

EVOLUTION IN THE GENUS *MYZOMELA*
(AVES: MELIPHAGIDAE)

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IN recent years many genera of birds, particularly of Polynesia and the Malay Archipelago, have been analyzed in terms of geographical distribution, speciation, and intra-generic evolution. Much of this work is discussed by Mayr (1940, 1942). The importance of these investigations in terms of evolutionary mechanisms has been ably summarized by Mayr and Moynihan (1946: 1). "As has been demonstrated in many recent papers, the knowledge of the systematics of birds has reached such a degree of completion, that it can be used safely as a basis for studies on evolution. Island birds are particularly favorable material for such studies, because each water gap acts as a barrier reducing population movements and gene flow. Subspecies found on a series of neighboring islands often show character progressions which one might expect in a fossil series but hardly in contemporary geographical representatives. It appears in some of these cases as if each colonization of a new island was correlated with a certain amount of evolutionary change." On the same page a number of genera of birds are mentioned as containing some of the most interesting cases of incipient and recently completed speciation, one of these being *Myzomela*. I have selected the genus *Myzomela* for study largely because geographical variation in the form of conspicuous color patterns is readily detected in most species in the genus.

The genus *Myzomela*, as here discussed, consists of a number of small, mostly rather brightly colored, honeyeaters (Meliphagidae), ranging from Celebes, Sumba (Lesser Sundas), and northwestern Australia, to Samoa, and from the northern Marianas Islands to southeastern Australia. They occur on almost all islands within this area, but in Australia they are found only in the well-watered regions of the northern and eastern coasts. They almost certainly form a natural group, but further taxonomic work on the honeyeaters may show that other forms should be added to the genus. In this case, the forms here discussed should be considered a subgenus of the larger genus *Myzomela*. This larger genus might or might not contain, among others, the species *pectoralis* and *niger*, by many considered to belong to the genus.

An attempt will be made in this paper to trace the relationships within the genus, the pattern of distribution, and something of the pattern and mode of evolution in connection with certain definite

plumage color characters. Though it doubtless has had an important bearing on evolution within the genus, differential selection exercised by the ecology in various parts of the range will not be discussed. Plumage color was selected as a means toward elucidating these evolutionary problems, inasmuch as in most other respects the various forms are very similar. Body size is rather untrustworthy, often differing considerably among closely related forms, yet being very similar among distantly related ones. (The wing length in the genus ranges from 49 mm. in *adolphinae* to 79 mm. in *cardinalis rubrata*.) In this study I have paid particular attention to the distribution of red and black in the plumage and to the degree of sexual dimorphism, including secondary masculinization of the female plumage, as these characters could be most easily analyzed throughout the genus. No attempt has been made to pass on the validity of the various subspecies which have been described.

Adequate material of all forms was examined with the exception of the following races: *cruentata coccinea* (none), *obscura mortyana* (type only), *cardinalis tucopiae* (type only), *pulchella* (1 male), *erythrocephala dammermani* (1 male), *nigrita ramsayi* (1 male), *obscura rubrobrunnea* (1 male), *cardinalis kurodai* (2 males), *nigrita pluto* (3 males), *cruentata kleinschmidti* (2 immature males, 1 female), *obscura aruensis* (3 males, 1 sex?), and *blasii* (5 males, 1 immature). For the particular purposes of this study, a series of a given form containing at least 1 adult of each sex was considered adequate, since individual variation in this genus is usually slight as shown by large series (over 50), which were available for several forms.

GENERAL SURVEY OF THE GENUS

In order to facilitate the tracing of relationships among the species here treated, they are grouped into three sections, based mainly on the presumed primary presence or absence of sexual dimorphism, but also, to some extent, upon color patterns in both sexes. A check-list of the species and subspecies is given in the appendix and the probable phylogeny is indicated in Figure 1.

Section I.—This section is characterized by a presumed primary absence of sexual dimorphism, both sexes being predominantly gray or brownish, in some cases with a more or less diffuse reddish tinge. Really bright spots of color, if present, are restricted to red on the throat. The members of this section are all of fairly large size. The general gray coloration prevalent in this section suggests that it is the most primitive in the genus.

The four subspecies of the more or less primitive *obscura*, namely

harterti, *obscura*, *aruensis*, and *fumata*, resemble each other closely, being grayish-brown and lacking more than traces of red on the throat. *M. o. simplex* and *o. mortyana* are also similar, but show traces of red on other parts of the body. Finally, in *o. rubrotincta* and *o. rubrobrunnea*, there are distinct, though somewhat dull, red areas on the back, wings, and tail, and a less distinct reddish "wash" elsewhere. A red plumage is apparently here acquired by a diffuse reddening rather than by spread from well-defined centers.

M. albigula is closely related to *obscura*, but the plumage is somewhat lighter and streaked with gray-brown. Traces of red appear

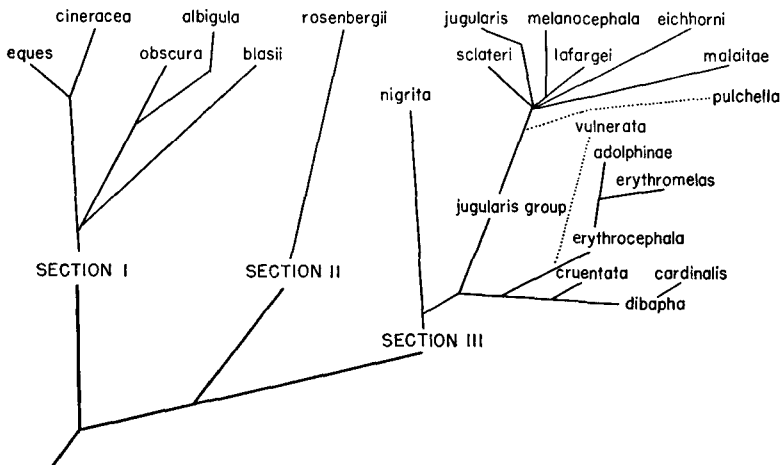


FIGURE 1. Phylogeny of the species in the genus *Myzomela*. Relationships indicated by dotted lines are extremely tentative.

on the throat, and in the case of the pale subspecies, *a. pallidior*, also on the forehead.

M. eques resembles *obscura* very closely except for having a bright red throat patch. Its three races are all very similar and have no red on the forehead.

M. cineracea is very similar to *eques*, but is grayer and has only slight traces of the red throat mark. This virtual absence of red may be secondary.

M. blasii resembles *a. pallidior* more than any other form, having faint traces of red on the throat and forehead. However, it also has a slight greenish-yellow wash over the body, and the throat and upper breast have a scaled pattern. It occupies a somewhat uncertain phylogenetic position.

It may be said that were it not that *eques* and *obscura fumata* live

side by side in southern New Guinea, all the forms of the *eques-obscura* group, which make up Section I, with the possible exception of *blasii*, would probably be considered conspecific. From the known characters, however, I am unable to group these five species even into two or more superspecies.

Evolutionary History of Section I.—The initial splitting-up of the *eques-obscura* group probably took place in the Pleistocene, before the last (Würm) glaciation. At this time, as Zeuner (1942) has pointed out, south-central New Guinea was an island, separate from the main New Guinea land mass. Zeuner believes that during at least some of the interglacial periods, even this southern island was submerged, but this probably was not the case for all of them, particularly not the last (Riss-Würm) interglacial, which represented a less complete retreat of the ice and therefore a less complete submergence than in the case of the second (Mindel-Riss) glaciation.

Somewhere within the general Moluccan-southern New Guinea area, Section I originated and the *eques-obscura* group became differentiated. The originally homogeneous stem form apparently became separated into three isolated subspecies, one on Seran (*blasii*), which never gave rise to any other form, one on the southern New Guinea island ("*obscura*") and one on northern New Guinea ("*eques*"). Somewhat later the northern and southern subspecies or incipient species each gave rise to another distinct form, the northern going to Umboi and New Britain (*cineracea*), the southern to the Louisiades (*albigula*). More recently, *obscura* has spread to the Moluccas, Biak, and Australia, where it has given rise to several more or less distinct subspecies. With the establishment of a land connection between northern and southern New Guinea, *eques* and *obscura* invaded each other's territory to some extent. Since, however, during the period of geographical separation, they had acquired reproductive isolation, they now live side by side as good species, though morphologically rather similar. *M. eques*, however, has a greater altitudinal range, probably owing to the more varied topography of the former north New Guinea island.

Section II.—This section contains only *r. rosenbergii* and *r. longirostris*, which differ only in the longer bill of the latter. Though sexual dimorphism has been developed in this species, the female plumage is quite different in appearance from that found in Section III, and hence *rosenbergii* is placed in a separate section. The head of the female is mottled black and brown; this is unique in the genus. The throat is black in both sexes, and neither sex has any red on the head, though red is present on the breast and rump in both, and on

the neck and back in the male. It may be noted that this is the first case to be mentioned here of melanization in *Myzomela*, as all parts not red in the male are black. The female plumage probably shows some secondary masculinization by darkening of the head, though this is difficult to determine in the absence of closely related forms.

The limited distribution of this species is probably to be explained by its extreme mountain habitat, widening the geographical barriers which must be crossed and severely limiting the number of nearby islands on which it could subsist. Though the range of the nominate race is considerably broken up by valleys separating the various mountain ranges, it shows no visible geographical variation.

Section III.—This section contains all the remaining forms of the genus and is distinguished from the other two sections by the female plumage. Except when secondarily masculinized, this is very characteristic. It is of a rather neutral olive-gray tone, with the back and belly somewhat yellowish, and shows traces of red on the forehead and throat. In both sexes, red, if present, is usually concentrated on the head, always being present there if it is present anywhere else.

The species of this section fall into four species groups, distinguished by basic differences in color pattern of the males. These are the *nigrita*, *cardinalis*, *cruentata* and *jugularis* groups, which will be discussed in turn.

M. NIGRITA group.—Though the plumage of unmasculinized females of *nigrita* is fairly typical of Section III, the group is in other respects rather different, and apparently more primitive than the other three groups of this section. The males of all but two forms are completely black and bright spots of color, if present, are restricted to red on the crown.

The only deviations from the all-black plumage of the typical male are in some of the island races. The male of *steini* is dark gray rather than black, thus resembling the typical female plumage considerably more than do the males of the other forms of *nigrita*. There are two possible explanations for this. *M. n. steini* may be the most primitive subspecies, in which sexual dimorphism, resulting from melanization, has not been completely developed. Actually both sexes of this race resemble *obscura* considerably except for their much smaller body size. An alternative explanation is that this is a case of secondary feminization of the male plumage (hen-feathering). It is impossible at the present juncture to choose between these alternatives.

The only other modification of the male plumage in this species is

found in *forbesi*. Here the male has a small red crown mark. Young males of *tristrami* have a yellow bill, unlike the black bill found in other subspecies.

The most interesting variation in this species entails the female plumage. In *steini*, *nigrita*, *pluto*, *forbesi*, *louisiadensis*, and the western populations of *meyeri*, it is quite typical of Section III. In *tristrami*, *pammelaena*, *ernstmayri*, *ramsayi*, and *hades*, all females are black like the males (cock-feathered), whereas in the eastern populations of *meyeri* both "normal" and black females occur side by side.

The distributional history of *nigrita* seems fairly simple and clear. (See Figure 2.) The species presumably originated on Waigeu or

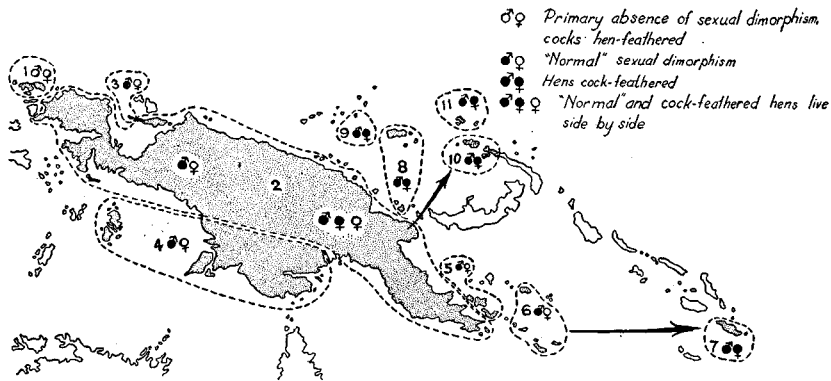


FIGURE 2. Geographical distribution of the subspecies of *Myzomela nigrita*, showing the presence or absence of sexual dimorphism: 1. *steini*, 2. *meyeri*, 3. *pluto*, 4. *nigrita*, 5. *forbesi*, 6. *louisiadensis*, 7. *tristrami*, 8. *pammelaena*, 9. *ernstmayri*, 10. *ramsayi*, 11. *hades*.

somewhere in New Guinea, and first spread over New Guinea, Japan, and Mios Num. From New Guinea it spread in two directions: east to the D'Entrecasteaux Islands, Louisiades, and San Cristobal, and north into the smaller islands of the Bismarck Archipelago. In spite of the great similarity in size and coloring between *tristrami* and the races in the Bismarck Archipelago, the absence of members of this group from all the Solomon Islands except San Cristobal makes it seem highly unlikely that there is any direct relationship between the forms of the two areas. They appear rather to represent independent offshoots from the New Guinea subspecies.

M. CARDINALIS group.—This may be considered the central group of the more specialized *Myzomelas* and has by far the greatest range and number of forms, all of which may be included in one superspecies. In this group, the entire head is almost always red in males, the

throat invariably so. The back, rump, and at least the upper part of the breast are also usually red. This wide distribution of intense red pigment is in sharp contrast with the condition met with in the groups hitherto considered. Melanization is quite frequent, but no general reddening of the plumage ever occurs. The *cardinalis* group may be divided into two subgroups according to whether or not the back is red.

In the *cardinalis* subgroup, the back is always red. The two included species differ in that in *cardinalis*, the male plumage is entirely red and black, whereas in *dibapha* the lower abdomen, at least, is whitish or yellowish and the wings may be brown. Another peculiarity of *dibapha* is that each belly feather has a light-colored bar running across it, though this is not clearly visible unless the feather as a whole is red. This character is absent in *cardinalis*. The extent of red on the ventral surface in males is quite variable in both species of this subgroup. It is almost restricted to the throat in *tucopiae*, but covers almost the entire abdomen in *elisabethae*, and there are many intermediate conditions. The distribution of red elsewhere on the body is much more uniform, covering, in all cases but one, the entire head, back, and rump. The sole exception is *chermesina*, in which the forehead, cheeks, and nape are black.

In the *erythrocephala* subgroup, the back is never red, but is black or brownish. Red is also always absent from the abdomen and lower breast, these parts being whitish. Though the absence of red on the back is an important character, this subgroup, particularly *erythrocephala*, resembles the *cardinalis* subgroup so closely in other ways, such as the pigmentation of the head, that it must be considered as representing the *cardinalis* group within its range, and as therefore belonging to the same superspecies.

M. erythrocephala, especially *e. kuehni*, resembles *dibapha* except for the important subgroup characters. *M. adolphinae* is also very similar except for its much smaller size (smallest of all *Myzomelas*), and for the red on the breast being even more restricted to the throat. In both these species the females have unmasculinized plumage. The males of *adolphinae* show little melanization, but the various races of *erythrocephala* show great variation in this respect, *kuehni* being lightest and *dammermani* darkest. *M. erythromelas* is somewhat similar to *adolphinae*, but melanization of the male plumage is very pronounced. Not only does black cover all parts not red, thus resembling *cardinalis*, but even the red area has been restricted to the head. The female plumage shows considerable masculinization.

M. vulmerata is a doubtful member of the *cardinalis* group. It re-

sembles *erythrocephala* somewhat but is darker than any of the races of *erythrocephala*. The female plumage is almost completely masculinized. Red is present on the nape in both sexes, but not on the forehead, cheeks, and back, these being black. In this way it resembles the *jugularis* group more than it does the *cardinalis* group.

Evolutionary history of the cardinalis group.—The *cardinalis* group, as here constituted, almost certainly originated somewhere in the Banda Sea area, since the most primitive members of both subgroups occur there. Here the initial splitting-up into subgroups took place, probably at a time when New Guinea was divided into northern and southern islands. The *erythrocephala* subgroup apparently reached the southern New Guinea island quite early. *M. adolphinae* was apparently at first only a north island subspecies of the south island *erythrocephala*. Taking advantage of the new upland habitat afforded, *adolphinae* became a mountain species. *M. erythromelas* apparently developed as a New Britain offshoot of *adolphinae*. Since the union of the north and south New Guinea islands, two races of *erythrocephala* (*erythrocephala* and *infuscata*) have invaded the general range of *adolphinae*, the two species living in close proximity, but retaining the extreme lowland habitats in which they evolved, these forms of *erythrocephala* have not really overlapped the range of the mountain form. Besides New Guinea, *erythrocephala* has also colonized Wetar (perhaps its center of distribution), Australia, and from the northwest coast of the latter continent, Sumba.

M. vulnerata of Timor poses a special problem. If its range were unknown, it would undoubtedly be put into the protean *jugularis* group, with which it agrees very well. However, between Timor, the habitat of *vulnerata*, and Karkar, the nearest island within the range of the *jugularis* group, lies the whole stretch of the Arafura Sea and New Guinea, uninhabited by any closely similar forms. It therefore appears more likely that *vulnerata* has evolved its *jugularis*-group-like characters independently from a form like *erythrocephala*. The extreme diversity in appearance among the various members of the *jugularis* group, the considerable masculinization of their females, together with the extreme masculinization of the female plumage in *vulnerata*, makes the problem more difficult of solution. Whether this form reached Timor from Wetar, New Guinea, Sumba, or Australia, is unknown.

The *cardinalis* subgroup, represented by its primitive species, *dibapha*, first spread in two directions. The first was north and west into the Moluccas and Celebes, giving rise to several well-marked races; the second, south and east, past territory perhaps only later occupied by the *erythrocephala* subgroup, to eastern Australia. From

Australia, *dibapha* invaded New Caledonia and also gave rise to *cardinalis*. *M. cardinalis* probably arose in the Loyalty Islands and spread through the New Hebrides to the Santa Cruz Islands. Samoa was also invaded, as were Rennell and San Cristobal. From San Cristobal, *cardinalis* reached Micronesia, spreading widely in the

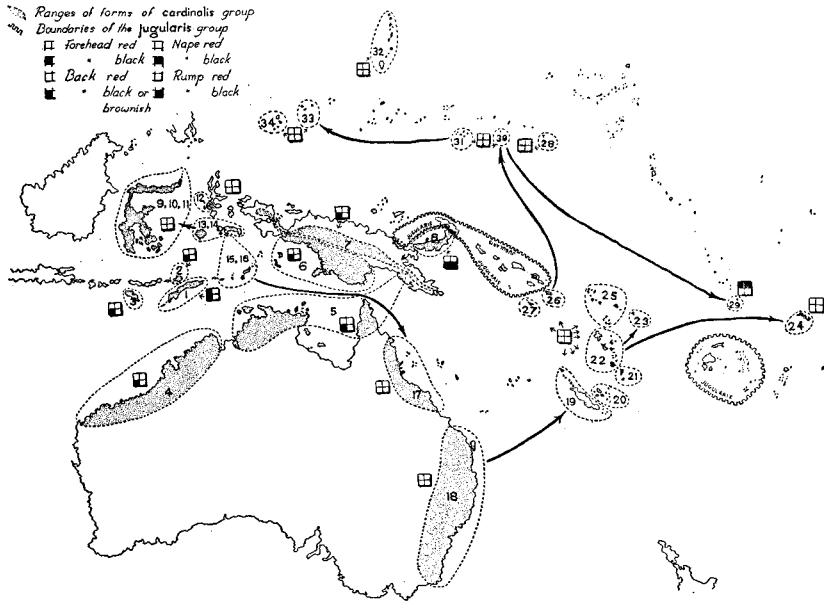


FIGURE 3. Geographical distribution of the species and subspecies of the *cardinalis* group in relation to the *jugularis* group, showing coloration of the forehead, nape, back, and rump: 1. *vulnerata*, 2. *erythrocephala kuehni*, 3. *e. dammermani*, 4. *e. derbyi*, 5. *e. erythrocephala*, 6. *e. infuscata*, 7. *adolphinae*, 8. *erythromelas*, 9. *dibapha eva* (Jampea, Selayar), 10. *d. juga* (South Celebes), 11. *d. chloroptera* (North Celebes), 12. *d. batjanensis*, 13. *d. wakaloensis* (Buru), 14. *d. elisabethae* (Seran), 15. *d. boiei* (Banda), 16. *d. annabellae* (Babber, Timorlaut), 17. *d. stephensi*, 18. *d. dibapha*, 19. *d. caledonica*, 20. *cardinalis lifuensis*, 21. *c. cardinalis* (southern New Hebrides), 22. *c. tenuis* (Efate, northern New Hebrides, Banks), 23. *c. tucopiae*, 24. *c. nigriventris*, 25. *c. sanctaerucis*, 26. *c. pulcherrima*, 27. *c. sanfordi*, 28. *c. rubrata*, 29. *cardinalis chermesina*, 30. *c. dichromata*, 31. *c. major*, 32. *c. saffordi*, 33. *c. kurodai*, 34. *c. kobayashi*.

Caroline and Marianas islands. There seems to be little doubt that *c. chermesina* reached Rotuma from the eastern Carolines, probably Ponape. The distribution of the members of the *cardinalis* group is shown on Figure 3.

M. CRUENTATA group.—Two groups occupy a somewhat uncertain position in relation to the *cardinalis* group but may be offshoots of it. Certainly they are more closely related to it than to *nigrita*.

The first is the *cruentata* group containing only the species *cruentata*.

It is distinguished from the other species of Section III by the fact that in males practically the entire plumage is red. In this character, *cruentata* is similar to the Moluccan-Biak races of *obscura*, these being the only other forms of *Myzomela* with red tails. In *obscura*, however, no well-defined patches of red were present, so that reddening was diffuse and never led to the entire plumage acquiring a bright color. In *cruentata*, on the other hand, bright red was probably already present on the belly, breast, rump, back, and entire head, as in a form such as *cardinalis elisabethae*, since the red in the New Guinea form of *cruentata* appears to be more intense in those areas. All that was then necessary for a completely bright red plumage to develop was an extension of red to the wings and tail.

In *c. cruentata* the red color is very bright but still seems concentrated on the belly, breast, back, and rump. As one goes through *kleinschmidti* and *coccinea* to *erythrina*, the red becomes duller and more diffuse, thus approaching the Moluccan-Biak races of *obscura* in appearance. The females of *c. cruentata* have a fairly typical feminine plumage of the Section III type, but this becomes considerably masculinized in the transition to *erythrina*.

M. cruentata apparently originated in western New Guinea as an offshoot of some Moluccan race of *cardinalis* such as *elisabethae*. It has spread all over the hill forest of New Guinea and Japen and up into the Bismarck Archipelago.

M. JUGULARIS group.—This group, all to be included in one super-species, is much more heterogeneous in appearance than any of the others. Hardly any positive characters distinguish the entire group, which can be recognized only by resemblances among the various forms belonging to it. None, however, have red backs, which are present in *cruentata* and in many of the members of the *cardinalis* group. With the exception of *pulchella*, tentatively placed here, none of the forms of this group has red on the forehead and cheeks. The female plumage always shows considerable masculinization.

M. eichhorni is a fairly typical member of the group. Red is confined to the throat and rump in males, the breast and belly being dirty yellow, the rest of the plumage olive to black. The three races differ chiefly in the general shade of color of the non-red areas, *e. eichhorni* being lightest and *e. atrata* darkest, melanization here progressing by a general darkening of the plumage, rather than by extension of black areas. The female plumage is considerably masculinized, this again being least in *e. eichhorni*, greatest in *e. atrata*. In some males of the latter race, traces of red appear on the nape. Whether red is here being lost or gained is difficult to say.

In *lafargei*, red is confined to the nape in males, the throat and dorsal parts being black, the breast and belly yellow. *M. melanocephala* is rather similar to it, but lacks red on the nape, whereas the yellow extends onto the back. Inasmuch as two such similar species as *obscura* and *eques* live side by side without interbreeding, it seems best to recognize *lafargei* and *melanocephala* as distinct species. The absence of red on the throat in these two species is certainly secondary. In both species the female plumage is considerably more masculinized than in *e. eichhorni*, less so in *lafargei* than in *melanocephala*.

Perhaps the most melanistic species of the group is *malaitae*. In its completely black and red coloration, it resembles *cardinalis* so much in general appearance, that it was originally described as a subspecies of *cardinalis*. However, though the abdomen, breast, throat, and rump are red, the forehead, nape, and back are black. Although red may be lacking from any of these parts in various members of the *cardinalis* group, red is never absent from all three, whereas this condition is common in the *jugularis* group. The female plumage is considerably masculinized, to about the same degree as in females of *cardinalis* from nearby islands.

In *jugularis*, as in *malaitae*, the throat and rump are red, but here the nape is also red, whereas the red on the breast and abdomen is replaced by bright yellow. The female plumage is almost completely masculinized, more so than in any other species of this group. This species also has the smallest body size of its group.

In *sclateri*, red appears on the throat and breast, the belly being yellow, the dorsal parts blackish. The female is partially masculinized.

M. pulchella is a very aberrant species. Red is confined to the forehead, cheeks, breast, and throat. It is a very doubtful member of the *jugularis* group, but resembles *sclateri* in general appearance more than any other form. It is the only member of the genus in which the forehead and cheeks, but not the nape, are red.

Evolutionary history of the jugularis group.—The original home of the *jugularis* group is uncertain, but was probably one of the islands to the northeast of New Guinea, perhaps in the Solomons. Unless *vulnerata* is a member of it, this group would appear to have remained always to the north and east of New Guinea. Whether any member of it ever inhabited the New Guinea mainland is unknown. Certainly its range seems small considering the number of very distinct forms which it contains. The group did manage, however, to spread over most of the Solomon Islands and even to the Fijis. It may be noted that although the *jugularis* group resembles the *cardinalis* group less,

perhaps, in basic color characters than does *cruentata*, it has, unlike the latter species, a completely allopatric distribution in relation to the *cardinalis* group. Indeed, all the diverse forms of the *jugularis* and *cardinalis* groups, different though many of them are from one another, replace each other as perfectly as subspecies of one species. *M. adolphinae* inhabits the mountains of New Guinea, *erythromelas* those of New Britain, but *pulchella* occupies only New Ireland, and *sclateri* only small islands off the coasts of New Guinea and New Britain. *M. cardinalis* occupies the New Hebrides, Samoa, the Santa Cruz Islands, Rennell, San Cristobal, and Rotuma; *malaitae* replaces it in Malaita, *melanocephala* on Guadalcanal, *jugularis* in the Fijis.

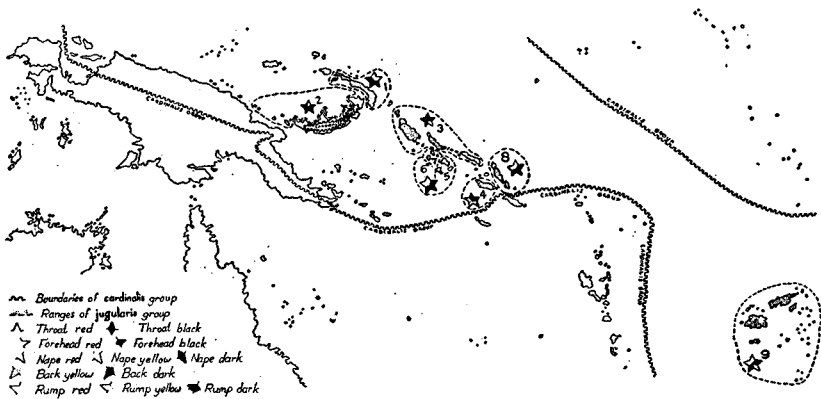


FIGURE 4. Geographical distribution of the species and subspecies of the *jugularis* group in relation to the *cardinalis* group, showing coloration of the throat, forehead, nape, back, and rump: 1. *pulchella*, 2. *sclateri*, 3. *lafargei*, 4. *melanocephala*, 5. *e. eichhorni*, 6. *e. ganongae*, 7. *e. atraia*, 8. *malaitae*, 9. *jugularis*.

Yet two such similar forms as *eques* and *obscura fumata* live side by side without any interbreeding. This interlocking of the ranges of the *cardinalis* and *jugularis* groups is shown in Figure 4.

As mentioned above, *malaitae* resembles *cardinalis* most closely in general appearance, but in its basic color characteristics it fits best into the *jugularis* group. These facts might be interpreted as showing relationships to both groups, a sort of link between the two. The origin of *cardinalis* is quite clear. It is rather obviously a specialized offshoot of *dibapha*. The origin of the *jugularis* group is, on the other hand, very obscure. It might then be postulated that the *jugularis* group arose from *cardinalis*, *malaitae* being an intermediate form, a race of *cardinalis* which had acquired most of the diagnostic characters of the *jugularis* group. It is very doubtful, however, that the very

diverse *jugularis* group is actually younger than *cardinalis* which, though having more geographical forms, is much less diverse. It is much more likely that the *jugularis* group is an older one, whereas *cardinalis* is a more recent invader into adjoining areas and has not had time to differentiate to any great extent. According to this view, *cardinalis* and *malaitae* developed their color resemblances independently by the extension of red and black pigmented areas over the entire plumage, perhaps in a parallel fashion. By chance, some of the more advanced races of *cardinalis* reached islands close to Malaita. In those races the female plumage happens to be at a stage of masculinization roughly comparable to that found in most forms of the *jugularis* group, particularly *malaitae*. In the general discussion an alternate explanation will be suggested.

GENERAL DISCUSSION

Following this survey of the characters and distribution of the various sections, groups, and species of *Myzomela*, certain conclusions may be drawn regarding the probable common ancestor of the various forms, as well as the general pattern of evolution in the genus. This will help to relate the facts concerning separate forms to the general evolutionary scheme.

Since, at present, New Guinea has the richest *Myzomela* fauna (7 species), it seems likely that it lies near the ancestral range. At least the initial stages in the splitting-up of the genus into sections and groups apparently occurred when New Guinea was divided into northern and southern islands, though just how long ago this began seems impossible to say. Such a situation in New Guinea would appear to offer ample opportunity for the early speciation, especially since the Moluccas and Timorlaut were probably involved, at least in a minor way.

By a comparison of the course of evolution in the various groups, it can be said that the ancestral *Myzomela* was probably of a nondescript gray, without any bright spots of color, without any extensive black areas, and without much sexual dimorphism. Such a state of affairs, relatively unchanged, is found in the Australian and New Guinea races of *obscura*, in *blasii*, *albigula*, *cineracea*, and *nigrita steini*. The typical female plumage of Section III is also not very different from this. It would seem to be the sort of pattern from which the various other plumage patterns could be most easily derived.

Dispersal.—It may now be asked, what evidence do the various living forms give concerning the modes of distribution and speciation prevalent in the genus? From the presence of *Myzomela* on such

clearly oceanic islands as Samoa and Rotuma, and in Micronesia, it is evident that no land bridges are necessary to explain the distribution. Indeed, one of the most striking things about the dispersal of *Myzomela* is the ability of these nectar-sucking birds to traverse wide expanses of open ocean to colonize isolated islands. Thus we have the invasions of San Cristobal from the Louisiades (*nigrita*), eastern Australia from Timorlaut (*dibapha*), and Samoa from the New Hebrides (*cardinalis*). The longest transoceanic invasions are of the Fiji Islands from Malaita by *jugularis* (1200 miles) and Rotuma from Ponape by *cardinalis* (2000 miles). It is not surprising, with such means of dispersal, that practically every ecologically suitable island within its general range has been colonized by one form or another. That successful colonization is often a random matter, however, is shown by the complete absence of *Myzomela* from such islands as the Trobriands, Kei Islands, Sula Islands, Halmahera, and most of the Lesser Sunda Islands.

Geographical speciation.—The question then arises as to whether speciation in *Myzomela* has occurred chiefly on continents or on groups of islands. This much can be said. Whenever two or more subspecies of one species occur on a continent or large island, like Australia or New Guinea, they are very similar, as, for example, the races of *eques*, the New Guinea races of *nigrita*, etc. Island races may also be very similar, as, for example, many of the races of *cardinalis*, the insular races of *nigrita*, etc. There are other cases, however, in which races or closely related species on different islands of a group are very different, such as the members of the *jugularis* group, *cardinalis chermesina* and the other races of *cardinalis*, the Moluccan-Biak races of *obscura* and its other races, etc. Hence it is highly probable that speciation has occurred mainly through isolation on islands.

Borderline cases.—If *Myzomela* is a genus in which active speciation is still proceeding, we would certainly expect to find some borderline cases, forms which, especially using ordinary taxonomic techniques, one finds difficult or impossible to decide to call distinct species or only subspecies of one another. Actually this is a common phenomenon in *Myzomela*, as might be gathered from the above accounts of the various forms. The forms within the following five groups apparently represent borderline cases (the forms in parentheses are ordinary subspecies of the others): 1. *albigula* (with *pallidior*), *obscura* (with *harterti*, *aruensis*, and *fumata*), *simplex* (with *mortyana*), *rubrobrunnea*, *rubrotincta*; 2. *eques* (with *nymani* and *primitiva*) and *cineracea* (with *rooki*); 3. *erythrocephala* (with *infusata*, *derbyi*, *dammermani*, and *kuehni*) and *adolphinae*; 4. *chermesina* and the other races of *cardinalis*;

5. *lafargei* and *melanocephala*. In some of these, the forms have been considered distinct species, in others, subspecies; but, to a large extent, the designation has been rather arbitrary. In all cases, I tried to compare the differences between the doubtful allopatric forms, with those present between sympatric species, particularly between the closely related *eques* and *obscura*, where the differences, aside from the presence or absence of the red throat mark, are very slight, since this was the only case of sympatric forms within the same group. The validity of these decisions, however, depends upon a parallel evolution of morphological differences and reproductive isolating mechanisms throughout the genus. There is no positive evidence either for or against this assumption, but of course no exact correlation would be expected.

Hybridization.—In a genus like *Myzomela* with such excellent facilities for dispersal, yet which is broken up into so many distinct forms, one might expect to find numerous hybrid populations. This is tied up with the problem of the possibility of hybridization in *Myzomela* between forms considered distinct species. However, such hybridization appears to be rather rare. There is only one place where it seems reasonably certain that hybridization between rather distinct forms occurs. That is between *nigrita tristrami* and *cardinalis pulcherrima* on San Cristobal, the only place where these two species occur together. The two forms are very similar in size, but strikingly different in color pattern. Here, however, the hybrids are rather rare (one probable and one doubtful hybrid as compared with 15 pure *cardinalis* and 42 pure *nigrita* from the zone of overlap), and the two species remain quite distinct (Mayr, 1932). There is no evidence concerning the fertility of these hybrids.

Two other cases, however, may be interpreted as stabilized hybrid populations between very distinct forms. These are *malaitae* on Malaita and *pulchella* on New Ireland. These two forms have several things in common. Both are here considered members of the *jugularis* group but have ranges which lie close to the boundary of the range of the *cardinalis* group, on islands which might be colonized by either group. Both occupy a rather uncertain position and are in certain respects intermediate between the two groups. This is particularly striking in the case of *malaitae*. Of these two populations, *malaitae* is no more variable than any other form of the *cardinalis* or *jugularis* groups; of *pulchella*, my material, consisting of a single male, is insufficient to make a decision one way or the other. If, however, these two forms do represent hybrid populations, it almost certainly would mean that introgressive hybridization can occur throughout

the *cardinalis* and *jugularis* groups. If this were shown to be the case, there would be, to my mind, no alternative but to combine all these exceedingly diverse forms into one species. Inasmuch as all the forms of the *cardinalis* and *jugularis* groups have strictly allopatric distributions, there is no real evidence against this. Some of the forms are, however, much more different from one another than are the sympatric *obscura* and *eques* and no less different than is *cruentata* from *adolphinae*, *erythromelas*, and *pulchella*, which occur within its range without interbreeding.

As has been mentioned above, there are several species such as *blasii*, *vulnerata*, *pulchella*, *malaitae*, and perhaps *jugularis*, whose position and relationships seem uncertain. Obviously a new line of attack is indicated. In this connection, Dr. Mayr informs me that each of the New Guinea species of *Myzomela* with which he is familiar has a distinctive song. Undoubtedly, in some of these, a comparison of the song of the doubtful form with those of possible relatives might help to clear up the relationship. I cannot help thinking, however, that in other cases of doubtful relationship, as well as where there is a question as to the specific distinctness of a form, only a genetic analysis of the forms involved, including tests to determine the presence and nature of reproductive isolating mechanisms will resolve these problems with certainty. Unfortunately, in such birds, this is apt to prove very difficult.

CHARACTER ANALYSIS

While the tracing out of the phylogeny and general evolutionary patterns are probably the most interesting results to be gained from a study of evolution in the genus *Myzomela*, much can also be gained from an elucidation of the character variation, that is, to see which characters vary and how. Two characters have been chosen for general analysis, the degree of sexual dimorphism, including secondary masculinization of the female plumage; and the degree of melanization of the male plumage. In addition, a special analysis is made of the geographical distribution of various male color characters in the *cardinalis* and *jugularis* groups.

Sexual Dimorphism.—In Section I, sexual dimorphism is absent, almost certainly primarily. It was apparently only developed in the evolution to Sections II and III, perhaps independently in each section. In *rosenbergii*, it is well-developed, but there is probably in addition some secondary masculinization of the females, though this is far from complete. It is impossible to say for sure, since *rosenbergii* has no close relatives. In Section III, a characteristic female plumage

type is always present except where secondarily masculinized. With one exception, the male plumage is always quite different from this. In *nigrita steini* of Waigeu, however, sexual dimorphism is poorly developed and the male has a plumage rather similar to that of *obscura* or the typical feminine plumage of Section III. Whether this condition is primary or secondary seems impossible to say. In all the other races of *nigrita*, the males are of a distinctive black. Females from the Louisiade and D'Entrecasteaux archipelagos, Woodlark, Japen, Mios Num, southern and western New Guinea, have a typical feminine plumage. Females from San Cristobal, Long, and the Bismarck Archipelago have a completely masculinized plumage. This is apparently dependent upon one gene difference, since in eastern New Guinea, both masculinized and unmasculinized females occur together, without any intermediates. Masculinization has here, then, developed by a single step, unlike its gradual evolution in other groups. (See Figure 2 for the geographical distribution of masculinization in *nigrita*.)

In the *cardinalis* group, the female plumage is unmasculinized except in *erythromelas*, *vulnerata*, and the northern races of *cardinalis*. In *erythromelas* it is only partially masculinized. In *cardinalis*, the female plumage of the races *lifuensis*, *cardinalis*, *tenuis*, *nigriventris*, and probably *tucopiae* is practically unmasculinized, that of *santaecrucis*, *sanfordi*, *pulcherrima*, *dichromata*, and *chermesina* shows varying degrees of intermediacy in that order, while in *rubrata*, *major*, *kurodai*, *kobayashi*, and *saffordi*, the female plumage is almost completely masculinized. Masculinization has apparently been initiated, therefore, three times, and gone to completion twice. From a geographical point of view, fully masculinized females are found on Timor, Kusaie, Truk, Yap, and the Marianas; intermediates on New Britain, Torres Islands, Santa Cruz Islands, Rennell, San Cristobal, Ponape, and Rotuma; unmasculinized females elsewhere. In the species *cardinalis* there is seen to be a cline, masculinization increasing from south to north.

In *cruentata*, the New Guinea females have only slightly masculinized plumage, but proceeding through New Britain to New Ireland, New Hanover, and the Tabar Islands, the female plumage becomes considerably more masculinized. In the *jugularis* group, the female plumage is always considerably masculinized but is virtually completely so only in *eichhorni atrata* of Vella Lavella and Bagga, and in *jugularis* from the Fiji Islands. Elsewhere it is incomplete in varying degrees. The two cases of complete masculinization were certainly acquired independently.

It is interesting to note that secondary loss of sexual dimorphism always occurs in peripheral insular areas rather than on large central land masses such as New Guinea or Australia. The reason for this is not clear but may be associated with the relative lack of predation on the smaller, more oceanic islands. Decrease in the selective value of sexual dimorphism for species recognition seems ruled out, since in the genus *Myzomela* loss of sexual dimorphism almost always involves masculinization of the inconspicuous female plumage rather than feminization of the distinctive and relatively conspicuous male plumage.

Melanization.—Like masculinization of the female plumage, melanization of the male plumage has occurred, in different degrees, a number of times independently in *Myzomela*, though usually not going to completion. Melanization may occur either by a general darkening of gray or brown plumage, or by extension of black areas, thus paralleling the two modes by which reddening is attained.

Melanization does not occur in Section I. In *rosenbergii* it is rather extensive but is confined to the anterior and posterior parts of the body, whereas the middle is red. In *nigrita* it is virtually complete except in *n. steini*, where it is poorly developed or reduced.

In the *cardinalis* group, melanization has been definitely initiated at least three times, being considerable in *erythrocephala dammermani*, *erythromelas*, and *cardinalis*, whereas several of the other races of *erythrocephala* and *dibapha* show earlier stages in the process. Melanization is also marked in *vulnerata*, but this form may have had a common origin with *erythrocephala dammermani*. In the case of *cardinalis*, melanization is clearly due to an extension of black areas, in *e. dammermani* to a general darkening, but in the other cases the mechanism is less clear. Melanized males are thus found in New Britain, Sumba, Timor, and Polynesia.

In the *jugularis* group, melanization is greatest in *malaitae*. The three races of *eichhorni* show an interesting evolutionary series, *e. eichhorni* being only slightly melanized, *e. ganongae* more so, and *e. atrata* considerably, the process being a gradual darkening. In none of the other forms is there much melanization.

M. cruentata shows no special melanization, reddening having occurred instead. Few of the members of Section III, however, are quite as unmelanized as are those of Section I.

Specific color characters.—Because specific color characters in males are so important in distinguishing the various species and super-specific aggregations within the genus, they will receive special treatment. Emphasis will be put upon distinct red patches on various

parts of the body, since these are by far the most important in indicating relationships. A detailed analysis will only be made in the *cardinalis* and *jugularis* groups, where they are widespread and have an interesting geographical distribution, but a few remarks will be made about their occurrence elsewhere.

In Section I, bright red patches are confined to the throat in *eques* and are absent in other forms. In *rosenbergii* (Section II) the entire middle part of the body is red, but the head and adjacent parts are black, this being in contrast to the usual "cephalization" of red found in Section III. In *nigrita* red is absent except in *n. forbesi*, which has a small crown patch. In *cruentata* the entire plumage is red, but, at least in *c. cruentata*, this is somewhat concentrated on the head, breast, belly, rump, and back.

In the *cardinalis* and *jugularis* groups, there are several specific areas where the presence or absence of red is of high taxonomic value, usually being constant among closely related forms. Some of these are, in addition, apparently centers of pigment dispersal. These areas will be treated in turn.

Throat.—This is always red except in the two closely related species, *lafargei* and *melanocephala*, in which it is black. The distribution of the red throat character is therefore the entire range of the two groups except for Buka, Bougainville, Fauro, Choiseul, Ysabel, Florida, and Guadalcanal, all in the Solomons. A red throat may act as a center for the spread of red pigment on the ventral side, in some cases reaching even the lower abdomen. The extent of this spread is, however, very erratic, often differing considerably among closely related subspecies, and is therefore not a very important taxonomic character. Red apparently cannot appear on the breast or belly unless it has been developed on the throat first.

Upper parts of the head.—These are divisible into two distinct regions, the forehead and the nape, which may vary together, as a genetic unit, or independently of one another. The cheeks are always of the same color as the forehead. Both forehead and nape are red in *erythromelas*, *adolphinae*, *erythrocephala*, *dibapha*, and all the races of *cardinalis* except *chermesina*. The geographical range is therefore New Britain, New Guinea, Moluccas, Celebes, Wetar, Timorlaut, Babar, Sumba, Aru Islands, northern and eastern Australia, southern Melanesia, Samoa, San Cristobal, Rennell, and the Carolines and Marianas islands. A red nape only is found in *vulnerata*, *lafargei*, and *jugularis*, whereas some individual males of *eichhorni atrata* have traces of it. This probably represents at least three independent occurrences. Its range is therefore Timor, Buka, Bougainville,

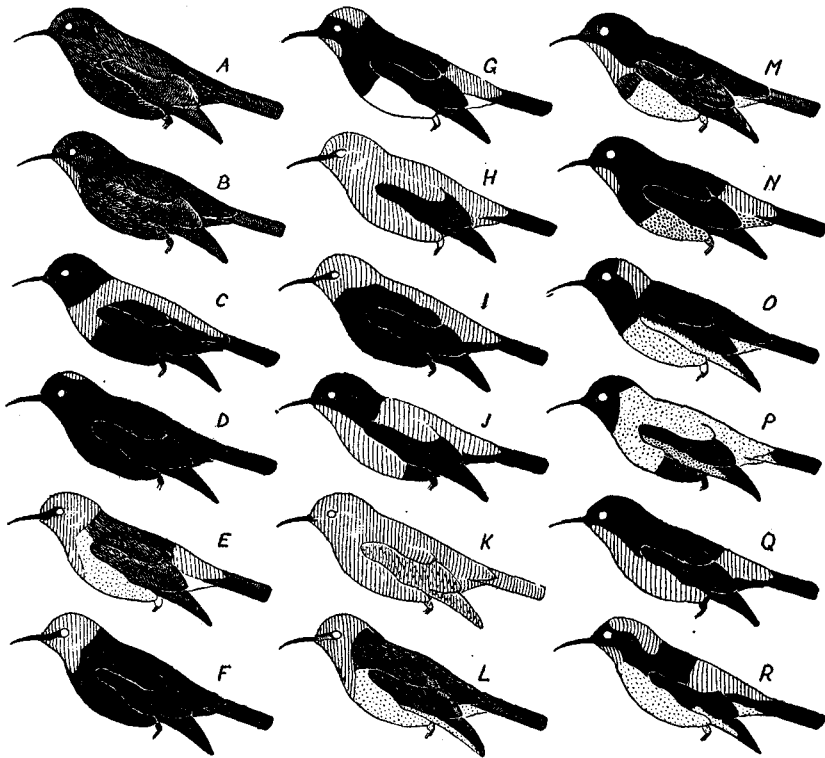


FIGURE 5. Color patterns in *Myzomela* (black, solid; white, blank; red, vertical lines; yellow, stippled; gray or brown, closely hatched); A. *obscura fumata*, B. *eques*, C. *rosenbergii*, D. *nigrita forbesi*, E. *erythrocephala*, F. *erythromelas*, G. *vulnerata*, H. *dibapha wakaloensis*, I. *cardinalis lifuensis*, K. *c. cruentata*, L. *pulchella*, M. *sclateri*, N. *eichhorni atrata*, O. *lafargei*, P. *melanocephala*, Q. *malaitae*, R. *jugularis*.

Choiseul, Fauro, Ysabel, Fijis, and to a slight extent on Vella Lavella and Bagga. A red forehead only is found in *pulchella* of New Ireland. Red is absent from both forehead and nape in *sclateri*, *melanocephala*, *malaitae*, *cardinalis chermesina*, and most individuals of *eichhorni*. In *chermesina* this is certainly secondary, in the others possibly primary. Its range is therefore Karkar, Long, Rook, small islands off the west coast of New Britain, Vella Lavella, Bagga, Ganonga, Kulambangra, Gizo, New Georgia, Vanganu, Rendova, Tetipari, Florida, Guadalcanal, Malaita, and Rotuma.

Rump.—The rump is another center of red pigment dispersal. For red to appear on the back, it must first appear on the rump. A red rump appears in all the forms under consideration except *erythromelas*, *sclateri*, *pulchella*, *melanocephala*, and *lafargei*. In

erythromelas it is certainly secondary, in the others probably primary. Its distribution is therefore the entire range except Karkar, Long, Rook, New Britain and neighboring islets, New Ireland, Buka, Bougainville, Fauro, Choiseul, Ysabel, Florida, and Guadalcanal.

Back.—Unlike the situation in regard to the breast and belly, extension of red from the rump onto the back apparently occurs by a single step. If the back is red at all, it is all red. The distribution

TABLE 1
CHARACTER ANALYSIS OF THE *cardinalis* AND *jugularis* GROUPS

<i>Presence or absence of red on various body parts in males</i>					
<i>Species or subspecies</i>	<i>throat</i>	<i>forehead</i>	<i>nape</i>	<i>back</i>	<i>rump</i>
<i>cardinalis</i> group					
<i>cardinalis</i> subgroup					
<i>cardinalis chermesina</i>	+	—	—	+	+
<i>cardinalis</i> (other races)	+	+	+	+	+
<i>dibapha</i>	+	+	+	+	+
<i>erythrocephala</i> subgroup					
<i>erythrocephala</i>	+	+	+	—	+
<i>adolphiinae</i>	+	+	+	—	+
<i>erythromelas</i>	+	+	+	—	—
<i>vulnerata</i>	+	—	—	—	—
<i>jugularis</i> group					
<i>pulchella</i>	+	+	—	—	—
<i>sclateri</i>	+	—	—	—	—
<i>lafargei</i>	—	—	+	—	—
<i>melanocephala</i>	—	—	—	—	—
<i>eichhorni</i>	+	—	—*	—	—
<i>malaitae</i>	+	—	—	—	+
<i>jugularis</i>	+	—	+	—	+

* Some individual males of *e. atrata* have traces of red on the nape.

of red backs, also unlike that of red breasts and bellies, is very constant and not at all erratic, being restricted to, and highly characteristic of, *dibapha* and *cardinalis*. It is, therefore, an important taxonomic character, its distribution being Celebes, the Moluccas, Babar, Timor-laut, eastern Australia, southern Melanesia, Samoa, Rotuma, San Cristobal, Rennell, and the Carolines and Marianas islands.

For a summary of the distribution of red in the *cardinalis* and *jugularis* groups, see Table 1; see also Figures 3, 4, and 5.

I am greatly indebted to Dr. Ernst Mayr for making available to me the material in the Whitney Rothschild Collections of the American

Museum of Natural History, as well as for many helpful suggestions during the study of the material and the preparation of the manuscript.

SUMMARY

The genus *Myzomela*, sensu stricto, may be divided into three sections, based upon female plumage and, to a certain extent, on color patterns in males.

Six species groups are recognized, only one of which includes more than one superspecies. These are based on color pattern in males.

Twenty-one species are tentatively recognized, many of which undoubtedly lie only on the border of specific distinctness.

New Guinea and the nearby islands have been the center of distribution for the genus, though some groups have spread far from the center. The number of species in a given area falls off rapidly, however, as one proceeds away from New Guinea in any direction.

In the ancestral *Myzomela*, both male and female were almost certainly of a similar dull coloration, but in most groups, by acquisition of striking color patterns by the males, a striking sexual difference has developed. Furthermore, the female plumage has been repeatedly masculinized, none of the sexually dimorphic superspecies being wholly free of the effects of this change. This masculinization may be gradual or may arise by one step.

Myzomela is essentially an island genus, being able to colonize new regions across wide stretches of open ocean. The sea has also usually been the primary isolating mechanism, permitting divergence of the isolated populations.

Color patterns in males, particularly the distribution of bright red areas, are of considerable taxonomic importance, especially in the more advanced groups. Two areas, the throat and the rump, may act as centers dispersal of red pigment to other body areas, from the throat to the breast and belly, and from the rump to the back. A completely red or black plumage may arise either by extension of the heavily pigmented areas, or by a general increase in pigmentation.

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APPENDIX
CHECKLIST OF THE SPECIES AND SUBSPECIES OF
MYZOMELA (SENSU STRICTO)

SECTION I

M. eques-obscura group

- M. blasii* Salvadori (Moluccas: Seran)
- M. albigula albigula* Hartert (Louisiades: Rossel)
- M. albigula pallidior* Hartert (west-central Louisiades)
- M. obscura harterti* Matthews (Australia: Cape York peninsula)
- M. obscura obscura* Gould (Australia: Northern Territory)
- M. obscura aruensis* Kinnear (Aru Islands)
- M. obscura fumata* Mueller (southern New Guinea, Misol)
- M. obscura simplex* Gray (Moluccas: Batjan)
- M. obscura rubrotincta* Salvadori (Moluccas: Obi)
- M. obscura mortyana* Hartert (Moluccas: Morotai)
- M. obscura rubrobrunnea* Meyer (Geelvink Bay: Biak)
- M. eques eques* Lesson (Waigeu, Salawati, Misol, New Guinea: Vogelkop, Onin Peninsula)
- M. eques nymani* Rothschild and Hartert (southern and eastern New Guinea)
- M. eques primitiva* Stresemann and Paludan (north-central New Guinea)
- M. cineracea rooki* Hartert (Bismarcks: Rook)
- M. cineracea cineracea* Sclater (New Britain)

SECTION II

M. rosenbergii group

- M. rosenbergii rosenbergii* Schlegel (High mountains of New Guinea)
- M. rosenbergii longirostris* Mayr and Rand (D'Entrecasteaux Islands: Good-enough)

SECTION III

M. nigrita group

- M. nigrita steini* Stresemann and Paludan (Waigeu)
- M. nigrita meyeri* Salvadori (Japan, New Guinea except south-central portion)
- M. nigrita pluto* Salvadori (Geelvink Bay: Mios Num)
- M. nigrita nigrita* Gray (south-central New Guinea)
- M. nigrita forbesi* Ramsay (D'Entrecasteaux Islands: Normanby, Goodenough, Dobu)
- M. nigrita louisiadensis* Hartert (Woodlark, Louisiades)
- M. nigrita tristrami* Ramsay (Solomons: San Cristobal, Ugi, Santa Anna)
- M. nigrita pammelaena* Sclater (Bismarcks: Long, Admiralty Islands)
- M. nigrita ernstmayri* Meise (Bismarcks: Ninigo Islands)
- M. nigrita ramsayi* Finsch (Bismarcks: New Hanover, northern New Ireland)
- M. nigrita hades* Meise (Bismarcks: St. Matthias)

M. cardinalis group

M. erythrocephala subgroup

- M. vulnerata* Mueller (Lesser Sundas: Timor)
- M. erythrocephala kuehni* Hartert (Lesser Sundas: Wetar)
- M. erythrocephala dammermani* Siebers (Lesser Sundas: Sumba)
- M. erythrocephala derbyi* Matthews (coast of northwestern Australia)
- M. erythrocephala erythrocephala* Gould (Australia: coast of the Northern Territory, Cape York; New Guinea: region of Hall Sound)

- M. erythrocephala infuscata* Forbes (coast of southern New Guinea)
M. adolphinae Salvadori (mountains of New Guinea)
M. erythromelas Salvadori (New Britain)

M. cardinalis subgroup

- M. dibapha eva* Meise (islands south of Celebes: Jampea, Selayar)
M. dibapha juga Riley (south Celebes)
M. dibapha chloroptera Walden (north Celebes)
M. dibapha batjanensis Hartert (Moluccas: Batjan)
M. dibapha wakoloensis Forbes (Moluccas: Buru)
M. dibapha elisabethae van Oort (Moluccas: Seran)
M. dibapha boiei Mueller (Moluccas: Banda)
M. dibapha annabellae Selater (Timorlaut, Babber Islands)
M. dibapha stephensi Matthews (north-central Queensland)
M. dibapha dibapha Latham (New South Wales, southern Queensland)
M. dibapha caledonica Forbes (New Caledonia)
M. cardinalis lifuensis Layard (Loyalty Islands)
M. cardinalis cardinalis Gmelin (southern New Hebrides)
M. cardinalis tenuis Mayr (Efate and northern New Hebrides, Banks Islands)
M. cardinalis tucopiae Mayr (New Hebrides: Tucopia)
M. cardinalis nigriventris Peale (Samoa)
M. cardinalis sanctaecrucis Sarasin (Santa Cruz and Torres Islands)
M. cardinalis sanfordi Mayr (Solomons: Rennell)
M. cardinalis pulcherrima Ramsay (Solomons: San Cristobal, Ugi)
M. cardinalis chermesina Gray (Rotuma)
M. cardinalis rubrata Lesson (Carolines: Kusiae)
M. cardinalis dichromata Wetmore (Carolines: Ponape)
M. cardinalis major Bonaparte (Carolines: Truk)
M. cardinalis kurodai Momiyama (Carolines: Yap)
M. cardinalis kobayashi Momiyama (Palau)
M. cardinalis saffordi Wetmore (Marianas)

M. cruentata group

- M. cruentata cruentata* Meyer (New Guinea, Japen)
M. cruentata kleinschmidti Sharpe (Bismarcks: New Britain)
M. cruentata coccinea Ramsay (Bismarcks: Duke of York)
M. cruentata erythrina Ramsay (Bismarcks: New Ireland, New Hanover, Tabar Islands)

M. jugularis group

- M. sclateri* Forbes (Bismarcks: Karkar, Long, Rook, small islands off the west coast of New Britain)
M. pulchella Salvadori (Bismarcks: New Ireland)
M. lafargei Pucheran (Solomons: Buka, Bougainville, Fauro, Choiseul, Ysabel)
M. melanocephala Ramsay (Solomons: Guadalcanal, Florida)
M. eichhorni eichhorni Rothschild and Hartert (Central Solomons: Gizo, Kulambangra, New Georgia, Vangunu, Rendova, Tetipari)
M. eichhorni ganongae Mayr (Central Solomons: Ganonga)
M. eichhorni atrata Hartert (Central Solomons: Vella Lavella, Bagga)
M. malaitae Mayr (Solomons: Malaita)
M. jugularis Peale (Fijis)

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