blue above with a crimson crown patch and yellow below with a red pectoral spot. A white malar stripe is present. The races are: *ignicapillus* (Malaya, Sumatra, Rhio Archipelago, Billiton, Banka, North Natuna Islands, Borneo), *regulus* (Tana Massa, Batu Islands), and *percussus* (Java).

4. *A. plateni* (*johannae* auct.). Like *percussus* but with the rump yellow as in the following species, *xanthopygius*. Since *plateni*, which is endemic to Palawan, is intermediate between *percussus* and *xanthopygius*, which coexist on Borneo, it cannot be safely united with either species

as a race (Mayr, 1945, p. 115). We may assume that the widespread *percussus*, or its ancestor, spread to Palawan, giving rise to *plateni* which has reentered Borneo to produce the third species, *xanthopygius*. According to a recent letter from Hachisuka, the name *plateni* (Braunsch. Anzeiger, no. 52, 1888) antedates *johannae*, published in the same year.

5. *A. xanthopygius*. This species is much like *plateni* but lacks the white malar stripes. It is found on Borneo and the North Natuna Islands.

6. *A. thoracicus*. A rather rare, monotypic species of Malaya, Borneo, and Biliton. The color pattern is distinctive: head and breast black, mid-breast and crown crimson, rump yellow, back citrine olive. This pattern suggests remote relationship with *Dicaeum trigonostigma* or *D. quadricolor*.

DICAENUM CUVIER (CRUENTATUM)

SYNONYMS: *Acmonorhynchus* Oates (*vincens*); *Chilociris* Oberholser (*aeruginosus*, a race of *agile*); *Chromatociris* Oberholser (*quadricolor*); *Cryptociris* Oberholser (*obsoletus*, a race of *agile*); *Pachyglossa* Blyth (*melano-xantha*); *Piprisoma* Blyth (*agile*); *Polisornis* McGregor (*anthonyi*).

Polisornis was proposed as a subgenus. McGregor also proposed a subgenus *Bournsia* with the same type (*aeruginosus*) as the earlier *Chilociris* of Oberholser.

DIAGNOSIS: Similar to *Anaimos* but tenth primary vestigial (in *D. melano-xanthum*, the only species of *Dicaeum* with a visible tenth primary, this primary is short and very narrow, only about 10 mm. long and 1 mm. wide, compared with about 13 mm. by 2.5 mm. in *Anaimos*); crown patch and malar stripe usually lacking; bill often thinner than in *Anaimos* with the lower mandible less upturned. In specimens preserved in fluid the tarsus is seen to be scutellate in front (probably the same is true of *Anaimos*) and hence more "primitive" than in the other genera (*Pardalotus*?) in which it is virtually booted.

The various genera that we synonymize were based primarily on differences in the thickness and shape of the bill, but these are not of a nature to indicate natural groups of

species as we have pointed out above. Mayr (1945, p. 114) has shown in more detail the drawbacks of further subdividing the genus *Dicaeum*.

As it has long been known that the tenth primary is vestigial in many flowerpeckers, it is surprising that Oberholser (1923) confused the ninth primary with the tenth in the species he studied (*quadricolor*, *vincens*, some races of *agile*) and stated that the tenth primary is not reduced in these species. Actually it is reduced to the vanishing point.

Although some of the species of *Dicaeum* are easily arranged into species groups, the natural arrangement of all species of the genus is difficult. As already noted, the bill tends to become thinner in the more advanced species, but this trend has been reversed several times. The coloration of most species of the presumably more primitive *Anaimos* is bright and varied, and hence the more simply colored species of *Dicaeum* are not necessarily primitive. *D. concolor*, *D. erythrorhynchos*, and *D. tristrami* probably owe their plain colors to secondary simplification. All three are closely linked with bright-colored species. Certain groups of forms that still are geographical representatives (superspecies) show great variation in shape of bill and in coloration, e.g., the *papuense-retrocinctum* group, the *bicolor-quadricolor* group, and the *erythrothorax* group (including *tristrami*). Some of the more unusual color patterns in *Dicaeum*, such as those of *chrysorrheum*, *agile*, *anthonyi*, and *annae*, suggest that *Dicaeum* may not be monophyletic in the narrowest sense of the term, but that various branches may have developed from different species of *Anaimos* or *Anaimos*-like ancestors. Thus *Dicaeum annae* resembles *Anaimos olivaceus* in some respects, and the streaked *D. chrysorrheum* (and perhaps *agile*) may be directly related to the streaked *A. maculatus*. Some of these resemblances are doubtless deceptive, and we cannot suggest any further subdivision of the genus that would not obscure rather than elucidate relationships. The only question is whether it is profitable to separate *Anaimos* and *Dicaeum*. We do so only tentatively.

The phylogeny of *Dicaeum* suggested in figure 5 and explained in the following account of the species attempts to reconcile the above difficulties, but will doubtless be improved as further knowledge of life histories, eggs, and anatomy accumulates. The first eight species listed in *Dicaeum* are the most primitive and most like *Anaimos* in the shape of the bill and in coloration.

SPECIES: 1. *D. annae*. This peculiar species occurs in the Lesser Sunda Islands, the nominate race on Flores and the race *sumbavensis* on Sumbawa. Records from other islands seem to be due to early confusion with *D. agile*. In *D. annae* the males have a half-concealed patch of bright yellow feathers on the lower back. This feature is unique in the family but possibly homologous with the yellow rumps or lower backs of such species as *Dicaeum quadricolor* or *Anaimos olivaceus*. It equally resembles *Dicaeum agile*, which also occurs in the Lesser Sundas, and since both of these species lack the tenth primary the relation may be closer than with *olivaceus*.

2. *D. agile*. Many of the races of this widespread species (or superspecies) are rare in collections. It is a dull species, grayish above and whitish below, usually more or less streaked. The bill is thick, short, and blunt. The eggs are spotted, and the nest, while in general like those of the genus, is said to be especially finely woven, so as to regain its shape even after being rolled up or crushed. The species must be considered rather aberrant but not necessarily primitive. Two forms of the *agile* group have been thought to occur together in the Malay Peninsula, but this seems doubtful (Deignan, 1945, p. 550). The heavily streaked Philippine form (*aeruginosum*) is linked with the others by *affine* of Palawan, while the unstreaked *obsoletum* of Timor is linked with the striated forms by *tinctum* of the nearby islands. We believe it will prove correct to unite all the forms listed below as races of *agile*. Oberholser (1923) divided them among three genera and five species, with two other species (*vincens*, *quadricolor*) sandwiched in between.

Most races of *agile* have white spots on the inner vanes of the outer tail-feathers (absent in *aeruginosum*). This suggests relationships to *vincens* and *melanozanthum* the only other species of *Dicaeum* with such marks.

The races of *agile* are: *zeylonense* (Ceylon); *agile* (India); *modestum* (? eastern India, Burma, Malay Peninsula; see Deignan, *loc. cit.*); *pallens* (Siam, Indo-China); *atjehense* (Sumatra); *finchii* (Java); *tinctum* (Sumba, Flores, Alor); *obsoletum* (Timor); *bungurensis* (North Natuna Islands); *everetti* (Borneo, Labuan); *affine* (Palawan); *aeruginosum* (Philippine Islands).

The name *atjehense* was proposed by Delacour (1946, p. 4) for *Piprisoma sumatranus* Chasen, preoccupied in *Dicaeum*. The older records of this species from Sumbawa are based on a mistake of Hartert's in identifying immatures of *D. annae* as the present species. We have found no definite records for Sumbawa.

3. *D. chrysorrheum*. This species contains three races which range from eastern and northern India through the Indo-Chinese countries and Malaysia. This and *agile* (some races) are the only species of *Dicaeum* having streaked underparts. *D. chrysorrheum* has a thin bill, very unlike that of *agile*. The yellow under tail coverts of *chrysorrheum* apparently link it with the following group of yellow-bellied species (nos. 4-8). The bright olive upperparts of *chrysorrheum* are also partly duplicated in *aureolimbatus* and *nigilore* of the group just mentioned. We thus tentatively place *chrysorrheum* as a link between the streaked *agile* and the species with partly yellow underparts but without conviction that the similarity to *agile* actually indicates close relationship.

4. *D. anthonyi*. The few known specimens of this species, which McGregor described from the moss forests of the northern Luzon mountains, were in the destroyed collection of the Manila Bureau of Science (for a colored plate see McGregor, 1914). It is the only species of *Dicaeum* with a yellow crown patch (male only) like that usual in *Anaimos*. The back is glossy black in the male, olive green in the female.

The throat is white; the breast and abdomen are yellow. This coloration plus the heavy bill, mountain range, and apparent rarity of *anthonyi* suggest that it is primitive. McGregor (1927, p. 522) clearly states that *anthonyi* has the tenth primary vestigial, so we must place it in *Dicaeum*. In color pattern *anthonyi* is rather similar to the four species that follow (nos. 5-8), all of which perhaps have a relict distribution.

5. *D. melanozanthum*. This Himalayan species is the largest of the genus and, as are many mountain species, is rather long winged. It is the only *Dicaeum* in which the tenth primary is visible, though very small. Like *anthonyi* it is bluish black above and yellow below with white throat and breast, but it lacks a crown patch, and the black has encroached on the sides of the breast. There are white spots on the outer tail feathers. The bill is broad and short. It was formerly separated in the genus *Pachyglossa*.

6. *D. vincens*. This species resembles *D. melanozanthum* in so many details of coloration as to leave little doubt they are related, as P. L. Sclater (1874) pointed out long ago when figuring them together in the Ibis. *D. vincens* is found in the lowlands and foothills of Ceylon. The tail feathers have large white spots near their tips that are undoubtedly homologous with those of *melanozanthum*.

7. *D. aureolimbatus*. This Celebes species resembles the three preceding ones, but the white of the breast extends back with yellow restricted to the sides. Above only the wings, tail, and sides of the head are blackish; the rest is yellowish olive. The bill is short and thick. A race occurs on Sangir.

8. *D. nigrilore*. A Mindanao species rather rare in collections (colored plate: Novitates Zool., 1920, vol. 26, pl. 6). Very similar to *aureolimbatus* but the back is brownish, only the crown and flight feathers olive. The bill is thin and decurved, but the coloration and distribution leave little doubt that *nigrilore* is a close relative of *aureolimbatus*. It helps link the heavy-billed species with those with thin bills. The species was apparently redescribed by Hachisuka (1941) as *Di-*

caelum isag. The original description does not mention a single character not applicable to *nigrilore*, and the colored plate looks like *nigrilore*.

9. *D. hypoleucum*. This Philippine species contains three races: *hypoleucum* of Basilan and Mindanao, *pontifex* of the Samar-Leyte group, and *obscurum* of Luzon. Although there is a considerable variation in color of plumage and soft parts from north to south, *pontifex* is intermediate between *hypoleucum* and *obscurum*, so that it seems justifiable to unite the three forms in a single species (Mayr, 1945, p. 115). Better material may show that Tweeddale's race *mindanense* is separable from typical *hypoleucum*. Mayr (1946) proposed the name *pontifex* as a substitute for *Dicaeum everetti* Tweeddale, which is preoccupied by *Prionochilus everetti* Sharpe, once the latter is transferred to *Dicaeum* as a race of *D. agile*. The rather attenuated bill and to some extent the coloration of *hypoleucum* resemble *nigrilore*, although the relationship may not be very close.

10, 11. *Dicaeum bicolor*, *D. quadricolor* (superspecies). Males of *D. bicolor* are bluish black above and gray below with a whitish mid-ventral area. Two races occur in the Philippines. On Cebu it is replaced by the little known *quadricolor* (colored plate: Proc. Zool. Soc. London, 1877, pl. 77, fig. 2), similar but with the upper back scarlet and the lower back ochraceous green. The two species agree in all structural details and seem to be geographical representatives despite these striking differences in coloration. Similar variation occurs in the following superspecies (*papuense*). Females and young of both species are dull and scarcely separable.

Dicaeum bicolor is like *D. h. hypoleucum* in color and perhaps related, but the bill is heavy as in *anthonyi* or *melanozanthum* and (together with *papuense*) it links these rather primitive, heavy-billed species with the more widespread and apparently advanced, thin-billed species that follow. Both *bicolor* and *hypoleucum* resemble some species of *Melanocharis* in their style of coloration.

12, 13. *D. papuense*, *D. retrocinctum* (superspecies). The ranges of the three

forms in this Philippine superspecies are as follows: *D. retrocinctum*, Mindoro; *D. papuense haematostictum*, Guimaras, Negros, Panay; *D. p. papuense*, most of the other Philippines from Luzon to Mindanao and Basilan. *D. p. papuense* is similar to *D. bicolor bicolor*, but the bill is thinner and longer, the back is duller black, and the mid-ventral area is crimson, not white. *D. papuense haematostictum* is similar, but the back is glossier and the ventral red area is partly encircled with black at the breast. In *D. retrocinctum* the bill is much thinner and the entire breast is black, meeting the black of the top of the head and neck. There is a patch of lanceolate red feathers on the throat and also a transverse crimson patch of red in the scapular region. Thus, a red dorsal patch is a variable character in this superspecies, as it is in *D. bicolor quadricolor*.

This superspecies provides another instance of the small taxonomic value of variation in the bill in flowerpeckers. It is the only brightly colored species of *Dicaeum* in which females have acquired the male type of coloration. *Dicaeum flaviventer* Meyer was probably based on a specimen of *D. papuense* discolored by alcohol (Mayr, 1945).

14. *D. trigonostigma*. This species occurs in the Philippines, Malaysia, and the southern Indo-Chinese countries. There are eight races in the Philippines alone and about an equal number in the rest of the range. This is a thin-billed species with a red or orange patch on the upper back and often with a yellow rump patch, which sometimes is joined with the back patch. Throat and breast are grayish and the rest of the underparts bright yellow. Females are dull greenish. This is one of the most specialized species of the genus; it is probably of Philippine origin for the color pattern suggests *D. retrocinctum*.

15. *D. erythrorhynchos*. This dull-colored, thin-billed, tiny species is found in peninsular India, with a race on Ceylon. The dull coloration is probably secondary. It is a close relative of *concolor* and so similar to it that occasional specimens may not be identifiable.

16. *D. concolor*. This is another dull-

colored, thin-billed species similar to *erythrorhynchos*, though they occur together in some parts of India. It is much more widespread, with the following races: *concolor* (southern India), ? *subflavum* (central India), *olivaceum* (Himalayas to Yunnan and Kwangtung, south through the Indo-Chinese countries), ? *sinense* (Szechwan), *uchidai* (Formosa), *virescens* (Andaman Islands), *minullum* (Hainan), *borneanum* (Malaya, Sumatra, Borneo, North Natuna Islands), *solicitans* (Java, Bali).

17. *D. pygmaeum*. This Philippine and Palawan species may be a representative of *concolor*, a species which it resembles in its dull coloration, thin bill, whitish spot before the eye, and small size. On the other hand, males of *pygmaeum* have a slight bluish gloss on the wings, a whitish mid-ventral area, and a yellowish rump, suggesting the following *cruentatum* group of species, also lacking in the Philippines unless represented by *pygmaeum*. Thus the latter seems to link *concolor* loosely with the *cruentatum* group.

THE *cruentatum* SPECIES GROUP

The ranges of the 13 species comprising this species group (species 18-30, below) are mapped in figure 6, and their supposed phylogeny is shown in figure 8.

Before the evolution of this group is discussed, the species will be listed and briefly described.

18. *D. nehrkorni*. In the male of this Celebes species, the crown, forehead, rump, and a small spot on the mid-breast are crimson, the back and wings glossy bluish black, the breast and sides gray, the belly and under tail coverts white with a blackish area medially. The female is similar but duller, with no crimson on the breast and only a suggestion of it on the head; the rump is red as in the male.

19. *D. vulneratum*. This monotypic species is found on Amboina, Seran, and Goram in the southeastern Moluccas. Like *nehrkorni* it is very grayish below, lighter in the female, with a red pectoral spot in the male. This red mark is much larger in *vulneratum* than in *nehrkorni*. Dorsally both sexes of *vulneratum* resemble the female of *nehr-*

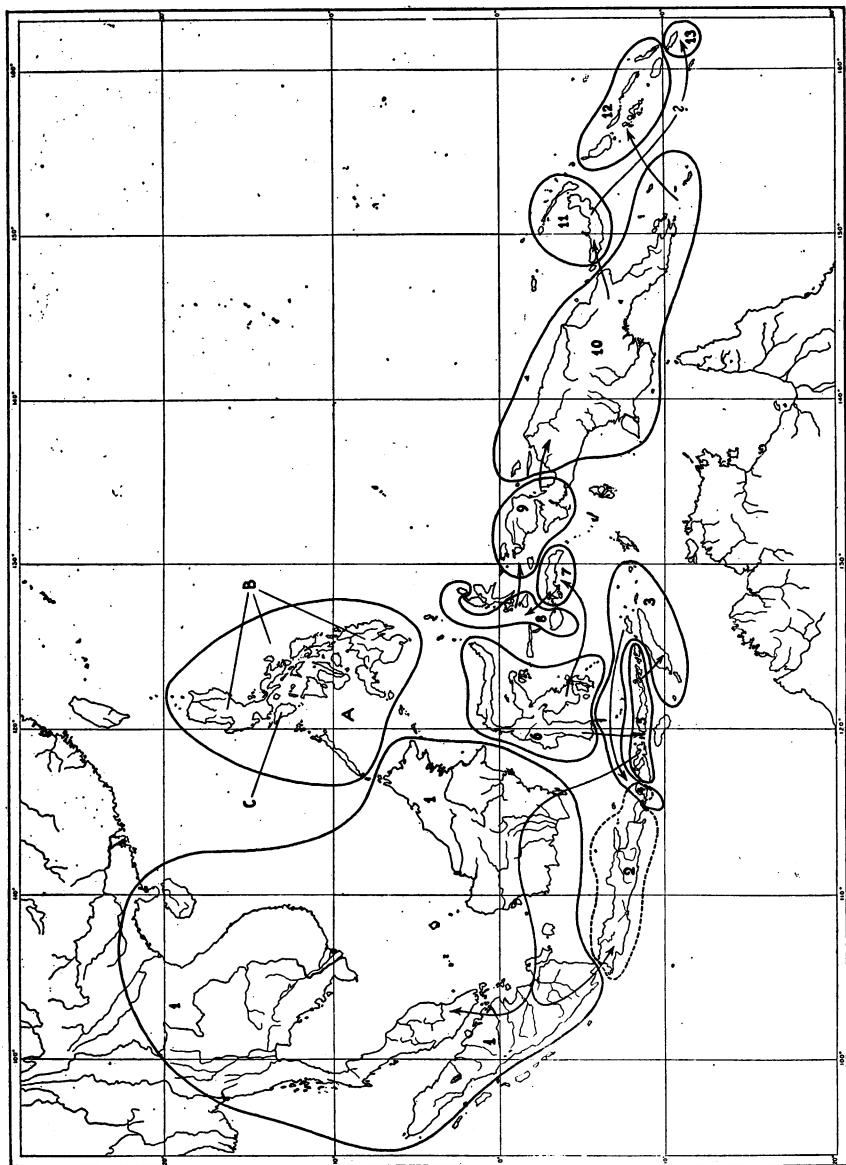


Fig. 6. Distribution and route of colonization of the *Dicaeum cruentatum* group; distribution of *Dicaeum pygmaeum*, *D. papuense*, and *D. retrocinclum*. 1. *D. cruentatum*, 2. *D. trochileum*, 3. *D. maugae*, 4. Overlap of *trochileum* and *maugae* on Lombok, 5. *D. igniferum*, 6. *D. nehrkorni*, 7. *D. vulnerum*, 8. *D. erythrothorax*, 9. *D. pectorale*, 10. *D. geelvinkianum*, 11. *D. ezimium*, 12. *D. aeneum*, 13. *D. tristrami*. A. *D. papuense*, B. *D. retrocinclum*.

korni: rump red; crown grayish like the back (not red!); no dark blue gloss as in the male of *nehrkorni*. Male without black ventral stripe.

20. *D. erythrothorax*. This species resembles *vulneratum*, but flanks and belly are washed with yellowish olive. The rump is not red, but the back is washed with olivaceous which becomes yellowish on the rump in the male (probably the final stage in the loss of the red rump). The male has a large red breast patch. The race *erythrothorax* with white throat occurs on Buru in the southern Moluccas, and *schistaceiceps* with gray throat on Obi, Batjan, and Morotai in the northern Moluccas. Its apparent absence on Halmahera is surprising.

The characters of the two Moluccan species leave little doubt that *vulneratum* is closest to *nehrkorni*, although the Buru race of *erythrothorax* is now more or less intermediate geographically. Probably *erythrothorax* (*schistaceiceps*) was originally limited to the northern Moluccas where it was an offshoot of *vulneratum*. Recently it spread south to Buru where *vulneratum* for some reason was absent.

21. *D. pectorale*. This species is found on the islands of Misol, Salawati, Batanta, and Waigeu west of New Guinea and on the coasts of western New Guinea. These islands are close to the northern Moluccas, and *pecturale* is evidently a descendant of *erythrothorax*. It is similar to *erythrothorax* but more olivaceous, less grayish throughout, even becoming greenish on the crown and back. There is no trace of a red rump patch. It is a smaller species.

22. *D. geelvinkianum*. The range is New Guinea (except the part occupied by *pecturale*), some of the nearby islands, and the Louisiade Archipelago. In the male the upperparts are almost as in *nehrkorni*, but glossed with purplish blue. Below it is very similar to *pecturale*. The female is like the male but duller with the crown and rump reddish. The two races of the Louisiades (*nitidum* and *rosseli*) are somewhat different: back glossed with greenish; tone of underparts ochraceous; crown duller, almost maroon. These are differ-

ences of degree, and we do not think it necessary to recognize *nitidum* as a species.

In this species the rump is red as is usual in the *cruentatum* group and not gray as in *pecturale* and *erythrothorax* from which *geelvinkianum* was presumably derived.

23. *D. eximium*. This species is found on the larger islands (New Britain, New Hanover, New Ireland) in the Bismarck Archipelago. The male is white below with a red breast spot bordered with grayish brown which extends back more or less on the sides and mid-ventral area. Above it is dull brownish olive with red rump, a maroon wash on the crown, and a faint blue gloss on the tail. The female is similar but entirely whitish below except along the flanks and sides. It is thus quite different in appearance from the neighboring species. Eye-ring, loreal and malar stripes are white. In the latter character it resembles *Anaimos*.

24. *D. aeneum*. In this Solomon Islands species there is a return to the brighter coloration usual in this group. The male is remarkably similar to *D. e. erythrothorax*, but the gray upperparts are more brightly glossed with greenish, without noticeable yellow wash even on the rump. There are other minor differences. The female is similar to that of *erythrothorax*.

25. *D. tristrami*. This very aberrant species is found on San Cristobal in the Solomons (where *aeneum* is lacking). It is entirely without lipochromes: white below, washed with gray on the sides, brownish across the chest. The back and sides of the head are brown, more or less mottled with whitish; darker and slightly glossy on wings, tail, and malar stripes. The sexes are alike. The bill is unusually heavy and large. *D. tristrami* carries much further tendencies apparent in the rather dull *eximium* of the Bismarck Archipelago. It is possible that *tristrami* was derived from *eximium*, while *aeneum* descended more recently and directly from *geelvinkianum* (probably *nitidum*). On the other hand, it may be merely another example of the parallelism that is common in the species group (e.g., the similarity of *aeneum* to *erythrothorax*).

All of the species of the *cruentatum* group just listed, with the possible exception of *nehrkorni*, may be considered members of a single superspecies, and all (except *tristrami*) are obviously closely related geographical representatives, though many are so distinct we think it better to consider them species. We now return to a group of more specialized species which are linked through *nehrkorni* to those listed above.

26. *D. igniferum*. The upperparts of the male are similar to those of *nehrkorni*, but the back is washed with red. Wings and tail are black glossed with dark purplish blue. The throat is white, the breast red. The sides of the head are black, and this extends around as a border below the red breast and then back as an indefinite line separating the white abdomen. The pattern below is thus similar to the geographically distant *eximium*. The female is whitish below, duller on the breast; the back is similar to that of the male but duller. This species occurs in the north central part of the Lesser Sunda Islands, the nominate race on Sumbawa and Flores, and *cretum* on the islets Pantar and Alor.

27. *D. maugei*. The underparts of the male in this species are almost the same as in its close relative *igniferum*. Above, only the rump is red; the rest of the plumage is black glossed with dark purplish blue as are the wings and tail of *igniferum*. The females of the two species are similar ventrally, while dorsally red occurs only on the rump in *maugei*.

The races of *maugei* are: *maugei* (Timor, Samau, Savu); *salvadorii* (Moa, Babar); *romae* (Roma, Damar); *splendidum* (Djampoa and Saleyer, between Celebes and the Lesser Sundas); *neglectum* (Lombok); and *mariae* (islet of Penida, south of Bali). The validity of Neumann's race *mariae* is doubtful, as Meise intimates (1941). The ranges of *igniferum* and *maugei* suggest that the former evolved in the western and the latter in the eastern part of the Lesser Sunda group. Recently *maugei*, which has been able to colonize small islands, extended its range to more or less encircle that of *igniferum* but without overlapping. On Lombok, however, it has

overlapped with the less closely related *trochileum*.

Rensch (1931, p. 616) mentions finding *trochileum* in the lowlands of Lombok up to 200 meters. *D. maugei neglectum* occurs in the lowlands also but ranges up to 2000 meters and is much more common. We lack material of the Lombok race of *trochileum* and cannot judge which of these subspecies is more differentiated (and hence perhaps older). Other evidence suggests that *trochileum* is the more recent arrival on Lombok. *D. maugei* has colonized the small island of Penida, but not adjacent Bali, suggesting that the presence of *trochileum* may have excluded it on Bali though not on Lombok.

28. *D. cruentatum*. Whereas *D. maugei* appears to be a relative of *igniferum* in which the red of the upperparts (except the rump) has been lost, in *cruentatum* the red has been intensified so that the entire crown, back, and rump are scarlet. The wings and tail are deep bluish black, the sides of the head and breast duller black, and a broad mid-ventral stripe is white. The female is duller, with only the rump red. The tone of the plumage is soft, suggesting *nehrkorni*, which some authors have considered the closest relative of *cruentatum*. It is possible, therefore, that the red back was independently acquired in *igniferum* and *cruentatum*, although *igniferum* is intermediate as regards the presence of red on the back.

The races of *cruentatum* are: *nigritum* (Borneo); *niasense* (Nias); *batuense* (Batu Islands); *sumatranum* (Sumatra); *ignitum* (Malay Peninsula, most of Burma); *siamense* (Siam, Indo-China); *erythronotum* (*coccineum* auct.; see Deignan, 1943; southern China); *hainanum* (Hainan); *cruentatum* (eastern India, northern Chin Hills).

29. *D. trochileum* (*flammeum* auct.). The entire upperparts, head, throat, and breast are light crimson in the male. The underparts are uniform gray; the wings and tail bluish black similar to *cruentatum*. The female is light grayish with a red rump. This is a very specialized species—the only one of the genus with the head entirely red. For this reason we place it after *cruentatum*,

although on geographical evidence, if these species were derived from *igniferum*, presumably this stock reached Java before Sumatra or Borneo. As noted above, an alternative theory is that *cruentatum* and later *trochileum* were independently derived from *nehrkorni*, the dispersal then being from Celebes to Borneo, Sumatra, and Java.

Dicaeum trochileum occurs on Java and Bali, with a race *stresemanni* on Lombok, where it overlaps with *D. maugei neglectum*. This is the only overlap of range in the *cruentatum* species group. *D. trochileum* is so distinct there could be little doubt of its specific status, even if this overlap did not exist.

EVOLUTION OF THE *cruentatum* SPECIES GROUP

It has already been pointed out that *pygmaeum* may be a plainly colored member of this group or it may represent the still more dully marked *D. concolor* in the Philippines. It thus serves to link the *cruentatum* group with *concolor*. The latter, along with *erythrorhynchos*, is perhaps an Indian equivalent or representative of some of the more brightly colored island species. The *cruentatum* group is basically one with a bright and varied color pattern. A suitable type of ancestral stock among existing species is provided to some extent by the *papuense-retrocinctum* superspecies of the Philippines which supplies a transition from the heavier-billed *Anaimos* type of species to the more advanced ones, although the relationship is not close.

Turning to the interrelationships of the members of the *cruentatum* group, the four species of the Sunda Islands (*cruentatum*, *trochileum*, *igniferum*, *maugei*) are more differentiated than the others, and it is here that the only instance of overlapping range in the group occurs (Lombok). This suggests that these species are older than the Moluccan-Papuan ones. On the other hand, the rather specialized characters of the Sunda species (such as the red back) do not make them likely immediate ancestors of the somewhat simpler Moluccan and Papuan species. *D. nehr-*

korni of Celebes does furnish an excellent transition from the Sunda to the Moluccan species, as it is obviously related to both. Perhaps the Sunda species are older than the Moluccan ones, but *nehrkorni*, though a member of the Sunda group, never acquired the red back and other specialized characters of that group. More recently, we may assume, *nehrkorni* stock radiated eastward, giving rise to the series of allopatric Moluccan and Papuan species. Another possibility is that the Moluccan and Papuan species are as old as, or older than, the Sunda ones, but that the former have been kept more or less similar by occasional stragglers from island to island with resultant gene exchange. Whichever of these hypotheses is favored, *nehrkorni* may be taken as a central point in the *cruentatum* species group (figs. 6, 8).

Dicaeum maugei is a relative of the red-backed *igniferum* in which the back is black. Its resemblance to the type of pattern of the Moluccan-Papuan species is apparently parallelism.

CHARACTER GEOGRAPHY IN THE *cruentatum* SPECIES GROUP

In the brightly colored species of *Dicaeum*, the color pattern often changes rather abruptly in closely related forms. This is true both of the *cruentatum* species group and of others already mentioned. Perhaps this means that some of these color characters are controlled by a few or single genetic factors. In several instances, however, it is obvious that red marks are only partially or dully indicated, suggesting a more complex genetic basis. This type of abrupt variation is favored by the insular distribution of many of these forms. The bright varied coloration of the ancestral *Anaimos* demonstrates that such patterns were already present when the species of *Dicaeum*, such as the *cruentatum* group, evolved. Some of the plainer species of *Dicaeum* are not primitive in this respect, but have lost the bright coloration of their relatives secondarily. This is obviously true of *tristrami* and probably of *pygmaeum* and *erythrorhynchos*.

In the above list of species some use was made of character analysis, as in point-

ing out the closer relationship of *vulneratum* than of *erythrothorax* to *nehrkorni*. The geographical variation in color characters is more fully analyzed here (table 1).

RUMP: In most species of the *cruentatum* group the rump is red (in both sexes), but four species *erythrothorax*, *pectorale*, *aeneum* and *tristrami*, are exceptions. The rump is still yellowish in *erythrothorax*, suggesting recent loss. In *pectorale*, which seems to have been derived from it, the rump is no longer yellow. In *aeneum* of the Solomon Islands the loss of the red rump was probably independent of that in *pectorale*, since in the intervening area two red-rumped species, *geelvinkianum* and *eximium*, occur. The fact that the rump is not red in *tristrami* might be interpreted to mean that it was derived from the other Solomons species, *aeneum*, but other features of the coloration indicate that *tristrami* may have been derived from the Bismarck Archipelago (*eximium*) and *aeneum* from New Guinea or the Louisiades (*geelvinkianum*).

CROWN AND BACK: A red crown is less

breast is characteristic of all the closely related species extending from Celebes (*nehrkorni*) eastward through the Moluccas and the New Guinea region to the Solomon Islands, except for the aberrant *tristrami*. This red breast spot may be a transmutation of the red abdominal stripe found in the superspecies *D. papuense*. This assumption is strengthened by the fact that the red spot is continued in *nehrkorni* and *eximium* by a dark abdominal stripe. A red spot on the lower throat is also found in some species of the Malaysian branch of the *cruentatum* group (*igniferum-maugei*), but is lost in the more specialized species *cruentatum* and *trochileum*. The red throat of *trochileum* seems not to be homologous with the red breast spot of the other species, but rather due to the encroachment of the red of the crown around the sides of the head onto the throat.

The accompanying chart (table 1) summarizes the variation of the more important color characters in the group.

TABLE 1

CHARACTER VARIATION IN *Dicaeum nehrkorni* AND RELATIVES

Males	Belly Stripe	Red Breast Patch	Crown	Back	Rump
<i>nehrkorni</i>	Black	Small	Red	Black, blue gloss	Red
<i>vulneratum</i>	—	Medium	Gray	Gray	Red
<i>erythrothorax</i>	—	Large	Gray	Olive	Olive
<i>pectorale</i>	—	Medium	Olive	Olive	Olive
<i>geelvinkianum</i>	—	Small	Red	Blue gloss	Red
<i>nitidum</i>	—	Medium	Red	Green gloss	Red
<i>aeneum</i>	—	Large	Gray	Gray, green gloss	Gray
<i>eximium</i>	Brown	Medium	Reddish brown	Brown	Red
<i>tristrami</i>	—	—	Mottled brown	Brown	Brown

characteristic of the *cruentatum* group than a red rump, occurring in fewer species and being absent in the female when present in the male. It occurs in *igniferum*, *cruentatum*, and *trochileum*, and in these the back is also more or less red. They are undoubtedly closely allied. The crown is also red in males of *nehrkorni*. The red crown has been lost in the two Moluccan species and in *pectorale* of the western New Guinea Islands but reappears in *geelvinkianum* and *eximium*, though reduced in the latter. It is entirely lost again in the two Solomon Islands species.

BREAST AND THORAX: A red spot on the

THE SUPERSPECIES

Dicaeum hirundinaceum

The species of this superspecies are very similar to some of the species of the *cruentatum* group, and there can be no question of a very close relationship. However, both groups occur together on Celebes and in most of the Greater and Lesser Sunda Islands, although they are usually altitudinally separated. The greatest similarity exists between the species *maugei* and *sanguinolentum* which represent the two groups on the Lesser Sunda Islands, and scarcely two authors have agreed as to how to associate these species with the species of the

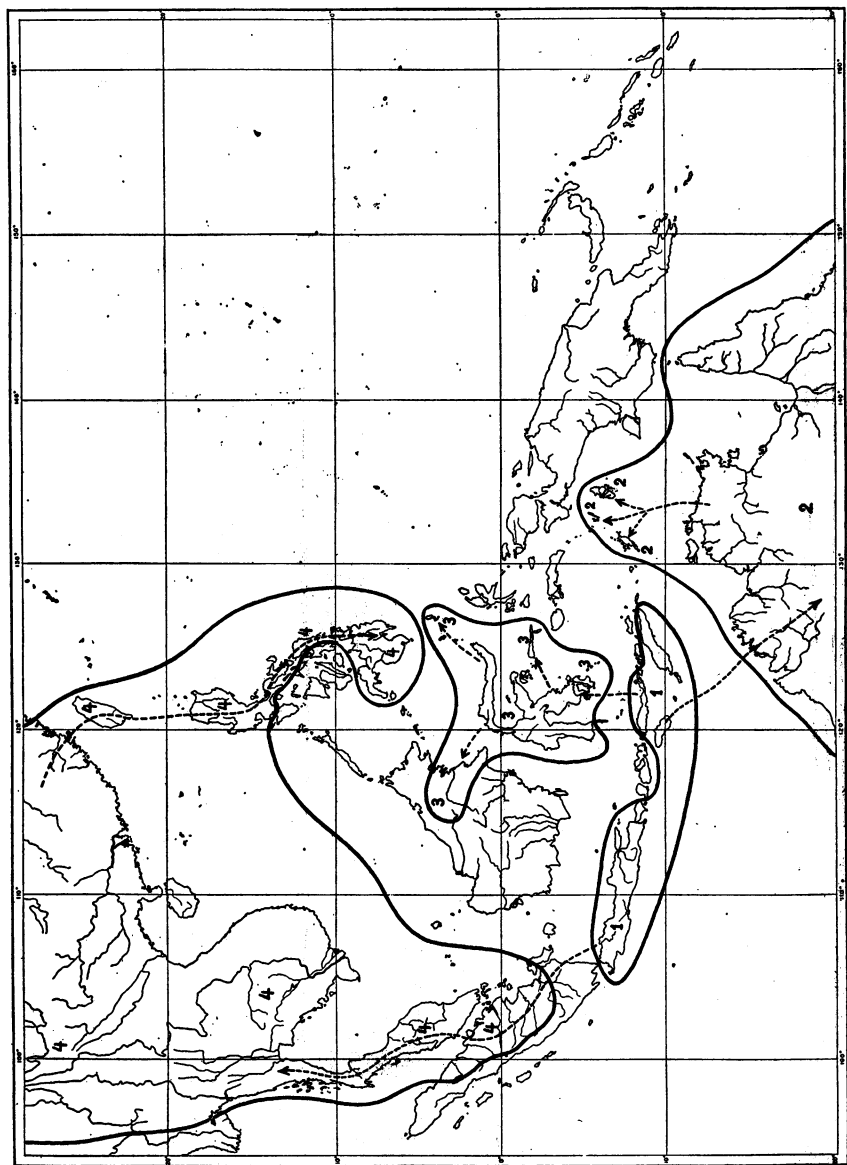


Fig. 7. Distribution and route of colonization of the superspecies *Dicaeum hirundinaceum*. 1. *sanguinolentum*. 2. *hirundinaceum*. 3. *celebicum*. 4. *ignipectus*.

neighboring islands. A close study suggests that *maugei* or the form ancestral to *maugei* gave rise to the *hirundinaceum* group, but the exact stages in which this speciation occurred were subsequently obscured by reinvasions and range changes. The most probable hypothesis is that the *hirundinaceum* group originated by the colonization of the western Lesser Sunda Islands (giving rise to *sanguinolentum*) by a *maugei*-like stock coming from the Timor group. Subsequent range expansions of *sanguinolentum* and *celebicum* and of descendants of these forms has led to the present distribution. The *cruentatum* and *hirundinaceum* groups still replace each other geographically on most smaller islands, especially in the area from Celebes and the Lesser Sundas eastward. The *hirundinaceum* group is considered to be the younger because of the lesser degree of differentiation among its members and, in part, because of its distribution (fig. 7).

The only constant character separating the *hirundinaceum* and *cruentatum* groups is the fact that the rump is never red in males of the former group. It is sometimes red in the female, especially in *sanguinolentum* which is nearest to the *cruentatum* group. Even this is not a very satisfactory distinction, as the red rump has been lost in a few Moluccan and Papuan species of the *cruentatum* group. The upperparts in males of *hirundinaceum* and allies are in general more glossy than in those of the other group, and there are other minor points which help in separating them. Here, too, the difference is least in the Lesser Sunda forms of *maugei* and *sanguinolentum*.

It is difficult to divide the *hirundinaceum* group satisfactorily into species. Deignan (1945, p. 548) has recently listed them all as races of *hirundinaceum*, although he confusingly uses the term superspecies. Since, in several other instances, forms of *Dicaeum* as similar as *sanguinolentum*, *hirundinaceum*, and *celebicum* occur together as good species, we prefer to recognize the following four groups of forms as species:

30. *D. sanguinolentum*. There are four races, as follows: *sanguinolentum* (Java and

Bali), *rhodopygiale* (Flores), *wilhelminae* (Sumba), *hanieli* (Timor). Robinson and Kloss described a race *ablutum* from eastern Java and Bali, of which the most striking character was the supposed absence of the red rump in the female. Others (Chasen, 1940, p. 265) surmised that an immature male may have been mistakenly considered a female. This seems to be the case, as the only female from the range of *ablutum* examined by us (Bali, Stresemann collector) has the rump as red as in any race of *sanguinolentum*. Chasen thought *ablutum* valid on the basis of other characters, but our material, which includes four males from Bali, makes this appear doubtful.

The upperparts of the male are glossed with dark bluish purple varying slightly in tone among the races. The underparts are buffy white with a large red pectoral spot in *s. sanguinolentum*. *D. s. rhodopygiale* is similar, but the breast spot is paler. In *hanieli* the red area is smaller, and the underparts are whiter. In all these races there is a small indistinct blackish area posterior to the red breast. In *wilhelminae*, the breast spot is large, extending to the chin, and the mid-belly and sides are extensively blackish. The females of all races are grayish or buffy white below and olive gray above with a red rump. The bill is small in *sanguinolentum* and *rhodopygiale*, medium in *hanieli*, and stout in *wilhelminae*. The Flores race is nearer to the Javan one in all particulars than is that of Sumba. This is a mountain species.

31. *D. hirundinaceum*. This we consider a separate species because the under tail coverts are red or pink in both sexes in all four races. The rump is no longer red in the female of *h. hirundinaceum* of Australia, but is still tinged with red in the three other races: *ignicolle* (Aru Islands), *keiense* (Kei Islands), *fulgidum* (Tenimber Islands). The back in the male is similar to that of *sanguinolentum*, but the gloss is a little more bluish. Ventrally there is a great resemblance to *D. s. wilhelminae* of Sumba, from which *hirundinaceum* was apparently derived, though the breast is redder, less orange. The bill is quite heavy as in *wilhelminae*. In this instance there is little doubt that Australia was

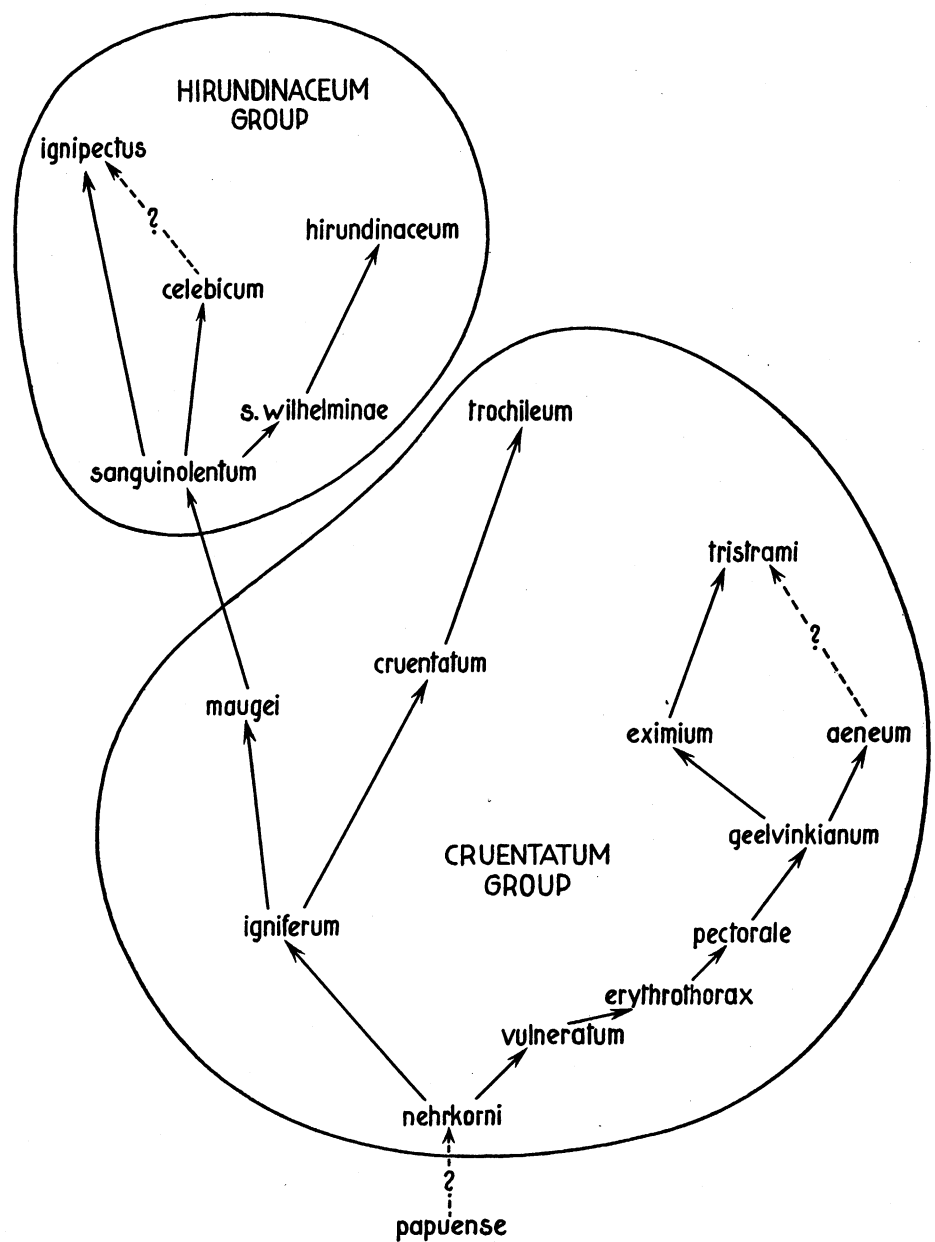


Fig. 8. Diagrammatic phylogeny of the *cruentatum* and *hirundinaceum* groups.

colonized from Sumba, not from Timor which is more usual (Mayr, 1944).

Dicaeum h. hirundinaceum is the common Mistletoe Bird of Australia, generally and commonly distributed, and, as would be expected, is mainly not a mountain bird. Mathews has described a number of Australian races now in need of scouting, of which perhaps *yorki* of northern Australia is valid.

32. *D. celebicum*. This is kept specifically distinct from *sanguinolentum* and *hirundinaceum* because the rump is not red in the female and the under tail coverts are never red. Although the back is dark purple in the Celebes race, some of the others on islands near Celebes are much bluer, almost like *monticola* of Borneo. As the latter form does not differ in any significant respect, we keep it in *celebicum*. Most of the races occur both in mountains and lowland, but *monticola* only in mountains.

Dicaeum celebicum is closely related to *sanguinolentum*. The distance between the races of the former occurring in the Lesser Sundas and *celebicum* is not great. *D. celebicum kühni* of the Tukang Besi Islands is very much like *D. sanguinolentum wilhelminae* in color (except for the red rump of the female in the latter), but the shape of the bill is more as in *D. s. rhodopygiae* of Flores. The females of most races of *celebicum* are glossier than in the allied species, while the males tend to be darker and suffused with black or gray ventrally.

The races of *celebicum* are: *kühni* (Tukang Besi Islands), *sulaense* (Sula Islands), *celebicum* (Celebes, Buton, Muna), *sanghirense* (Sangir Islands), *talautense* (Talaut Islands), and *monticola* (Mts. Kinabalu and Dulit, Borneo).

33. *D. ignipectus*. The races and distribution are as follows: *beccarii* (northern Sumatra); *cambodianum* (Cambodia, Indo-China); *dolichorhynchum* (peninsular Siam and Malaya); *ignipectus* (Indo-Chinese countries, southern China, Himalayas); *formosanum* (Formosa); *luzoniense* (Luzon); *bonga* (Samar); *apo* (Mt. Apo, Mindanao). In this species the upperparts are glossed with greenish blue, it

being the most distinct member of the superspecies in this respect. The rump is not red in the female. The derivation of this species is somewhat puzzling. The Philippine races bear a strong resemblance ventrally to *monticola*, but it seems rather unlikely that the species originated in the Philippines from *monticola* (Borneo) stock, then spread north through Formosa to China and back through southeastern Asia to Sumatra. On the other hand, the Sumatran and Malayan races resemble *D. sanguinolentum* ventrally. There is no trace of the red rump of females of *sanguinolentum* in any form of *ignipectus*, while the color of the back is also very different.

The Philippine and Formosan subspecies have an extensive red area on the breast and throat; in *ignipectus* and *dolichorhynchum* it is smaller and in *cambodianum* (not seen) and *beccarii* it has faded to cinnamon buff. Females are like those of *monticola* but even greener and lighter above. This species ranges as high as 12,000 feet in parts of Asia, but on Luzon ranges down almost to the lowlands.

SUMMARY OF *hirundinaceum* GROUP

This group of four closely related allopatric species probably was derived from the *cruentatum*' species group in the general region of the Lesser Sunda Islands, where *D. sanguinolentum* bears a strong resemblance to *D. maugei* of the *cruentatum* group. The *hirundinaceum* group is characterized by the absence of a red rump in the males and by a tendency to lose it in the females. This mark still exists in the females of *D. sanguinolentum*, it is either absent or present, but pale, in the various subspecies of *D. hirundinaceum* of Australia and the nearby islands, and is absent in the females of the other two species. *D. hirundinaceum* resulted from colonization of Australia by *sanguinolentum* stock from the Lesser Sundas, probably Sumba. *D. celebicum* of Celebes, Borneo, and adjoining islands also seems to have been derived from *sanguinolentum* of the Lesser Sundas. *D. ignipectus* is more distinct, but seems closest to *sanguinolentum*, though in some races it is similar to *D. celebicum monticola*.

Aside from the disappearance of the red rump, the other color variation within the superspecies does not exhibit any very pronounced trends, but several of the characters are useful in trying to determine the interrelationships of the species, as shown above. The bill varies considerably within the species *sanguinolentum*. In the eastern part of their ranges, the *cruentatum* and *hirundinaceum* groups replace each other (except in the Lesser Sundas). *D. hirundinaceum* has reached Australia but avoided the Moluccas and Papua where the other group is present. The two groups coexist in the larger western islands and on the mainland—the *hirundinaceum* group usually at higher altitudes. In Celebes this is reversed, and *nehrkorni* of the *cruentatum* group ranges at higher levels, while *celebicum* occurs both in the lowlands and mountains.

ABERRANT GENERA

The three remaining genera of the Dicaeidae are aberrant. They appear to be specialized offshoots of the family and seem properly assigned to it. In all three the tenth primary is vestigial and the bill is not serrated. Two of them, *Oreocharis* and *Paramythia*, are monotypic and restricted to New Guinea. They seem to be strictly fruit eaters which suggests that they are distantly related to the fruit-eating primitive New Guinea genera, *Melanocharis* and *Rhamphocharis*. The third genus, *Pardalotus*, of Australia and Tasmania, though insectivorous, appears distantly related to *Oreocharis*.

OREOCHARIS SALVADORI (ARFAKI)

DIAGNOSIS: Tenth primary vestigial. Bill much as in *Melanocharis* but not serrated. The male has the head and throat glossy black with bright yellow cheek patches; underparts bright yellow with a medial chestnut brown area; back olive green; flight feathers dark with yellow patches near the tips of the secondaries on the outer vanes; tail dark washed with blue. In the female the throat and cheeks are gray; the upperparts similar to the male but the crown also green; the underparts duller yellow than in the male, with-

out chestnut and with the feathers margined with black.

The tail is rather short and the general appearance like that of a titmouse (*Parus*) in which genus the species was first described. There are hair-like filoplumes on the napes and flanks, a character tending to ally it with the Dicaeidae, as similar feathers are found in some species of *Anaimos* and *Dicaeum*. Tarsus booted except basally.

PARAMYTHIA DE VIS (MONTIUM)

As in *Oreocharis* there is only one species. It is endemic to New Guinea. The systematic position of *Paramythia* had been uncertain until Mayr (1933) showed that it resembles *Oreocharis* in so many respects that there can be no doubt it is a specialized relative of that genus. Similarity between the two had been casually indicated by one or two earlier authors.

DIAGNOSIS: Similar to *Oreocharis* but much larger and with a full nuchal crest of pointed feathers; tail relatively longer. In both sexes, which are colored alike, the head is black as in *Oreocharis*, but the bases of the crown feathers are white (a character suggested in the crown feathers of *Oreocharis*). The dull bluish coloration of the tail of *Oreocharis* has extended in *Paramythia* until it occupies the upper back and most of the underparts except the black throat and a small area on the belly and under tail coverts which are yellow as in *Oreocharis*. The back is similar to *Oreocharis* but duller. In immatures of *Paramythia* the breast feathers are tipped with yellow, suggesting a previous more extensive distribution of that color. There are long filoplumes on nape and flanks. Tarsus booted except basally.

PARDALOTUS VIEILLOT (PUNCTATUS)

SYNONYMS: *Dipardalotus* Mathews (*rubricatus yorki*); *Nesopardalotus* Mathews (*quadragintus*); *Pardalotinus* Mathews (*striatus*). Mathews later synonymized these genera himself.

The genus *Pardalotus* is rather aberrant both structurally and in habits. It agrees with *Oreocharis* in lacking serrations on the bill and in the vestigial tenth primary.

Some of the species, such as *P. punctatus*, have terminal spots on the outer vanes of the secondaries, very suggestive of those of *Oreocharis*. In addition they have many other spots and streaks, producing a rather variegated pattern and suggesting the names *Pardalotus* and Diamond Bird. They are stumpy, short-tailed, and short-billed little birds and thus resemble to some extent their rather distant relatives, *Dicaeum*. The internal anatomy has apparently not yet been studied.

DIAGNOSIS: Bill not serrated; short, deep, with strongly arched culmen and sometimes slightly compressed (modified for burrowing). Tenth primary vestigial. Small, short-tailed, rather long-winged birds, similar to *Dicaeum* in proportions but averaging somewhat larger. Sandy-colored birds, often with bright yellow, especially on the throat and sometimes tiny yellow or red marks on the wing coverts; crown, wings, and tail usually black, much spotted and streaked with white; feet and claws stout. The tarsus appears booted in dried skins, but this may be deceptive.

THE SPECIES OF *Pardalotus*

The seven species of *Pardalotus* can be divided into two groups, the spotted-wing group (*punctatus* and *quadragintus*), and the striped-wing group (the other five species). Since the spotted-wing pattern is very similar to that of *Oreocharis arfaki* (New Guinea) it seems likely that this is the more primitive pattern. The two groups are quite similar, except for the

wing. The proportions are the same; there is a tendency for a light-colored rump and for white tail tips.

1. *Pardalotus punctatus*. Eastern, south, and southwest Australia, Tasmania. The arid country form *xanthopygius* appears to be a race of this species. Male and female are strikingly distinct in this species. The superciliary is indistinct.

2. *Pardalotus quadragintus*. Tasmania. Male and female are hen feathered and rather similar to the female of *punctatus*. This is probably another case of double invasion on Tasmania, with *quadragintus* the first, and *punctatus* the second colonization. The primitive color of this species appears to be a secondary simplification.

3. *Pardalotus rubricatus*. North and central Australia to New South Wales. This arid country species leads in some respects from the spotted to the striped pardalotes. The superciliary with the loreal spot (reddish in this species) is, however, typical for the striped pardalotes. There is no sexual dimorphism.

4. *Pardalotus striatus*

5. *Pardalotus ornatus*.

6. *Pardalotus substriatus*. The differences, the geographical distribution, and the reasons for the specific distinctness of these three species have been discussed recently by Hindwood and Mayr (1946).

7. *Pardalotus melanocephalus*. This more or less tropical species with the plain black crown is very close to the other three striped pardalotes, particularly to *substriatus*. It ranges from northwest Australia through northern Australia into northern New South Wales.

REFERENCES

- ALI, SALIM A.
1931. The role of sunbirds and flowerpeckers in the propagation and distribution of the tree-parasite, *Loranthus longiflorus* Desf., in the Konkan (W. India). Jour. Bombay Nat. Hist. Soc., vol. 35, pp. 114-149.
1936. The ornithology of Travancore and Cochin. Part 5. Jour. Bombay Nat. Hist. Soc., vol. 38, pp. 759-790.
- ALI, SALIM, AND HUMAYUN ABDULALI
1938. The birds of Bombay and Salsette. Part 4. Jour. Bombay Nat. Hist. Soc., vol. 40, pp. 148-173.
- BAKER, E. C. STUART
1934. The nidification of birds of the Indian Empire. London, Taylor and Francis, vol. 3, vii + 568 pp.
- CHANDLER, L. G.
1910. Notes on pardalotes. Emu, vol. 10, pp. 113-118.
1912. Notes on the mistletoe-bird (*Dicaeum hirundinaceum*). Ibid., vol. 12, pp. 130-133.
- CHASEN, F. N.
1939. In Robinson, H. C., and F. N. Chasen, The birds of the Malay Peninsula.

- London, H. F. and G. Witherby, Ltd., vol. 4, xiii + 485 pp.
1940. Notes on some Javan birds. *Treubia*, vol. 17, pp. 263-266.
- COOMANS DE RUITER, L.
1936. Het goed verborgen nest van den Geelromp Bastaard-Honingvogel (*Anaimos xanthopygius* [Salv.]). De Tropische Natuur: Jubileum-Uitgave, pp. 132-133.
- DEIGNAN, HERBERT G.
1943. Two preoccupied names of Oriental birds. *Proc. Biol. Soc. Washington*, vol. 56, p. 70.
1945. The birds of northern Thailand. *Bull. U. S. Natl. Mus.*, no. 186, v + 616 pp.
- DELACOUR, JEAN
1944. A revision of the family Nectariniidae (sunbirds). *Zoologica*, vol. 29, pp. 17-38.
1946. Notes on the taxonomy of the birds of Malaysia. *Ibid.*, vol. 31, pp. 1-8.
1947. Birds of Malaysia. New York, The Macmillan Co., xvi + 381 pp.
- DELACOUR, JEAN, AND ERNST MAYR
1946. Birds of the Philippines. New York, The Macmillan Co., xv + 309 pp.
- DESSELBERGER, HERMANN
1931. Der Verdauungskanal der Dicaetiden nach Gestalt und Funktion. *Jour. für Ornith.*, vol. 79, pp. 353-370.
- GADOW, HANS
- 1890-1899. In Wilson, Scott B., and A. H. Evans, *Aves Hawaiiensis: The birds of the Sandwich Islands*. London, A. H. Porter, xxv + 257 pp.
- GARDNER, LEON L.
1925. The adaptive modifications and the taxonomic value of the tongue in birds. *Proc. U. S. Natl. Mus.*, vol. 67, pp. 1-49.
- HACHISUKA, MASAUJI
1941. Description of a new species of bird from the Philippine Islands. *Bull. Biogeogr. Soc. Japan*, vol. 11, p. 1.
- HILL, G. F.
1911. Field notes on the birds of Kimberley, north-west Australia. *Emu*, vol. 10, pp. 258-290.
- HINDWOOD, K. A., AND ERNST MAYR
1946. A revision of the striped-crowned pardalotes. *Emu*, vol. 46, pp. 49-67.
- LAWRENCE, S. A., AND R. T. LITTLEJOHNS
1916. Nesting habits of the mistle-toe bird (*Dicaeum hirsutinaceum*). *Emu*, vol. 15, pp. 166-169.
- LUSHINGTON, CICELY
1940. Notes on the nesting of Legge's flower-pecker (*Acmonorhynchus vincens* [Slater]). *Jour. Bombay Nat. Hist. Soc.*, vol. 42, pp. 186-187.
- MCGREGOR, RICHARD C.
1914. Description of a new species of *Prionochilus* from the highlands of Luzon. *Philippine Jour. Sci.*, vol. 9, ser. D, p. 531.
1927. New or noteworthy Philippine birds. *Philippine Jour. Sci.*, vol. 32, pp. 513-525.
- MAYR, ERNST
1931. Die Vögel des Saruwaged- und Herzoggebirges (NO-Neuguinea). *Mitt. Zool. Mus. Berlin*, vol. 17, pp. 639-723.
1933. Zur systematischen Stellung von *Paramythia* De Vis. *Ornith. Monatsber.*, vol. 41, pp. 112-113.
1941. List of New Guinea birds. New York, American Museum of Natural History, xi + 260 pp.
1944. Timor and the colonization of Australia by birds. *Emu*, vol. 44, pp. 113-130.
1945. In Delacour, Jean, and Ernst Mayr, Notes on the taxonomy of the birds of the Philippines. *Zoologica*, vol. 30, pp. 105-117.
1946. A new name for a Philippine flower-pecker. *Ibid.*, vol. 31, p. 8.
- MEISE, WILHELM
1941. Ueber die Vogelwelt von Noesa Penida bei Bali. *Jour. für Ornith.*, vol. 89, pp. 345-376.
- OBERHOLSER, HARRY C.
1923. A review of the genus *Prionochilus* Strickland and its closest allies. *Ohio Jour. Sci.*, vol. 23, pp. 287-294.
- PORSCH, OTTO
1929. Kritische Quellenstudien über Blumenbesuch durch Vögel, 4. *Biologia Generalis*, vol. 5, pp. 157-210.
- RAND, A. L.
1937. In Mayr, Ernst, and A. L. Rand, Results of the Archbold expeditions. No. 14. Birds of the 1933-1934 Papuan expedition. *Bull. Amer. Mus. Nat. Hist.*, vol. 73, pp. 1-248.
1942. Results of the Archbold expeditions. No. 43. Birds of the 1938-1939 New Guinea expedition. *Ibid.*, vol. 79, pp. 425-516.
- RENSCH, BERNHARD
1931. Die Vogelwelt van Lombok, Sumbawa and Flores. *Mitt. Zool. Mus. Berlin*, vol. 17, pp. 451-637.
- ROBERTS, N. L.
1937. The red-tipped pardalote. *Emu*, vol. 37, p. 102.
- SCLATER, P. L.
1874. On the *Prionochili* of British India. *Ibis*, pp. 1-3, pl. 1.
- SHARPE, R. BOWDLER
1885. Catalogue of the birds in the British Museum. London, vol. 10, xiii + 682 pp.
- STEINBACHER, GEORG
1935. Ueber den Bau des Magens von

- Euphonia*. Ornith. Monatsb., vol. 43, pp. 41-45.
- WETMORE, ALEXANDER
1914. The development of the stomach in the euphonias. Auk, vol. 31, pp. 458-461.
- WHISTLER, HUGH
1934. The Vernay scientific survey of the Eastern Ghats. Part 8. Jour. Bombay Nat. Hist. Soc., vol. 37, pp. 281-297.