

A GENERIC REVISION OF FLY-  
CATCHERS OF THE TRIBE  
MUSCICAPINI

CHARLES VAURIE

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## INTRODUCTION

THE PRESENT STUDY was undertaken at the suggestion of Dr. Ernst Mayr who felt that a generic revision of the subfamily Muscipinae was needed. On account of the very large size of this group, it was decided, however, to limit the study to the tribe Muscipini (for the division of the Muscipidae, see Mayr and Amadon, 1951). Of the other tribes of this subfamily, the Monarchini and the Rhipidurini are well defined, but in the present study it was found impossible to draw a line between the Muscipini and the Pachycephalini. As a result, all the species of these two tribes were examined, and my original intention was to revise both as a unit. Owing to the pressure of other work, however, I had to stop the actual writing part way. This paper is limited, then, to *Muscicapa* and related genera, which constitute the most controversial group of the Muscipinae, and includes also all the other Muscipini from the Ethiopian region and Madagascar. About one-third of the 378 species computed for the subfamily by Mayr and Amadon are included.

### ACKNOWLEDGMENTS

I would like to express my appreciation to a number of persons and institutions for the help that I have received. First of all to my friends and colleagues at the American Museum: Dr. Mayr and Mr. Jean Delacour, who have had much experience with the flycatchers, have given me many very helpful and friendly suggestions, but I am responsible for the present arrangement and the conclusions reached. Dr. Mayr has also very kindly read and criticized the manuscript. Dr. James P. Chapin has most obligingly discussed with me the Ethiopian species and has made available a copy of his manuscript on the birds of the Belgian Congo. Dr. Dean Amadon and Dr. J. T. Zimmer have helped in other ways, Dr. Zimmer with the synonymies and Dr. Amadon with the ratio diagrams and other suggestions.

I have drawn freely upon the following institutions: the Academy of Natural Sciences of Philadelphia, the Chicago Natural History Museum, the Museum of Comparative Zoölogy, and the United States National

Museum. I acknowledge with pleasure my debt to Mr. R. M. de Schauensee, Dr. A. L. Rand, the late Mr. J. L. Peters and Mr. J. C. Greenway, and to Dr. H. Friedmann and Mr. H. G. Deignan for their gracious cooperation in lending me material under their care.

### METHOD

This study is based on the material in the collection of the American Museum of Natural History supplemented by the loan of specimens from the other institutions mentioned above. All specimens were compared for coloration, pattern, and texture of the plumage. When suitable specimens were available, the post natal and juvenal plumage were examined. In the case of the wing formula and of the structural characters that can be measured, a number of specimens in good plumage were selected, consisting, if possible, of 10 fully adult males from the same population or, failing this, from the same subspecies in the case of polytypic species. Unfortunately, such an ideal selection is impossible in many instances, and the desired series of 10 measurements was rounded out by adult females or unsexed adults, but subspecies that differ appreciably in size were not mixed. Further, it is obvious, of course, that the rarer species may be represented by only a very few specimens and that in a number of cases the young are not known. Because the measurements given are only the mean of the specimens measured and are to be used only for comparison of general structure, I have thought it desirable to give a list of the species in which fewer than 10 specimens were examined. This list (see Appendix) shows how many specimens of the rarer species are present in the leading American collections, the location of these specimens, and if a young is available. Only one species was not examined, this species (*Newtonia fanovanae*) being known only from a unique specimen in the Stockholm museum.

In the text the treatment of the genera usually follows this order: synonymy, general distribution, characters of the genus, including habits, presumed relationships,

and a list of the species. In these lists it is not always possible to arrange the species in one continuous linear sequence, but the species of each branch are placed, as nearly as possible, in what appears to be their correct systematic order. In these lists are

included, occasionally, some short systematic remarks which deal directly with the species concerned and would be out of place in the discussion of the genus.

The nomenclatural aspects of this study are listed separately (see Appendix).

## CHARACTER VARIATION AND ITS ANALYSIS

### GENERIC CHARACTERS

THE MORPHOLOGICAL CHARACTERS that have been used for the generic separation of the Muscicapini, in the order most frequently used, are: shape of bill, pattern of plumage and its pigmentation, shape of wing (i.e., the relative lengths of the first, second, longest, and tenth primaries, with or without a statement of the wing formula), general body size, and relative lengths (proportions) of various parts, such as the wing, tarsus, and tail. Other characters occasionally mentioned are: development of the rectal bristles and of the frontal feathers at the base of the culmen, shape of tail, scutellation and relative thickness of the tarsus and strength or weakness of the claws, texture of the plumage, and sexual dimorphism in coloration. The spotting or lack of spotting of the young should be mentioned, although this character is used not so much for generic separation as for a "family" character.

All the characters are analyzed below. Although the extent to which they seem to be valid for generic separation is evaluated in a concluding section it may be stated here that they are of unequal value and that most of the structural characters are of doubtful phylogenetic significance. Since similarity of function usually results in similarity of structure, general habits must be discussed with the variations in structure.

### MEASUREMENTS

Nine direct measurements were taken of each specimen: the length of the longest primary (wing length), the length of the first,<sup>1</sup> second, and tenth primaries, the length of the primary coverts (expressed as the excess of the first primary over the primary coverts), the length of the tail and tarsus, and the length and width of the bill. All measurements were taken to the nearest millimeter except in the case of the length of the tarsus and bill which were taken to the nearest half millimeter. The bill was measured from its insertion in the skull. The width of the

bill was measured not at the gape but at the level of the middle point of the nostrils. This results in a smaller but more accurate measurement. It was found possible in many specimens to estimate a measurement smaller than a half millimeter, that is, two-tenths and eight-tenths of a millimeter. In the case of species with narrow bills such fractional measurements modify slightly the mean.

Since, as stated, only mean measurements are given and some of the series are mixed as to sex and locality, the measurements are to be used only for a comparison of general structure. From the mean measurements the ratio diagrams of proportions were constructed in the manner explained by Amadon (1950).

### BODY SIZE

The species studied vary a good deal in general body size. Some are small and slender, while others are large and heavily built. The over-all range in size as expressed by wing length varies from 49 to 112 mm. Generally speaking, the species most arboreal in their habits are small and slender, the species that come to the ground to feed are large and heavily built, and those that live in the undergrowth or range part way up into the trees are intermediate. Although probably adaptive these variations seem to be of taxonomic and phylogenetic importance, but their significance is often obscured by many contradictions.

Unrelated species or species groups with different habits may be similar in body size and build, while very closely related species may vary abruptly. For instance, the species of the genus *Ficedula* are small and slender, although many of them live in thickets or close to the ground; *Fraseria ocreata*, *Niltava hoëvelli*, and *N. sanfordi*, which are species of the tall tree tops that do not come near the ground, are very large and exceptionally heavily built, with thick shrike-like heads; *Niltava concreta*, another species of the tree tops, is also very large and heavy. *Niltava grandis*, which is very closely related to *N. macgrigoriae*, is almost twice as large. Other instances could be cited.

It is often stated that size and wing length

<sup>1</sup> Throughout this paper the primaries are counted in the European manner, that is, starting from the outermost, which is called the first.

are closely correlated, but that this may not always be so is shown by some of the species studied. In these species the length of the wing is definitely correlated with certain factors such as migration or highly arboreal habits rather than to general size. For instance, in the genus *Muscicapa* (see table 6) the species that are very arboreal and almost swallow-like in their habits (*infusata* = *fuliginosa* auct.<sup>1</sup> and *ussheri*) and some of the species that breed far north and have a long migration such as *striata*, *sibirica*, and the northern populations of *griseisticta*, have a long wing, the wing length of the five species ranging from about 82 to 87 mm., but these species are clearly not "bigger" than some of the non-migratory or less arboreal species such as *aquatica*, *olivascens*, or *cassini* in which the wing length ranges from 67 to 74. It is also not clear why in migratory species, which appear to be the same in size, some should have a short wing while others have a long one. In *latirostris* and *sibirica*, which have identical habits, breed at the same latitudes, and have the same migration, the wing lengths are 72 (*latirostris*) and 83 (*sibirica*).

Weight or body length, possibly a combination of both, would be a better indication of size. Weight, unfortunately, is available for only a few isolated specimens of some species, and it may vary at different points of the life cycle, as when fat accumulates for migration. Dr. Chapin has suggested that a fair index to body length can be determined in well-made skins by measuring the distance from the wrist to the circlet of feathers at the cloacae.

#### SHAPE OF THE WING

The shape of the wing can be expressed in terms of the wing formula and the distance between certain key feathers, such as between the second or longest primary and the tenth.

The shape of the wing seems to be of taxonomic and phylogenetic importance, but as in the case of body size its significance is obscure for, although it remains remarkably constant in certain genera and groups of species despite changes in habits and manner

of feeding, it is very variable and purely adaptive in others. Thus in *Muscicapa* and *Ficedula* the migratory species have a pointed wing and the non-migratory species a rounded one. In *Muscicapa* the non-migratory but swallow-like *infusata* and *ussheri* have a pointed wing, and in both *Muscicapa* and *Ficedula* the closer the species lives to the ground the rounder the wing becomes. In the 21 species of *Muscicapa* proper no more than two species, whether migratory or not, have an identical wing formula, and the range in variation between pointed and rounded wing is extreme.

In *Niltava* and *Rhinomyias* the shape of the wing remains essentially the same, and the basic formula is constant whether the species be arboreal or not. In the migratory populations of some species of *Niltava* the basic formula is the same as in the non-migratory populations. In *Fraseria* which is arboreal and in *Bradornis* and *Melaenornis* which come to the ground to feed, the shape of the wing and its formula are basically the same. It is of interest to note also that variations in body size and shape of wing are not correlated. In *Muscicapa* and *Ficedula*, where the shape of the wing varies, all the species are small and relatively slender; in *Niltava*, *Rhinomyias*, *Bradornis*, or *Fraseria*, where body size varies, the shape of the wing and its formula remain the same. In *Niltava grandis* and *N. macgrigoriae* the shape and formula of the wing are virtually the same, although the body size of the former is almost twice as large as that of the latter.

#### MODIFICATION OF THE PRIMARIES

It is interesting to test whether the pointed or rounded shape of the wing is caused by a differential rate in the development of the individual feathers, that is, whether or not the pointed shape of the wing is caused by a lengthening of the second and longest primaries, accompanied by a decrease in length of the first and tenth primaries, and whether or not the rounded shape is due to a shortening of the second and longest primaries, with an elongation of the first and tenth. Figure 1 suggests that such is the case.

For the purpose of this figure, the 21 species of *Muscicapa* proper were selected, for, as

<sup>1</sup> For the name of this species, see Appendix.

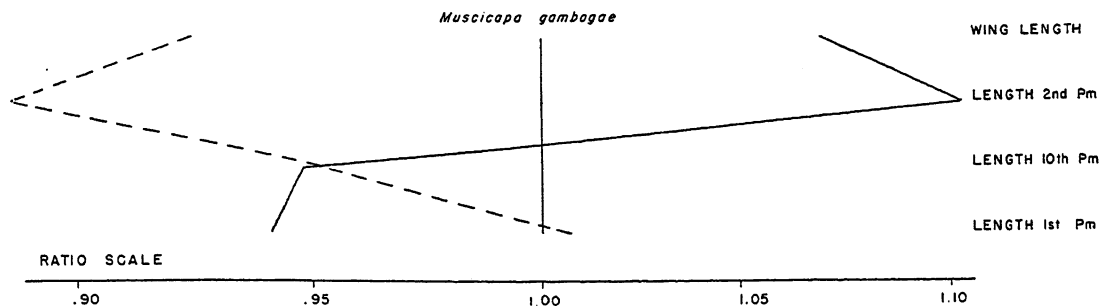


FIG. 1. Comparison through ratio diagram of the modification of the primaries in the migratory species (solid line) and the non-migratory species (broken line) of the genus *Muscicapa*. Standard of comparison: *M. gambagae*; see text. The pointed shape of the wing of the migratory species is caused by a lengthening of the longest (wing length) and second primaries accompanied by a decrease in the lengths of the tenth and first primaries. The reverse is true in the rounded-wing, non-migratory species.

stated, the shape of the wing is most variable in this genus. The species were divided into two groups and were compared by means of a ratio diagram to *M. gambagae* which, although non-migratory, is about intermediate in the shape of wing tip between the migratory and non-migratory species, that is, its wing is neither very pointed nor very rounded. The nine species of the first group (solid line) consist of the migratory and partly migratory species and of *infuscata* and *ussheri*, all of which have a pointed wing. The 11 species of the second group (broken line) all have rounded wings and are non-migratory. It can be seen that in the species with pointed wings the length of the wing (that is, of the longest primary, either the third or fourth or both the third and fourth) and the length of the second primary increase while the length of the tenth and first primaries decrease, and that the reverse is true in the species with rounded wings. Apparently, the rate of increase or decrease of the longest and second primaries is about the same in both groups but more rapid in the case of the second group. In the species with pointed wings the length of the tenth primary decreases faster than it increases in the species with rounded wings, and in the latter the first primary increases at a much more accelerated rate than it decreases in the species with pointed wings.

Another measure of the differential rate in development is shown by the length of the first primary as compared to that of the

primary coverts (see table 6). In *M. gambagae* the first primary exceeds the coverts by 6.6 mm., in the species with rounded wings the excess is 6.2 to 15.3 (10.0), while in the species with pointed wings the first primary may be shorter or longer, the range being from minus 5.5 to plus 5.4, with an average of plus 1.1 for nine species.

#### SHAPE, LENGTH, AND PATTERN OF THE TAIL

The shape of the tail usually varies from squarish to slightly rounded, but it may be well rounded in some species and slightly forked in others. These variations appear not to be of phylogenetic importance, for the shape of the tail may vary abruptly between two species that are very closely related. For instance, in the genus *Melaenornis* the tail is well rounded in *edolioides* where the outer rectrices fall short of the long central pair by a distance about equal to 24 per cent of the total length of the tail, but in *pammelaina* the tail is forked. Other closely related species may vary as shown in figure 2 where of the two *Microeca* the tail is rounded in *leucophaea* while it is squarish or even slightly forked in *brunneicauda*.

The length of the tail is correlated with the length of the wing, and figure 3 shows that this correlation, with the exception of a group of species, is almost perfectly linear. In this group of 14 species (enclosed in broken lines) where the tail tends to be shorter, it is interesting to note that 10 of these species are

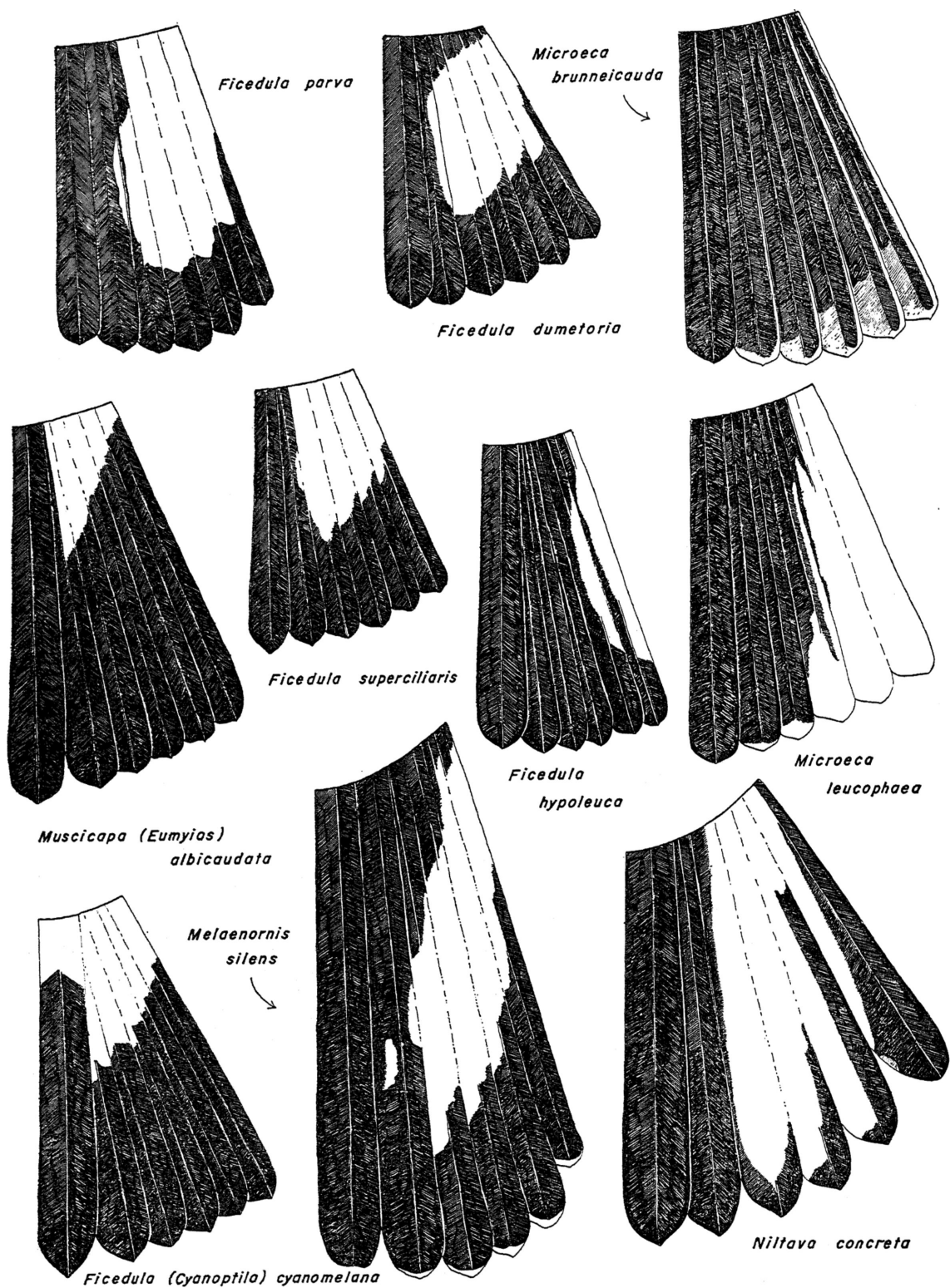


FIG. 2. Tail pattern in the genera of Muscicapini included in this study. Natural size.



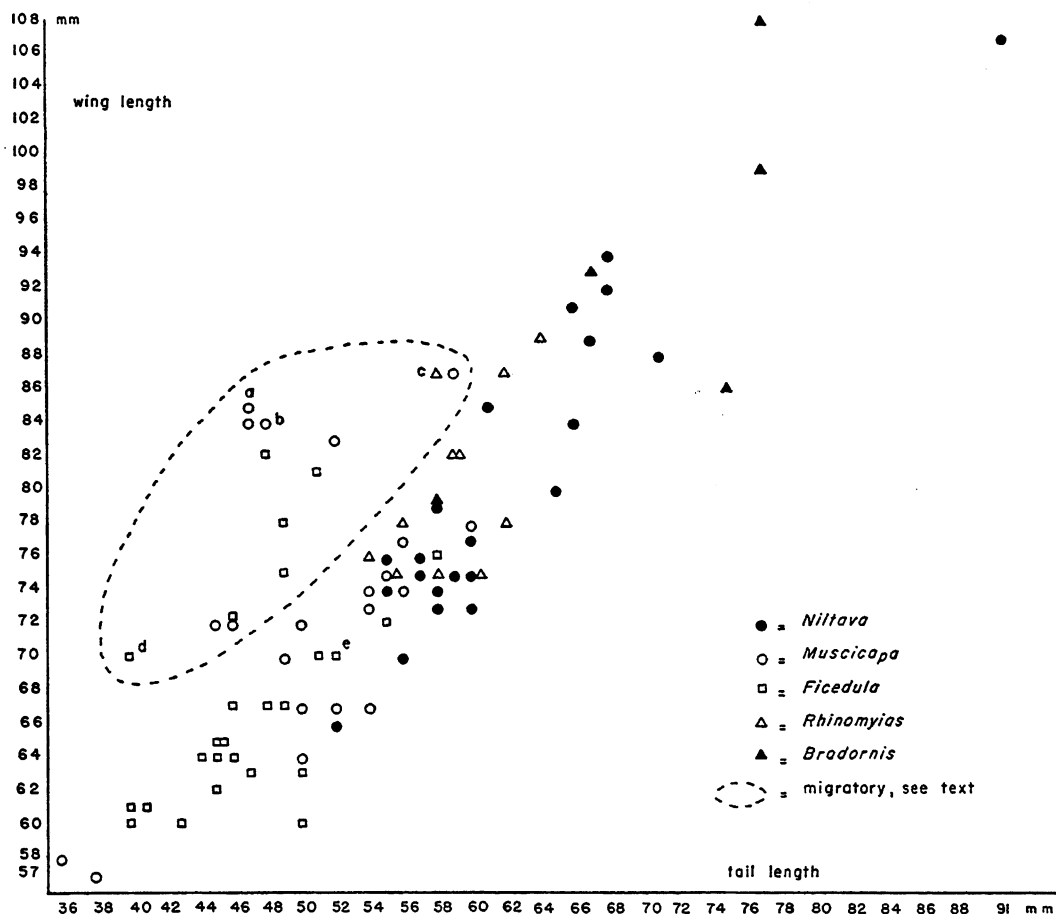


FIG. 3. Correlation between the length of the wing and the length of the tail.

highly migratory and that two others, *Muscicapa ussheri* (a) and *Muscicapa infuscata* (b) are very aerial in their habits and hunt from the top of the tallest trees. A shorter tail may be more efficient in species that have long migrations or that maneuver freely in the open air. There are some exceptions: in the "migratory" group, *Ficedula basilanica* (d) and *Rhinomyias g. gularis* (c), which are not migratory, have a proportionately shorter tail, while *Ficedula parva* (e) has a longer one. *F. parva*, however, is the only highly migratory species studied which does not fit in the group of species with shorter tail, while *R. g. gularis* is on the borderline between the species with shorter or longer tails.

The pattern of the tail, in contrast to its shape and length, seems to be of certain phylogenetic importance. In the great ma-

jority of the 113 species studied the tail is without pattern, but a white or pale area, variable in shape and extent (fig. 2), is present in 19 species. The fact that this white area is common in some groups of species and lacking or of seemingly fortuitous appearance in others seems significant. In the genus *Ficedula* proper a white area is present in 11 of the 26 species and occurs in this genus only in the groups of species that seem to be more closely related. A white area is present also in the monotypic subgenus *Cyanoptila* of *Ficedula*. In the groups of *Ficedula* where a white area is present in the tail the phylogenetic importance of this pattern character is supported by the presence of other white areas in the plumage, namely, on the head and on the wings.

In *Microeca* a white or pale area occurs in

three of the seven species of this genus, and there are traces of it in a fourth species. In this genus there appears to be a great contrast in the shape of the white area of *leucophaea* and the white and pale areas of *brunneicauda* (fig. 2), but these two species are nevertheless very closely related; and *brunneicauda* in all other characters grades into *leucophaea*, then in turn grades, in respect to the pattern of the tail and all other characters, into two other species. The presence of a white area in the tail of *Microeca* and *Ficedula* does not necessarily show, of course, that these two genera are related. The white pattern, furthermore, is dissimilar.

In the genera other than *Ficedula* and *Microeca* a white area is present in four species: twice in the subgenus *Eumyias* of

*Muscicapa*, in the closely related *albicaudata* and *indigo* where it is identical in shape and extent, once in *Melaenornis* in *silens*, and once in *Niltava* in *concreta*. As shown in figure 2 the white area is dissimilar in these species. The phylogenetic significance of its presence in these species is obscure, and its appearance may be fortuitous and an instance of parallelism. *Eumyias* and *Cyanoptila*, however, are possibly distantly related to each other and to *Ficedula*, but *silens* and *concreta* are not related and seem very far removed from *Ficedula*.

### THE TARSUS

Under this heading the relative length and thickness of the tarsus and of the strength of the claws and the scutellation may be con-

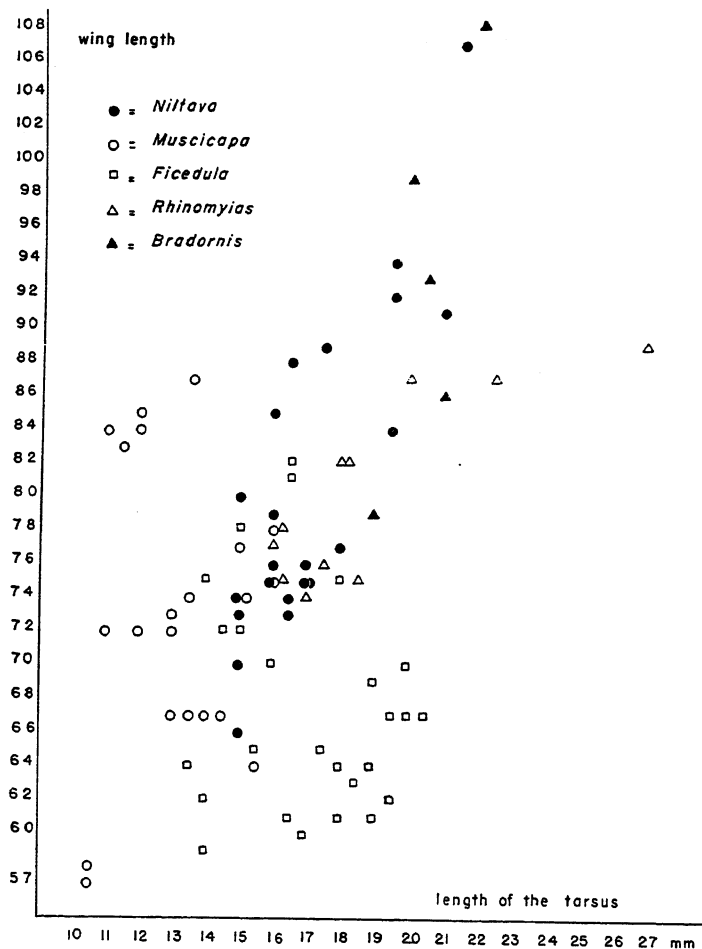


FIG. 4. Correlation between the length of the wing and length of the tarsus.

sidered. The length and thickness of the tarsus and the strength of the claws seem to be purely adaptive, but the phylogenetic or adaptive significance of the scutellation, if any, is obscure.

Although generally speaking there is a definite correlation between the length of the tarsus and size, as shown by the length of the wing, this correlation (fig. 4) is far from being so close as is that between the length of the wing and of the tail. This figure shows that most *Ficedula* have a long tarsus although their wing is short, and that many *Muscicapa* have a shorter tarsus than their size seems to warrant. It would be tedious to discuss the position of each individual symbol, but by checking the position of some of these symbols with the measurements given in tables 4 and 6 it can be seen that the *Ficedula* with the shortest tarsus are those that depart from the habits of this genus by being more arboreal, such as *westermanni*, *superciliaris*, and *sapphira*. Conversely, in *Muscicapa* the species with the longest tarsus are *griseigularis*, *caerulescens* (= *cinerea* auct.<sup>1</sup>), and *tessmanni*. The habits of *tessmanni* are not known; *griseigularis* is not truly arboreal and searches the foliage for food in the manner of a warbler; and *caerulescens* does not ascend high into the trees but hunts from bushes or low trees in savanna or at the edge of clearings.

It may be observed also that in the three races of *Rhinomyias gularis*, which are plotted separately on account of their wide variation in the length of the tarsus, the tarsus lengthens while the wing length remains unchanged or virtually so. The habits of this species are very poorly known, except that the races with a long tarsus are dwellers of the thick undergrowth in deep mossy forest. It may be fairly stated as a "rule of thumb" that in the flycatchers studied the closer the species feeds to the ground the longer its tarsus becomes.

The *Ficedula* with a shorter tarsus which overlap with *Muscicapa* are all highly migratory species. It is possible that, as in the case of the tail, a shorter tarsus is more efficient in species with a long migration, but this shortening of the tarsus seems to be

secondary, for in the highly migratory species of the short-tarsus genus *Muscicapa*, with a migration similar to that of the migratory *Ficedula*, the tarsus is generally even much shorter.

The thickness of the tarsus is not directly correlated with either the length of the wing or the length of the tarsus but rather with the general build of the species. Heavily built species, whether long-winged or not, always have a thick tarsus, whether short or long, and slender species have a slender tarsus. This is well illustrated by *Muscicapa comitata* (fig. 5G) and *tessmanni* (fig. 5F) and by *Fraseria ocreata* and *cinerascens*. In both pairs the species are virtually identical in appearance and appear to be closely related. Their wing length does not differ very abruptly (the wing of *comitata* averages 67.3; of *tessmanni*, 75.0; of *ocrea*, 98.1; and of *cinerascens* 82.4), but the larger species in each pair is much more heavily built than the relatively small difference in wing length indicates and has a very much thicker tarsus, the tarsus being almost twice as thick (fig. 5). The tarsus is proportionately very much thicker than the relatively small difference in its length would seem to warrant, the length of the tarsus in *comitata* averaging 14.5, in *tessmanni* 16.3, in *ocrea* 21.3, and in *cinerascens* 17.8.

In all species the strength of the claws is directly correlated with the thickness of the tarsus, the species with a thick tarsus having heavy and powerful claws, whereas the claws are slender and may be very weak in the species with a slender tarsus.

It may be stated as a rule that species that are arboreal and feed on the wing or those that roam through the undergrowth have a slender tarsus and weak or slender claws and those that drop to the ground to pick up insects (*Bradornis* and *Melaenornis*) have a thick tarsus and strong claws. However, in *Fraseria ocreata* and *Niltava concreta* which appear to be strictly arboreal and in *Niltava grandis* which seems to be largely a dweller of the undergrowth, the tarsus is as thick as in *Bradornis* and *Melaenornis*, these three species and the species of *Bradornis* and *Melaenornis* being all heavily built species, or very large (*grandis*). In this last species it may be noted that although the tarsus is thick, the claws are relatively weak.

<sup>1</sup> For the name of this species, see Appendix.

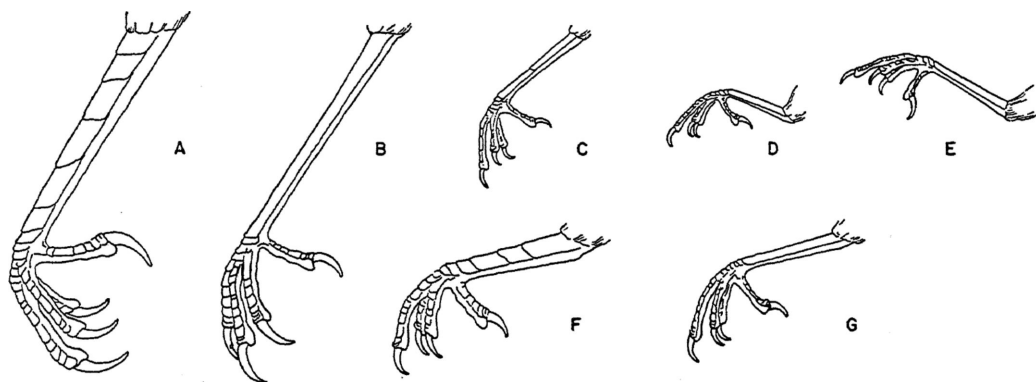


FIG. 5. Variation in the shape and scutellation of the tarsus in some of the Muscicapini included in this study. A. *Bradornis infuscatus*. B. *Rhinomyias gularis insignis*. C. *Muscicapa striata*. D. *Muscicapa epulata*. E. *Ficedula westermanni*. F. *Muscicapa tessmanni*. G. *Muscicapa comitata*. Natural size.

The significance of the scutellation is obscure. In speaking of the scutellation I do not refer to the very closely spaced scutes which are always present at the base of the tarsus but to the scutellation of the shank. Examination was made only in skins and under a magnification of  $\times 15$ . Scutes visible in life or in alcoholic specimens might not show in dried specimens, but it is believed that this magnification would show true scutes if present. Some of the variations in the shape of the tarsus and its scutellation or lack of scutellation are shown in figure 5.

The presence or absence of scutes is usually correlated with the thickness of the tarsus, the tarsus being scutellated in the species with a thick tarsus and not scutellated in those in which it is slender, but there are some exceptions. It is well scutellated in *Bradornis*, *Melaenornis*, and *Fraseria* but not in *Niltava grandis* and *concreta*, although these two species also have a thick tarsus. It is scutellated in *Fraseria cinerascens*, which has a relatively thin tarsus, and scutes are sometimes more or less well indicated in species which have a really slender or weak tarsus. For instance, scutes or traces of them are found in seven of the 21 species of *Muscicapa*, in four of the 22 species of *Niltava*, in three of the 26 species of *Ficedula*; traces of scutes are occasionally visible in the eight species of *Rhinomyias* in which the tarsus is normally booted.

The presence or absence of scutes is not

correlated with habits; it varies between two closely related species; and it varies individually. In the very closely related *Muscicapa infuscata* and *ussheri* two clear-cut scutes are present on the shank of the former but none in the other. In the sibling pair *Niltava davidi* and *sundara* two clear-cut scutes are present in *davidi* and none in *sundara*. In *Fraseria ocreata* scutes are almost always very clearly indicated, but they may be faint in some specimens and not visible in others. It may be recalled that Bonaparte erected the genus *Fraseria* for this species on the ground that the "anterior part of the tarsus was made all in one piece," i.e., that it was booted.

#### THE BILL

In this section the shape of the bill, the feathering at the base of the culmen and over the nostrils, and the rictal bristles are considered. These characters are very difficult to evaluate for, although they remain constant and seem to be of phylogenetic significance in some groups of species, they vary in other groups where the changes seem to be purely adaptive.

The phylogenetic significance of the bill characters, which have been used so much for generic separation, must always be questioned, for they are usually very plastic and may be adapted to even apparently small differences in the manner of feeding. In most of the species groups studied it may be stated

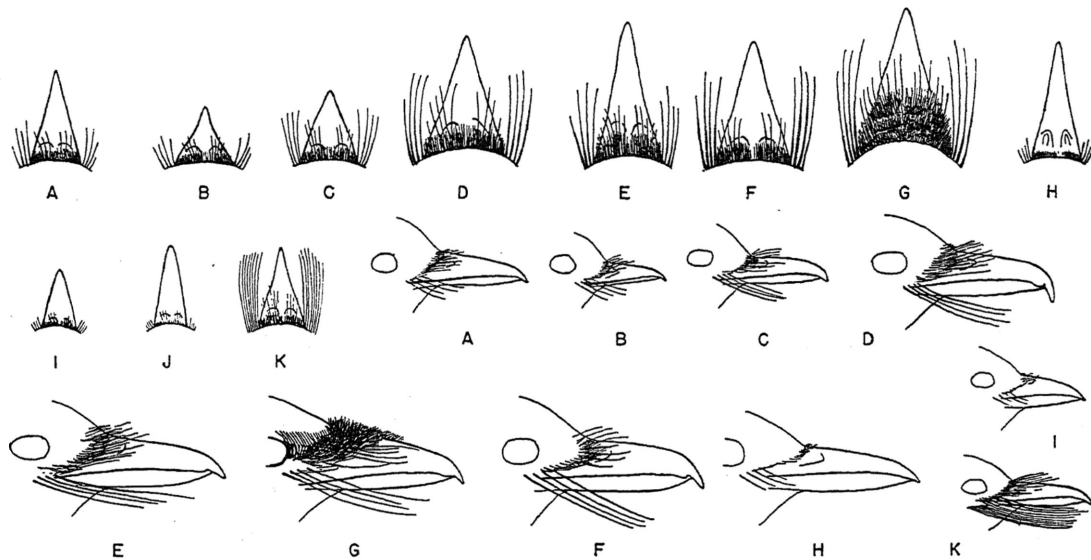


FIG. 6. Principal variations of the bill characters in the Muscicapini included in this study. A. *Muscicapa striata*. B. *M. ferruginea*. C. *M. (Eumyias) panayensis*. D. *Niltava hoëvelli*. E. *N. concreta*. F. *Rhinomyias gularis albigularis*. G. *Niltava grandis*. H. *Bradornis infuscatus*. I. *Ficedula hypoleuca*. J. *F. timorensis*. K. *Culicicapa ceylonensis*. Natural size.

that these characters seem to be purely adaptive. That is to say, the bill is more or less flycatcher-like in the species that are arboreal but becomes warbler-like in the species that normally search the foliage for insects, or thrush-like in the species that feed in the undergrowth and on or close to the ground.

The bill characters of all the species are illustrated throughout the text, and the chief variations are brought together in figure 6. In this figure the bill of *Muscicapa (Eumyias) panayensis*, an arboreal species, is a perfect example of the flycatcher bill, i.e., it is triangular in shape, very broad at the base, and not attenuated, depressed (flattened) above, with a shallow ridge and moderately hooked at the tip, the nostrils are almost entirely concealed by hair-like feathers and antrorse bristles which extend from the base of the culmen, and the rictal bristles are long and strong. The arboreal species may depart from this type as follows: the bill may be swallow-like as in *Muscicapa rufilata ferruginea*<sup>1</sup> or *M. infuscata* or it may be more attenuated as in *Muscicapa striata*, *Niltava hoëvelli*, and *N. concreta*. In the species in which it becomes well attenuated, as in *N. concreta*, it may cease to be flattened above

<sup>1</sup> For the name of this species, see Appendix.

and become strongly compressed laterally (this is not shown in fig. 6). The terminal hook may become weak or, as in *N. hoëvelli*, very strong, and it may be mentioned that on the sole basis of this strong hook a monotypic genus was erected for this species. The most striking instance of adaptive variation encountered in this study occurs within the limits of a single species. *Rhinomyias gularis*, in which the bill in its shape, feathering, and bristles varies from that of a typical flycatcher to one indistinguishable from that of a typical thrush (Vaurie, 1952a).

Although the species studied show much evidence of adaptive variation, apparent similarity of function does not always result in similarity of structure. In *Bradornis* and *Melaenornis*, in which all the species appear to have precisely the same feeding habits, there is a striking difference in the bill characters. The bill of *Melaenornis* is flycatcher-like in every character, but the bill of *Bradornis* (figs. 6H, 9) is thrush-like, these bill characters being constant in each genus (figs. 9, 11). The arboreal *Culicicapa* has a well-flattened bill which, though a little too attenuated, is very flycatcher-like, but it is not clear why this genus, if a Muscicapini, has developed twice as many rictal bristles

(fig. 6K) than are found in all the other genera studied, the bristles being arranged in two rows, one above the upper half of the bill and the other below the insertion of the mandible.

Further, the amount of variability varies from genus to genus. Of the three largest genera (*Muscicapa*, *Ficedula*, and *Niltava*), the bill characters are more variable in *Muscicapa*, although the basic feeding habits vary little, whereas in *Ficedula* and *Niltava*, each of which includes some species with widely different feeding habits, the bill characters remain fairly constant. One may conclude that in some groups of species the bill characters are of phylogenetic importance.

#### TEXTURE OF THE PLUMAGE

The texture of the plumage with the exception of that of *Humblotia* and *Newtonia* differs little. It is soft and rather full. In the species with blue coloration, however, the texture of the blue parts of the plumage averages less soft, the glossy areas being smoothest and least soft. In the monotypic and insular *Humblotia* (fig. 24) the plumage has become unusually soft and fluffy. In this species (*flavirostris*, restricted to Grand Comoro) the feathers of the crown also show a tendency to be modified into a vague sort of crest, being distinctly elongated while those of the fore crown are squamose and semi-erect. Despite these characters, *Humblotia* is still very closely related to *Muscicapa*. In *Newtonia*, which may possibly have been derived from the same branch that gave rise to *Humblotia*, the plumage is very soft also, but less soft than in *Humblotia*. A softening of the plumage often occurs in insular forms.

#### PLUMAGE OF THE YOUNG

The plumage of the young, whether spotted or not, is usually taken to be a significant "family" character rather than a generic character. In the Muscapini studied, however, the young of the genus *Newtonia* are not spotted, and the nature and extent of the spotting often vary in the other genera. In *Muscicapa* the young of *comitata* are described as not spotted. In the only young of this species examined, however, a few slight but distinct spots are present, but apparently the young are not usually spotted, or, if

spotted, the spots are few and not conspicuous. In the other large genera (*Ficedula* and *Niltava*) the young of some species are boldly spotted with rounded spots, whereas in other species they are more streaked or mottled than spotted. Unrelated genera often have similarly spotted young. In some species, as in *Ficedula* (*Cyanoptila*) *cyanomelana*, the spotting is present only in the nestling and is lacking in the juvenal plumage.

In addition to *Newtonia* the young are not spotted in *Horizorhinus* and *Culicicapa*. These three genera are not related; *Horizorhinus*, although provisionally included in this study, may not be a flycatcher, and the affinities of *Culicicapa* may be with the Rhipidurini rather than with the Muscapini. *Newtonia*, on the other hand, although aberrant, appears to belong to the Muscapini and may be distantly related to *Muscicapa*.

The spotting of the young is probably not a character suitable for generic separation, and it is a poor "family" character for it does not separate the spotted Muscapinae from the spotted Turdinae.

The young of not all the species were examined. The list of such species is given in the Appendix, the young of not a few of these species being unknown.

#### PATTERN AND COLORATION

The pattern and coloration are much more conservative than the structural characters, for they remain constant or relatively constant in most genera, or groups of species as in *Ficedula*, where the structural characters and habits vary.

There are, however, a number of cases where the coloration or a detail of pattern common in one genus recurs in another. Most of these cases seem to be instances of parallelism, some of which may be adaptive or, in relatively few cases, may indicate more or less distant relationship. For instance, black is found in *Melaenornis* and *Ficedula* and yellow in *Culicicapa*, *Ficedula*, and *Microeca*, but these genera are not related, and in every case the pattern differs. The adaptive significance of a concealing coloration in many species of unrelated genera needs no elaboration. The presence of a conspicuous superciliary stripe is more interesting, for it occurs

only in *Ficedula* and in the races of *Rhinomyias gularis* that are dwellers of the undergrowth; since most of the species of *Ficedula* are not arboreal and many feed in thickets and in the undergrowth, this character may be adaptive. In *Bradornis*, which inhabits open arid regions, a superciliary streak is, however, more or less clearly indicated. The appearance of a white pattern in the tail and its possible phylogenetic significance are discussed above.

Although characterized by a blue coloration one group of species was divided and placed in different genera. This includes one species (*sapphira*) of the *Muscicapula-Digenea* group of *Ficedula* and all the species of the subgenera *Eumyias*, *Cyanoptila*, and *Muscicapella*. *Eumyias* consists of five species; *Cyanoptila* and *Muscicapella* are monotypic. All these species are probably more or less distantly related, but since, with the exception of *sapphira* which intergrades back very well into *Ficedula*, the degree of the relationship of the others is more or less uncertain, they have been kept separate as subgenera. In the other two subgenera recognized, *Empidonis* and *Myopornis*, both of which are monotypic, the pattern or coloration is unique.

Sexual dimorphism in coloration has occasionally been used for generic separation, but the phylogenetic significance of this character is uncertain, because, although it is always lacking in some genera and present in others, the degree of dimorphism varies between related species and may even vary in the races of a single species.

#### HABITS AND THE VALIDITY OF CHARACTERS

In the preceding discussion some of the general habits of the species are mentioned, such as feeding habits, migratory or sedentary habits, or whether the species is arboreal or terrestrial. Other habits, such as song, gregarious or solitary habits, nesting habits or structure of the nest, or participation of the male in incubation, are mentioned below in the discussions of the separate genera whenever such information is available.

Habits are of importance in the determination of relationships, but in habits as in morphological characters a discrimination

must be made between taxonomically important and unimportant characters. This study indicates that feeding habits are among the taxonomically less important characters. Similarity of feeding habits is usually directly correlated to similarity of structure and function but is not always a good clue to relationships. The closely related species of the genus *Rhinomyias* vary in their habits, and if feeding habits were taken as automatically indicating relationship some races of *R. gularis* should be placed among the flycatchers and others in the thrushes. If the larger genera recognized in this study, *Muscicapula*, *Ficedula*, and *Niltava*, are admitted, it will be seen that the feeding habits or other so-called "field" characters may diverge widely between some of the closely related species in each of these genera. In *Muscicapula*, where the species are chiefly typical arboreal flycatchers, one species (*griseigularis*) is warbler-like in structure, voice, and habits. In *Ficedula*, which is chiefly not arboreal, a few species (*hodgsonii* and some of the species of the *Muscicapula-Digenea* group) are arboreal and *Muscicapula*-like in their manner of feeding. This is also true in *Niltava-Cyornis* in which a few species are restricted to the tree tops although these species are nevertheless closely related to the other *Niltava-Cyornis* and share a common and distinct blue coloration and pattern. *Fraseria*, far removed from *Muscicapula*, is arboreal and has similar feeding habits. In *Bradornis* and *Melaenornis*, which are separated by coloration and bill characters, habits are similar, and so on. Furthermore, ecology and behavior may not be any more fixed than the morphological characters. Many arboreal flycatchers which hawk insects from an exposed perch search the foliage for insects and, occasionally, come to the ground to feed, and, vice versa, ground-feeding species may catch food on the wing, as in *Bradornis* and *Melaenornis*.

Internal characters have not been examined, but it may be presumed that in the relatively poorly differentiated species studied they are not necessarily more significant than the external characters. For instance, recent attempts have been made to establish relationships on the basis of variations in the jaw muscles. In the genera studied, how-

ever, related species may differ in the structure of the bill which may be depressed, very broad and short, and swallow-like, or long and slender and compressed laterally. Presumably these variations are adaptations to a different manner of feeding and result in adaptive variations in the jaw muscles and bones of the skull.

In conclusion, it is evident that habits and morphological characters (whether functional or not) must always be weighed together. Structural (functional) characters, non-structural characters (in this sense coloration and pattern), and habits may be equally valid for generic separation, but the emphasis on certain characters, or a complex of characters and habits, may shift if apparently natural relationships are not to be obscured.

In this study the genera have usually been recognized on a combination of characters, but precedence has been given by me to coloration and pattern, for these characters appear, as in many other groups of birds, to be the most conservative. In many instances these characters are supported by constant or fairly constant structural characters and similarity in general habits. It must be emphasized again, however, that structural characters that may or may not be correlated with feeding habits will oc-

asionally vary between species that are shown to be closely related by their similarity in pattern and coloration. In a few instances the structural characters seem more significant than coloration or pattern, as in *Melaenornis*, *Culicicapa*, and the monotypic subgenus *Muscicapella* and *Humblotia*, or a combination of structural characters and habits, as in *Newtonia*. Habits have been the principal deciding factor in only a few cases, the chief of these being in the case of *böhmi* for which a monotypic subgenus (*Myopornis*), related to *Muscicapa*, is admitted, and of *Fraseria* which, although apparently related to *Melaenornis*, has shifted into a major new ecological niche. It must be admitted that my recognition of *Myopornis* and *Fraseria* on the basis of habit is strongly influenced by the unique color patterns of their under parts.

Throughout this study an attempt has been made to place the species in what seems to constitute natural groups which when well, or relatively well, defined have been considered to form separate genera. When single species, or in one case a group of species (*Eumyias*), do not seem to fit well in any one natural group I have recognized a few subgenera, rather than obscure relationships.



## GENERAL DISCUSSION

### LIST AND SYNOPSIS OF THE GENERA

THE GENERA RECOGNIZED are listed below in what appears to be a natural order. A statement of the distribution of each genus and the number of its species are given, and a brief description of the characters in general terms is included. These summary descriptions may seem to be superfluous, but since no key can be given it is hoped that this synopsis will be helpful.

If desired, the genera can be divided into two groups, with the genus *Rhinomyias* intermediate. The first, the *Bradornis* group, includes the generally larger and more heavily built species from *Bradornis* to *Fraseria* which seem farthest removed from the more typical flycatchers. The second, the *Muscicapa* group, comprises the true flycatchers. *Horizorhinus*, provisionally included in this study among the Muscicapini, is placed in the list in the order in which it appears in the text. *Culicicapa*, which may possibly be related to the Rhipidurini, is placed last.

*Bradornis* (five species) and the monotypic subgenus *Empidornis*. Drier parts or savannas of the Ethiopian region. Moderately large to large species with a thick and relatively short tarsus; wing rounded; bill well attenuated and strongly compressed laterally, very poorly feathered (nostrils exposed), rictal bristles very short and weak. Concealing drab sandy coloration. Drops to the ground to feed. Somewhat gregarious, usually silent. *Empidornis* differs in its silvery and very strong rufous coloration.

*Melaenornis* (five species). Distribution, structure (except bill characters), and habits similar to those of *Bradornis*. Bill broad or relatively broad, well feathered, and with well-developed rictal bristles. Coloration not concealing: black, black and white, or slate to brown.

*Fraseria* (two species). Rain forests of western and central Africa. Similar in structure to *Melaenornis*. Dark slate above but with white squamated under parts. Arboreal. Very silent or very noisy with peculiar buzzing note.

*Horizorhinus* (monotypic). Restricted to Principe Island in the Gulf of Guinea. Of very uncertain affinities. Characters given in the text.

*Rhinomyias* (eight species). Indo-Malayan. Medium sized; tarsus short to long and relatively slender; wing rounded; bill broad and rather depressed, short or rather attenuated, thrush-like in

one species, very well feathered with long bristles or poorly feathered with short bristles. Coloration more or less rufous olive brown, streaked or unstreaked below, with more or less well-indicated pectoral band. Habits variable, arboreal or in the undergrowth. The song has not been described.

*Ficedula* (26 species) and the monotypic subgenus *Cyanoptila*. Palearctic and Indo-Malayan. Small species, with moderately long to long slender tarsus; wing variable, pointed or rounded; bill small, not well broadened at the base, sometimes well attenuated, not or feebly hooked, feathering and bristles poor or rather poor. Pattern and coloration most variable but not streaked and with white markings on the head and tail in about two-thirds to one-half of the species. With very few exceptions not truly arboreal, comes often to the ground; many species are dwellers of the undergrowth. Usually a varied and pleasing song. A very complex and difficult group, in which a number of more or less clearly defined subgroups can be distinguished. *Cyanoptila*, of somewhat dubious affinities with this genus, is a large species in which the male has a brilliant blue coloration above.

*Niltava* (22 species) and the monotypic subgenus *Muscicapella*. Indo-Malayan. Medium-sized to large species, with relatively short tarsus of medium thickness; wing rounded, slightly variable; bill large, not well depressed, broadened at the base and moderately attenuated, moderately to strongly hooked, with feathering and bristles very well developed; tail moderately long to long. Coloration characteristic, not streaked and with very well-developed blue and rufous markings, without white head markings and, except in one species, without white in the tail. Habits variable, arboreal or in the undergrowth. All species are said to be very good singers. *Muscicapella* differs in being of very small size, in having a needle-like bill, and in being a leaf-warbler or a *Regulus* in habits.

*Muscicapa* (21 species) and the subgenera *Eumyias* (five species) and the monotypic *Myopornis*. Palearctic, Ethiopian, and Indo-Malayan. The "typical" flycatchers. *Muscicapa* proper: small species with short to very short tarsus, usually very weak; wing very variable, very pointed to very rounded; bill variable, broad to very broad and depressed, moderately to weakly hooked, feathering and bristles usually moderate; tail moderately long to short or very short. Coloration dull, streaked or with indications of streaks, no white on the head or tail, drab gray brown to blue gray or slate, one species rufous. Arboreal, usually perches stolidly and feeds entirely or mostly on the wing. Poor singers.

*Eumyias* differs in its blue coloration and a longer tail. *Myopornis* presents some of the characters of *Bradornis* but is arboreal, and the under parts are well spotted with triangular spots.

*Humblotia* (monotypic). Restricted to Grand Comoro Island. Differs from *Muscicapa* to which it is related by the unusually soft texture of the plumage, modification of the crown feathers, and by having a longer tarsus. Habits unknown.

*Newtonia* (four species). Restricted to Madagascar. Small to very small species, with a very long tarsus; wing extremely rounded; bill fairly broadened at base but well or very well attenuated, feathering and bristles moderately to well developed; plumage very soft; tail long. Brown tinged with rufous below or on thighs and tail. Gregarious and tit- or warbler-like. Song loud and rich.

*Microeca* (seven species). Australo-Papuan. Medium-sized but rather small to small species with short to moderately long tarsus, slender or of medium thickness; wing rounded, slightly variable; bill depressed, well broadened at base, feathering and bristles well developed. Gray brown to yellow and yellow green, four species with white, pale, or yellowish markings or traces of them in the tail. Arboreal and typical flycatchers. Good or fairly good singers. The Australo-Papuan representative of *Muscicapa*.

*Culicicapa* (two species). Southeastern Palearctic (central China) and Indo-Malayan. Small and very frail species with a short and very weak tarsus; wing rounded; bill very depressed, well broadened at base but coming to a fine point, well feathered, rictal bristles very long, twice as numerous and arranged differently than in the other *Muscicapini*. Yellow green and very bright yellow with gray head and breast in one species. Very arboreal and very restless and active. Good singer.

#### THE GENUS *PARISOMA*

This Ethiopian genus, which consists of seven species to which *Muscicapa griseigularis* is sometimes added, is discussed here, as it is placed near *Muscicapa* in modern classifications. Because examination shows, however, that it is a composite and unnatural group, some species of which are almost certainly warblers, it is omitted from this study, with the exception of *griseigularis* which is a true, though somewhat aberrant, *Muscicapa*.

The vicissitudes of *Parisoma* have been many. Although Sclater (1930) places it next to *Muscicapa* he states, "The affinity of this genus is by no means settled. It was

placed by Sharpe among his Timelidae, by Shelley as a distinct family, and by Reichenow and Hellmayr among the Tits. Recent writers regard it as best placed near *Muscicapa*, though it does not seem to have a spotted juvenile plumage. *P. leucomelaena* (= *blanfordi*) and its allies have often been placed with *Sylvia*, and perhaps this will be the eventual position of the whole genus." Recent writers support Sclater. Meinertzhagen (1949) states that *leucomelaena* belongs in *Sylvia* and that *P. buryi* probably does. Benson (1951) has also called attention to *P. lugens* which "in its movements seems more typically a warbler than a flycatcher."

Bates (1930) states that *Muscicapa griseigularis* "seems to form a connecting link between the genera; and the young of *Parisoma plumbeum* are spotted." Bannerman (1936) states, however, that they are not, and my own examination of five immature specimens of *plumbeum*, some of them very young, supports Bannerman fully. Dr. Chapin informs me that he places *griseigularis* in *Parisoma* because it seems to have a somewhat similar voice and manner of feeding. The shape of the bill of *griseigularis* approaches somewhat that of *plumbeum*, that is, the bill of *griseigularis* (fig. 21 O) is more attenuated and more compressed laterally than is normal in *Muscicapa*, but a bill adapted to a similar manner of feeding is not necessarily a proof of relationship.

The characters of *Parisoma*, including those of *plumbeum*, do not grade at all into the characters of *Muscicapa*. In addition to warbler-like habits and lack of spotting in the young, *Parisoma* has very different proportions. Its first primary averages longer to very much longer, its tail is very long, is slightly or well graduated, and its outer feathers are white or broadly tipped with much white, its bill is very slender and much compressed laterally, and its rictal bristles are very short and very weak. The *Parisoma* are also more slender birds.

Bates was not sure whether he should call *plumbeum* a "flycatcher or Tit or Warbler." Until further study clarifies the true position of *plumbeum* and that of the other *Parisoma*, it seems advisable to remove these species from the flycatchers to the warblers.

THE *MUSCICAPA* COMPLEX

The 77 species divided in this study among the genera *Ficedula*, *Niltava*, and *Muscicapa* were formerly divided in a host of more or less ill-defined genera, most of them monotypic, or, except in the case of *Niltava* (includes *Cyornis*), consisting of but two or three species. The 21 species of *Muscicapa* were divided in 10 genera, the 26 species of *Ficedula* in 16 genera, the 22 species of *Niltava* in six, and to these must be added the four subgenera that I recognize. Hartert (1907) combined about a third of these genera with *Muscicapa*, but he was not followed. Stresemann, for instance (1912), testing the concept of Hartert with a number of Indo-Malayan species, divided about three-quarters of the 26 species that I have placed in *Ficedula* in eight genera, several of which had been merged with *Muscicapa* by Hartert. About 25 genera continued to be more or less generally recognized: the four treated by me as subgenera, eight in *Muscicapa*, 11 in *Ficedula*, and two in *Niltava*.

Mayr in 1945 revived the concept of an all embracing genus *Muscicapa*, stating that in their morphological characters as well as in their habits the species could be arranged in a complete series showing a "complete intergradation between the extremes." Delacour (1946b) and Deignan (1947) added still other genera to *Muscicapa*.

Mayr, however, was aware that such a large complex of species in which a number of natural groups with varying degree of relationship can be distinguished required testing, and, as stated, it was at his suggestion that the present analysis was undertaken. As shown in the synopsis where the characters are briefly summarized, the 77 species have been divided into three main genera and four subgenera, three of which are monotypic, the subgenera representing strongly specialized species or species of uncertain affinities. It is hoped that in this manner the affinities of the species are maintained and better expressed than by treating them all as congeneric.

It is true, as Mayr states, that all the species can be arranged in a complete series, but if the division advocated is admitted, the cases in which the coloration and pattern

of one genus are repeated in another are very few. The most troublesome consist of the species with a blue coloration that I have divided among the subgenera *Eumyias*, *Cyanoptila*, and *Muscicapella*. The three subgenera present no true intergradation, and the monotypic *Muscicapella* is but a very specialized offshoot of *Niltava* and does not intergrade with any known species. The cases of similarity in feeding habits are more numerous, but, as stated, similarity in feeding habits does not appear to be an important taxonomic character and does not invalidate, I believe, the main thesis. Similarity of feeding habits which, it is to be expected, will result in more or less close adaptation of structure is neutral when the affinities seem otherwise to be clear as shown by the similarity of pattern and coloration.

## PHYLOGENY OF THE GENERA

The presumed relationships of the genera and subgenera studied are shown diagrammatically in figure 7. In this diagram and throughout this study it is assumed that this group does not include polyphyletic elements. This is not certain, for *Newtonia*, although it seems to be an aberrant flycatcher distantly related to *Muscicapa* via *Humblotia*, is not very flycatcher-like in its morphology or habits and could be a warbler. *Culicicapa* may be related to the Rhipidurini, the genera of the *Bradornis* group may represent a distinct branch of the Muscicapini, the affinities of *Rhinomyias* remain somewhat dubious, and *Ficedula* and perhaps *Muscicapa* may contain some polyphyletic elements. *Horizorhinus* is omitted from this discussion, for its affinities are too uncertain.

On the assumption that the genera are not polyphyletic, they may be arranged in a rather complicated sequence in which the genera of the *Bradornis* group represent a primitive element in the sense that in these genera the characters and habits of the more typical flycatchers have not become well developed. Conversely, *Muscicapa*, *Microeca*, and *Culicicapa* represent the extreme development of the flycatcher type. These three genera are not, however, necessarily related. *Muscicapa* was probably directly derived from a less arboreal type such as is

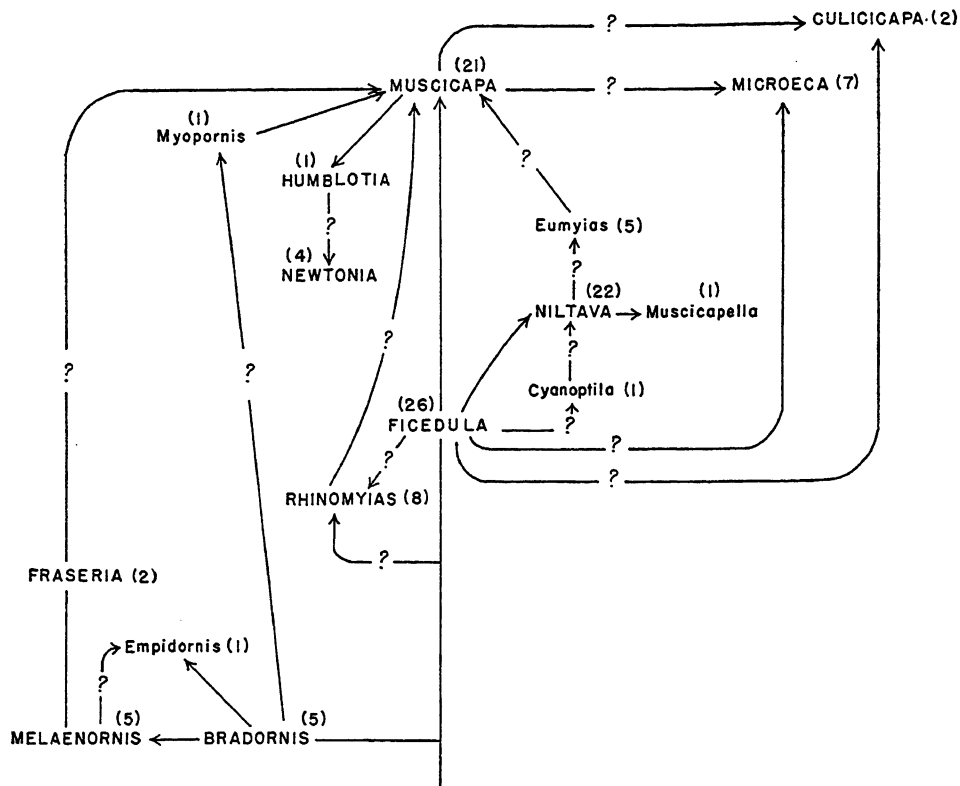


FIG. 7. Diagrammatic representation of the presumed relationships of the genera and subgenera (lower-case letters) studied. Arrows suggest derivations. Figures in parentheses indicate the number of species.

represented today by most of the species of *Ficedula*, and *Microeca* and *Culicicapa* may have been derived independently from such a type.

*Humblotia* appears to have been directly derived from *Muscicapa*, but its lone species has become differentiated on its isolation on Grand Comoro and has lost some of the characters of the more typical arboreal flycatchers. It has developed a very long tarsus, although it retains the streaked plumage and short broad bill of *Muscicapa*. *Newtonia* may have reached Madagascar via the same branch that gave rise to *Humblotia*, similarities in the tarsus and texture of the plumage supporting this opinion, but it has lost most of the muscipine characters and has become tit- or warbler-like.

*Myopornis* is placed near *Muscicapa* on account of its very streaked plumage and arboreal habits, but some of its characters suggest that it may be an offshoot of *Bradornis*

converging towards *Muscicapa*. *Fraseria* is shown in the diagram to have possible affinities with *Muscicapa*, for in *Muscicapa* the dark slate *comitata*, and particularly *tessmanni*, have something in common with *Fraseria*, *tessmanni* being distinctly more heavily built than the other *Muscicapa* and possessing strong claws and a very thick tarsus which is well scutellated (fig. 5F). This, on the other hand, may be merely an instance of convergence.

The genera of the *Bradornis* group are closely related, as shown in the diagram, *Fraseria* being probably directly derived from *Melaenornis* via *M. ardesiaca*.

The other genera (*Rhinomyias*, *Ficedula*, and *Niltava*, with their related subgenera) are more or less intermediate between the genera of the *Bradornis* group and the genera placed near *Muscicapa*. *Rhinomyias*, which varies in structure and habits and in which some forms are thrush-like and others very

close to *Muscicapa*, is of uncertain affinities. It is probably an independent and fairly primitive branch of the Muscicapini, but some similarities with the species of the *platenae* group of *Ficedula* suggest that *Rhinomyias* may possibly be an offshoot from *Ficedula*.

It can be seen that *Ficedula* is given a central position. It definitely belongs in the *Muscicapa* group taken in its broad sense, but *Ficedula* is in itself an old group in the sense that it is very broadly distributed and contains by far the most diversified species. This diversity is well reflected by the unusually large number of genera among which its species were formerly split, as, for instance, by Stresemann (1912). All the species, however, appear to retain something in common to a greater or lesser degree, the most questionable species being *F. timorensis* which may be of different origin.

In *Ficedula*, one of its group (the *Muscicapula-Digenea* group) leads directly to *Niltava* via *F. sapphira*. That *Niltava* is a much younger genus than *Ficedula* is well shown by the fact that, although *Niltava* is almost as rich in number of species as *Ficedula*, it has remained relatively quite homogeneous. *Muscicapella* is but a very specialized offshoot of *Niltava*. The position of *Cyanoptila* and *Eumyias* is more uncertain; the former, which shows some similarities with *Niltava*, may have been derived independently from *Ficedula*, and *Eumyias*, though retaining the blue coloration of *Niltava*, represents another group of typically arboreal species which closely approach *Muscicapa*.

#### GENUS BRADORNIS SMITH

*Bradornis* SMITH, 1847, Illustrations of the zoology of South Africa, Aves, pl. 113. Type, by

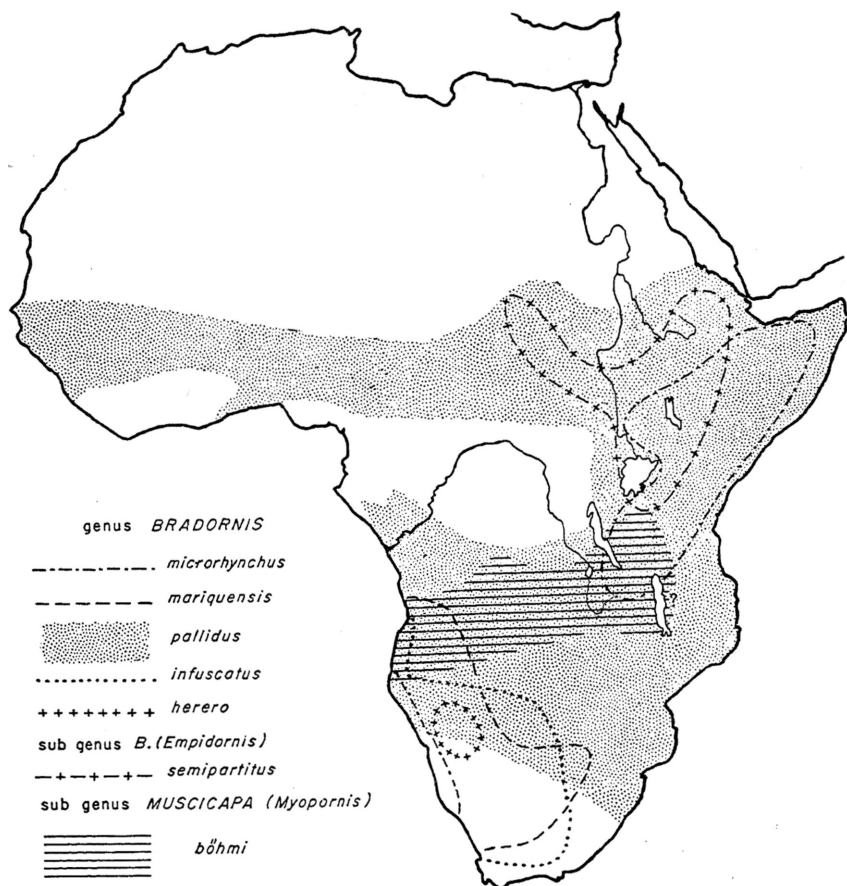


FIG. 8. Distribution of the genus *Bradornis* and of the subgenus *Muscicapa (Myopornis)*.

original designation, *Bradornis mariquensis* Smith.

*Bradyornis* SUNDEVALL, 1850, Övers. K. Vetensk. Akad. Förhandl. Stockholm, p. 106. *Nomen emendatum* for *Bradornis* Smith.

*Agricola* BONAPARTE, 1854, Compt. Rendus Acad. Sci. Paris, vol. 38, p. 6. Type, by original designation, *Saxicola infuscata* Smith [= *Bradornis infuscatus* Smith].

*Empidornis* REICHENOW, 1901, Jour. f. Ornith., vol. 49, p. 285. Type, by original designation, *Muscicapa semipartita* Rüppell.

*Haganopsornis* ROBERTS, 1922, Ann. Transvaal Mus., vol. 8, p. 225. Type, by original designation, *Bradornis infuscatus* Smith.

*Namibornis* BRADFIELD, 1935, Description of new races of Kalahari birds and mammals. (This publication, a privately printed and very rare leaflet published at Benoni, Union of South Africa, is reprinted in *The Auk*, 1936, vol. 53, p. 131.) Type, by original designation, *Bradornis herero* de Schauensee.

#### GENERAL DISTRIBUTION OF THE GENUS

This genus consists of five species (*micro-rhynchus*, *mariquensis*, *pallidus*, *infuscatus*, and *herero*), and one species (*semipartitus*) in the subgenus *Empidornis*. The distribution of these six species, which are restricted to the savannas and to the dry and more arid parts of the Ethiopian region, is shown in figure 8. The distribution of *Muscicapa* (*Myopornis*) *böhmi* is also shown in this figure, but the affinities of this species, which is briefly discussed below, seem to be with *Muscicapa* of which I consider it to form a subgenus. *Bradornis* is best represented in the arid regions of southwestern Africa, where four species occur.

#### CHARACTERS OF THE GENUS

**STRUCTURAL CHARACTERS:** This genus consists of medium-sized but rather large to large species (table 1). The tarsus is well scutellated anteriorly, relatively short proportionately, averaging (fig. 10) from about 20 to 25 per cent of the length of the wing. It is powerful and thick, and the claws are strong and large. The bill (fig. 9) is slender, attenuated, sharply ridged, strongly compressed laterally, and rather weakly hooked, and in *semipartitus* is proportionately slightly stouter. The opening of the nostril is oval and rather small and not concealed, or but slightly so; in *semipartitus* one or two short

bristles extend over the nostril. The rectal bristles are weak and short, hardly extending beyond the nostrils, and in *herero* are minute. The wing is rather long but rounded, the basic formula being 3, 4, 5, 6 subequal (usually 4=5 slightly longest, 3 slightly > or =6) >7>8, 2 subequal >9>10; 7=2 in the three specimens of *herero* examined and in some of the specimens of *mariquensis*; in *semipartitus* and *infuscatus* the wing is slightly more pointed, being 3=4=5 usually slightly >6 in *semipartitus* and 3=4=5 (or 3=4 slightly >5) >6> or =2 in *infuscatus*. The tail, which is squarish or slightly rounded in *Bradornis* proper, is very well rounded in *semipartitus* where the outer rectrices fall short of the longest by a distance about equal to the length of the tarsus.

**PATTERN AND PIGMENTATION:** In *Bradornis* proper the coloration is very drab. The upper parts are dull gray brown, darker brown on the wing and tail, and the under parts are creamy or dingy white, more or less washed with grayish or tawny or cinnamon in *infuscatus* and *herero*, the throat and center of the abdomen being whiter. In all the species there is a vaguely defined whitish area in front and above the lores which is sometimes prolonged, more or less well indicated, into a superciliary streak, this streak being best indicated in *herero*. A narrow whitish eye ring is present. The ear coverts vary from gray-brown to gray-brown very slightly tinged with rufous in *infuscatus* to chocolate brown in *herero*. The crown, and sometimes the mantle, are more or less faintly streaked with dusky. The lower throat, the breast, and the flanks are streaked in *herero* but not in the other species with the exception of one of the races of *infuscatus* which shows narrow and faint dusky shaft streaks on the breast, the streaks averaging about 1 to 1½ mm. in width on the breast of *herero* where they are broadest. The upper wing coverts, tertials, and secondaries edged with whitish or buff, the outer webs of the primaries edged with buff or dull rufous, the outer webs of the outer rectrices edged with whitish, buff, or dull rufous. In *herero* where the rufous pigments are best developed, the lower part of the mantle, the rump, the upper tail coverts, and the outer webs of the rectrices are dull rufous (cinna-

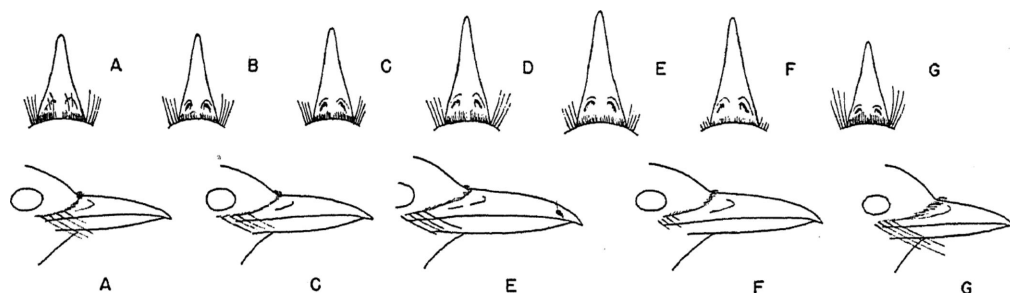


FIG. 9. Bill characters in the genus *Bradornis* and the subgenera *Empidornis* and *Myopornis*. A. *Bradornis* (*Empidornis*) *semipartitus*. B. *Bradornis microrhynchus*. C. *B. mariquensis*. D. *B. pallidus*. E. *B. infuscatus*. F. *B. herero*. G. *Muscicapa* (*Myopornis*) *böhmi*. Natural size.

mon). A slight tinge of this color also appears in *infuscatus*. The inner webs of the rectrices are dusky except for a dull rufous wedge of decreasing size at the tips of the outer rectrices. A color plate of *herero* is given by de Schauensee (1932), but in this plate the pattern and especially the shade of the rufous pigments are overemphasized; the rufous pigments are not bright chestnut as in my copy of this plate, but much duller,

cinnamon rufous, as stated in the original description of *herero* (1931).

The pattern and pigmentation of *semipartitus* are very different. This species is silvery gray above, including the sides of the face, and the whole of the under parts is bright orange-brown. This species has no whitish markings on the head and is not streaked, although a few faint dusky shaft streaks occasionally show on the crown.

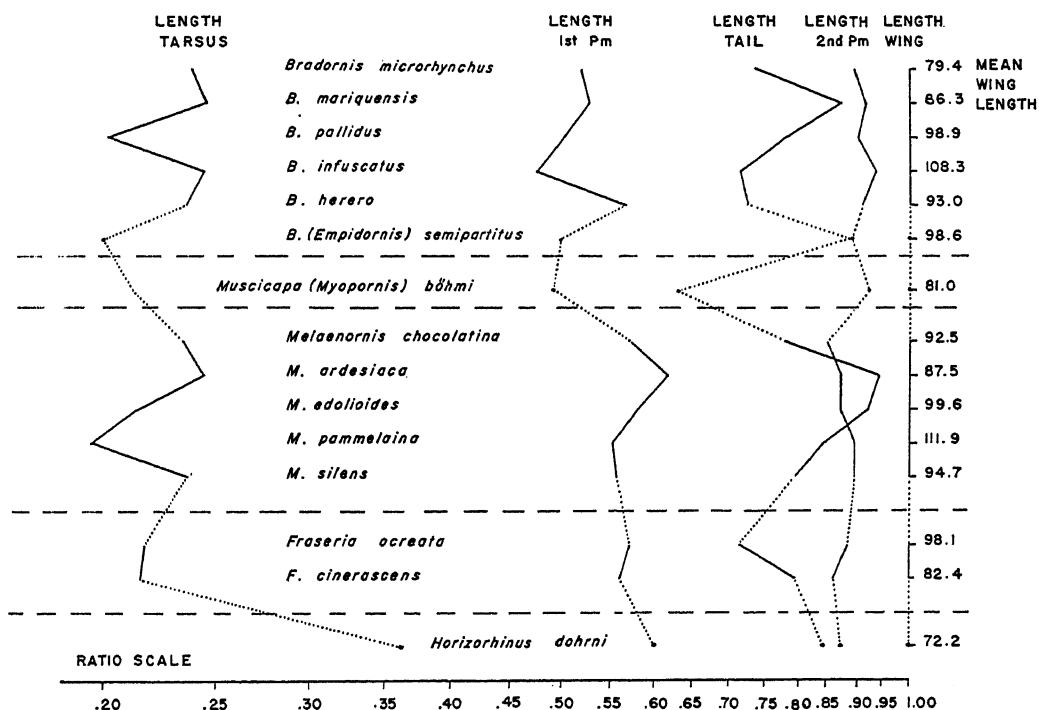


FIG. 10. Comparison through ratio diagram of the proportions in *Bradornis*, *Muscicapa* (*Myopornis*), *Melaenornis*, *Fraseria*, and *Horizorhinus*.

The sexes are alike in coloration in all the six species. The young of *herero* is not known. The young of the other species, including *semipartitus*, are well spotted.

**HABITS:** The habits of the six species are similar or differ but little. According to the literature, the birds perch rather low, on bushes or in the lower branches of trees from which they often drop to the ground to capture insects. De Schauensee (1931) found that *herero* "flitted from rock to rock, occasionally landing on the small bushes, which grew sparsely among the stones." Hoesch (1938) states that he has not observed this species perching on rocks and that it comes to the ground only to feed. All the authors agree that the species feed much on the ground. I have not found records of other types of feeding habits in *herero*, *infuscatus*, and *semipartitus*. The last is said to "run on the ground," *mariguensis* to "pick insects from the ground," and *pallidus* to "hop on the ground in search of insects and ants." Virtually nothing is recorded of *microrhynchus*, but presumably the habits of this species do not differ appreciably from those of its close relatives. However, although most of the food, perhaps the whole of it in the case of some species, is picked from the ground, *mariguensis* and *pallidus* also catch some of their food on the wing, darting from their perches in pursuit of flying insects. Some of the other species may do likewise or the feeding habits may vary according to local conditions, but at any rate the birds are not truly arboreal, for their big feet with their stout tarsus and their slender and compressed bill with its weak and short rectal bristles seem to be adaptations for ground feeding.

All the species seem to be shy or cautious and do not allow close approach. Four of the six species (*mariguensis*, *pallidus*, *infuscatus*, and *herero*) are said to associate in small parties consisting of some three to five individuals, and *microrhynchus* and *semipartitus* do perhaps likewise. The birds, with the possible exception of *semipartitus*, are usually silent other than for some whistling and scolding notes; *semipartitus* is said to have a song that is quite musical and pleasing but not very powerful. The nest, which is cup shaped and more or less well constructed, is placed not very high above the ground.

It is composed of twigs, rootlets, grasses, or straws and may be unlined or, in the cases of *microrhynchus* and *mariguensis*, may be lined with feathers. The breeding habits of *mariguensis*, *pallidus*, and *infuscatus* have been described by Vincent (1947). The nest of *herero* has not been described.

#### RELATIONSHIPS OF THE SPECIES

*Bradornis microrhynchus*, *mariguensis*, *pallidus*, and *infuscatus* are much alike in every way and are obviously very closely related. *B. herero* is more distantly removed but appears to come closest to *infuscatus* in which dull rufous (cinnamon) pigments are rather well developed, though less so than in *herero*. One of the races of *infuscatus* has also, as stated, some faint dusky shaft streaks on the breast.

Hoesch (1938) has stated that *herero* has little in common with the other four *Bradornis*, and Hoesch and Niethammer (1940) have gone so far as to remove *herero* from the Muscicapinae and to place it in the Turdinae, stating that Steinbacher has found upon dissection that *herero* is a thrush. Hoesch and Niethammer do not say in what the anatomical differences consist, and Steinbacher has, apparently, not published his findings. One may be permitted to doubt that details of the internal anatomy, which may be adaptive in character, separate with certainty the thrushes from the flycatchers. Externally, as well as in habits, some thrushes and flycatchers show a great resemblance. In a separate paper I have shown in detail (1952a) that in the small muscicapine genus *Rhinomyias* some species behave like flycatchers and others like thrushes. In a single species, indeed, some races of *R. gularis* are not separable morphologically from the flycatchers and others are indistinguishable from the true thrushes.

The only difference, much emphasized by Hoesch and Hoesch and Niethammer, which may be of some possible significance is the manner of flight. According to these authors, the flight of *herero* is wavy, and it is straight in the other *Bradornis*. This difference is not necessarily conclusive and does not justify the removal of *herero* to the Turdinae, since *herero* in virtually every character appears to be a typical *Bradornis*. De



Schauensee has stated (1932) that in the field *herero* is "very *Bradornis*-like," and that "the wing formula, proportion of tail, wings and [shape of the] beak make it evident that it cannot be placed anywhere else." To this may be added, as shown in the discussion of the characters of the genus, that it has the same feet and the same habits. In my opinion, de Schauensee was undoubtedly correct when, supported by Chapin, he described *herero* as a *Bradornis*. The relationship of *herero* to the other four *Bradornis* was thought by de Schauensee to be "rather obscure, the color pattern not resembling that of any other *Bradornis*." However, the pattern and coloration of *herero* are not truly different but seem to me to be an emphasis of a pattern and coloration that are foreshadowed by those of *infuscatus*.

In the case of *semipartitus* no close relation to any of the other *Bradornis* can be demonstrated. The differently shaped tail and the very different pattern and pigmentation seem to deserve subgeneric recognition, but the similarities in the other structural characters and the similarity of habits show conclusively, I believe, that it would be misleading to separate *semipartitus* from *Bradornis* by treating it as a monotypic genus. *E. semipartitus*, however, might equally well be treated as a subgenus of *Melaenornis*.

*Myopornis böhmi* was mentioned in the distribution of *Bradornis*. Its wing formula

is the same as in *Bradornis*, and the bill (fig. 9) is of the same shape though proportionately broader at the base and with longer bristles, but its tarsus is proportionately shorter than that of a *Bradornis* of the same general size; much more slender, and with weaker claws (in *B. microrhynchus* the wing length averages 79.4 and in *M. böhmi* 81.0). *M. böhmi* is also of more slender general build. These structural differences are correlated with habits, for *böhmii* does not come to the ground to feed. According to Benson (1940) "It has the erect posture and rather confiding habit of a typical flycatcher such as *Muscicapa*," and according to White (1943) it is a typical flycatcher in its habits. The affinities of *böhmii* being seemingly with *Muscicapa* rather than with *Bradornis*, I have placed it in *Muscicapa* but have retained it as a subgenus. The under parts of *böhmii*, which with their strange spotting are different from those of either *Muscicapa* or *Bradornis*, are illustrated in figure 23.

#### LIST OF THE SPECIES

##### *Bradornis microrhynchus* Reichenow

RANGE: East Africa from Northern Rhodesia to British Somaliland.

##### *Bradornis mariquensis* Smith

RANGE: Western south Africa from southern Angola to Great Namaqualand east to Cape Province, western Transvaal, and western Southern Rhodesia.

TABLE 1  
AVERAGE MEASUREMENTS IN THE GENUS *Bradornis* AND THE SUBGENUS *Empidornis*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess of 2d Over 10th Primary	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
Genus <i>Bradornis</i>										
<i>microrhynchus</i>	79.4	71.1	65.9	5.2	41.1	8.6	58.5	19.0	17.1	4.6
<i>mariquensis</i>	86.3	79.0	70.6	8.4	45.3	10.5	75.0	21.2	17.9	4.5
<i>pallidus</i>	98.9	89.3	78.2	11.1	49.7	8.9	77.3	20.1	19.0	4.9
<i>infuscatus</i>	108.3	101.0	81.5	19.5	51.3	4.3	77.0	26.4	22.0	5.4
<i>herero</i>	93.0	84.7	77.0	7.7	52.7	14.0	67.3	22.0	20.3	4.8
Subgenus <i>Empidornis</i>										
<i>semipartitus</i>	98.6	88.0	78.6	9.4	48.9	9.6	88.0	19.8	17.9	5.2

<sup>a</sup> Longest primary.

**Bradornis pallidus** Müller

RANGE: From Senegal east, in savannas, to Eritrea, Abyssinia, south in east Africa to Zululand, west to Damaraland, north to Angola, and the lower Congo.

**Bradornis infuscatus** Smith

RANGE: Southwestern Africa.

REMARK: For a recent revision of this species, see Vaurie (1952b).

**Bradornis herero** de Schauensee

RANGE: Southwest Africa (Damaraland).

**Bradornis (Empidornis) semipartitus** Rüppell

RANGE: Abyssinia and Anglo-Egyptian Sudan to northern Tanganyika.

GENUS **MELAENORNIS** GRAY

*Melasoma* SWAINSON, 1837, Birds of western Africa, pt. 1, p. 257, pl. 29. Type, by monotypy, *Melasoma edolioides* Swainson.

*Melaenornis* GRAY, 1840, A list of the genera of birds, p. 35. New name for *Melasoma* Swainson preoccupied by *Melasoma* Dillwyn, 1831, for a genus of Coleoptera.

*Melanopepla* CABANIS, 1850, Museum Heineanum, vol. 1, p. 54. Type, by monotypy, *Muscicapatronitens* Cabanis = *Bradyornis ater* Sundevall [= *Melaenornis pammelaina* Stanley].

*Sigelus* CABANIS, 1850, Museum Heineanum, vol. 1, p. 68. Type, by monotypy, *Lanius silens* Shaw.

*Dioptrornis* FISCHER AND REICHENOW, 1884, Jour. f. Ornith., vol. 32, p. 53. Type, by original designation, *Dioptrornis fischeri* Reichenow.

## GENERAL DISTRIBUTION OF THE GENUS

This genus consists of five species: *chocolatina*, *ardesiaca*, *edolioides*, *pammelaina*, and *silens*. *Melaenornis*, like *Bradornis*, to which it seems to be related, is restricted to the Ethiopian region but neither occurs in the rain forest, the distribution of *Melaenornis* avoiding, however, the more arid region where *Bradornis* is well represented.

## CHARACTERS OF THE GENUS

*Melaenornis* differs from *Bradornis* (including *Empidornis*) in coloration and pattern, but both genera have some structural characters in common, and the habits of their species are similar or rather similar.

STRUCTURAL CHARACTERS: As in *Bradornis*, the five species of *Melaenornis* are rather large to large (table 2) and have a similar tarsus. The tarsus of *Melaenornis* is well scutellated anteriorly, relatively short pro-

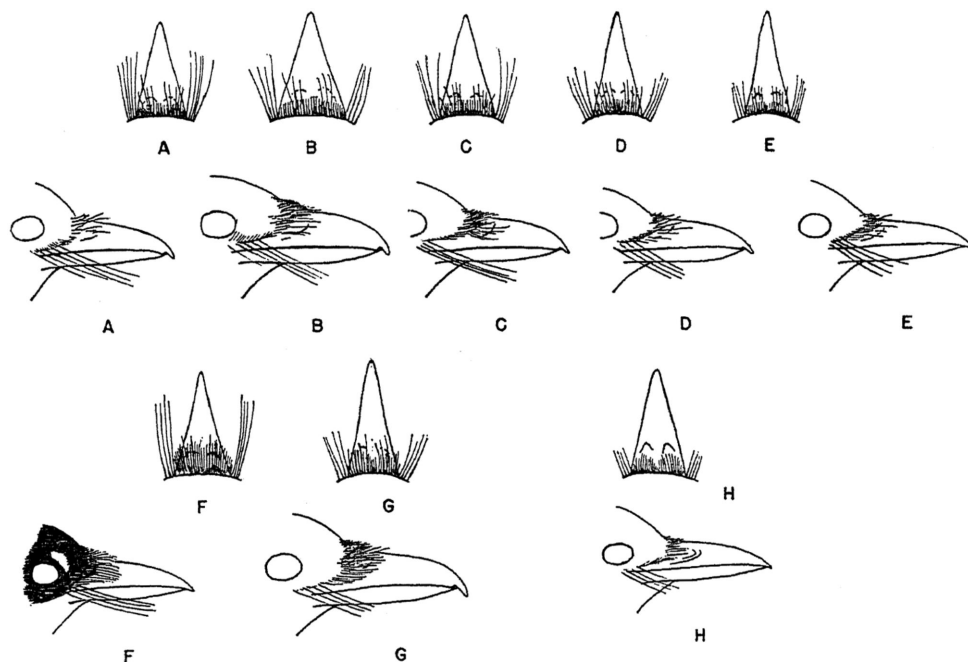


FIG. 11. Bill characters in the genera *Melaenornis*, *Fraseria*, and *Horizorhinus*. A. *Melaenornis chocolatina*. B. *M. ardesiaca*. C. *M. edolioides*. D. *M. pammelaina*. E. *M. silens*. F. *Fraseria cinerascens*. G. *F. ocreata*. H. *Horizorhinus dohrni*. Natural size.

portionately, averaging (fig. 10) from about 20 to 25 per cent of the length of the wing, but is powerful and thick, and the claws are strong and large. The shape of the bill and its feathering differ, however, from those of *Bradornis*. The bill (fig. 11) of *Melaenornis*, with the exception of that of *silens*, is broader at the base, less attenuated, more rounded (less sharply ridged and less compressed laterally), and rather more strongly hooked. The opening of the nostrils, except in *silens*, are better concealed, and the feathers at the base of the bill are well developed, much more so than in *Bradornis*. Short bristles (present but less well developed in *silens*) project over the nostrils, and the rictal bristles vary from moderately long but not very strong to long and strong, rictal bristles being notably short and weak in *Bradornis*.

The wing of *Melaenornis* is rounded and very similar in shape to that of *Bradornis*. The chief difference, which is a very slight one, is that the second primary tends to be shorter in *Bradornis* where 8 and 2 are subequal or occasionally  $7=2$  or  $6=2$  (see also tables 1 and 2). In *chocolatina*, *ardesiaca*, and *edolioides* the wing formula is  $4=5=6>3=7>8>9=2>10$ ; in *chocolatina*, 2 being slightly shorter is  $9>2$  slightly  $>10$  or  $2=10$ . In *pammelaina* the wing is a little more pointed, the formula being  $3=4=5$  slightly  $>6>7>2>8>9>10$ ; in *silens*, 3, 4, 5, 6 are subequal  $>7>8$ , 2 subequal  $>9>10$ . With the exception of *ardesiaca* where only three specimens are available the formula in all the other species often varies to  $4=5>3=6>7$ , etc. In *ardesiaca* a larger number of specimens would probably show the same variation.

The shape of the tail varies in *Melaenornis*. In *chocolatina* the tip is squarish or slightly rounded; in *ardesiaca* and *edolioides* it is well rounded, and the outer rectrices fall short of the longest by a distance about equal to the length of the tarsus. In *silens* the tail is rounded but less so than in *ardesiaca* and *edolioides*. In *pammelaina* the tail is slightly forked as in *Dicrurus ludwigii*. In *Bradornis* the tail is usually squarish but may be slightly rounded and in the subgenus *Empidornis* is very well rounded to about the same extent as in *ardesiaca* and *edolioides*. The shape of the tail may not be of phylogenetic

significance, for it is most abruptly different in the two species (*edolioides* and *pammelaina*) which are obviously very closely related.

The tail of *Melaenornis* tends to be longer proportionately (fig. 10) than that of *Bradornis* but in *semipartitus* and in *mariguensis* and *pallidus* in *Bradornis* proper, the tail is as long proportionately as in *Melaenornis*. The rest of the proportions are similar and, as stated, are exactly the same in the case of the tarsus.

**PATTERN AND PIGMENTATION:** Black and slate pigments predominate in *Melaenornis*. *M. ardesiaca*, *edolioides*, and *pammelaina* are slate or black above and below with no white in the plumage. *M. ardesiaca* is dark blue slate, *edolioides* is dull black or blackish slate without gloss, and *pammelaina* is blue-black with a metallic sheen and resembles *Dicrurus ludwigii* very strongly. *M. chocolatina* varies from dark slaty blue to brown above; the under parts are paler but of the same color as the back down to the level of the middle or lower breast and dull white from there down. In some of the races of this species a more or less restricted white area encircles the eye. The pattern of *silens* is the most varied; the upper parts are glossy black and the under parts white, the white, which is fairly clear on the throat, being tinged with grayish on the breast and flanks. The axillaries and the feathers at the bend of the wing are white, the wing and tail are black except in the following areas which are pure white: the outer webs of the tertials, the base of the secondaries and inner primaries, and (fig. 2) most of the basal half or two-thirds of the four outer rectrices.

The sexes are alike in coloration, or, in *edolioides* and *pammelaina*, the females are duller and browner, the dimorphism being best indicated in *silens* in which the female is dark brown and the male black. The young in all five species are well spotted. The young of *ardesiaca* has not been described in the literature and was unknown until recently, but Dr. Chapin kindly informs me that one of his correspondents writes that it is well spotted.<sup>1</sup>

**HABITS:** The habits of *Melaenornis* are similar to those of *Bradornis* (*Empidornis*

<sup>1</sup> This is confirmed by a specimen received when the present paper was in proof.

included), that is, *Melaenornis* hawks insects on the wing or picks them from the ground, but one gets the impression from the literature that *Melaenornis* feeds more on the wing than *Bradornis*. This impression seems to be supported by the shape of the bill which in *Melaenornis* is better adapted for catching insects on the wing. In *Melaenornis* the bill is or tends to be broader at the base, to be less compressed laterally, and even in *silens* is very much better supplied with rictal bristles.

The habits of *fischeri* (a race of *chocolatina*) are described as follows by Moreau (1936): "As a rule these Flycatchers occupy a perch several feet above the ground, but do not make purely aerial circular flights like an *Alseonax* or *Muscicapa*. They prefer to drop on their prey after the manner of a Drongo; but one was feeding on the ground beside a water-channel, hopping along, and occasionally flicking its tail like a Chat. The call and song are very much like those of a *Bradornis*, soft and sibilant." *M. edolioides* perches on bushes and small trees "now and again darting out, after the manner of a Drongo, at a passing insect, or settling on the ground to pick up a beetle," according to Jackson and Sclater (1938). Concerning *pammelaina*, Roberts (1942) states that this species "has a habit of perching on the projecting branches of large trees and much resembles the plainer-coloured *Bradornis* species in hawking insects or dropping to the ground to pick them up," adding that it is often mistaken for *Dicrurus ludwigii*. Vincent (1947) states that *pammelaina* "Like [*Bradornis*] is mostly a silent bird, usually seen in pairs, and has much the same habits." Roberts and Vincent both state that *silens* perches prominently on telegraph wires, fences, or projecting branches and hawks insects or picks them from the ground. The feeding habits of *ardesiaca* have not been described, but this species is said to be silent, to occur in small parties, and to perch conspicuously in the open.

All the species of *Melaenornis*, like those of *Bradornis*, apparently occur in pairs or small parties and are usually silent. The nest is cup shaped or a shallow bowl and is more or less well constructed of twigs, stems, dry leaves, straws, fibers, or other material and

is usually placed rather high in the fork of two branches; *edolioides* and *pammelaina* occasionally build their nests in a hollow, niche, or crevice in a tree and relined old nests of other birds.

#### RELATIONSHIPS

The authors quoted above have emphasized that *Melaenornis* and *Bradornis* are very similar in life, and in the discussion of characters I show that all the structural characters with the exception of the bill and its feathering are the same or tend to be similar. Despite the differences in coloration, *Bradornis*, *Empidornis*, and *Melaenornis* appear to be related, and the similarity in behavior suggests that this group of 11 species could be treated as one genus. This treatment, however, obscures the relationship of some of the species. For instance, the four species of *Bradornis* proper (*microrhynchus*, *mariquensis*, *pallidus*, and *infuscatus*), to which *herero* may be added, are obviously more closely related to one another than to the other species which, with the exception of *edolioides* and *pammelaina*, are not so closely related. On the other hand, a generic splitting based solely on the differences in coloration and pattern appears unsound in this case, for this would result in the recognition of at least five genera (*Bradornis* for five species, *Melaenornis* for three, and *Empidornis*, *Dioptrornis*, and *Sigelus* for one species each). These could be further subdivided if, based on some small peculiarities of coloration and structure, *Namibornis* is recognized for *herero*, *Agricola* for *infuscatus*, and a new genus is erected for *ardesiaca*, for, as Berlioz states (1936), this species is quite distinct from *edolioides* or *pammelaina*. It would lead much too far to recognize monotypic or oligotypic genera for 11 related species. I have divided them into two genera, recognizing a subgenus (*Empidornis*) for *semipartitus*. This subgenus, which I have placed in *Bradornis*, could perhaps be equally well placed in *Melaenornis*. In recognizing *Melaenornis*, however, I am guided by the fact that the species that I have placed under it seem to depart from *Bradornis*, and perhaps *Empidornis*, because they are somewhat more flycatcher-like in their habits.

In *chocolatina*, the species in *Melaenornis*

that seems closest to *Bradornis* proper, I include *fischeri* from east Africa and *brunnea* from Angola. Benson (1946) has already shown that the first two should be regarded as conspecific but *brunnea* should also be included, for all three are geographical representatives, the various races differing only in a matter of degree. *M. ardesiaca*, despite its uniform coloration, is not directly related to *edolioides* or *pammelaina* and may represent a link to the two species of *Fraseria* which are strictly restricted to the rain forest. This is suggested by its ecological requirements which are intermediate between those of *Fraseria* and *Melaenornis*; *ardesiaca*, though not truly a bird of the forest, occurs on its edges and in forest clearings and occupies a relatively small range in a fairly humid region west of the Albertine Rift.

Many authors have mentioned that the habits of *Melaenornis* are similar to those of drongos, and, of course, the resemblance between *pammelaina* and *Dicrurus ludwigii* is so very striking that the two are often confused in the field, and the great similarity, even in skins, is remarkable. In my review of the Dicruridae (1949) I stated that their nearest relatives are in doubt, but that there was "no difficulty in recognizing any member of this family as a drongo." This statement is still true, generally speaking, but after reading about the habits of *Melaenornis* and comparing *pammelaina* and *D. ludwigii* I am less sure that this applies to this drongo. The genus *Dicrurus* has 10 tail feathers, but the primitive drongo of New Guinea (*Chaetorhynchus papuensis*) has 12 tail feathers as in the flycatchers, and *divaga* (a pure synonym of *papuensis*) was described as a flycatcher. It must be noted that there are no significant structural differences between *Melaenornis* and the more primitive drongos, and that the texture of the plumage, which is less soft in the drongos than in the flycatchers, is just as soft in *pammelaina* and *ludwigii*, and its metallic sheen is the same.

The drongos, perhaps on account of their metallic plumage or ornamental feathers, have been placed near the top of the classification of bird families, among or next to the crow-like birds, and Mayr and Amadon (1951) have recently placed them in the same group as the orioles and starlings, though

stating that these groups are not necessarily related. The possibility that the drongos are descended from a group of primitive flycatchers, such as the present-day *Melaenornis*, in which the typical flycatcher habits are not fully developed, deserves consideration. A study of the Dicruridae shows very definitely that the development of the metallic gloss, its distribution, and the development of ornamental appendages are secondary characters which have arisen independently several times in the family as a series of successive steps that still can easily be traced.

#### LIST OF THE SPECIES

##### *Melaenornis chocolatina* Rüppell

RANGE: East Africa from Abyssinia to central Nyasaland (Dezda), eastern Katanga, and Angola.

##### *Melaenornis ardesiaca* Berlioz

RANGE: Mountain slopes (about 5000 to 7000 feet) west of Lake Edward and Ruzizi Valley.

##### *Melaenornis edolioides* Swainson

RANGE: Senegal east, in savannas, to Abyssinia, south to Lake Victoria.

##### *Melaenornis pammelaina* Stanley

RANGE: Eastern Cape Province north through Ngamiland to Angola, lower and middle Congo, and east Africa north to north central Kenya.

##### *Melaenornis silens* Shaw

RANGE: South Africa from Capetown to Natal, Transvaal, and Bechuanaland.

#### GENUS *FRASERIA* BONAPARTE

*Fraseria* BONAPARTE, 1854, Compt. Rendus Acad. Sci., Paris, vol. 38, pp. 386, 536. Type, by original designation, "*Tephrosia ochreata*, Strickland."

*Eucnemidia* HEINE, 1860, Jour. f. Ornith., vol. 8, p. 134. Type, by subsequent designation, Sharpe, 1877, Catalogue of the . . . birds in the . . . British Museum, vol. 3, p. 303, *Fraseria ochreata* (sic) Strickland.

#### DISTRIBUTION AND CHARACTERS

This genus consists of two species (*occreata* Strickland and *cinerascens* Hartlaub) which are strictly restricted to the rain forests of western and central Africa. The first species ranges from Sierra Leone to Fernando Po, northern Angola, the Congo, and Uganda;

*cinerascens*, from Portuguese Guinea to the lower Congo, southern Kasai, and the lower Ituri and Uelle rivers.

**STRUCTURAL CHARACTERS:** These two species differ from each other in some structural characters, but both fall within the range of structural variation of *Melaenornis*. *F. ocreata* is fairly large (table 2), robustly built, with a shrike-like head and beak and a very thick tarsus with large claws. *F. cinerascens* is medium sized, more slender throughout, with a proportionately thinner tarsus and weaker claws, and its beak (fig. 11), though broader at the base, is less heavy, feebly hooked, and more highly ridged though less compressed laterally. All the other structural characters of *ocreata* and *cinerascens* are similar: proportions (fig. 10), feathering of the bill, scutellation of the tarsus, shape of the tail, and wing formula. The bill is well feathered at the base, with well-developed bristles over the nostrils and with moderately long to long but rather weak rictal bristles. The tarsus is usually well scutellated anteriorly, but in some specimens the scutes may be hardly visible. The tail is slightly rounded. The basic wing formula is  $4=5$  slightly  $>3=6>7>8>2>9>10$ , in *ocreata* 2 and 8 or 2 and 9 are sometimes equal, and in *cinerascens* 2 and 9 are subequal.

As stated, these structural characters are similar to, or differ very little from, those of

*Melaenornis*. The proportions are the same, though generally speaking the tail tends to be longer in *Melaenornis*. The basic wing formula is the same. In *Melaenornis* (see this genus) the tail may be slightly rounded. *F. ocreata* is robustly built but no more so than *M. ardesiaca*; both have a thick tarsus, a thick head, and a heavy beak (fig. 11), though in *ardesiaca* the bill is broader and rounder. *F. cinerascens* and *M. chocolatina* have a similar build and tarsus, and the shape of the bill (fig. 11) does not differ appreciably, though it is usually somewhat less heavily feathered at the base in *chocolatina*.

**PATTERN AND PIGMENTATION:** The pattern and pigmentation of the two species are virtually identical. They are slaty above and white below, the feathers of the lower throat and breast having crescentic slaty margins which give these parts a squamated appearance. The only difference consists of the presence in *cinerascens* of a small but conspicuous white patch above the lores and in front of the eye. Some species of *Melaenornis* are slaty above but are not squamated below. In *Fraseria*, the sexes are identical in coloration, and the young are well spotted.

**HABITS:** I have not been able to find a clear statement on how these two species capture their insect prey, but to judge from their forest habitat it must be inferred that

TABLE 2  
AVERAGE MEASUREMENTS IN THE GENERA *Melaenornis*, *Fraseria*, AND *Horizorhinus*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess of 2d Over 10th Primary	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
Genus <i>Melaenornis</i>										
<i>chocolatina</i>	92.5	78.5	77.9	0.6	52.9	14.2	72.2	21.7	18.3	4.9
<i>ardesiaca</i>	87.5	76.0	73.0	3.0	54.0	17.0	82.5	21.4	19.5	6.6
<i>edoloides</i>	99.6	86.5	83.8	2.7	57.5	16.3	91.7	21.4	19.0	5.2
<i>pammelaina</i>	111.9	100.1	89.2	10.9	61.6	16.4	94.2	21.9	19.2	5.3
<i>silens</i>	94.7	84.6	75.6	9.0	52.6	13.4	75.4	22.4	19.7	5.0
Genus <i>Fraseria</i>										
<i>ocreata</i>	98.1	86.9	83.4	3.5	56.0	15.3	70.1	21.3	21.0	5.7
<i>cinerascens</i>	82.4	70.8	69.2	1.6	46.1	13.1	65.5	17.8	18.1	5.9
Genus <i>Horizorhinus</i>										
<i>dohrni</i>	72.2	62.9	62.6	0.3	43.2	15.8	60.8	26.1	18.6	5.1

<sup>a</sup> Longest primary.

they feed only on the wing. *F. cinerascens* is apparently restricted to river banks where stolidly and silently it perches over the water on overhanging branches or roots. Bates (1930) compares it to a little kingfisher, though its food, of course, is insects. It may, however, occasionally occur in the forest undergrowth away from streams where it was collected once by Chapin (in press). *F. ocreata* is apparently arboreal. Bates (1930) states that it "is found in the trees on swampy borders of streams in the forest," and Chapin (in press) states that "in the Ituri Forest it was noted usually in parties of three to six about the edges of old plantations or in tall trees even in the uncut forest." Chapin adds that, although its food usually consists of insects, some of the specimens he collected had eaten fruits. *F. cinerascens* is said to be very silent, but *ocreata* is said to be noisy, its note usually consisting of a peculiar buzzing sound, occasionally with snatches of a varied musical song and imitations of other birds. The nest of *ocreata*, according to Bates, is composed of rough rootlets and has been found in knotholes and in the forks of trees. I have found no description of the nest of *cinerascens*.

#### RELATIONSHIPS

These two species appear to be very closely related, but Chapin, who has skinned both, tells me that he was impressed that they are more distinct than their great external resemblance would lead one to believe. The differences, which are described above, appear, however, to be of no more than specific importance. They are no greater, or even are less well marked, than the differences that separate any two species of *Melaenornis*. Compare, for instance, the two most closely related species of *Melaenornis*, *pammelaina* and *edolioides*, which are obviously very closely related to each other; *pammelaina* has a forked tail and a glossy plumage, and *edolioides* has a well-rounded tail and a dull plumage.

In my opinion *F. ocreata* and *cinerascens* appear to be related to *Melaenornis*, to which they seem to be linked through *M. ardesiaca*. They cannot be separated generically from *Melaenornis* on the basis of structural characters, and, although their under parts are

squamated and those of *Melaenornis* are not, a generic separation solely on the basis of pattern appears to be unsound in this case. If *Fraseria* and *Melaenornis* are separated on this basis alone, there is no reason, as stated under *Melaenornis*, why all the variations in pattern and coloration in this genus cannot be made the basis for the recognition of a number of monotypic or oligotypic genera.

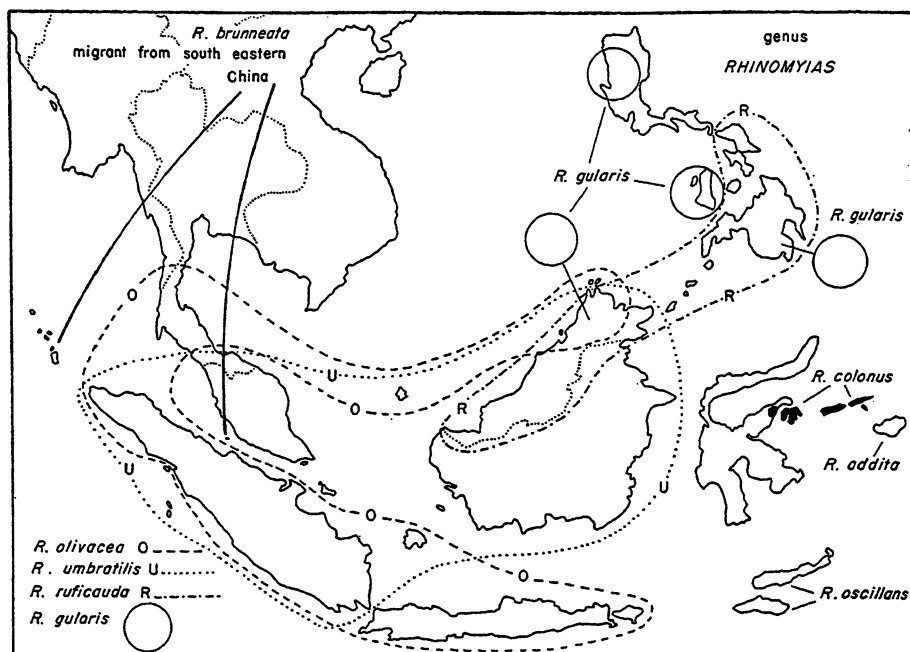
A valid generic separation of *Fraseria* and *Melaenornis* can, however, be defended on the basis of ecology. *F. ocreata* and *cinerascens*, having shifted into a major new ecological niche (from savannas and ground-feeding habits to the rain forest and arboreal habits), may be recognized as a new genus (see Mayr, 1952). The facts that *ocreata* still seems to be close to *M. ardesiaca* and that both *ocreata* and *cinerascens* have not become well differentiated structurally from *Melaenornis* may show that the separation is a fairly recent one.

#### GENUS *HORIZORHINUS* OBERHOLSER

*Cuphopterus* HARTLAUB, 1866 (June), Proc. Zool. Soc. London, p. 326. Type, by original designation and monotypy, *Cuphopterus dohrni* Hartlaub.

*Horizorhinus* OBERHOLSER, 1899, Proc. Acad. Nat. Sci. Philadelphia, vol. 51, p. 216. New name for *Cuphopterus* Hartlaub, preoccupied by *Cuphopterus* Morawitz, 1866 (January), for a genus of Hymenoptera.

This puzzling monotypic genus, which is restricted to Principe Island in the Gulf of Guinea, is of very uncertain affinities. Usually placed in the babblers (Sclater, 1930; Bannerman, 1936), it is considered to be a flycatcher by Delacour (1946a), and Amadon (1953), although he considers that it is possibly an aberrant member of the Muscapinae, has suggested that "the possibility that it is a thrush deserves consideration." According to Dohrn (1866) its habits, and according to Snow (1950) its manner of feeding, are those of a warbler. It may provisionally be kept in the flycatchers next to *Sigelus* (included by me in *Melaenornis*) and *Fraseria* where Delacour has placed it, and where, tentatively, Amadon has retained it. In my opinion, however, its affinities are not with these two genera, and it seems to have little in common with the other Muscapinae included in this

FIG. 12. Distribution of the genus *Rhinomyias*.

study. Chapin informs me that although he thought once that it might be a flycatcher he now very strongly believes that it is a babbler.

#### CHARACTERS

The sexes are identical in coloration. The young has not been described, and the very young has not been examined by me, but an undoubted juvenal collected by Correia on September 26 is not spotted or streaked. In the adult the whole of the upper parts and sides of the face are gray-brown tinged with olive, and the under parts are creamy white with a faint yellowish tinge and with a pectoral band of olive brown, this pigment extending to the flanks and "thighs." The bill (fig. 11) is attenuated but is neither very well broadened at the base nor compressed laterally. It is very feebly hooked, the nostrils are exposed, the frontal feathers being very poorly developed and without antrorse bristles, and the rictal bristles are short and weak. The tarsus, which is poorly scutellated anteriorly and rather slender, is relatively very long, averaging (fig. 10) a little more than 36 per cent of the length of the wing. In all the other *Muscipinae* included in this study, with the exception of the aberrant

*Newtonia*, the proportions of the tarsus do not exceed 30 per cent of the length of the wing. The wing is very rounded, the formula being 3, 4, 5, 6, 7, subequal (or  $4=5=6>3=7>8>9>10=2$  or 2 very slightly  $>10$ ).

According to Snow (1950) *H. dohrni* occurs in many varied habitats, feeds like a warbler at all levels in bushes and trees but avoids the ground. It sings a great deal, the song being loud and melodious. The nest is a plain cup of dead grass, with a thin bottom and no lining. The nest described by Snow was 11 feet up in the fork of a small bough. The nests described by Dohrn (1866) were in bushes from 4 to 8 feet high and were built like those of a *Sylvia*.

The average measurements of *H. dohrni* are given in table 2. A to me uncharacteristic drawing of this species is given by Bannerman (1936, fig. 34), but a good color plate is given by Dohrn (1866, pl. 34).

#### GENUS RHINOMYIAS SHARPE

*Rhinomyias* SHARPE, 1879, Catalogue of the ... birds in the ... British Museum, vol. 4, p. 367. Type, by subsequent designation, Mathews, 1930, *Systema avium Australasianarum*, p. 499, *Alcippe pectoralis* Salvadori = *Rhinomyias umbratilis* Strickland.



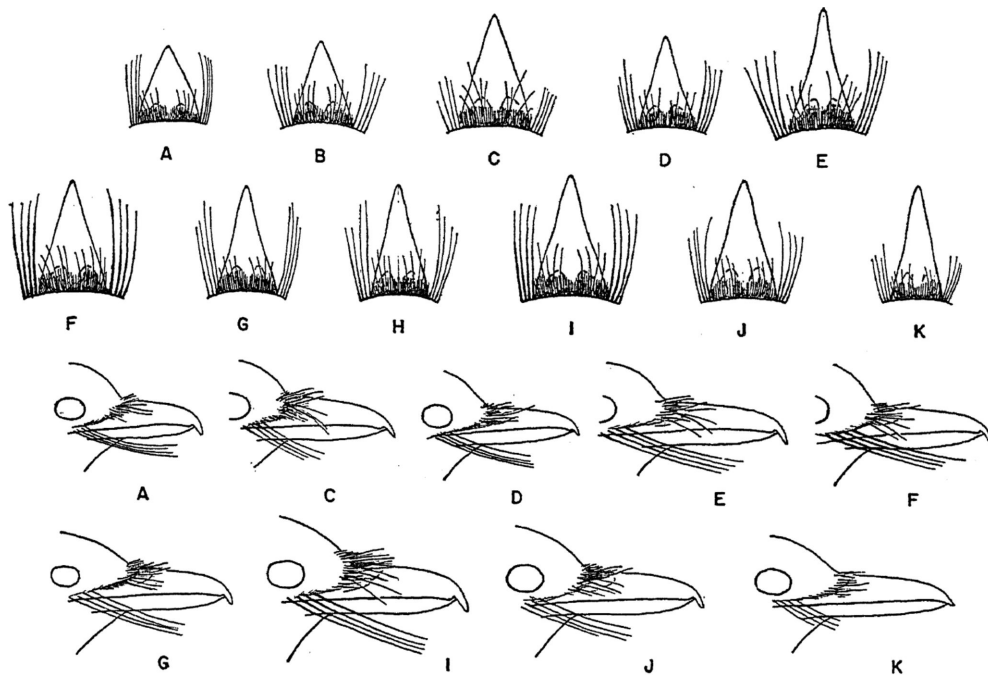


FIG. 13. Bill characters in the genus *Rhinomyias*. A. *R. addita*. B. *R. oscillans oscillans*. C. *R. oscillans stresemanni*. D. *R. olivacea*. E. *R. brunneata*. F. *R. umbratilis*. G. *R. ruficauda*. H. *R. colonus*. I. *R. gularis albigularis*. J. *R. gularis gularis*. K. *R. gularis insignis*. Because geographical variation is marked in *oscillans* and *gularis*, the bill characters of their races are figured separately. Natural size.

*Addoea* MATHEWS, 1925, Bull. Brit. Ornith. Club, vol. 45, p. 93. Type, by original designation, *Microeca addita* Hartert.

*Olcyornis* BAKER, 1930, The fauna of British India, vol. 7, p. 137. Type, by original designation, *Cyornis olivacea* Hume.

#### GENERAL DISTRIBUTION OF THE GENUS

This genus has been reviewed in a detailed preliminary paper (Vaurie, 1952a). It consists of eight species, seven of which are Indo-Malayan and non-migratory and one (*brunneata*) which breeds in eastern China from Chekiang south to Kwangtung and Kwangsi and migrates to winter in the Nicobars and lower Malay Peninsula. The distribution is shown in figure 12.

#### CHARACTERS OF THE GENUS

**STRUCTURAL CHARACTERS:** This genus consists of medium-sized to rather large species (table 3), one of which is rather heavily built. The tarsus is not scutellated anteriorly, or shows but a trace of one or two scutes and is relatively slender with rather weak

claws; it is relatively short, averaging between 21 and 25 per cent of the length of the wing, but in one species (*gularis*) it becomes moderately long, the proportions (fig. 14) of the tarsus ranging in the various races of this species from about 22 to 30 per cent of the length of the wing. The bill (fig. 13) is broadened at the base and is more or less attenuated, rather flattened but usually well ridged, moderately or well hooked, well feathered at the base, with very well-developed antrorsal bristles; the nostrils are concealed; and the rictal bristles are long and strong, sometimes very strong. In *gularis*, in which most characters vary geographically, the bill becomes strongly compressed laterally, feebly hooked, and the bristles are weaker. (For a detailed analysis of the geographical variations in this interesting species, see my 1952a paper.) The tail is squarish. The wing is rounded, even in the migratory *brunneata*, the basic formula of the genus being  $4=5>3=6>7>8>9>2>10$  which may vary individually to  $4=5=6>7>3>8>9>2>10$ . Sometimes,

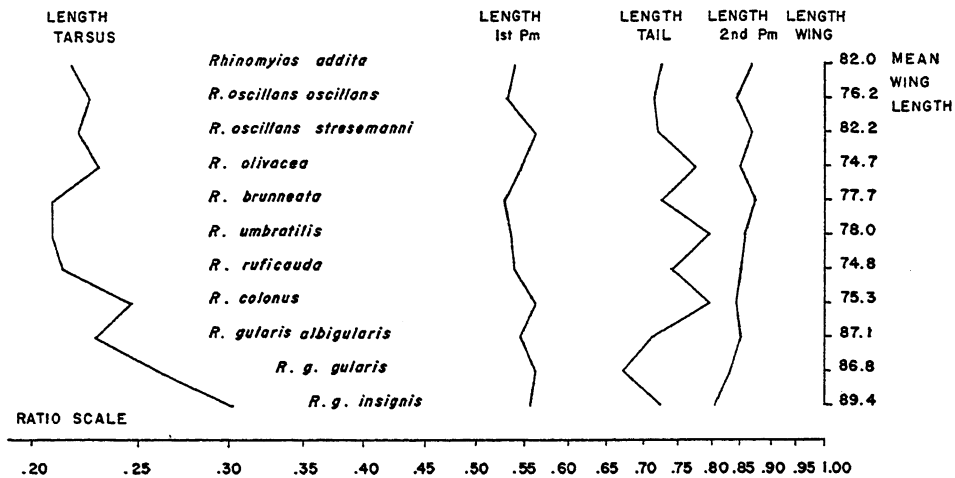


FIG. 14. Comparison through ratio diagram of the proportions in *Rhinomyias*. The races of *oscillans* and those of *gularis* are shown separately, because geographical variation is very marked in the latter species.

2 = 10 or in nominate *gularis* averages slightly shorter than 10.

**PATTERN AND PIGMENTATION:** The pattern is simple and together with the pigmentation is quite uniform, the exceptions being in *addita*, *oscillans*, and *gularis*. In all the species, with the exception of *R. gularis goodfellowi*, which is dark slate, the upper parts and sides of the face are rufous brown more or less tinged with gray or olive, the tail varying from chocolate brown to rather bright reddish chestnut. With the exception of *addita* and nominate *oscillans* a more or less distinct buffy, grayish, or whitish loreal spot is present, or in *gularis* is lacking but replaced by a superciliary streak which is buffy or in some races is pure white and very conspicuous. The under parts are dingy white or white and are more or less heavily pigmented on the flanks; in six species the white of the throat and breast is separated by a vaguely or very well-indicated pectoral band varying in width. The pigments of this band and of the flanks vary from gray-brown to olive brown or rufous olive or, in *R. gularis insignis*, to bright red-fawn. In *oscillans* and *addita* there is no pectoral band. In *oscillans* the throat and breast are uniform gray with a slight trace of whitish on the center of the throat; in *addita* these parts are whitish much washed with gray, and the center of the feathers, being darker, form faint but distinct streaks.

The sexes are identical in coloration. The young of *addita* and *oscillans* are apparently unknown. The young of *olivacea*, *brunneata*, *ruficauda*, *colonus*, and *gularis* are well spotted. No very young specimen of *umbratilis* has been examined, and apparently none are reported, but in a first year bird there are still one or two large spots on the crown, and the upper wing coverts are tipped with rufous.

**HABITS:** The habits are not too well known, but some species (*addita*, *olivacea*, and *umbratilis*) apparently behave like typical flycatchers and hawk insects from the tree tops, while the others are dwellers of the thick undergrowth where they may occasionally feed on the ground. *R. oscillans* (Vaurie, 1952a) is a bird of neither the tree tops nor the undergrowth. It perches under cover in trees and bushes and has been observed feeding on the ground. Its food, as in the case of *ruficauda* and perhaps other *Rhinomyias*, includes fruit as well as insects. The song has not been described except in *brunneata* where it is said to be short but powerful. The only nest described is that of *R. gularis albigularis*. In this form the nest is composed of moss and is lined with fine roots, and the only nest found was placed in a hole of an old rotten tree 6 feet from the ground. The clutch consisted of two eggs which resembled those of the Common Robin.

TABLE 3  
AVERAGE MEASUREMENTS IN THE GENUS *Rhinomyias*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess or Deficit of 2d Over 10th Primary	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
<i>addita</i>	82.0	71.0	67.0	4.0	44.0	10.4	59.4	17.8	15.9	6.5
<i>oscillans</i> <sup>b</sup>	76.2	64.2	63.2	1.0	40.5	9.0	54.5	17.2	15.8	6.2
<i>stresemanni</i>	82.2	71.0	67.5	3.5	46.0	12.6	59.0	18.1	18.1	6.8
<i>olivacea</i>	74.7	63.2	61.4	1.8	40.7	11.7	58.0	17.2	16.3	5.9
<i>brunneata</i>	77.7	67.6	62.8	4.8	40.9	8.2	56.2	16.2	18.6	6.5
<i>umbratilis</i>	78.0	66.6	65.0	1.6	41.5	11.7	62.0	16.3	18.0	6.4
<i>ruficauda</i>	74.8	63.5	61.6	1.9	40.2	10.9	55.1	15.9	17.5	6.0
<i>colonus</i>	75.3	63.4	62.1	1.3	42.2	12.3	60.0	18.5	17.6	5.7
<i>albigularis</i>	87.1	73.6	71.8	1.8	47.5	13.3	61.8	19.9	19.6	7.0
<i>gularis</i> <sup>b</sup>	86.8	72.2	73.6	-1.4	48.7	15.9	58.0	22.5	20.1	5.9
<i>insignis</i>	89.4	72.2	68.0	4.2	49.6	14.8	64.4	27.0	20.1	4.7

<sup>a</sup> Longest primary.

<sup>b</sup> *Rhinomyias oscillans* and *R. gularis* vary geographically. The races of *oscillans* (nominate *oscillans* and *oscillans stresemanni*) and the races of *gularis* (nominate *gularis*, *gularis albigularis*, and *gularis insignis*) are tabulated separately.

#### RELATIONSHIPS

The interspecific relationships have been discussed in my 1952a paper.

The exact position of the genus is uncertain as stated in the discussion of phylogeny. Wolters (1950) has stated that *Rhinomyias* cannot be separated generically from *Muscicapa* for, in his opinion, *Rhinomyias* is "a primitive group which in some ways unites the gray flycatchers [*Muscicapa*] with the other *Muscicapa* species," and in his diagram of relationships he places *Rhinomyias* between the "*Bradornis* Group" and the many other genera reduced in this paper to *Ficedula*, *Niltava*, and *Muscicapa*. This arrangement, which I follow, seems to be sound, but *Rhinomyias* may, as stated, represent an independent evolutionary line, for in my opinion it is not manifestly derived from the *Bradornis* group or a *Bradornis*-like ancestor.

Similarity in coloration between *Rhinomyias* and the species of the *platenae* group of *Ficedula* may possibly indicate that *Rhinomyias* is an offshoot of *Ficedula*, the *platenae* species and some *Rhinomyias* being also dwellers of the undergrowth. On the other hand, other *Rhinomyias* are typically arboreal, and one species is streaked below as in *Muscicapa*,

and if the thrush-like races of *R. gularis* are excepted, the bill of *Rhinomyias* is more typically flycatcher-like than that of *Ficedula*. Nevertheless, if *Rhinomyias* is related to the *Muscicapa* group of genera, it is more likely to have been derived from the more diversified *Ficedula* than from *Muscicapa* which seems to represent the peak of a specialized evolutionary line.

#### LIST OF THE SPECIES

##### *Rhinomyias addita* Hartert

RANGE: The highlands of Buru.

##### *Rhinomyias oscillans* Hartert

RANGE: Flores and Sumba.

##### *Rhinomyias olivacea* Hume

RANGE: Southern Tenasserim and peninsular Siam, Sumatra, Billiton, Java, Bali, North Natunas, northern Borneo, Balambangan, and Banguey Islands off northern Borneo.

##### *Rhinomyias brunneata* Slater

RANGE: Eastern China from Chekiang south to Kwangtung and Kwangsi; migrates to Malay States and Nicobars.

##### *Rhinomyias umbratilis* Strickland

RANGE: Malay Peninsula south of Trang, Sumatra, western Sumatran islands (Batu and

Mansalar), Lingga, Billiton, Karimata, North Natunas, the whole of Borneo except the mountains of the north.

**Rhinomyias ruficauda** Sharpe

RANGE: Philippines (Samar, Leyte, Bohol, Mindanao, Basilan, Sulus), northern and western Borneo.

**Rhinomyias colonus** Hartert

RANGE: Sulas, Peling, and eastern peninsula of Celebes.

**Rhinomyias gularis** Sharpe

RANGE: Philippines (mountains of northern Luzon, Negros, Guimaras, mountains of eastern Mindanao), and mountains of northern Borneo.

GENUS **FICEDULA** BRISSON

*Ficedula* BRISSON, 1760,<sup>1</sup> Ornithologia, vol. 3, p. 369. Type, by tautonymy, "*Ficedula*" = *Motacilla hypoleuca* Pallas.

*Stoparola* BLYTH, 1836, in White, The natural history of Selborne, p. 119. Type, by monotypy, *Stoparola luctuosa* Scopoli [= *Ficedula hypoleuca* Pallas].

*Siphia* HODGSON, 1837, India Rev., vol. 1, p. 651. Type, by monotypy, *S. strophilata* Hodgson (this paper not available).

*Erythrosterina* BONAPARTE, 1838, A geographical and comparative list of the birds of Europe and North America, p. 25. Type, by monotypy, *Muscicapa parva* Bechstein.

*Dimorpha* HODGSON, 1841, Jour. Asiatic Soc. Bengal, vol. 10, p. 29. New name for *Siphia* Hodgson.

*Muscicapula* BLYTH, 1843, Jour. Asiatic Soc. Bengal, vol. 12, p. 939. Type, by subsequent designation, Gray, 1855, Catalogue of the genera and sub-genera of birds... in the... British Museum, p. 52, "*Muscicapa saphira* Tickell" [= *saphira* Blyth].

*Synornis* HODGSON, 1844, in Gray, The zoological miscellany, p. 83. Type, by monotypy, *Muscicapa leucura* [= *Ficedula parva albicilla* Pallas].

*Digenea* HODGSON, 1845, Proc. Zool. Soc. London, p. 26. Type, by subsequent designation, Gray, 1855, Catalogue of the genera and sub-genera of birds... in the... British Museum, p. 146, *Digenea tricolor* Hodgson.

*Hedymela* SUNDEVALL, 1846, Övers. K. Vetensk. Akad. Förhandl. Stockholm, p. 225 (this paper

not available). Type, [by?], *Muscicapa atricapilla* Linnaeus [= *Ficedula hypoleuca* Pallas].

*Anthipes* BLYTH, 1847, Jour. Asiatic Soc. Bengal, vol. 16, p. 122. Type, by monotypy, *A. gularis* Blyth = *Dimorpha* ? *monileger* Hodgson [= *Ficedula monileger* Hodgson].

*Zanthopygia* BLYTH, 1847, Jour. Asiatic Soc. Bengal, vol. 16, p. 123. Type, by subsequent designation, Gray, 1855, Catalogue of the genera and sub-genera of birds... in the... British Museum, p. 53, *Zanthopygia leucophrys* Blyth [= *Ficedula zanthopygia* Hay].

*Cyanoptila* BLYTH, 1847, Jour. Asiatic Soc. Bengal, vol. 16, p. 124. Type, by monotypy, *C. cyanomelana* Temminck.

*Oreicola* BONAPARTE, 1854, Compt. Rendus Acad. Sci., Paris, vol. 38, p. 6. Type, by subsequent designation, Gray, 1855, Catalogue of the genera and sub-genera of birds... in the... British Museum, p. 143, *Saxicola pyrrhonota* Müller [= *Ficedula timorensis* Hellmayr, see Mayr (1944)].

*Charidhylas* BONAPARTE, 1854, Compt. Rendus Acad. Sci., Paris, vol. 38, p. 651. Type, by original designation, *Muscicapa hylocharis* Temminck and Schlegel [= *Ficedula narcissina* Temminck and Schlegel].

*Menetica* CABANIS, 1866, Jour. f. Ornith., vol. 14, p. 391. New name for *Siphia* Hodgson.

*Dendrobiastes* SHARPE, 1877, Trans. Linnean Soc. London, ser. 2, vol. 1, p. 332. Type, by original designation, *Dendrobiastes basilanica* Sharpe.

*Erythromyias* SHARPE, 1879, Catalogue of the... birds in the... British Museum, vol. 4, p. 199. Type, by subsequent designation, Salvadori, 1889, Aggiunte alla Ornithologia della Papuasie e delle Molucche, p. 83, *Saxicola dumetoria* Wallace.

*Poliomyias* SHARPE, 1879, Catalogue of the... birds in the... British Museum, vol. 4, p. 201. Type, by subsequent designation, Salvadori, 1881, Ornithologia della Papuasie e delle Molucche, vol. 2, p. 81, *Motacilla luteola* Pallas [= *Ficedula mugimaki* Temminck].

*Dammeria* HARTERT, 1899, Bull. Brit. Ornith. Club, vol. 8, p. 57. Type, by original designation, *Dammeria henrici* Hartert.

*Takatsukasaia* HACHISUKA, 1935, The birds of the Philippine Islands, pt. 4, p. 296. Type, by original designation, *Siphia platenae* Blasius.

GENERAL DISTRIBUTION OF THE GENUS

This genus consists of 26 species and of one monotypic subgenus (*Cyanoptila*) which is discussed below. Of the 26 species, six are Palearctic, 19 are Indo-Malayan, one of them reaching the Moluccas, and another is restricted to the Moluccas. The Palearctic species are highly migratory, four of these six

<sup>1</sup> Not preoccupied by *Ficedula* Moehring, 1758 (Geschl. Vogeln, pp. 2, 26). This name, cited by Sherborn (1902, Index animalium, p. 365), is not tenable, for the 1758 edition is an exact copy of the original edition of Moehring (published in 1752) and is therefore, according to Opinion 57 of the International Code of Zoological Nomenclature, not entitled to consideration under the Law of Priority.

species migrating in winter to Indo-Malaya, the other two (*hypoleuca* and *albicollis*) migrating to central Africa.

#### GENERAL CHARACTERS AND COMPARISON OF *Ficedula* WITH *Muscicapa*

The 26 species included in this study in the genus *Ficedula* are quite variable. They vary structurally (chiefly in their wing formula and relative length of the tarsus), as well as in the pattern of the plumage and its pigmentation, and to a certain extent in their habits also and as a result were formerly divided into many poorly defined genera. Finsch (1901) dealing with many of these species divided them into seven genera. Stresemann (1912) divided a larger list of these species into eight genera. To these must be added *Ficedula* for *hypoleuca* and *albicollis*, and *Zanthopygia* for *zanthopygia* and *narcissina* which were not studied by Stresemann, and *Oreicola* as well, for, as Mayr (1944) has shown, the type species of this genus is *pyrrhonota* = *timorensis*, a species included by Stresemann in one of his eight genera. This splitting, although it emphasizes the variability of the genus *Ficedula* as here understood, is not warranted, but, as shown in figure 17, the 26 species seem to arrange themselves in a number of more or less closely related groups. The high diversification of *Ficedula* is of phylogenetic significance, for it seems to show that this genus is probably older than the less variable *Muscicapa*, which seems to represent a specialization of more recent origin.

These 26 species were the chief target of Mayr (1945), Delacour (1946b), and Deignan (1947) who have merged all their 11 genera into *Muscicapa*. In my opinion, this reaction went too far, for the 26 species taken as a whole differ distinctly in several respects from the more typical flycatchers of the genus *Muscicapa*. Since I believe that the two genera can be separated, my thesis is better defended through comparison than by a mere description of *Ficedula*. In this comparison all the general characters of *Ficedula* will be described, the characters of the individual groups being described in a following section.

The differences between the two genera consist in differences of structure, pattern, and coloration, accompanied, apparently,

in most instances by significant differences in habits and biology.

**STRUCTURE:** Both genera are composed of small or rather small species (tables 4 and 6) which differ generically in the relative proportions of the tarsus and to a lesser extent of the first primary, in the shape of the wing tip in the migratory species, and, in *Ficedula* taken as a whole, in the shape of the bill and in the development of the rectal bristles.

The differences in the relative length of the tarsus and their correlation with habits are discussed (and illustrated in fig. 4) in the general discussion of the tarsus in the introductory section of this paper. It may be stated here that in 20 of the 21 species of *Muscicapa* (the exception being *M. griseigularis* which is aberrant in structure and warbler-like habits), the tarsus (fig. 22) ranges from about 13 to 20 per cent of the length of the wing, in *Ficedula* (fig. 16) from about 19 to 31 per cent, the average being about 17 in *Muscicapa* and 26 in *Ficedula*. In *M. griseigularis* the tarsus is 25 per cent of the length of the wing. In *Ficedula* the claws are usually weak or moderately strong, but less variable than in *Muscicapa*. Fewer *Ficedula* have a scutellated tarsus (three out of 26) than *Muscicapa* (seven out of 21).

In *Ficedula* the first primary tends to be slightly longer than in *Muscicapa*. Compare for instance the proportions in the migratory species of both genera (figs. 16 and 22). In these migratory species the wing tip of *Ficedula* is never so pointed as in *Muscicapa*, although the distances traveled may be the same. For instance, in *F. mugimaki* and *F. parva* the wing formula is  $3=4=5>6=2>7>8>9>10$ , whereas it is  $3>2=4>5>6>7>8>9>10$  in *M. griseisticta* and  $3>4>2>5>6$ , etc., in the northern populations of *M. sibirica*, although *mugimaki* and *griseisticta* and the northern populations of *sibirica* and the eastern populations of *parva* have the same migration, from eastern Siberia, Kamchatka, Bering, or Sakhalin to Indo-Malaya. The wing is rounder in *F. hypoleuca* than in *M. striata*, although both migrate from Lapland to tropical Africa. In terms of actual measurements (tables 4 and 6) the differences between the second and tenth primaries are: *hypoleuca* 17.8 mm., *striata* 23.3, *mugimaki*, 12.4, *parva* 11.1, *sibirica* 24.2, *griseisticta*

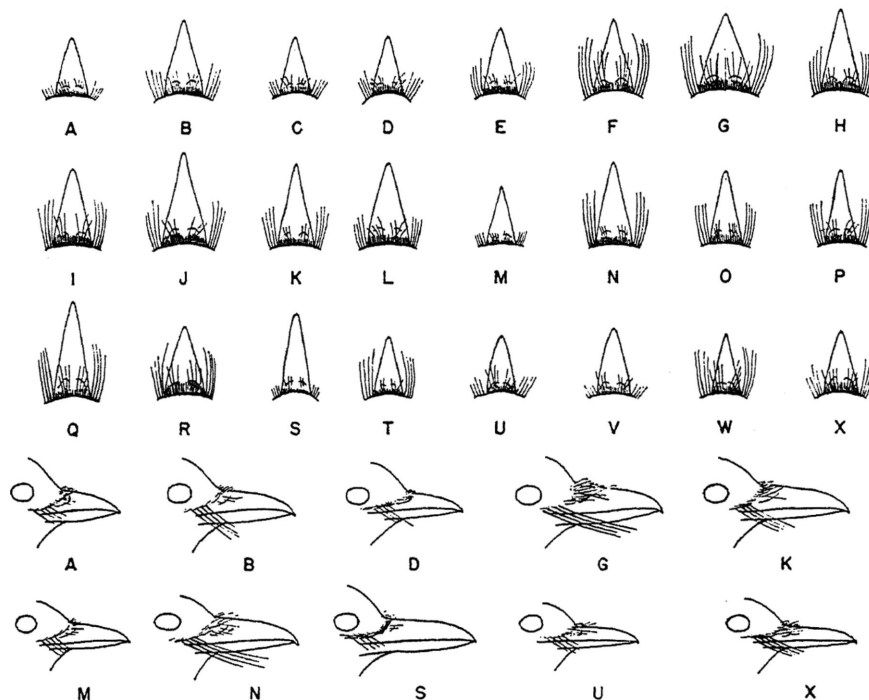


FIG. 15. Bill characters in the genus *Ficedula*. A. *F. hypoleuca* and *albicollis*. B. *F. zanthopygia* and *narcissina*. C. *F. mugimaki*. D. *F. parva*. E. *F. strophinata*. F. *F. monileger*. G. *F. solitaria*. H. *F. basilanica*. I. *F. dumetoria*. J. *F. buruensis*. K. *F. rufigula*. L. *F. henrici*. M. *F. hodgsonii*. N. *F. platenae*. O. *F. crypta*. P. *F. bonthaina*. Q. *F. harterti*. R. *F. nigrorufa*. S. *F. timorensis*. T. *F. hyperythra*. U. *F. westermanni*. V. *F. superciliaris*. W. *F. tricolor*. X. *F. sapphira*. Natural size.

28.3. The differences between the longest and tenth primaries would show a still greater gap. The differences in the shape of the wing are apparent even in the southern species of both genera with a limited migration. In *F. strophinata* the wing formula is  $4=5>6=3>7>2=8>9>10$  and the difference between the second and tenth primaries 5.0 as against, in *M. ferruginea*,  $3=4>5=2>6>7>8>9>10$  and 17.4. Both species are Himalayan; *strophinata* reaches Tenasserim and Indochina and *ferruginea* goes a little farther to Java and Borneo, but the relatively small difference in distances traveled cannot account for the much rounder wing of *strophinata*.

Comparison of the bill characters in *Ficedula* (fig. 15) and *Muscivora* (fig. 21) show clearly that the bill of *Ficedula* is of a more generalized type, is less triangular, not so broad at the base, generally weaker, and less hooked. Although not shown in the figures,

the bill of *Ficedula* is more highly ridged, less depressed, except in the *Muscivora-Digenea* group. Taken as a whole, the bill is less heavily feathered and the rictal bristles are shorter in *Ficedula*, although a few of its species have the bristles as long as in *Muscivora*.

PATTERN AND COLORATION: The pattern and coloration are highly developed and very variable in *Ficedula* but relatively constant and restricted in *Muscivora*. Although variable, the pattern of *Ficedula* presents two characters that are relatively constant. These characters, which are always lacking in *Muscivora*, consist of a white area in the tail which occurs in the great majority of the species other than the six species of the *Ochromela-Oreicola* and *platenae* groups, and of conspicuous white markings (yellow in one species) on the head. In *hypoleuca* and *albicollis* (fig. 2) the white is restricted almost entirely to the outer webs of the two outer pairs of rectrices, but in the other species

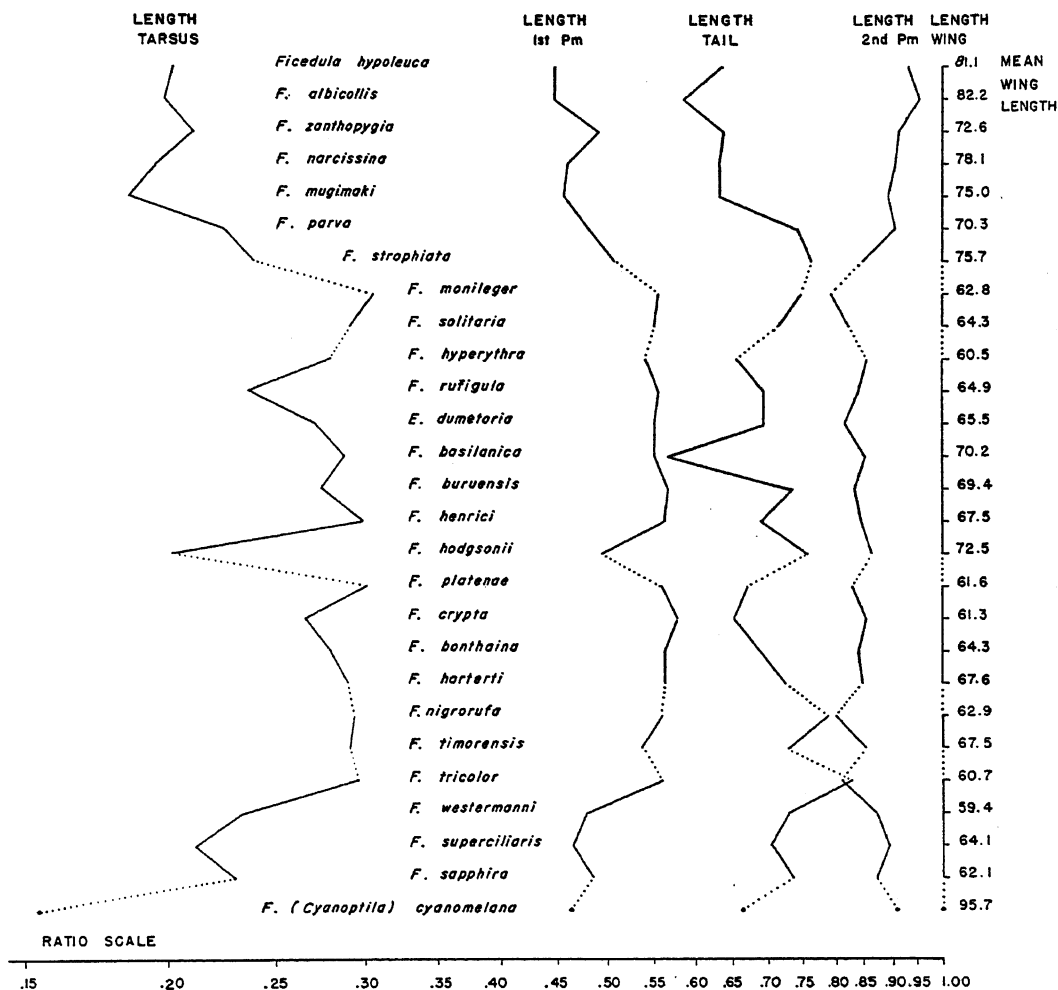


FIG. 16. Comparison through ratio diagram of the proportions in *Ficedula* and in the subgenus *Cyanoptila*. The species with a short tarsus are all highly migratory (*hypoleuca* to *parva* and *cyanomelana*) or arboreal (*hodgsonii*, *westermanni* to *sapphira*).

with white in the tail, to the basal half or more of the four outer pairs. The head markings, present in virtually all species, may be restricted to the fore crown or to the region behind the eye, but usually take the form of a broad superciliary streak which sometimes reaches the nape. Other conspicuous details of pattern which may occur in *Ficedula* but are lacking or poorly shown in *Muscicapa* consist of very sharply delimited throat patches, a strong contrast between the pigmentation of the breast and abdomen or that of the back and rump, and bands of white on the wings. The pattern is much simpler in *Muscicapa* and consists of some streaking of

the fore crown, throat, and breast, or the throat may be white or whitish and the breast pigmented, but these two areas are not too sharply contrasted, conspicuous head markings are lacking, and, as stated, there is no white in the tail. The females of the western Palearctic *Ficedula* have been said to have a plumage similar to that of *Muscicapa*, but the resemblance is superficial and this statement is very misleading. It is true that these females are grayish brown above, but they are not streaked and they have white in the tail.

The range of pigments or colors is very much greater in *Ficedula*. Bright yellow or

orange, blue, pure black, and pure white present in *Ficedula* do not occur in *Muscicapa* where drab gray-browns, blue-grays, or slate predominate. In *Ficedula* the range of rufous which occurs in many species is very much greater than in *Muscicapa* where this pigment is well developed in only one species (*ferruginea*).

Sexual dimorphism may be mentioned. In some groups of *Ficedula* the sexes are dimorphic in pattern and coloration. The dimorphism is usually very strong or well marked as in *parva* and *strophitata*, whereas the sexes are identical in all the species of *Muscicapa*.

**HABITS AND BIOLOGY:** In cases where information is available the morphological differences between *Ficedula* and *Muscicapa* are usually supported by clear-cut differences in habits and biology. The habits of the western Palearctic species described by Niethammer (1937) and by Witherby *et al.* (1938) differ in several significant respects from those of the typical *Muscicapa* such as *striata*. The *Ficedula* "seldom, if ever, returns to the same twig," they often alight on the ground, or, tit-like, cling to the trunk and branches, or, warbler-like, search the foliage. In these species, only the female incubates, not as in *striata* where both sexes incubate. In the typical western and eastern Palearctic *Ficedula*, with the exception of *parva*, the breeding plumage acquired at the prenuptial molt is very different from that of the "rest" plumage acquired at the postnuptial molt, whereas these two plumages are similar in all *Muscicapa*.

The habits of many Indo-Malayan species are summarized by Stresemann (1912), and some information is given by Baker (1924, 1933). These species, with apparently the exceptions of *hodgsonii* and some species of the *Muscicapula-Digenea* group, are not truly arboreal as they do not ascend high into the trees but usually inhabit thickets or the undergrowth but a few feet from the ground. As in *Muscicapa*, the nest of *Ficedula* varies in its structure and location, but is usually placed lower down, in some species directly on or very close to the ground, and moss is less often used. Globular nests, unknown in *Muscicapa*, are built by such *Ficedula* as *monileger*, *solitaria*, and *nigrorufa*. It may be added that, unlike most *Muscicapa*, many

*Ficedula* have a varied and pleasing song and have a stronger habit of jerking and flicking the tail. In *parva*, *strophitata*, and *monileger*, and probably in most species where there is much white in the tail, the tail is often spread open in display.

#### RELATIONSHIPS WITHIN THE GENUS *Ficedula*

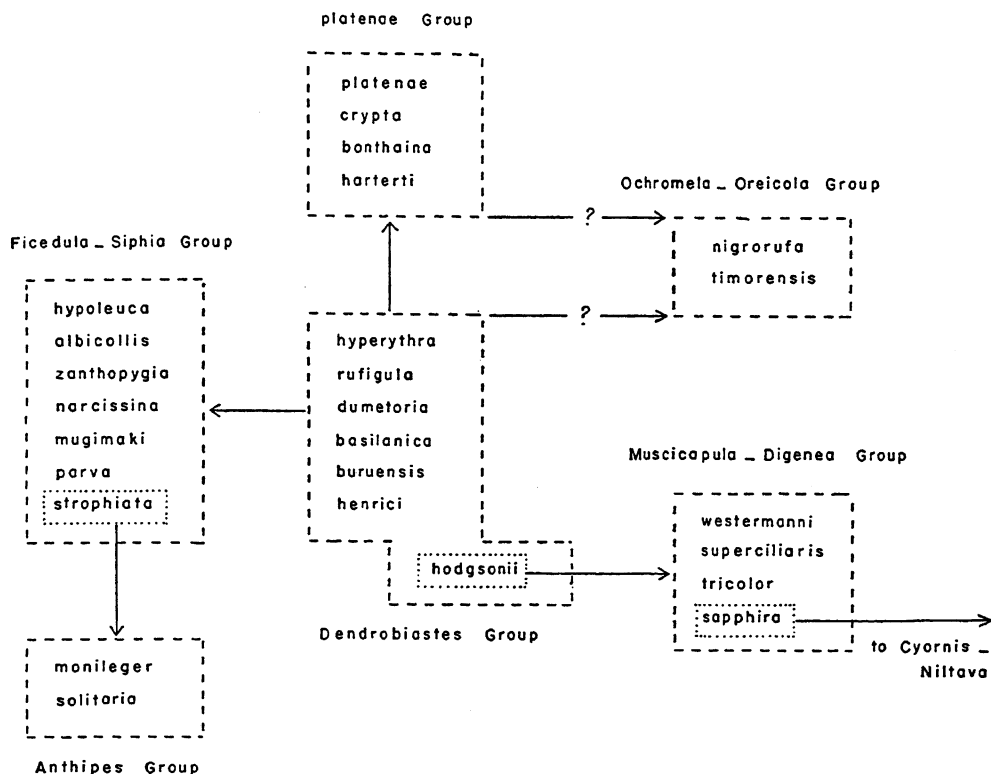
As stated in the discussion of the general characters, the 26 species can be divided in a number of groups, the presumed relationships of which are shown in figure 17. These groups are not to be taken as the equivalent of subgenera for, as shown below, they are of unequal value and include, in some cases, dissimilar though apparently related forms. It is not certain, however, that the two species of the *Ochromela-Oreicola* group are related to each other or to the other species of the genus.

In Stresemann's arrangement (1912) the eight genera recognized were separated on the basis of the wing formula, which this author considers to be an important and exact character, but in my opinion this character, which is probably adaptive, does not necessarily indicate that the species with the same wing formula are "obviously closely related," as stated by Stresemann. For instance, *dumetoria* and *pyrrhonota* (= *timorensis*) placed in the same genus (*Erythromyias*) by Stresemann, have nothing in common except the wing formula, and it is not even certain that *timorensis* is a flycatcher. Or, on the other hand, *leucomelanura* (= *tricolor*), which appears to be closely related to *superciliaris* and *sapphira*, is separated as the monotypic *Digenea* on account of its different wing formula. Further, the wing formula differs in such sibling species as *hypoleuca* and *albicollis* or *zanthopygia* and *narcissina*.

In my opinion, the wing formula is but one character which, although possibly significant in one group, is not so in another, or it may be of unequal value along with all the other characters such as pattern, pigmentation, dimorphism, proportions, shape of the bill, as well as habits and general distribution. All the characters must be weighed together. Based on such a combination of characters the 26 species appear to permit the following arrangement in six groups.

**THE *Ficedula-Siphia* GROUP:** This group comprises all the Palearctic species and



FIG. 17. Presumed relationships of the species in the genus *Ficedula*.

*strophhiata* which appears to be not too distantly related. These species, including *strophhiata*, are migratory and perhaps as a result of such habit have similar proportions (fig. 16). In *strophhiata*, in which the migratory habit is not so well established and the migrations are less extensive, the proportions diverge somewhat, but the proportions of the highly migratory *parva* are intermediate between those of *strophhiata* and the other species.

Sexual dimorphism in coloration is very strong in this group except in *parva* and *strophhiata* where it is relatively slight. In the strongly dimorphic species (*hypoleuca*, *albicollis*, *zanthopygia*, *narcissina*, and *mugimaki*), although the pigmentation of the males in breeding plumage may vary (the under parts are white in the first two, yellow in the next two, and strongly rufous in *mugimaki*), the rest of the plumage presents some strong similarities, being black with conspicuous white markings in the wings. The back may be all black, or, as in *albicollis*, there may be

a white nuchal band and whitish rump, and in *zanthopygia* and *narcissina* a yellow rump, the yellow extending halfway up or more over the back. The females of these five species and female *parva* and the males of the five species in winter plumage are very similar. They are whitish or buffy below, and the upper parts are gray-brown, with variable whitish markings on the tertials and inner greater upper wing coverts. The rump is greenish in *narcissina* and yellow in *zanthopygia*. In *elisae*, a race of *narcissina*, the male is olive above. The male of *parva*, in breeding and winter plumage, is gray-brown above, with a large rufous patch on the throat and upper breast. In *strophhiata* the pattern and pigmentation are very different. The male is olive brown above, with a blackish tail. The lores and throat are deep black, and the sides of the face and the upper breast are slate, the slate of the breast and the black of the throat being separated by a conspicuous gular patch of bright brownish orange. The flanks and sides of the abdomen are slaty changing to

olive, only the center of the abdomen and under tail coverts being whitish. Female *strophata* has only a trace of white on the fore crown, no black on the throat, and a much smaller and paler gular patch.

In the males of all the species, except in *parva* where the fore crown is grayish white, there is a very conspicuous band of pure white (sulphur yellow in *narcissina*) across the fore crown and/or above and behind the eye. All the species, with the exceptions of *zanthopygia* and *narcissina* and female *mugimaki*, have some white in the tail in both sexes.

The tarsus and the first primary are proportionately shorter than in the other groups (fig. 16) with the exception of the species which in these groups are most arboreal, such as *hodgsonii*, *melanoleuca*, *superciliaris*, and *sapphira*. The second primary is longer. The bill is not very flattened above, and in this group, taken as a whole, the rectal bristles are relatively not very well developed (fig. 15) and are not very strong. The wing formula varies. In *hypoleuca* and *narcissina* it is  $3=4>5>2>6>7>8>9>10$ ; in *albicollis*  $3=4>5=2$  or rarely  $2$  slightly  $>5>6>7>8>9>10$ ; in *zanthopygia*, *mugimaki*, and *parva*  $3=4=5>6=2>7>8>9>10$  with slight variations in *zanthopygia* and *parva* where  $3=4$  may be slightly  $>5$ , or  $3, 4, 5$ , subequal or  $6$  slightly  $>2$ ; in *strophata* the wing is more rounded,  $4=5>6=3>7>2=8>9>10$ .

In this group it may be mentioned that the species do not grade into one another, and, with the exception of the two sibling pairs (*hypoleuca-albicollis* and *zanthopygia-narcissina*), they have all been separated as monotypic genera. The possible affinities of the species cannot be expressed in a linear sequence such as the one followed in this paper; *mugimaki*, *parva*, and *zanthopygia-narcissina* can probably be said to "radiate" to a varying degree around *hypoleuca-albicollis*, though *mugimaki* and *parva* are probably not too distantly related to the latter and to each other; *strophata*, which stands farther apart but which may be distantly related to *parva*, seems to lead directly to the following group.

THE *Anthipes* GROUP: This group consists of two forms, *monileger* and *solitaria*, which seem to be geographically representative and which, since they have a similar pattern, are

usually treated as conspecific. Examination, however, shows some slight differences such as the lack of a pigmented area around the eye in *monileger*. In this form the white throat patch is completely surrounded by a broad border of black which is only faintly indicated in *solitaria*, mainly at the base of the patch, and the rufous pigments which are very well developed in *solitaria* are largely replaced by olive in *monileger*. These differences may be only of subspecific importance, but the bill is quite different in the two forms (fig. 15). This figure shows only the outline of the bill, but it is also more highly ridged and more compressed laterally in *monileger*.

There is no sexual dimorphism, and the wing formula is the same in both forms,  $4=5=6>7$  which is slightly  $>$  or  $=3>8>9>10>2$ . The tarsus is long. As might be expected from the very round wing and long tarsus, these two forms live only in the undergrowth very close to the ground. They build a globular nest largely made of grasses and bamboo leaves which they place directly on or not far from the ground. They have a conspicuous broad but short, white or fulvous superciliary streak almost meeting on the fore crown, but no white in the tail, although they are said to spread it open when perched as in some of the species of the *Ficedula-Siphia* group.

THE *Dendrobiastes* GROUP: This group, which is fairly homogeneous, comprises the seven species which appear to be most nearly related to the species of the *Ficedula-Siphia* group. Its limits, however, are somewhat uncertain, for some of its species such as *hodgsonii* appear to lead directly in their structure and habits to the species of the *Muscicapula-Digenea* group, while on the other hand the females of *hyperythra*, *rufigula*, and *dumetoria* are very similar in pattern and coloration to the four species of the *platenae* group in which the males are "hen feathered."

"*Dammeria*" *henrici* fits well in the *Dendrobiastes* group, although the plumage of the male, which is dark slate below, differs from that of the males of the other species which, with the exception of *basilanica*, are strongly rufous on the breast. The plumage of the females shows, however, that *henrici* and *basilanica* are clearly related to the other species. With the exception of *buruensis*, in

which the females are like the males though duller, all the other species are sexually dimorphic, the females being olive brown above more or less tinged with rufous or gray, with the area in front of the lores more or less prolonged into a short superciliary streak and the eye ring buffy or brownish.

In the males of the *Dendrobiastes* group the white markings of the genus *Ficedula* are gradually reduced and are lost in some species. They are most conspicuous in *dumetoria*. This species, in which the upper parts are black and very similar to those of a typical *Ficedula* such as *albicollis*, is probably the species of the *Dendrobiastes* group closest to the species of the *Ficedula-Siphia* group. In *basilanica* the white head markings that are conspicuous in one race (*samarensis*) are much reduced in another (nominate *basilanica*). The head markings are not conspicuous in *hodgsonii*, are reduced to a very faint trace in *rufigula*, and are lacking altogether in *buruensis*. The white tail markings, which are conspicuous only in *dumetoria* and *hodgsonii*, are reduced to the base of the tail in *hyperythra* and are lacking in the other species. They are lacking also in the races of *hyperythra* from the Philippines and the Moluccas. The males vary above from black (*dumetoria*) to black slate or slate and always lack the distinct blue pigments of the males of the *Muscicapula-Digenea* group.

The *Dendrobiastes* group varies little structurally, the chief variations being in the proportions of *hodgsonii*, which, more arboreal, has a shorter tarsus, and *basilanica*, which has a shorter tail. Taken as a group the *Dendrobiastes* species, which, with the exception of *hodgsonii*, are notably not arboreal, have a shorter second primary and a longer tarsus, tail, and first primary than the species of the *Ficedula-Siphia* group. The bill, which varies scarcely in shape (fig. 15), is longer, except in *hodgsonii* and *hyperythra*, than that of the species of the *Ficedula-Siphia* group, and though more attenuated than in these species is more powerful and, especially, is more highly ridged and more strongly compressed laterally. Their wing is more rounded, even in *hodgsonii*. The wing formula, which varies relatively little, is  $4=5=6>3=7>8>9>10$ , 2 subequal or sometimes 9, 10, 2 subequal in *dumetoria*, *basilanica*, *rufigula*, and *buruensis*;

$4=5=6>3>7>8>9$ , 10, 2 subequal in *henrici* and *hyperythra* or sometimes  $8=2>9>10$  in *hyperythra*; in *hodgsonii* with arboreal habits the wing is a little more pointed,  $4=5>6=3>7>2=8>9>10$ .

THE *platenae* GROUP: This group, which, properly speaking, forms but a subgroup of the *Dendrobiastes* group, is exceptionally homogeneous and consists of four species that appear to have been directly derived from the same ancestral stock that gave rise to *hyperythra* and *rufigula*. Unlike these two species of the *Dendrobiastes* group, the species of the *platenae* group are not sexually dimorphic, the males being "hen feathered." Above, the plumage is rufous brown (strongly tinged with olive in *bonthaina*, most rufous in *harterti*), the tail is chestnut or red-brown, the under parts are white on the abdomen, the throat and breast being whitish in *harterti*, rust or orange in *platenae* and *bonthaina*, tinged with pale olive brown in *crypta* in which the throat is whitish. There is no white in the tail, and the facial markings are much reduced, being conspicuous only in *bonthaina* where they consist of an orange spot on the lores reaching from the base of the bill to the top of the eye; in the other species there is a vaguely defined grayish white or buffy spot on the lores.

Structurally, these four species differ but very slightly from one another; proportions are similar (fig. 16), as is the bill (fig. 15) which is attenuated and well ridged. The wing is rounded and differs little in its formula. In *bonthaina* and *harterti* it is  $4=5$  slightly  $>3=6$  or  $3, 4, 5, 6$  subequal  $>7>8>9$ , 10, 2 subequal; in *crypta*  $4=5$  slightly  $>6$  slightly  $>3$  or  $4, 5, 6$  subequal  $>3=7>8>9>10$ , 2 subequal; in *platenae*  $4=5=6>3=7>8>9>10>2$ . Structurally, these four species do not differ, or differ but little, from most of the species of the *Dendrobiastes* group.

As may be inferred from their structure, the species of the *platenae* group are not arboreal in their habits. Information is lacking in the case of *crypta* or unavailable in the case of *harterti*, but *bonthaina*, according to Stresemann (1940), and *platenae*, according to Mayr (1946), live near the ground in the undergrowth of the forest. Being small and plain species they are probably not con-

spicuous in such a habitat for they are rare or uncommon in collections; *harterti* Siebers was described only in 1928, and *crypta* even more recently by Vaurie (1951).

THE *Ochromela-Oreicola* "GROUP": This "group" consists of two species, *nigrorufa* for *Ochromela* and *timorensis* for *Oreicola*. Mayr (1944), who has discussed these two species, stated that they seem to be related and that *timorensis* is not very far removed from *buruensis* and *dumetoria*. These four species may be related, although the pattern of their plumage differs widely. In *buruensis* and *dumetoria* the tail and the whole of the upper parts are black or blackish, whereas the upper parts are strongly rufous in *nigrorufa* and *timorensis* from the hind neck down. In *nigrorufa* the tail and the whole of the under parts are rufous also as on the back, but in *timorensis* the tail is dark brown without rufous pigments and the under parts are pure white with a broad and very sharply defined pectoral band of pure glossy black. Both species are black on the sides and top of the head, but the black which is always dull in *nigrorufa* is glossy in *timorensis*. The sexes are identical in *timorensis*. In *nigrorufa* the female differs from the male in having the black of the head replaced by dark olive brown, and the wings, which are black in the male, are dark brown in the female. In *timorensis* the wings are dark brown with conspicuous broad buffy markings on the outer webs of the tertials.

These differences in pattern and pigmentation are hard to evaluate, for in *buruensis* and *dumetoria*, which appear to be unquestionably related to each other, there are also differences in pattern and pigmentation. In *buruensis* the whole of the under parts including the under tail coverts are strongly rufous, but the rufous pigments are weak in *dumetoria* and end sharply at the level of the lower breast, the abdomen and under tail coverts being pure white. In *dumetoria* the upper parts are pure black with conspicuous white markings in the tail, on the wings, and on the sides of the head; in *buruensis* there are no white markings and the upper parts are more dark slate than black.

The proportions (fig. 16) and wing formula of the four species are similar or differ little. The wing of *nigrorufa* and *timorensis* is

rounded, the formula of *nigrorufa* being  $4=5=6$  or  $4, 5, 6$  subequal and slightly  $>7$  slightly  $>8$  slightly  $>$  or  $=3>9>10>2$ ; and that of *timorensis*, which is the same as that of *buruensis* and *dumetoria*,  $4=5=6>3=7>8>9>10, 2$  subequal. The tip of the tail is rounded to about the same extent in all four species. The shape of the bill (fig. 15) differs, however: in *buruensis* and *dumetoria*, which have a similar bill, it is sharply attenuated and sharply or highly ridged; in *nigrorufa* it is more triangular and rather depressed; in *timorensis* it is strongly compressed laterally and blunt at the tip, and the rectal bristles of this species are unusually weak and short. The bill of *timorensis* contrasts strongly with that of the other species of the genus *Ficedula*.

I have retained *timorensis* in this genus, but its true position is not certain. Delacour, pointing to its unusual pattern and bill, has suggested (orally) that this species may be a robin rather than a flycatcher. However, at least until *timorensis* can be studied in life, it is probably better to place it close to *nigrorufa*, as Mayr suggests (orally) and to place both not far from the species of the *Dendrobiastes* group.

All observers agree that *nigrorufa* in life is far from being a typical flycatcher. It is a bird of the dark dense evergreen forests and shady thickets where it frequents the thickest undergrowth, seldom ascending far from the ground. It catches insects on the wing or on the ground. Whistler (1949) states "that whatever it does or wherever it goes you will notice that it seldom leaves the neighbourhood of the ground, usually keeping within a foot or two of it . . . reminding the English observer of a Robin in its ways." These habits are similar to those of the species of the *Dendrobiastes* and *platenae* groups with the exception of *hodgsonii*. *F. nigrorufa* has apparently no true song but is far from silent. Its nest, as stated, is globular and is placed at a height of 2 to 3 feet from the ground or lower.

THE *Muscicapula-Digenea* GROUP: This group is a good link between the genus *Ficedula* and the *Cyornis* group of the genus *Niltava* in both habits and appearance. It consists of four small species (*westermanni*, *superciliaris*, *tricolor*, and *sapphira*) which, although they are obviously closely related,

grade in their pigmentation and pattern from the typical plumage of *Ficedula* to that of typical *Cyornis*.

All four species are strongly dimorphic in coloration. In *westermanni* the male has a pied black and white plumage that is virtually identical with the breeding plumage of the males of some typical *Ficedula*, such as *hypoleuca* or *albicollis*, and the females of all these three species are very similar. In *sapphira* both male and female are virtually identical with the male and female of a typical *Cyornis* such as *rubeculoides*, the type species of *Cyornis*. Distinct blue pigments are present in the males of *superciliaris* and *tricolor*, but they are not so rich nor so brilliant as in *sapphira*; *superciliaris* is dull blue above, *tricolor* is dull blue on the forehead and sides of the crown, but the rest of its plumage is slaty above as in *hodgsonii* of the *Dendrobiastes* group, though bluer. Female *superciliaris* is similar to female *westermanni*, that is, grayish above and whitish below, but differs by showing a rather slight admixture of rufous best shown on the fore crown and cheeks, while female *tricolor* is very similar to female *sapphira*, that is, strongly rufous above and below, with a conspicuous rufous eye ring. In the males the basal half of the tail is white in the first three species, and a conspicuous white superciliary streak is present in the first two. These white markings are lacking in *sapphira* as in all *Cyornis* except *concreta*. In *concreta*, however, the white area in the tail is completely different in its distribution (fig. 2) from that of *superciliaris* and the other *Ficedula*.

The habits of three of these species (*westermanni*, *superciliaris*, and *sapphira*, which constitute *Muscicapula* proper) are similar to those of some of the species of the *Cyornis* group that are more or less arboreal, but the more rounded wing of *tricolor* (which has been separated as the monotypic *Digenea*) and its different proportions, especially its distinctly longer tarsus, suggest strongly that *tricolor* is not strictly arboreal.

The wing formula of *tricolor* is  $4=5=6>3=7>8>9>10$ , 2 subequal, and that of the *Muscicapula* species  $3=4=5>6>2=7>8>9>10$ . In these last three species, the bill (fig. 15) is triangular in shape, blunt, and well flattened above; in *tricolor* it is atten-

uated and well ridged. Despite these structural differences, *tricolor*, as shown by the plumage of the female, is probably much closer to *sapphira* than it is to *westermanni* and *superciliaris*.

Although *tricolor* is apparently quite closely related to *sapphira*, its structural characters (wing formula, proportions, and bill) are the same as those of the species of the *Dendrobiastes* group with the exception of *hodgsonii* which, being almost entirely arboreal in its habits, has a more pointed wing and the same proportions as the arboreal *westermanni*, *superciliaris*, and *sapphira*. The two groups thus seemingly grade into another in every character of structure, coloration, and habits and grade at the other extreme directly into *Cyornis* with *sapphira*.

#### LIST OF THE SPECIES

##### *Ficedula hypoleuca* Pallas

RANGE: Western Palearctic east to western Siberia (Tomsk, Barnaul) and from Lapland south to north Africa, east to the Balkans; migrates to northern tropical Africa.

##### *Ficedula albicollis* Temminck

RANGE: Western Palearctic, chiefly in central and southeastern Europe, north and east to central European Russia (Penza, Moscow), west to southern Baltic, east to the Caucasus, Asia Minor, Iran, and Transcaspia; migrates to central and eastern Africa.

##### *Ficedula zanthopygia* Hay

RANGE: Eastern Palearctic from eastern Mongolia and southern Transbaikalia to the Amur Basin, Ussuriland, Manchuria, and Korea, south to northern and central China; migrates to Indo-Malaya.

REMARK: On the relationships of *zanthopygia* and *narcissina*, see Steinbacher (1937).

##### *Ficedula narcissina* Temminck

RANGE: Eastern Palearctic in Sakhalin, Japan to Riu Kiu, northern China in northern Hopeh (*elisae*); migrates to Indo-Malaya.

##### *Ficedula mugimaki* Temminck

RANGE: Eastern Palearctic from northeastern Altai to Sakhalin and Japan; migrates to Indo-Malaya.

##### *Ficedula parva* Bechstein

RANGE: Western and eastern Palearctic; in the west, from Leningrad south to western, central,

TABLE 4  
AVERAGE MEASUREMENTS IN THE GENUS *Ficedula*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess or Defi- cit of 2d Over 10th Primary	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
Genus <i>Ficedula</i>										
M <sup>b</sup> <i>hypoleuca</i>	81.1	75.5	57.7	17.8	36.3	2.9	51.8	16.5	13.7	4.5
M <i>albicollis</i>	82.2	78.1	58.2	19.9	37.0	2.2	48.2	16.4	13.5	4.5
M <i>zanthopygia</i>	72.6	66.2	54.9	11.3	35.6	4.2	46.2	15.3	14.9	4.6
M <i>narcissina</i>	78.1	70.9	58.7	12.2	36.1	3.0	49.3	15.3	14.9	4.7
M <i>mugimaki</i>	75.0	67.1	54.7	12.4	34.3	3.4	49.8	13.9	13.3	3.6
M <i>parva</i>	70.3	63.9	52.8	11.1	33.8	4.4	52.3	15.8	13.9	4.2
PM <sup>c</sup> <i>strophiala</i>	75.7	64.0	59.0	5.0	38.5	10.5	57.9	18.1	14.3	4.4
<i>monileger</i>	62.8	50.1	54.5	-4.4	35.0	12.0	47.1	19.3	14.2	4.8
<i>solitaria</i>	64.3	52.8	54.0	-1.2	35.5	10.8	45.8	18.8	15.1	6.3
<i>hyperythra</i>	60.5	51.7	50.5	1.2	32.7	10.0	39.8	17.0	13.0	3.7
<i>rufigula</i>	64.9	54.6	54.2	0.4	36.1	12.2	44.9	15.3	15.6	4.8
<i>dumetoria</i>	65.5	53.5	55.0	-1.5	36.1	11.8	45.3	17.7	15.0	5.0
<i>basilanica</i>	70.2	59.8	59.4	0.4	38.6	12.0	39.9	20.2	16.7	5.1
<i>buruensis</i>	69.4	57.9	58.3	-0.4	39.5	13.9	50.8	19.0	16.6	4.7
<i>henrici</i>	67.5	57.0	56.1	0.9	38.0	12.0	46.3	20.3	15.4	5.1
<i>hodgsonii</i>	72.5	62.7	57.8	4.9	35.7	7.8	55.1	14.7	13.0	3.6
<i>platenae</i>	61.6	51.0	54.2	3.2	34.6	11.5	41.3	18.7	15.1	5.1
<i>crypta</i>	61.3	52.3	51.7	0.6	35.5	12.5	39.9	16.3	14.3	4.4
<i>bonthaina</i>	64.3	54.2	53.3	0.9	36.3	11.8	44.2	18.0	14.3	4.5
<i>hartertii</i>	67.6	57.4	56.8	0.6	38.0	12.8	48.8	19.6	16.2	4.4
<i>nigrorufa</i>	62.9	50.6	55.0	-4.4	35.3	12.8	49.9	18.5	14.2	4.9
<i>timorensis</i>	67.5	57.5	56.6	0.9	36.3	11.5	49.2	19.7	15.0	4.4
<i>westermanni</i>	59.4	51.6	45.3	6.3	28.3	5.1	43.2	13.8	13.0	4.0
<i>superciliaris</i>	64.1	57.5	49.2	8.3	29.8	4.0	45.0	13.6	14.7	4.1
<i>tricolor</i>	60.7	49.2	51.8	-2.6	33.9	12.2	50.4	17.9	12.6	3.9
<i>sapphira</i>	62.1	53.9	48.0	5.9	30.0	6.0	45.4	14.3	13.5	4.2
Subgenus <i>Cyanoptila</i>										
M <i>cyanomelana</i>	95.7	86.9	68.2	18.7	44.1	1.3	63.4	14.7	16.4	5.3

<sup>a</sup> Longest primary.

<sup>b</sup> Migratory.

<sup>c</sup> Partly migratory.

and, occasionally, southern Europe, east to north-western Himalayas; in the east, from central and eastern Siberia, Bering, and Kamchatka south in central Asia from northern Mongolia to Tibet and Himalayas; migrates to India, Indochina, and southern China, and, occasionally, northeast Africa.

***Ficedula strophiala* Hodgson**

RANGE: Himalayas from Kashmir to western China, northern Burma, Shan States, southern Annam; migrates to Bengal and Tenasserim to Indochina.

***Ficedula monileger* Hodgson**

RANGE: Sikkim to Indochina.

***Ficedula solitaria* Müller**

RANGE: Malay Peninsula, Sumatra.

***Ficedula hyperythra* Blyth**

RANGE: Central Himalayas (Garhwal) to Timor, Moluccas, Celebes, and Philippines.

***Ficedula rufigula* Wallace**

RANGE: Celebes.

***Ficedula dumetoria* Wallace**

RANGE: Malay Peninsula, Greater and Lesser Sundas.

***Ficedula basilanica* Sharpe**

RANGE: Philippines (Basilan, Mindanao, Samar, and Leyte).

***Ficedula buruensis* Hartert**

RANGE: Moluccas (Buru, Ceram, Kei).

***Ficedula henrici* Hartert**

RANGE: Damar Islands.

***Ficedula hodgsonii* Verreaux**

RANGE: Szechwan to central Himalayas (Nepal), Assam, and Burma.

***Ficedula platenae* Blasius**

RANGE: Palawan.

***Ficedula crypta* Vaurie**

RANGE: Mindanao.

***Ficedula bonthaina* Hartert**

RANGE: Southeastern Celebes (Lompobatang Massif).

***Ficedula harterti* Siebers**

RANGE: Sumba.

***Ficedula nigrorufa* Jerdon**

RANGE: Southern India.

***Ficedula timorensis* Hellmayr**

RANGE: Timor.

***Ficedula westermanni* Sharpe**

RANGE: Central Himalayas (Garhwal) east to northwestern Yunnan, north in Indo-Malaya to Timor, Celebes, and Philippines.

***Ficedula superciliaris* Jerdon**

RANGE: Himalayas from Afghanistan to Yunnan, Szechwan, Assam, and Burma.

***Ficedula tricolor* Hodgson**

RANGE: Himalayas from Kashmir to Burma, Yunnan, and western China to Kansu and Shensi, Khasia, Manipur, and Chin Hills.

***Ficedula sapphira* Blyth**

RANGE: Eastern Himalayas from Sikkim to Yunnan and Burma to upper Laos.

***Ficedula* (*Cyanoptila*) *cyanomelana* Temminck**

RANGE: Eastern Palearctic in Amurland, Ussuriland, Korea, Manchuria to Hopeh, Kansu, Kuriles, Sakhalin, and Japan; migrates to Indo-Malaya.

**GENUS *NILTAVA* HODGSON**

*Niltava* HODGSON, 1837, India Rev., vol. 1, p. 650. Type, by monotypy, *N. sundara* Hodgson (this paper not available).

*Chaitaris* HODGSON, 1841, Jour. Asiatic Soc. Bengal, vol. 10, p. 29. New name for *Miltava*, error for *Niltava* Hodgson.

*Cyornis* BLYTH, 1843, Jour. Asiatic Soc. Bengal, vol. 12, p. 940. Type, by subsequent designation, Gray, 1855, Catalogue of the genera and subgenera of birds . . . in the . . . British Museum, pp. 53, 146, *Phoenicura rubeculoides* Vigors.

*Bainopus* GRAY, 1846, Catalogue of the . . . birds of Nepal, p. 91. Type, by original designation, *Chaitaris grandis* Blyth.

*Schwaneria* BONAPARTE, 1857, Rev. Mag. Zool., p. 54. Type, by original designation, *Schwaneria caeruleata* Bonaparte.

*Nitidula* BLYTH, 1861, Proc. Zool. Soc. London, p. 201. Type, by monotypy, *Nitidula campbelli* Blyth [= *Nemura hodgsoni* Moore].

*Muscicapella* BIANCHI, 1907, Ann. Mus. Zool. Acad. Imp. Sci. St. Pétersbourg, vol. 12, pp. 14, 43. New name for *Nitidula* Blyth, preoccupied by *Nitidula* Fabricius, 1775, for a genus of Coleoptera.

*Microbainopus* BIANCHI, 1907, Ann. Mus. Zool. Acad. Imp. Sci., St. Pétersbourg, vol. 12, pp. 70, 73. Type, by original designation, *Phoenicura macgrigoriae* Burton.

*Rileyornis* MATHEWS, 1927, Bull. Brit. Ornith. Club, vol. 48, p. 48. Type, by original designation, *Siphia hoëvelli* Meyer.

*Briantia* CHASEN AND KLOSS, 1930, Bull. Brit. Ornith. Club, vol. 50, p. 69. New name for *Nitidula* Blyth.

**GENERAL DISTRIBUTION OF THE GENUS**

This genus consists of 22 species and one monotypic subgenus (*Muscicapella*) which is discussed below. The 22 species are virtually restricted to the Indo-Malayan region, the range of four species extending part way into southeastern China or the mountains of western China, and the range of another to Formosa. They are not migratory except for the northern populations of *rubeculoides* and *banyumas*, the southern populations of which are not migratory. The northern populations of *rubeculoides* from China mi-

grate to peninsular Siam and the Himalayan populations to southern India and Ceylon; of *banyumas* the Himalayan populations migrate to peninsular Siam.

#### LIMITS OF THE SPECIES

Some of the 22 species, particularly the females, are very similar, and this has resulted in a great deal of confusion in correct identification. Further confusion, this time as to the limits of the various species, has been caused by the fact that a number of these species are geographically representative. Four reviews have dealt with some or all of the species of the *Cyornis* group (the 18 species listed in table 5, starting with *vivida* and ending with *turcosa*). These reviews are by Stresemann (1925), Robinson and Kinnear (1928), Chasen and Kloss (1929), and Stresemann and de Schauensee (1936). The review by Robinson and Kin-

near is the only one that includes all of the species with the exception of *sanfordi*, described in 1931. All the four reviews differ as to the limits of the species, but, since a new revision of the complicated *Cyornis* group does not fall within the scope of this paper, I follow the review of Stresemann and de Schauensee which, being the most recent, comments on the others. I differ from this review, however, in treating *lemprieri* from Palawan not as a distinct species but as a race of *banyumas*; in this I follow Mayr (in Delacour and Mayr, 1946). I also do not follow Stresemann (1940) in keeping the *djampeana* group as distinct specifically from *rufigastra*.

#### GENERAL CHARACTERS AND COMPARISON WITH *Ficedula* AND *Muscicapa*

The authors of the four reviews cited do not refer to the species of *Niltava* proper

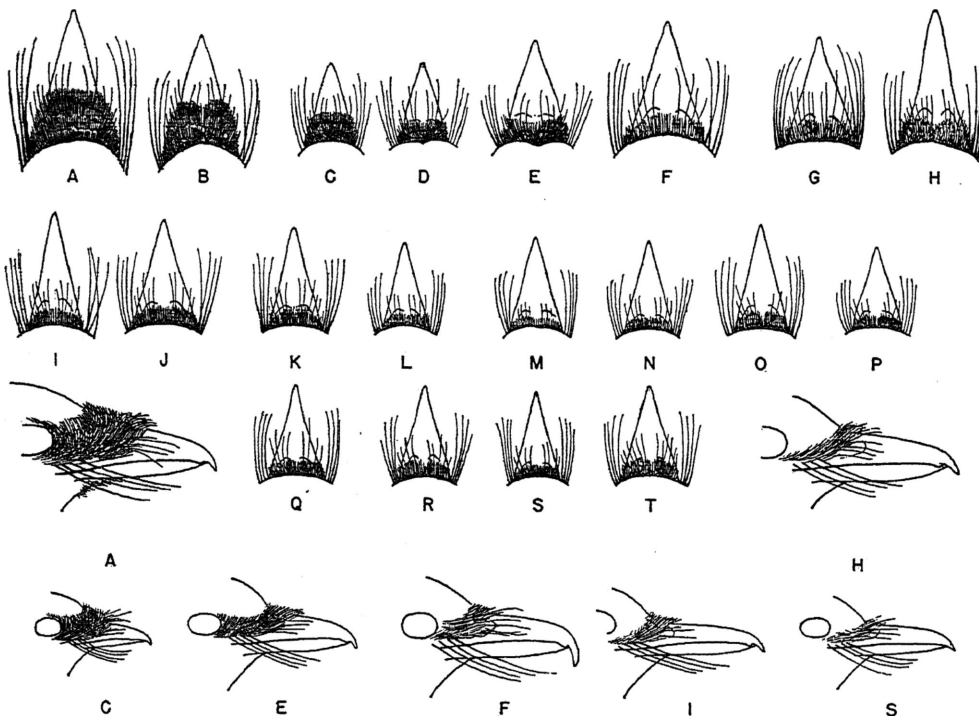


FIG. 18. Bill characters in the genus *Niltava*. A. *N. grandis*. B. *N. davidi* and *sundara*. C. *N. macgrigoriae*. D. *N. vivida*. E. *N. hyacinthina*. F. *N. hoëvelli*. G. *N. sanfordi*. H. *N. concreta*. I. *N. ruecki*. J. *N. herioti*. K. *N. pallipes*. L. *N. hainana*. M. *N. poliogenys*. N. *N. unicolor*. O. *N. superba*. P. *N. rubeculoides*. Q. *N. caerulata*. R. *N. banyumas*. S. *N. tickelliae*. T. *N. turcosa*. The bill of *rufigastra* (not shown) is similar to that of *tickelliae* and *turcosa*. Natural size.



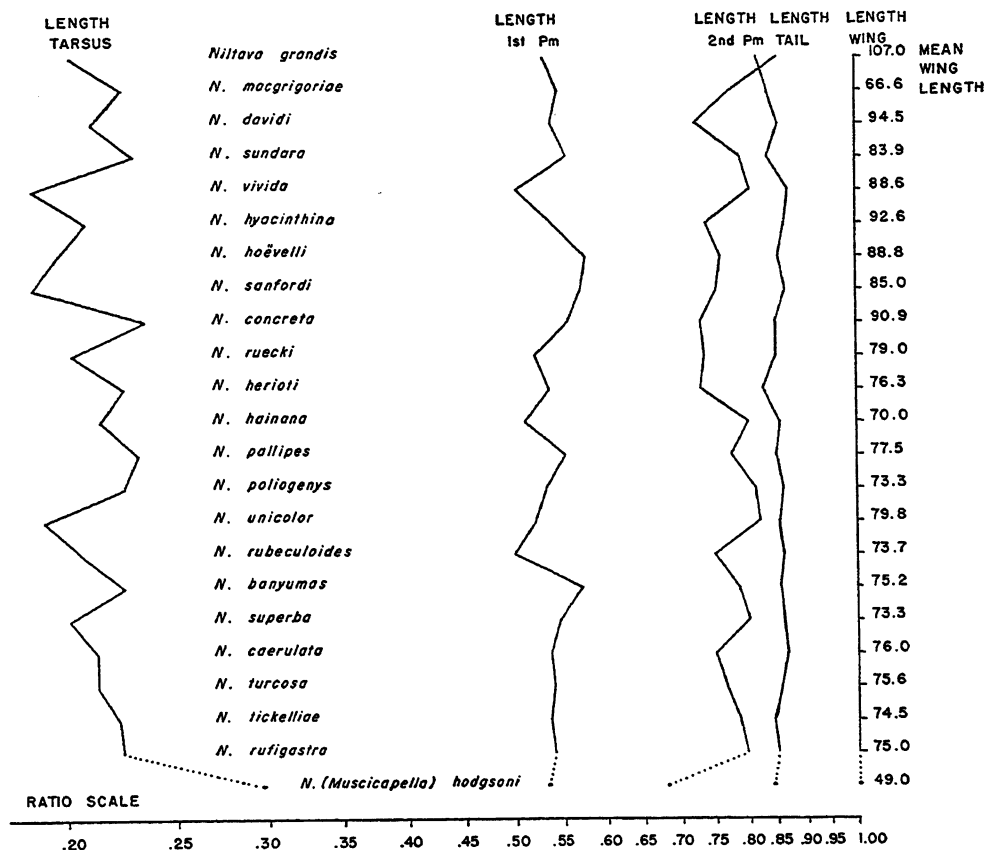


FIG. 19. Comparison through ratio diagram of the proportions in *Niltava* and in the subgenus *Muscicapella*.

(*grandis*, *macgrigoriae*, *davidi*, and *sundara*) but, as discussed below, these four species grade very smoothly in every character and in habits into the *Cyornis* species, and a generic separation is impossible at any point within the 22 species.

The genus *Niltava* is well defined and homogeneous in structure, coloration, and pattern, much more so than the genus *Ficedula* and more so structurally than the genus *Muscicapella*, despite the fact that its habits are much more variable than in this last genus.

**STRUCTURAL CHARACTERS:** This genus consists on the whole of larger species than those of *Ficedula* and *Muscicapella*, the species of *Niltava* being medium sized to rather large or large (table 5). The proportions (fig. 19) vary relatively very little, especially when compared to the proportions of *Muscicapella* (fig. 22) and *Ficedula* (fig. 16). In *Niltava*, taken as a whole, the tarsus is distinctly

shorter than in *Ficedula* and averages about the same (17 per cent of the length of the wing) as in *Muscicapella*, although species with a very short tarsus do not occur in *Niltava* as they do in *Muscicapella*. The claws are moderately strong in *Niltava*; very weak feet do not occur as they may in species of *Ficedula* and *Muscicapella* of the same size as those of *Niltava*. The tail and second primary are longer in *Niltava* than in *Muscicapella*. The bill (fig. 18) is much more powerful in *Niltava* than in *Ficedula*, more powerful and less variable than in *Muscicapella*. The rectal bristles are very well developed, more so than in the other two genera, and the tip of the bill is more strongly hooked, some *Niltava*, such as *hoëvelli* and *sanfordi*, having an exceptionally strongly hooked bill. In *Niltava* the nostrils are more concealed, the antrorse bristles over the nostrils tend to be more developed, and there is a strong tend-

ency for the feathers at the base of the bill to be developed forward, forming in some species a dense, brush-like cover over the nostrils.

The wing formula, which is so variable in *Ficedula* and even more so in *Muscicapa*, is remarkably constant in *Niltava*. In 15 species it is  $4=5>6=3>7>8=2>9>10$  with slight variations in the length of 2 which sometimes is equal to 7 or 9. The other species depart only slightly from this formula by having a somewhat more rounded wing,  $4=5=6>7=3>8>9=2>10$  in *herioti* and *turcosa*,  $4=5$  slightly  $>6$  slightly  $>3$  (or  $4=5=6$  slightly  $>3$ )  $>7>8>9=2>10$  in the remaining species (*grandis*, *sundara*, *macgrigoriae*, *concreta*, and *pallipes*).

**PATTERN AND PIGMENTATION:** The genus *Niltava* is strongly sexually dimorphic with the exceptions of the unrelated *sanfordi* and *poliogenys* in which the males are "hen feathered," the reverse being true in the related *rufigastra*, *tickelliae*, and *turcosa* where the females are very similar to the highly colored males. The males of *Niltava* are blue above (in *hoëvelli* this pigment is restricted to the head), more or less glossed, the fore crown and sometimes other parts of the plumage being brilliantly so. The under parts are blue or varying shades of orange, and the abdomen may be white or whitish to a varying extent. The species with an orange breast have a blue or blue-black throat, and a more or less sharply defined black mask is present. The contrast with *Muscicapa* is very striking. In that genus, which is not sexually dimorphic, the pigments are always dull except in *ferruginea* which is rufous and fairly colorful, most of the other species being gray-brown, a few being gray-blue or slate but without really blue pigments. The females of *Niltava*, with the three exceptions noted, are brownish above, more or less strongly tinged with rufous, but do not resemble *Muscicapa*. Below they are brownish or orange with or without whitish abdomens. Some have a well-defined crescentic patch of white at the base of the throat, and some of these have a patch of brilliant blue at the sides of the neck. In most females a vague or fairly well-defined spot of whitish or buffy is present in the region of the lores, and a narrow eye ring may be present. These facial

markings and the presence of a pale or whitish abdomen seem to be of very dubious phylogenetic importance, for they occur in many unrelated flycatchers or other small birds of diverse families. It may be added that streaking, a character so very typical of *Muscicapa*, is lacking in *Niltava*.

In the subgenus *Eumyias*, which has some affinities with *Niltava* but which seems to be closer to *Muscicapa*, a black facial mask and blue pigments predominate also, but orange pigments are lacking in *Eumyias*, and the nature of the blue pigment is rather different, being azure or Prussian blue rather than the richer ultramarine and cobalt of *Niltava*.

The genus *Ficedula* being much more varied in its pattern and pigmentation than *Muscicapa* presents some details of pattern and some pigments that occur in *Niltava*, but the two characters most constant in *Ficedula*, namely, the presence of conspicuous white markings on the head and at the base of the tail, are lacking in *Niltava*. White markings in the tail are present in *Niltava*, but they occur in only one species (*concreta*), and the distribution of the white (fig. 2) is utterly different from that of *Ficedula*. Furthermore these markings are not constant within this species, for they are lacking in the males of one of its races (*everetti*). Other details of pattern that occur in *Ficedula* but not in *Niltava* are the presence in some species of conspicuous white bands in the wings and of a strong contrast between the coloration of the back and rump. Pure blacks without a trace of blue which cover very large areas of the plumage in many *Ficedula* occur very sparingly in *Niltava* where they are restricted to the facial mask and to the sides of the face and to the throat of *grandis* and to the chin in a few other species. Some *Ficedula* are slaty, but real blue pigments occur only in some species of the *Muscicapula-Digenea* group where *sapphira* has the typical pattern and pigmentation of the *Cyornis* species of *Niltava*. The genus *Ficedula* may contain polyphyletic elements, but *sapphira* is unquestionably a direct link to *Niltava*.

**HABITS:** The ecological requirements and the feeding habits vary. In the case of the species where some information is available, some (*hoëvelli*, *sanfordi*, and *concreta*) are

apparently species of the tall tree tops and, typical flycatchers in their habits, do not come to the ground to feed. Others (*grandis*, *davidi*, and *sundara*) live in the undergrowth, in the brush or lower trees, and feed often on the ground. *N. macgrigoriae*, which is very closely related to the last three species and hardly differs from *grandis* except in size, is much more active and feeds almost entirely on the wing and does not come to the ground. According to Betts (1951) *pallipes* is a bird of the undergrowth which is "sluggish . . . seldom catching insects on the wing, but working through the thickets or dropping to the ground." The majority of the species, however, seem adaptable and feed successfully at different levels and in different habitats; *vivida*, which is said to catch insects in the "usual flycatcher manner," feeds indifferently in the tops of tall trees or in the underbrush; *unicolor* at the top of tall trees or in the "densest tangles"; *poliogenys*, *rubeculoides*, *tickelliae*, and *rufigastra* feed part way up or in small trees or in the scrub and bushes.

Ecology and habits may vary geographically. For instance, *rufigastra*, which in certain regions inhabits only mangroves, is found in other regions in deep forest or in open country in isolated groves or clumps of bamboo; *tickelliae* may breed in dense forest, shady ravines, or in gardens and even in houses. Some species are montane forms and others lowland forms, but most of them occur in both high and low country. The nest is not known in all species, but in those that are known it varies little in its structure and location. It is cup shaped and is almost always built of moss or contains moss and is placed in natural hollows in banks, rocks, or ledges, or in holes in stumps not far from the ground; it is often placed near streams. Unlike most *Muscicapa*, all *Niltava* have a melodious song which is said to be very beautiful in some species and "magnificent and rich" in *unicolor*.

Since the ecological requirements of the majority of the species do not appear to be rigidly fixed and all species are relatively very homogeneous structurally, in pattern and pigmentation, or in nesting habits and song, the arboreal or terrestrial habits of some species suggest that these are secondary

specializations of recent origin. In the arboreal species the tarsus has not become proportionately shorter nor has it become longer in the terrestrial species, the size of the claws remains proportionately the same, and the wing formula does not change. The feeding organ, being the most plastic character, has, however, begun to diverge. In the arboreal *concreta* the bill is strongly compressed laterally at the tip and strongly hooked; in *hoëvelli* and *sanfordi* it is very strongly hooked though not compressed laterally; in the terrestrial *grandis*, *davidi*, and *sundara* it is relatively more highly ridged and is hidden at the base under a dense brush of feathers; in the other species (fig. 18) it varies hardly at all.

One may further speculate that *Niltava* is of more recent origin than *Muscicapa*, which is very variable structurally though quite homogeneous in other characters, and that it is undoubtedly more recent than *Ficedula*, which is variable not only in structure but in all other characters and in biology as well. *Niltava* is restricted to a single zoogeographical region, whereas *Muscicapa* and *Ficedula* have spread to several. Secondary phylogenetic grouping of species cannot be recognized in *Niltava* or *Muscicapa* as they can in *Ficedula*.

#### RELATIONSHIPS OF THE SPECIES

The relationships of the various species do not appear to be complicated. Phylogenetically, some of the *Cyornis* species are not far from *sapphira* of *Ficedula*, or perhaps *Eumyias*, but since definite intergrades cannot be demonstrated I have arranged the species in a sequence starting with the best-characterized forms, although these, being the most specialized, are no doubt the farthest removed from *Ficedula* or *Eumyias*. Some species grade into one another, but many are so similar or differ only in a matter of degree that the order followed does not necessarily indicate linear progression.

The most specialized species, judging by the pattern of the females and the peculiar feathering over the base of the bill, consist of the four species (*grandis*, *macgrigoriae*, *davidi*, and *sundara*) that are usually separated from the other species as the genus *Niltava*, the other species forming the "genus"

*Cyornis*. The females of these four species are generally speaking brownish above and below, more or less olive or rufous above, more or less grayish below, and in *davidi* and *sundara* whitish on the abdomen. The pileum varies from dull rufous olive to grayish or bluish in some races of *grandis*. The tail is red-brown. A small patch of brilliant blue feathers is present at the sides of the neck, and in *davidi* and *sundara* there is a crescentic and sharply defined patch of white at the base of the throat, this patch being buffy and ill defined in *grandis* and *macgrigoriae*. The male plumage shows also that *grandis* and *macgrigoriae* on the one hand and *davidi* and *sundara* on the other are most closely related. In the first pair the males lack orange pigments, the throat and sides of the face being pure black in *grandis*, grading into blue-black on the breast and into slate to grayish on the abdomen; *macgrigoriae* is merely a smaller and brighter *grandis*, being brighter blue above, blue-black on the throat and sides of the face, and grayish from the lower breast down. *N. davidi* and *sundara* are sibling species which have long been confused. The males are blue-black on the throat and sides of the face and are bright orange below; male *davidi* is brighter blue above and richer orange below; female *davidi* is somewhat darker below. The size difference (table 5) which is very abrupt between *grandis* and *macgrigoriae* (*grandis* is almost twice as large) is relatively slight between *davidi* and *sundara*, *davidi* being a little larger.

*Niltava vivida* grades very smoothly into *davidi* and *sundara*, and, in the following order, *vivida*, *hyacinthina*, *hoëvelli*, and *sanfordi* grade smoothly into one another. In *vivida* and *hyacinthina* a clear trace of the brush of feathers over the base of the bill persists, but in *hoëvelli* and *sanfordi* this character is lost, though in these, as well as in virtually all the species of the genus, there is a tendency for the feathers at the base of the bill to be well developed forward. Male *vivida* is virtually identical with male *davidi* or *sundara*, and female *vivida* is very similar but lacks the little patch of brilliant blue feathers at the sides of the neck, its throat patch is buffy and less sharply indicated, and its crown is bluish slate. Male *hyacinthina* is

similar to male *vivida* but duller blue above, and the blue pigments of the throat come farther down, reaching the upper breast; female *hyacinthina* differs abruptly from the females of the preceding species in being uniformly orange below. Female *hyacinthina* and female *hoëvelli* are similar below, but in the latter the orange pigments of the throat and upper breast are invaded by grayish; in male *hoëvelli*, which is orange below with a blue throat, the blue pigments of the upper parts are restricted to the crown and grade into grayish brown on the nape. In *sanfordi*, in which the males are "hen feathered," both sexes are identical, the crown being grayish as in female *hoëvelli* and the back and rump grayish brown grading into rufous olive as in male and female *hoëvelli*. The blue pigments which in male *hoëvelli* are becoming reduced are lost altogether in *sanfordi*, and the orange pigments, which in female *hoëvelli* are already invaded by gray on the throat and upper breast, are restricted to the under tail coverts in *sanfordi* and are present, though weak and much invaded by gray, on the lower abdomen. *N. sanfordi* is perhaps not a true species, but merely a very localized and small population of *hoëvelli*.

*Niltava concreta* is not directly related to the four species just discussed, but through a mixture of characters it links the first four species discussed (*Niltava*, *sensu stricto*) to the remaining species listed in table 5 from *ruecki* on. The male of *concreta* is not rufous (orange) but blue below, with whitish abdomen, and differs only in a matter of degree from the males of *grandis*, *macgrigoriae*, *ruecki*, *herioti*, *pallipes*, *hainana*, and *unicolor*. Female *concreta* has a sharply defined crescentic patch of white at the base of the throat identical with that of *davidi* and *sundara*, and, as in these species, its abdomen is white or whitish. In these two species and in the northern race of *concreta*, the brownish coloration shows an admixture of olive and gray, but in the southern and insular races of *concreta* the pigments are much more rufous and are similar to those of virtually all the females from *ruecki* on. In size also, the measurements of *concreta* range from those of the species discussed, which are larger, to those of the species from *ruecki* on, which are smaller. In the species discussed (*grandis* to

*sanfordi*) the wing length ranges from 107 to 84 (*macgrigoriae* is so small that it is excepted as being "aberrant"); in the species from *ruecki* on, from 80 to 73. In the northern race of *concreta* (which is the race for which measurements are given in table 5), the wing length averages 91, but in the race from Borneo (*everetti*) the wing length in the five males available averages 82. *N. concreta* presents a character unique in *Niltava*, a patch of white in the tail, but this character varies geographically also, for although present in *everetti* in the female, it is lacking in the male.

The species from *ruecki* on are, as stated, smaller than the species discussed and are of generally slighter build than these and *concreta*. They scarcely differ structurally, having the same shape of bill (fig. 18), a wing formula that is identical or varies but slightly, and very similar proportions (fig. 19). The pigmentation and pattern are virtually identical in many species.

In *ruecki*, *herioti*, *hainana*, *pallipes*, and *unicolor* the males, as stated, are not orange or rufous below but are blue with a white or whitish abdomen. In *herioti*, *hainana*, and *pallipes*, the blue ends more or less on the breast. In *ruecki* and *unicolor* the abdomen is grayish white slightly tinged with blue, the blue reaching to the abdomen. The shades of blue above and below vary somewhat from species to species. They differ only slightly in *herioti*, *hainana*, and *pallipes*, are richest and most glossy in *ruecki*, and palest in *unicolor*. The axillaries in both sexes vary from gray in *ruecki*, buffy or whitish in *herioti*, *hainana*, and *unicolor*, to white in *pallipes*. The females of *herioti*, *hainana*, and *pallipes* are virtually identical in pattern and pigmentation. They are fulvous olive brown above with a chestnut or red-brown tail. Below, the rufous pigments, which are identical in *herioti* and *hainana* and somewhat more orange in *pallipes*, end at the same level on the breast, and the abdomen is whitish. They vary very slightly in the coloration of the fore crown. The region in front of the eye, which is rufous and brownish in *herioti*, is rufous and grayish in *hainana* and whitish in *pallipes* in which the point of the chin is whitish also. The characters of *herioti*, *hainana*, and *pallipes* are described in detail,

for my findings are the opposite of those of Stresemann and de Schauensee (1936), who state, "The females of both *pallipes* and *herioti* are very different from those of *hainana*, and the males of the three species show at best only a superficial resemblance to each other." In my opinion, these authors give too much weight to the slight differences, and they are wrong in stating that the three forms are not closely related. I agree with Robinson and Kinnear (1928) that they are very closely related, although they may not be conspecific, as believed by these last two authors. On the other hand, other authors such as Mayr (1945) believe that *herioti* may be only the geographical representative of *banyumas* on Luzon.

I believe also that *ruecki*, *unicolor*, and *poliogenys* are not far removed from the last three species. The female of *ruecki*, which is a very rare species, was not examined, but according to Robinson and Kinnear (1928), its pattern and pigmentation seem to be not far removed from those of female *herioti*, *hainana*, and *pallipes*. In a juvenal male of *ruecki* examined, the breast is rufous and the abdomen whitish. The female of *unicolor* and both sexes in *poliogenys*, in which the male is "hen feathered" and identical with the female, are so very similar above to female *herioti*, *hainana*, and *pallipes* that on this character alone the five species cannot be identified, but the pattern and pigmentation of the under parts differ in *unicolor* and *poliogenys*. In female *unicolor* the whole of the under parts are brownish gray, with faint tinges of rufous on the throat, lower abdomen, and under tail coverts and a vague trace of grayish white on the center of the lower breast and abdomen. In *poliogenys* the under parts are orange buff, the center of the abdomen is buffy white, the point of the chin is whitish, and the lores are gray white. These whitish markings show, perhaps, that *poliogenys* is not far from *pallipes*.

The remaining species from *rubeculoides* on appear to be very closely related. All the males and females have, to a varying degree, well-developed orange or buffy orange pigments on the throat and breast, the abdomen being paler or whitish to white. This pattern is reversed in some races of *rufigastri*, in which the abdomen is orange and the lower

throat or both the throat and breast are white. In all the species there is a strong tendency in the males for blue, blue-black, or black to invade the throat. These colors, to a variable extent, extend mesially from the sides of the throat and in most species join under the chin. In *rubeculoides* most of the throat is blue except at the lower center, and in *turcosa* the blue usually joins across the lower throat. This pattern, which seems to be a male character, is present also in the females of some of the races of *rufigastra*.

The species follow no certain gradation, and the present arrangement is based on the coloration of the females which presumably is the most conservative character. *N. rubeculoides* and *banyumas* are placed first, followed by *superba* and *caerulata*. In the first two the females are dull olive brown above or dull grayish brown and are least conspicuous; *superba* is rufous and brighter especially on the rump and tail, but lacks the blue of the male, the blue color first appearing in *caerulata* where it replaces the brown or rufous pigments on the rump and tail. In *turcosa*, *tickelliae*, and *rufigastra* both sexes are equally blue above, but the females are slightly duller above and slightly paler in the first two species, and in *rufigastra* both sexes are as highly colored above as they are below. Female *turcosa* has no blue color on the throat. In female *tickelliae* blue color is often present at the sides of the throat, but it is duller and does not join under the chin as it does in the male. In some races of *rufigastra* the female is as heavily pigmented at the sides of the throat and under the chin as the male.

The races of *rufigastra* from Celebes and the islands to the south have been accorded specific rank as *omissa* by Robinson and Kinnear (1928) or have been separated into two species (*rufigastra* and *djampeana*) by Stresemann (1940). But since all the forms replace one another geographically and intergrade, they are better treated, I believe, as one species.

#### LIST OF THE SPECIES

##### *Niltava grandis* Blyth

RANGE: Nepal to Assam, Burma, northwestern Yunnan, northern Siam, Indochina, Malay Peninsula, and Sumatra.

##### *Niltava macgrigoriae* Burton

RANGE: Himalayas from northern Punjab, to Burma, Yunnan, northern Siam, northern Tenasserim, northern Indochina to southern Kwangtung.

##### *Niltava davidi* La Touche

RANGE: Southeastern China, Yunnan to upper Laos and Annam.

##### *Niltava sundara* Hodgson

RANGE: Himalayas from northern Punjab to Burma, northern Siam, Yunnan to upper Laos.

##### *Niltava vivida* Swinhoe

RANGE: Assam, Burma, Yunnan, Tonkin, Formosa, Malay States, and western Sumatra.

##### *Niltava hyacinthina* Temminck

RANGE: Timor and Wetar.

##### *Niltava hoëvelli* Meyer

RANGE: Central Celebes and southeastern peninsula.

##### *Niltava sanfordi* Stresemann

RANGE: Restricted to Matinan Range in the northern peninsula of Celebes.

##### *Niltava concreta* Müller

RANGE: Upper Assam, Naga Hills, Tonkin, Laos, Malay Peninsula, Sumatra, and Borneo.

##### *Niltava ruecki* Oustalet

RANGE: Malay States (Malacca) and low country of northeastern Sumatra.

##### *Niltava herioti* Ramsay

RANGE: Philippines (Luzon).

##### *Niltava hainana* Ogilvie-Grant

RANGE: Southeastern China, Hainan, Indochina, Siam, and Tenasserim.

##### *Niltava pallipes* Jerdon

RANGE: Southwestern and southern India.

##### *Niltava poliogenys* Brooks

RANGE: Foothills of the Himalayas from Nepal to Assam.

##### *Niltava unicolor* Blyth

RANGE: Nepal to Assam, Burma, Malay Peninsula, and Greater Sunda.

TABLE 5  
AVERAGE MEASUREMENTS IN THE GENUS *Niltava*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess of 2d Primary Over Primary Coverts	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
<b>Genus <i>Niltava</i></b>										
<i>grandis</i>	107.0	87.8	85.8	2.0	56.8	14.2	91.1	21.7	21.5	6.6
<i>macgrigoriae</i>	66.6	55.5	54.5	1.0	36.2	11.4	51.7	15.0	13.5	4.0
<i>davidi</i>	94.5	80.7	74.2	6.5	50.7	11.0	68.2	19.5	17.4	5.2
<i>sundara</i>	83.9	70.3	67.4	5.9	46.7	12.4	66.6	19.3	17.5	5.0
<i>vivida</i>	88.6	77.2	65.6	1.6	44.3	7.0	71.5	16.6	16.3	5.5
<i>hyacinthina</i>	92.6	80.2	73.6	6.6	49.8	13.5	68.6	19.3	18.2	6.3
<i>hoëvelli</i>	88.8	75.5	72.3	3.2	50.9	14.5	67.1	17.5	19.7	7.4
<i>sanfordi</i>	85.0	73.6	69.2	4.4	48.3	15.0	61.0	16.0	19.1	7.3
<i>concreta</i>	90.9	76.8	74.8	2.0	50.5	14.5	66.0	21.3	22.1	6.0
<i>ruecki</i>	79.0	67.0	64.0	3.0	41.0	11.0	58.0	16.0	18.5	6.5
<i>herioti</i>	76.3	62.7	61.6	1.1	40.6	12.6	55.3	17.1	18.1	6.3
<i>hainana</i>	70.0	59.6	56.4	3.2	35.5	8.2	56.0	15.0	15.3	5.0
<i>pallipes</i>	77.5	65.6	63.3	2.3	42.9	12.5	60.0	17.9	18.1	5.9
<i>poliogenys</i>	73.3	63.0	59.3	3.7	38.8	11.1	59.5	16.5	15.7	5.1
<i>unicolor</i>	79.8	68.1	62.2	5.9	41.4	9.6	65.3	15.3	17.0	6.0
<i>rubeculoides</i>	73.7	63.2	57.1	6.1	36.6	7.6	55.2	15.1	15.4	5.1
<i>banyumas</i>	75.2	64.1	61.5	2.6	42.8	13.3	59.2	16.9	16.7	6.1
<i>superba</i>	73.3	63.0	60.0	3.0	40.0	11.1	58.6	14.8	17.0	5.5
<i>caerulata</i>	76.0	65.5	62.5	3.0	40.6	11.8	56.9	16.1	17.3	6.6
<i>turcosa</i>	75.6	64.4	61.6	2.8	40.6	11.0	57.5	16.1	16.6	5.7
<i>tickelliae</i>	74.5	62.7	59.8	2.9	39.6	10.2	58.5	16.5	16.2	5.4
<i>rufigastra</i>	75.0	63.6	61.7	1.9	40.2	10.7	59.6	16.8	16.3	5.6
<b>Subgenus <i>Muscicapella</i></b>										
<i>hodgsoni</i>	49.0	41.2	41.0	0.2	26.0	7.7	33.3	14.5	11.8	2.5

<sup>a</sup> Longest primary.

***Niltava rubeculoides* Vigors**

RANGE: Himalayas from Kashmir to Szechwan and Hupeh, Yunnan, Assam, Burma, western and peninsular Siam, central and southern Annam, southern Laos; northern populations migrate from China to peninsular Siam and from the Himalayas to southern India and Ceylon.

***Niltava banyumas* Horsfield**

RANGE: Sikkim, Cachar, Assam, Burma, Yunnan, northern Tonkin and northern Laos, parts of Siam and Cambodia, Malay Peninsula, Java, Borneo, and the Palawan group; the Himalayan populations migrate to peninsular Siam.

***Niltava superba* Stresemann**

RANGE: Borneo.

***Niltava caerulata* Bonaparte**

RANGE: Borneo and Sumatra.

***Niltava turcosa* Brüggeman**

RANGE: Malay States, Sumatra, and Borneo.

***Niltava tickelliae* Blyth**

RANGE: India (except Sind), Ceylon, Siam, Indochina, peninsular Siam, Malay States, north-eastern Sumatra.

***Niltava rufigastra* Raffles**

RANGE: Malay States and the greater part of the Malay Archipelago including Celebes and Philippines.

***Niltava (Muscicapella) hodgsoni*  
Horsfield and Moore**

RANGE: Nepal east to Bhutan, the hills of Assam, northern Burma, Malay States, Sumatra, and Borneo.

THE SUBGENERA *CYANOPTILA*,  
*MUSCICAPELLA*, AND *EUMYIAS*<sup>1</sup>

These three subgenera consist of seven species (*Cyanoptila cyanomelana*, *Muscicapella hodgsoni*, and *Eumyias sordida*, *thalassina*, *panayensis*, *albicaudata*, and *indigo*). Although these subgenera are not directly related to one another, they are more conveniently discussed together, I believe, than under the genera with which they have more or less distant affinities and in which they may be placed, *Cyanoptila* under *Ficedula*,

and pigmentation of many *Niltava*, a blue plumage above in the male with dark blue colors on the cheek extending towards the sides of the throat, and very bright buffy orange under parts, and, in the female, a rufous olive brown plumage above with the under parts similar to but paler than those of the male. The pattern and pigmentation of *hodgsoni* are generally similar to those of *sapphira* of the *Muscicapula-Digenea* group of *Ficedula*, but the resemblance is superficial only; *sapphira* differs structurally, has a

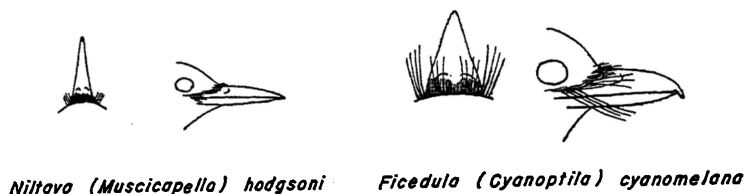


FIG. 20. Bill characters in *Niltava (Muscicapella) hodgsoni* and *Ficedula (Cyanoptila) cyanomelana*. Natural size.

*Muscicapella* under *Niltava*, and *Eumyias* under *Muscicapa*.

Because the position of *Muscicapella hodgsoni* is clearest, this species may be discussed first. It appears to be a specialized offshoot of *Niltava* which has become strongly adapted structurally to a different manner of feeding and different habits. *M. hodgsoni* is said to be gregarious and to flutter on bushes and in the lower trees searching for and taking insects from the leaves and twigs more often than it snaps them from the air. The habits of *Niltava*, discussed under that genus, vary, but its species do not behave like a leaf-warbler or a *Regulus*, as *hodgsoni* seems to do. As a result of its habits, *hodgsoni* has become very small and has developed a much longer tarsus and a very narrow and slender bill which, needle-like, is not hooked at the tip (fig. 20). The very distinct habits and strong specialization of *hodgsoni* seem to deserve subgeneric recognition.

This specialization, however, has been along structural lines only, for *hodgsoni* in both sexes still retains the typical pattern

triangular and very flattened bill, and behaves like a typical flycatcher.

The wing formula of *hodgsoni*, which is  $4=5=6>7=3>8>9>10=2$ , differs only very slightly from that of *Niltava*. It builds a similar nest, and, as are all the *Niltava*, is Indo-Malayan in distribution. The young of *hodgsoni* have not been examined, and I have found no description of them, but presumably they are spotted. The proportions of *hodgsoni* (fig. 19) and its bill (fig. 20) are very different from those of *Cyanoptila cyanomelana* or *Eumyias*.

The position of *Eumyias* is less certain. Its five species are perhaps intermediate between *Niltava* and *Muscicapa*, but since they are all typical flycatchers in their habits they seem better treated as a subgenus of *Muscicapa*, differing from it in their pattern and blue coloration, a tendency towards a shorter second primary, a longer tarsus, and a slightly to considerably longer tail. The same differences separating *Eumyias* from *Muscicapa* separate *Niltava* from *Muscicapa*, but, although *Eumyias* and *Niltava* have in common a blue coloration and a black mask from the bill to the eye, the rest of the pattern and the nature of the blue differ. *Eumyias* lacks the orange and strong rufous pigments so common in *Niltava*. The under tail coverts,

<sup>1</sup> The synonymy of *Cyanoptila*, *Muscicapella*, and *Eumyias* is included in that of the genera in which these three subgenera are placed. The species are listed under the respective genera, with their ranges, and the average measurements are given in the respective tables.



which may be blue bordered with white, differ. The shades of blue which in *Eumyias* range from ashy gray tinged with blue (*sordida*) to greenish azure "verditer" (*thalassina*) to dull azure (*panayensis*) to "indigo" and Prussian blue (*albicaudata* and *indigo*) are replaced in *Niltava* by ultramarine, a much richer and more intense color. Cobalt, which occurs very sparingly in *sordida*, *albicaudata*, and *indigo*, is more prevalent in *Niltava* where it extends over larger and different parts of the plumage. The contrast between the pattern and the coloration of the females is more significant. In *Eumyias* the males and females are blue or bluish above and below, but in female *Niltava* the under parts are never blue and are orange, rufous, or brownish, and the females of only three of the 22 species are blue above.

The differences in proportions between *Eumyias* and *Muscicapa* and the similarities of these proportions in *Eumyias* and *Niltava* may be due to similarity of function and do not necessarily indicate relationship or the lack of it. In the closely related species of *Muscicapa*, for instance, the proportions of the more aerial and of the migratory species differ very distinctly from those of the less aerial and non-migratory species. The difference between *Eumyias* and *Niltava* in the shape of the bill, although one of function, may be valid. *Eumyias* has a very typical flycatcher bill (fig. 21), flatter than that of *Niltava*, less attenuated, and proportionately broader at the base.

The problem of the affinities of *Eumyias* has been solved by most authors by treating this small group of species as a distinct genus, but, while convenient, this treatment is obviously unsound for it gives to these species the same "weight" that I have accorded to *Ficedula* or *Niltava* and *Muscicapa* and obscures the relationships of all the species which divide themselves or seem to divide themselves among these three genera.

**RELATIONSHIPS IN *Eumyias*:** The least-specialized species and the one that is perhaps closest to *Muscicapa* is *sordida*, judging by the facial pattern and blue coloration which are rather poorly developed in this species. *E. thalassina* and *panayensis* are very closely related and, since they replace each other geographically and are so similar,

constitute perhaps but one species. Their greenish azure coloration is so unusual that they may be considered, in this sense, as the most specialized. *E. indigo* and *albicaudata*, which, in turn, are closely related, are closer to *Niltava* in their pattern and coloration. The former, which is not truly indigo at all but Prussian blue, is quite variable geographically, one of its races (n nominate *indigo*) being a very greenish shade of this color and another (*cerviniventris*) rather dull Prussian as in *albicaudata*. It is in *indigo* that the cobalt is best developed and the pattern approaches most closely the pattern of some of the males of *Niltava*, the lower belly being whitish and the under tail coverts, in some races, rufous or tinged with rufous. In *indigo* and *albicaudata* the base of the tail is white (fig. 2); this character, very common in *Ficedula*, is lacking in *Muscicapa* and *Niltava*. In *Niltava*, one species (*concreta*) has some white in the tail, but the distribution of the white area is very different (fig. 2).

The wing formula of *Eumyias* is  $4=5>6=3$  (or 3, 4, 5, 6 subequal)  $>7>8>9>2$  (or  $9=2$ )  $>10$  in *sordida*, *panayensis*, and *indigo*, and the same in *albicaudata* with the exception that  $2=10$ . This formula is the same or differs very little from that of *Niltava*, but some non-migratory *Muscicapa* have a similar formula. In *thalassina* which is partly migratory the wing is a little more pointed, the wing formula being  $3=4=5>6>2>7$  (or  $2=7$ )  $>8>9>10$ . The nest, as in *Niltava* and *Muscicapa*, is cup shaped and made, or often made, of green moss. The young are well spotted. *Eumyias* is Indo-Malayan in distribution, the range of *thalassina* extending to Szechwan.

The position of *Cyanoptila cyanomelana* is uncertain. This very striking species, which breeds in the eastern Palearctic region and migrates to Indo-Malaya, is a true flycatcher in structure and is said to be one in its habits. Although a larger species than any *Muscicapa*, its proportions are similar to those of a typical migratory *Muscicapa* such as *striata*. Its wing formula ( $3=4>5>2>6>7>8>9>10$ ) and wing tip index are the same as in *latirostris*, another typical *Muscicapa* that breeds in the same regions as *cyanomelana* and has the same migration. The bill of *cyanomelana* (fig. 20) though not

well depressed is flycatcher-like in outline. These structural similarities, however, are probably due to similarity of function, for the coloration and pattern of the male of *cyanomelana* are completely different from those of any *Muscicapa*.

In *cyanomelana* the sexes are strongly dimorphic in coloration. The coloration and pattern of the female are not diagnostic, the upper parts, the sides of the face and throat, and breast being brownish gray, the center of the throat buffy white, and the abdomen and under tail coverts whitish. This inconspicuous coloration is generally similar to that of most *Muscicapa* and of the females of some species of *Ficedula* and *Niltava*. The males are blue above and present all the range in the shades of blue that occur in *Eumyias* and *Niltava* in which no one species is nearly so varied. The pattern and coloration of the under parts are different. *C. cyanomelana* is black and white below, the sides of the face and the whole throat are usually pure black, the black area ending sharply at the level of the upper or middle breast, the rest of the under parts being snow white. In *Niltava* the under parts are orange or strongly rufous, with a blue throat in some species. In *Eumyias* and in the species of *Niltava* that are not orange or rufous below, the under parts are blue-back (*N. grandis*) or blue with no white or little or much less white on the abdomen, and the white when present is always less pure than in *cyanomelana*.

In *cyanomelana* the mesial half of the outer tail feathers is white (fig. 2) as in many species of *Ficedula*, but the same tail pattern is present also in *Eumyias* in two species (*indigo* and *albicaudata*). The white area which in these two species is present in both males and females is lacking in female *cyanomelana*. In *Ficedula* the white area when present is normally present in both sexes, but is missing in the females of one species (*mugimaki*).

The possible phylogenetic significance of the pattern and coloration of *cyanomelana* is difficult to evaluate. These characters show, I believe, that *cyanomelana* is not directly related to *Muscicapa*, but its blue coloration shows, perhaps, that it is more or less distantly related to *Eumyias* or *Niltava*. It should be noted that in the male of *cyno-*

*melana* the black of the throat and breast is occasionally tinged with blue and that in the female the lower part of the buffy area of the throat expands sometimes into an ill-defined patch somewhat reminiscent of the throat patch of the females of some species of *Niltava*, but a throat patch is present also in some *Ficedula*. The juvenal plumage of *cyanomelana* is perplexing. Hartert (1907) states that the nestling "is said to be spotted," but juvenal individuals, apparently as soon as they leave the nest, are not spotted, whereas such individuals are well spotted in *Ficedula*, *Niltava*, *Eumyias*, and *Muscicapa*, at least in the species in which such specimens were available. In *Muscicapa comitata*, in which the young are said to be not spotted, I found that the young are faintly spotted on the breast. No nestling of *cyanomelana* was available. Juvenal specimens resemble the adult female but have the upper wing coverts well tipped with rufous, the rump, wings, and tail being bluish in the juvenal male.

I have treated *Cyanoptila* as a subgenus of *Ficedula*, although its blue coloration shows, perhaps, that its affinities are with *Niltava* or *Eumyias*. However, as discussed under *Ficedula*, the species of the *Muscicapula-Digenea* group of this genus grade perfectly into the blue coloration of the *Cyornis* species of *Niltava*. It is possible that either all the species with a blue coloration are more or less distantly related or that a blue coloration has arisen independently on several occasions. The nearest relatives of *cyanomelana* are not obvious, but I have placed this species under *Ficedula*, for this genus, being by far the most diversified in every character, is in my opinion older than the other more homogeneous genera and subgenera, which seem to be offshoots of more recent origin.

#### GENUS MUSCICAPA BRISSON

*Muscicapa* BRISSON, 1760, Ornithologia, vol. 1, p. 32. Type, by tautonymy, "*Muscicapa*," i.e., *Muscicapa striata* Brisson, 1760, Ornithologia, vol. 2, p. 357.

*Butalis* BOIE, 1826, Isis, p. 973. Type, by monotypy, *Muscicapa grisola* Linnaeus = *Muscicapa striata*.

*Hemichelidon* HODGSON, 1845, Proc. Zool. Soc. London, p. 32. Type, by subsequent designation, *Hemichelidon fuliginosa* Hodgson, 1845 (Gray, 1855, Catalogue of the genera and sub-genera of

birds . . . in the . . . British Museum, p. 53 [= *Muscicapa sibirica cacabata* Penard, see Appendix].

*Stoporola* (sic)<sup>1</sup> BLYTH, 1847, Jour. Asiatic Soc. Bengal, vol. 16, pt. 2, p. 125 (not *Stoparola* Blyth, 1836 = *Ficedula*, q. v.). Type, by original designation, "*St. melanops*" = *Muscicapa melanops* Vigors, 1831 = *Muscicapa thalassina* Swainson, 1838, because *M. melanops* Vigors is preoccupied by *Muscicapa melanops* Vieillot, 1822.

*Alseonax* CABANIS, 1850, Museum Heineanum, vol. 1, p. 52. Type, by subsequent designation, *Muscicapa undulata* Vieillot, 1822 (Gray, 1855, Catalogue of the genera and sub-genera of birds . . . in the . . . British Museum, p. 52 [= *Butalis adusta* Boie, 1828, because *M. undulata* Vieillot is preoccupied by *Muscicapa undulata* Gmelin, 1788]).

*Eumyias* CABANIS, 1850, Museum Heineanum, vol. 1, p. 53. Type, by monotypy, *Muscicapa indigo* Horsfield.

*Glaucomyias* CABANIS, 1850, Museum Heineanum, vol. 1, p. 53. [New name for *Stoparola* Blyth, 1849, see footnote below, not *Stoparola* Blyth, 1836 = *Ficedula* q. v.].

*Artomyias* J. AND E. VERREAUX, 1855, Jour. f. Ornith., vol. 3, p. 103. Type, by monotypy, *Artomyias fuliginosa* J. and E. Verreaux, 1855 (March) [= *Butalis infuscatus* Cassin, 1855 (April) = *Muscicapa infuscata*, see Appendix].

*Hypodes* CASSIN, 1859, Proc. Acad. Nat. Sci. Philadelphia, vol. 11. Type, by original designation and monotypy, *Eopsaltria cinerea* Cassin, 1856 [= *Butalis caerulea* Hartlaub, 1865 = *Muscicapa caerulea*, see Appendix].

*Pedilorchynchus* REICHENOW, 1892, Jour. f. Ornith., vol. 40, p. 34. Type, by monotypy, *Pedilorchynchus stuhlmanni* Reichenow [= *P. comitatus stuhlmanni* = *Muscicapa comitata stuhlmanni*].

*Myopornis* REICHENOW, 1901, Jour. f. Ornith., vol. 49, p. 285. Type, by original designation, *Bradyornis böhmii* Reichenow.

*Apatema* REICHENOW, 1905, Die Vögel Afrikas, vol. 3, p. 523. Type, by monotypy, *Parisoma olivascens* Cassin.

*Cichlomyia* OBERHOLSER, 1905, Proc. U. S. Natl. Mus., vol. 28, p. 908. Type, by original designation, *Butalis caerulea* Hartlaub.

*Arizelomyia* OBERHOLSER, 1905, Proc. U. S. Natl. Mus., vol. 28, p. 910. Type, by original designation, *Muscicapa latirostris* Raffles.

#### GENERAL DISTRIBUTION OF THE GENUS

This genus consists of 21 species, and of two subgenera (*Myopornis* and *Eumyias*)

<sup>1</sup> A typographical error is obvious, since Blyth corrected the name to *Stoparola* in 1849, Catalogue of the birds in the Museum Asiatic Society (p. 174).

which are discussed elsewhere, the first of these being monotypic and the other consisting of five species. *Muscicapa* is the most widespread genus of the Muscicapini, occurring in the Ethiopian and Palearctic regions and in Indo-Malaya. It is best represented in the Ethiopian region, with 13 species. Of the eight other species, one (*segregata*), which zoogeographically is the most interesting of the genus, is confined to Sumatra, the other species being Palearctic or Himalayan and highly or partly migratory. The partly migratory species consist of the Himalayan *muttui* and *ruficauda*, the northern populations of which (or a part of them) wander to the plains or to central and southern India after the breeding season. Of the five highly migratory species, one (*striata*) migrates to tropical and southern Africa, or, in the case of its eastern populations, to northwestern India, the other four species migrating to Indo-Malaya. The Ethiopian species are sedentary.

#### CHARACTERS OF THE GENUS

This genus consists of small or rather small species (table 6), all the general characters of which are compared with those of the other genera in the above discussions. However, since only a few of the individual species of *Muscicapa* are discussed, the characters of the genus and its variability may be described below. These species, although variable, comprise the typical flycatchers, some of which represent the extreme development of the flycatcher type. The variability is chiefly one of structure (where variability is high), the coloration and pattern being rather homogeneous, and the habits, except in one species (*griseigularis*), more or less similar.

**STRUCTURAL CHARACTERS:** The tarsus is usually short or very short, varying (fig. 22) from about 13 to 20 per cent of the length of the wing except in one species (*griseigularis*) where it is about 25 per cent of the wing. This species, however, is aberrant in the sense that it is more warbler-like than flycatcher-like in its habits and manner of feeding. The tarsus and claws are usually weak, but the tarsus is thick and the claws are strong in one species (*tessmanni*). The tarsus is usually not scutellated, but scutes or traces

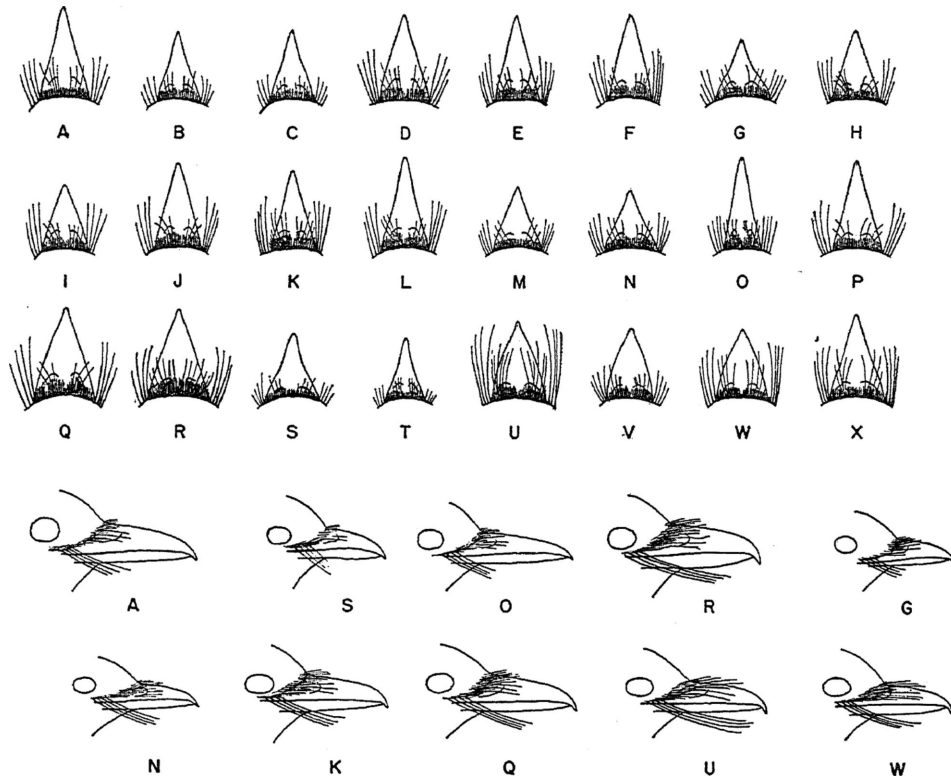


FIG. 21. Bill characters in the genus *Muscicapa* and the subgenus *Eumyias*. A. *Muscicapa striata*. B. *M. sibirica*. C. *M. griseisticta*. D. *M. latirostris* and *segregata*. E. *M. muttui*. F. *M. ruficauda*. G. *M. ferruginea*. H. *M. gambagae*. I. *M. adusta*. J. *M. aquatica*. K. *M. olivascens*. L. *M. cassini*. M. *M. epulata*. N. *M. seth-smithii*. O. *M. griseigularis*. P. *M. caerulescens*. Q. *M. comitata*. R. *M. tessmanni*. S. *M. infuscata*. T. *M. ussheri*. U. *Eumyias sordida*. V. *E. thalassina*. W. *E. panayensis* and *indigo*. X. *E. albicaudata*. For the subgenus *Myopornis*, see figure 8. Natural size.

of them are present in seven of the 21 species. These variations, which often occur between two closely related species, are discussed in the general discussion of the tarsus in the introductory section.

The proportions (fig. 22) may also vary between related species. However, in *Muscicapa* taken as a whole, the tail, tarsus, and first primary average distinctly shorter and the second primary longer than in all the preceding genera.

The bill although very variable in outline (fig. 21) is usually broad or very broad at the base and well or much depressed (again with the exception of *griseigularis* in which it is slender, very attenuated, and compressed laterally). The rictal bristles vary. They may be rather short and weak but usually

are fairly long and strong. In *Muscicapa*, as might be expected, the highest development of the flycatcher bill is reached, and in some species the bill is so well adapted for catching insects on the wing that it has become swallow-like.

The shape of the wing is extremely variable, from long and very pointed to long but blunt, to very round, and no more than any two species, whether migratory or not, have an identical wing formula. The migratory species have, of course, a very pointed wing, the formula ranging from  $3 > 4 > 2 > 5 > 6 > 7 > 8 > 9 > 10$  in *sibirica* to  $3 > 2 = 4 > 5$ , etc., in *griseisticta*, to  $3 = 4 > 2 > 5$ , etc., in *striata*, to  $3 = 4 > 5 > 2 > 6$ , etc., in *latirostris* and the partly migratory *muttui*, to  $3 = 4 > 5 = 2 > 6$ , etc., in *ferruginea*, to  $3 = 4 = 5 > 6 > 2 > 7$ , etc.,

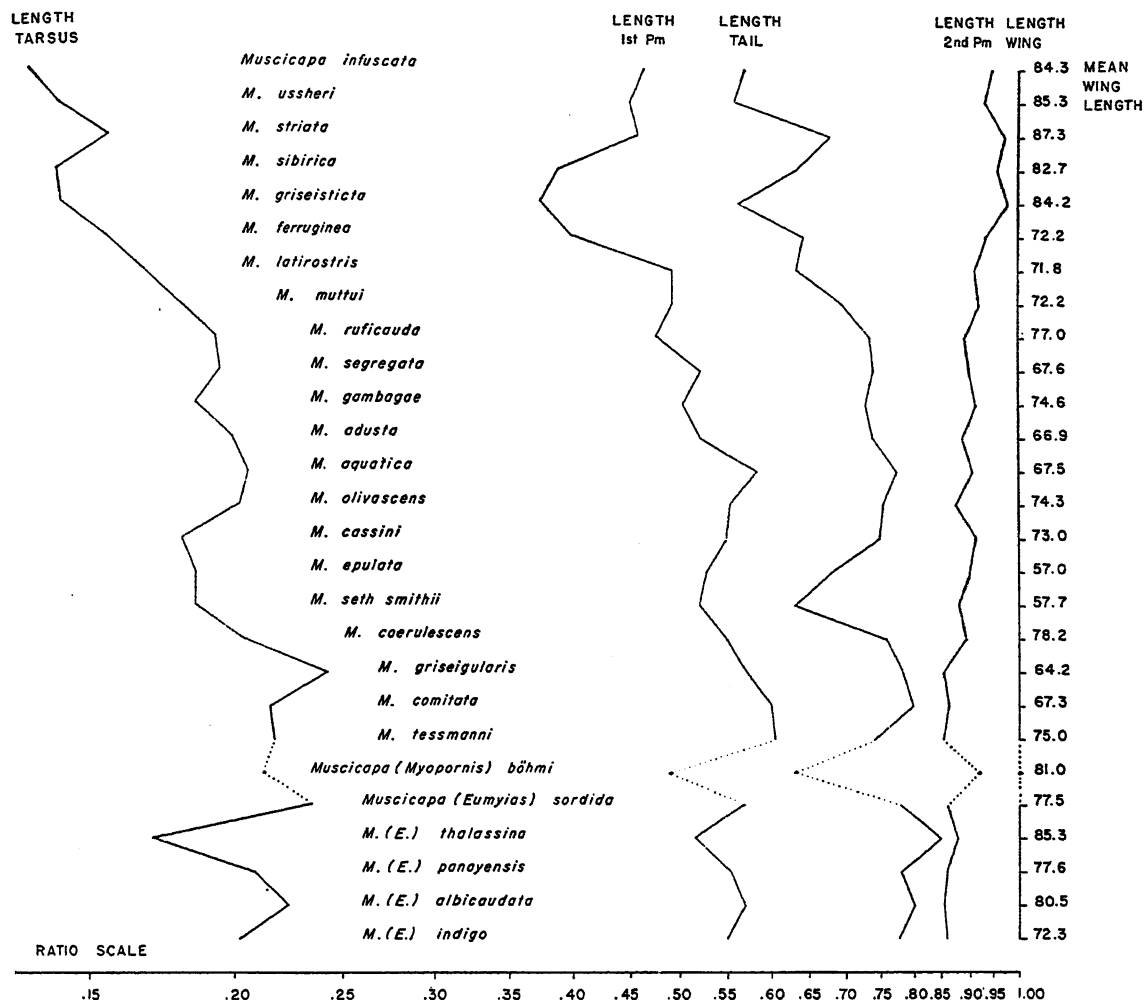


FIG. 22. Comparison through ratio diagram of the proportions in *Muscicapa* and in the subgenera *Myopornis* and *Eumyias*. In this diagram the Ethiopian species *infuscata* and *ussheri* are placed ahead of the highly migratory Palearctic species (*striata* to *latirostris*), as their proportions are much closer to the proportions of these species than they are to those of the other Ethiopian species. All Ethiopian species are non-migratory. *M. segregata* is separated from its close relative (*latirostris*) by two partly migratory Indian species, *segregata* from Sumba being non-migratory.

in the partly migratory *ruficauda* and in *segregata* from Sumba which though not migratory is probably very closely related to *latirostris*.

In the Ethiopian species which are all sedentary the wing becomes progressively very round. In *gambagae*, as stated in the introductory section, the wing is intermediate in shape between the pointed wing of the migratory species and the round wing of the other Ethiopian species, the wing formula

of *gambagae* being  $3=4=5>6=2>7>8>9>10$ . The formula of the other species ranges from  $3=4=5>6>2=7$ , etc., in *cassini*, to  $3=4=5>6>2>7$  in *epulata* and *seth-smithii*, to  $3=4=5>6>7>2$  or  $7=2>8$ , etc., in *adusta*, to  $4=5>3=6>7>2=8>9>10$  in *olivascens*, to  $3=4=5>6>7>2=8>9>10$  in *caerulescens*, to  $3=4=5=6>7>8>9>2>10$  in *aquatica*, to  $4=5=6>3=$  or  $7>8>9>2=10$  in *griseigularis*, to  $4=5>6>7=3>8>9>2=10$  in *tessmanni*, to  $3=$

4=5=6>7 or 4=5=6>3=7>8>9>2> or= or<10 in *comitata*. The two very arboreal *infuscata* and *ussheri*, although they have a long wing (the difference between the second and tenth primaries averages about 19 mm. as in some migratory species), do not have a sharp wing tip, the wing formula, which is the same in both species, being 3=4>5>or=2>or=6 (or 2, 3, 4, 5, 6 subequal)>7>8>9>10.

In the preceding list it can be seen that the shape of the wing often varies between two closely related species. For instance, in *sibirica* and *striata* or in *adusta* and *aquatica*, the formulas of the last two are quite far apart. Further, the formula may vary intraspecifically in the migratory or non-migratory species. For instance, in the less highly migratory southern races of *sibirica* the wing is rounder, and in *aquatica*, which is not migratory, the formula varies from 3=4=5=6>7>8>9>2>10 to 7=2>8>9>10 or 2 may be equal to 8, to 9, or to 10.

The fact that the structural characters vary considerably even in closely related species suggests that these characters are adaptive and are correlated with variations in habits and ecological requirements. Some of these instances of correlation, the most obvious of which are with migration or the height at which the species feed, are discussed in the introductory section.

**PATTERN AND PIGMENTATION:** In contrast to the high variability in structure the coloration and pattern are quite constant. The sexes are identical, the coloration is dull and the range of pigments very restricted, and the pattern is simple. The majority of the species (15 out of 21) are gray-brown more or less saturated, tinged with olive and/or rust in four species, only one of which (*ferruginea*) shows really well-developed rufous pigments. In the other six species the grayish and brown pigments are replaced by dull blue-gray, ashy, or slate. The under parts are whitish, more or less heavily pigmented with gray-brown or ashy on the throat, breast, and flanks, or the throat or its center may be white or whitish. The pigments may be more or less uniformly distributed, but in most species the shafts of the feathers on the throat and breast, and sometimes on the crown, are darker and form streaks. The

streaking may be vague, resulting in a mottled appearance, or the streaks may be well defined but faint, or they may be sharp and conspicuous, or very bold and heavy. In almost all species the lores, or the region immediately above or in front, are white, whitish, or buffy white, and the eye is often surrounded by a ring, often very narrow, of the same color. Conspicuous head markings are lacking, however, and the tail is uniformly colored, without a white area. A streaked pattern and dull coloration are characteristic of this genus.

**HABITS:** All the species, with the exception of *griseigularis*, are typical flycatchers. That is, they perch more or less stolidly and silently on some exposed vantage point from which they frequently sally forth after some passing insect, returning often to the same perch. They do not usually search the foliage for insects, and they seldom or never come to the ground. Their habitat requirements are nevertheless quite varied. Some species are restricted to the deep and shady virgin forest; others occur only in the clearings, others only in the open forest or in open country, or in evergreen forest, wooded savannas, thorn bush or acacia country, or in gardens, and so on. Some species are never found away from water, such as *cassini* and *aquatica*, which hunt over the water from projecting branches or snags; *cassini* along the banks of the wider rivers of the forest, *aquatica* in swamps, near pools, lakes, or the smaller streams. To some, such as *infuscata* and *ussheri*, tall dead trees or tall dead limbs of the trees of the high forest are essential. Others, such as *striata*, hunt from the lower branches and seldom at the top. Others hunt from low trees, the top of bushes, dead snags, fence posts, the top of reeds, or from hanging loops of vines and creepers.

The information on some species is scanty or lacking, but probably no two species occurring in the same regions have identical ecological requirements, these variations resulting, as stated, with the presence or absence of migration, in wide adaptive variations in structure.

All the species build a cup-shaped nest in which moss or lichens and often cobwebs are used very frequently. The height of the nest and its location are very variable. It may be

placed high or very low in thickets, against a stump, a branch, a tree trunk, or a wall, or it may be built on a branch, in hollows and holes in stumps and trees, masonry, and even earth banks. In *comitata* the nest is built in the abandoned nests of weavers, and in *striata* the nest is often built in the old nests of many species of birds. The species are silent or rather silent, or their song is usually poor and not very melodious.

#### DIVISION OF THE GENUS

The 21 species placed in this study in the genus *Muscicapa* are divided by some current authors among eight genera. Baker (1924) divides the six species that occur in India among three genera (*Muscicapa*, *Hemichelidon*, and *Alseonax*), separating *Alseonax* from the first two by five genera. This arrangement is very misleading, for it separates very widely such closely related and typical *Muscicapa* as *striata* and *latirostris* by the *Cyornis* species of *Niltava* or other unrelated species placed by me in *Ficedula*, *Rhinomyias*, *Eumyias*, and *Muscicapella*. The 13 Ethiopian species are divided in four (Bates, 1930; Sclater, 1930) to seven genera (Chapin, in press).

Since the coloration and pattern of these 21 species are quite homogeneous and the habits (with the exception of those of *griseigularis*) are similar, these "genera" are all perforce based on the variations in structure, chiefly those in the shape of the bill and length and shape of the wing. All these characters, however, grade insensibly into one another and, as I have emphasized, appear to be purely adaptive.

The Ethiopian genera recognized by Bates and Sclater are *Artomyias*, *Muscicapa*, *Alseonax*, and *Pedilorchynchus*. The first, which consists of *infuscata* and *ussheri*, can be defended if these two species are contrasted only with the rest of the Ethiopian species, the degree of distinction of *Artomyias* vanishing completely, however, when its two species are compared to *sibirica*, *griseisticta*, and *ferruginea* from the eastern Palearctic and India. The last three species, which make up the "genus" *Hemichelidon*, have, as in *infuscata* and *ussheri*, a very depressed and swallow-like bill with short and/or weak rectal bristles; fuscous, fulvous, or rufous pigments

are also present in *ferruginea* and *infuscata*, and *infuscata* is very heavily and broadly streaked as is *griseisticta*. All five species have similar proportions, a short tarsus, a short tail, a short first and second primary, and a long wing, but all these proportions grade into those of *striata*.

The inconsistency of the various attempts to distribute the 11 other Ethiopian species in different genera has been reviewed by Bates (1927) who, although he states that "much may be said in favour of uniting them all in *Muscicapa*," nevertheless recognizes *Alseonax* and *Pedilorchynchus* on the basis of differences in the shape of the wing and bill. Bates supports *Pedilorchynchus* by stating also that the base of its bill is more heavily feathered and that the young of *comitata* are not spotted. The denser feathering of the bill does not seem to warrant generic separation, and, as I have stated, I have found that the young of *comitata* are spotted. *Pedilorchynchus* consists of two species, *comitata* and *tessmanni*, which, as discussed in the introductory section, are quite distinct structurally. *M. tessmanni* is much more heavily built, has a very much thicker tarsus and much stronger claws, and a different wing formula. If, therefore, the species of *Muscicapa* are to be separated on structural characters, consistency requires the erection of a new monotypic genus for *tessmanni* which is certainly more distinct structurally from *comitata* than *cassini* or *aquatica*, placed by Bates and Sclater in *Alseonax*, are from *gambagae*, placed by these authors in *Muscicapa*. Further, there is no agreement as to the limits of *Alseonax*, and *cassini* and *aquatica* are shown conclusively to be true *Muscicapa* by Chapin (in press).

The monotypic *Apatema* and *Hypodes* for, respectively, *olivascens* and *caerulescens*, are recognized by Chapin (in press). These two "genera" are based on the shape of the bill. The bill of *Apatema* is more highly ridged than usual in *Muscicapa*, but the bill of *Hypodes*, although said to be more slender than the bill of *Muscicapa*, does not differ appreciably (fig. 21P) from that of *striata* (21A).

*Muscicapa griseigularis* is placed in *Alseonax* by both Bates and Sclater and, on the advice of Chapin, in *Parisoma* by Banner-

man (1936). *Parisoma* and *M. griseigularis* are discussed above in the introductory section where it is shown that *Parisoma* is a composite group, some species of which are almost certainly warblers. Chapin's observations that *griseigularis* behaves somewhat like a warbler are supported, as stated, by adaptive differences in structure, a more slender and compressed bill, and a longer tarsus. Nevertheless, for reasons given, I do not believe that *griseigularis* can be placed in *Parisoma*, and I consider that *griseigularis*, though aberrant in its manner of feeding, is closely related to the other gray-blue *Muscicapa*. It may be added that even the most typical *Muscicapa* occasionally search, singly or in groups, the foliage of trees and bushes.

#### RELATIONSHIPS OF THE SPECIES

The presumed relationships of the 21 species, which cannot be expressed in one continuous linear sequence, appear to be as follows:

If the long pointed wing of the Palearctic species be discounted as a secondary adaptation correlated with the development of migratory habits, the pattern and coloration of the Ethiopian *gambagae* suggest that this species is closely related to the Palearctic *striata*, *sibirica*, *latirostris*, and *griseisticta*; *segregata* of Sumba is merely a *latirostris* which has become sedentary and has, as a result, lost the pointed wing. As *latirostris* migrates to the Malay Archipelago, *segregata* is very probably directly derived from *latirostris*, or otherwise it would be difficult to account for the presence of an isolated colony of *Muscicapa* in the Lesser Sundas. *M. muttui* and *ruficauda*, which appear to be very closely related to each other, are but slightly differentiated from *latirostris*. The rufous pigments, which first appear and are weakest in *muttui*, are better developed in *ruficauda* and most highly developed in *ferruginea*. The bill of *ferruginea* is very broad and quite distinct from that of *muttui* and *ruficauda*, but these two species are shy birds of the heavy forest whereas *ferruginea* lives in the open and is very aerial in its habits.

The bill of *ferruginea* is identical with that of *infuscata* and rather similar to that of *ussheri*, and the proportions of these two Ethiopian species (long wing, short tarsus, and short

tail) also seem to bring these two species close to the migratory Palearctic and Indian species, but this seems to be an instance of parallel adaptation, for *infuscata* and *ussheri*, which like *ferruginea* are very aerial in their habits, probably represent an independent offshoot from some less specialized type such as the present-day *gambagae*. *M. infuscata* and *ussheri* are presumed to be very closely related and are geographical representatives. It has been suggested that they are conspecific. They differ clearly, however, in the pattern of the plumage; *infuscata* is very broadly streaked and *ussheri* is not streaked; the feet of *ussheri* are distinctly heavier, and its tarsus is not scutellated, whereas that of *infuscata* is clearly and well scutellated.

*Muscicapa cassini*, *aquatica*, *adusta*, and *olivascens* appear to be closely related to *gambagae*; *aquatica* and *adusta* appear to be especially close, although placed in two different genera by Chapin, the only fairly obvious difference being in the shape of the bill. With *cassini* blue-gray and slaty pigments make their appearance, but this species despite its different pigmentation is still clearly and closely related to *gambagae*. The blue-gray or slaty species may have followed two or more evolutionary lines, one leading to a general reduction in size with the small *epulata* and *seth-smithii*, the other line or lines to the larger *caerulescens*, *griseigularis*, *comitata*, and *tessmanni*. *M. epulata* and *seth-smithii* are very similar and obviously are very closely related. The larger species, including *cassini*, are better differentiated from one another, although some are still generally similar, so much so that, as Neumann (1914) and Bates (1926) have shown, *caerulescens* and *cassini* have often been confused with each other. As a comment on the generic splitting of these species, it may be added that some of the confusion arose with the author who erected *Hypodes* for *caerulescens*.

#### LIST OF THE SPECIES

In this list the Palearctic and Indo-Malayan species are placed first, followed by the Ethiopian species, and ending with *infuscata* and *ussheri*. The Ethiopian species are followed by the Ethiopian subgenus *Myopornis*, followed by the Indo-Malayan subgenus *Eumyias*. This order appears to be the most



logical possible but does not imply phylogenetic progression, although the species of each branch are placed as nearly as possible in what appears to be their natural order.

***Muscicapa striata* Pallas**

RANGE: Western Palearctic east to Lake Baikal, Transbaikalia, and northern Mongolia, and from Lapland and Archangel south to Morocco east to western Himalayas; migrates to northwestern India and tropical and southern Africa.

***Muscicapa sibirica* Gmelin**

RANGE: Eastern Palearctic from central Altai to Kamchatka, Bering, and Japan, in China from Szechwan to northwestern Yunnan, and Himalayas to Baluchistan; migrates to southeastern China and Indo-Malaya.

***Muscicapa griseisticta* Swinhoe**

RANGE: Eastern Palearctic from the upper Lena to Kamchatka, Bering, Kuriles, Sakhalin, Ussuriland, and eastern Manchuria; migrates to Indo-Malaya, Moluccas, and New Guinea.

***Muscicapa latirostris* Raffles  
(*daurica*, *auct.*)**

RANGE: Eastern Palearctic from Minussinsk to northern Mongolia, Transbaikalia, Amurland, Sakhalin, Kuriles, Ussuriland, Manchuria, Korea, and Japan; India in the Himalayas, central India, and western parts of the peninsula; migrates to southern China and Indo-Malaya.

***Muscicapa (latirostris) segregata* Siebers**

RANGE: Restricted to Sumba.

***Muscicapa muttui* Layard**

RANGE: Eastern Himalayas to Assam, central Szechwan, and northern Siam; partly migratory to southern India and Ceylon.

***Muscicapa ruficauda* Swainson**

RANGE: Western Himalayas from Baluchistan, Bukhara, and Afghanistan to central Nepal; partly migratory in western India south to Travancore, recorded in eastern India in Cachar.

***Muscicapa ferruginea* Hodgson**

RANGE: Himalayas from Garhwal to Assam, northern Burma, and Yunnan to Szechwan, also Manipur, southern China, and Formosa; migrates to southern China and Indo-Malaya.

***Muscicapa gambagae* Alexander**

RANGE: Interior of Gold Coast east to Uganda, Somaliland, and Yemen.

***Muscicapa adusta* Boie**

RANGE: South Africa north to Mt. Cameroon and Fernando Po in the west to northern Abyssinia in the east.

***Muscicapa aquatica* Heuglin**

RANGE: Gambia east to White Nile south, in east Africa, to Northern Rhodesia.

***Muscicapa olivascens* Cassin**

RANGE: Heavy forest from Gold Coast to Gaboon east to Semliki Valley.

**(*Muscicapa lendu*)?**

*Alseonax lendu* Chapin was described from a single specimen taken at Djugu, west of Lake Albert. In this specimen some of the characters of *aquatica* and *olivascens* appear to be combined. Above, *aquatica* and *lendu* are identical in coloration or virtually so, that is, both are darker and browner and lack the olive tinge of *olivascens*. In *lendu* the color of the under parts is very similar to that of *aquatica*, but the breast band is less well defined and the white area of the throat is restricted, as in *olivascens*. In *lendu* the throat, breast, and abdomen are faintly streaked or mottled; in *aquatica* these markings are restricted to the breast; and they are lacking in *olivascens*. In *lendu* the facial markings are similar to those of *olivascens*, but the white in front of the eye is more restricted, the lores are dark, and the white is restricted to a narrow and small supraloral streak. The bill of *lendu* is similar in shape to that of *aquatica* and *olivascens* (fig. 21J, 21K) but is slightly smaller than in *olivascens* and is intermediate in coloration. In *lendu* the base of the mandible is yellow and its tip is black, whereas the whole mandible is yellow in *olivascens* and black in *aquatica*.

Dr. Chapin kindly informs me that in his opinion, *lendu*, no other specimen of which has been collected, is either a separate species or an aberrant specimen of *olivascens*. The characters of the present specimen strongly suggest, I believe, that it is a hybrid of *aquatica* and *olivascens*.

***Muscicapa cassini* Heine**

RANGE: Forested regions from Liberia to northern Angola, east to Uganda, south to Northern Rhodesia.

***Muscicapa epulata* Cassin**

RANGE: Same as that of *olivascens*.

***Muscicapa seth-smithii* van Someren**

RANGE: Heavy forest from Fernando Po, Cameroon, and Gaboon east to Semliki Valley and Budongo Forest in Uganda.

***Muscicapa caerulescens* Hartlaub**

RANGE: Gold Coast and Cameroon east to Kenya, south to Natal.

***Muscicapa griseigularis* Jackson**

RANGE: Forests from Cameroon and Gaboon east to Semliki Valley and forests of Uganda.

***Muscicapa comitata* Cassin**

RANGE: Lowland forests from Sierra Leone south to northern Angola, east to Uganda.

***Muscicapa tessmanni* Reichenow**

RANGE: Forests from Gold Coast to southern Cameroon, east to Ituri.

***Muscicapa infuscata* Cassin**

RANGE: Forests from southern Nigeria to northern Angola, east to Uganda.

***Muscicapa ussheri* Sharpe**

RANGE: Sierra Leone to Gold Coast.

***Muscicapa (Myopornis) böhmi* Reichenow**

RANGE: See figure 8. Angola east to central Nyasaland and western Tanganyika.

***Muscicapa (Eumyias) sordida* Walden**

RANGE: Restricted to Ceylon.

***Muscicapa (Eumyias) thalassina* Swainson**

RANGE: Western China to Himalayas south to Malaysia; wanders in winter to central and southern India.

***Muscicapa (Eumyias) panayensis* Sharpe**

RANGE: Philippines, Celebes, and Moluccas.

***Muscicapa (Eumyias) albicaudata* Jerdon**

RANGE: Hills of southern India.

***Muscicapa (Eumyias) indigo* Horsfield**

RANGE: Sumatra, Java, and Borneo.

**THE SUBGENUS MYOPORNIS**

This monotypic subgenus was briefly discussed under *Bradornis*. Like the species of this genus, *Myopornis böhmi* occupies (fig. 8) a dry part of Africa from southern Angola to western Tanganyika.

The structural characters combine some of the characters of *Bradornis* and *Muscicapa*. As stated and illustrated under *Bradornis* (fig. 9), the bill of *böhmi* is similar in shape to that of *Bradornis* and has similarly exposed nostrils but, unlike the species of this genus, *böhmi* has a slender tarsus. Proportionately (fig. 22) the tarsus of *böhmi* is longer than in most *Muscicapa* but is similar in length to that of such non-migratory *Muscicapa* from the Ethiopian region as *caerulescens* or *co-*



FIG. 23. Spotting of the under parts in *Muscicapa (Myopornis) böhmi*. Natural size.

*mitata*, that is, about 20 per cent of the length of the wing, and is about as slender, though the claws are stronger in *böhmi* than in any other *Muscicapa* with the exception of *tessmanni*. The tail of *böhmi* is shorter than that of *Bradornis* (fig. 10) and fits very much better in the range of variation of *Muscicapa* (fig. 22). The wing formula of *böhmi* is  $3=4=5$  slightly  $>6>7=2>8>9>10$ . This formula is very similar to that of *Bradornis*, but this is probably of no phylogenetic significance, for some non-migratory *Muscicapa* such as *adusta* or *cassini* also have the same formula.

The general coloration of *böhmi* (gray-brown above and whitish below) is similar to that of *Bradornis* or to the gray-brown species of *Muscicapa*, but this is not necessarily diagnostic, for the upper parts of *böhmi* are far better streaked, more boldly and more abundantly, than any *Bradornis* or *Muscicapa*, and below (fig. 23) *böhmi* presents a unique triangular spotting. Both sexes are alike, and the young are well spotted.

TABLE 6  
AVERAGE MEASUREMENTS IN THE GENUS *Muscicapa*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess or Deficit of 2d Over 10th Primary	1st Pri- mary	Excess or Defi- cit of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
Genus <i>Muscicapa</i>										
M <sup>b</sup> <i>striata</i>	87.3	84.8	61.5	23.3	40.1	2.3	59.0	13.6	17.1	5.3
M <i>sibirica</i>	82.7	79.5	55.3	24.2	32.1	-4.5	52.2	11.6	13.8	5.4
M <i>griseisticta</i>	84.2	82.2	53.9	28.3	31.6	-5.5	47.5	11.9	14.3	5.2
M <i>latirostris</i>	71.8	65.7	50.1	15.6	33.7	2.2	45.5	12.0	14.7	6.0
<i>segregata</i>	67.6	61.0	53.6	7.4	35.0	6.9	49.9	13.2	16.4	6.0
PM <sup>c</sup> <i>muttui</i>	72.2	66.4	54.3	12.1	35.4	5.3	50.1	12.9	17.4	6.1
PM <i>ruficauda</i>	77.0	68.8	59.3	9.5	36.5	5.4	56.4	14.9	15.7	4.8
M <i>ferruginea</i>	72.2	67.3	49.9	17.4	28.7	-1.9	46.5	11.2	14.1	6.1
<i>gambagae</i>	74.6	68.2	59.3	8.9	37.4	6.6	54.5	13.8	14.3	5.5
<i>adusta</i>	66.9	59.6	53.9	4.7	34.8	8.9	49.4	13.4	13.8	5.3
<i>aquatica</i>	67.5	61.1	58.0	3.0	39.4	12.0	52.1	13.9	15.9	5.4
<i>olivascens</i>	74.3	65.0	60.3	4.7	41.0	10.3	56.0	15.1	15.0	5.3
<i>cassini</i>	73.0	66.5	59.6	6.9	40.1	9.5	54.4	13.2	17.5	5.6
<i>epulata</i>	57.0	51.5	46.4	5.1	30.0	6.5	38.7	10.6	12.4	5.2
<i>seih-smithii</i>	57.7	52.0	46.6	5.4	29.9	6.2	36.3	10.7	12.2	5.3
<i>caerulescens</i>	78.2	69.8	63.7	6.1	43.0	10.7	59.2	16.0	16.0	5.4
<i>griseigularis</i>	64.2	54.9	55.4	-5	36.7	11.1	50.5	15.6	15.0	4.1
<i>comitata</i>	67.3	58.2	57.6	-6	40.3	13.0	54.1	14.5	14.7	6.9
<i>tessmanni</i>	75.0	64.0	64.0	0	45.3	15.3	55.3	16.3	16.0	7.1
<i>infusca</i>	84.3	79.6	61.0	18.6	39.2	3.7	48.3	11.2	11.8	5.3
<i>ussleri</i>	85.3	79.9	60.3	19.6	38.5	3.5	47.6	12.0	12.2	5.4
Subgenus <i>Myopornis</i>										
<i>böhmi</i>	81.0	74.7	65.3	9.4	39.6	6.7	51.0	17.2	15.2	4.4
Subgenus <i>Eumyias</i>										
<i>sordida</i>	77.5	66.6	64.8	1.8	44.0	13.3	60.4	18.2	16.6	6.0
<i>thalassina</i>	85.3	74.9	67.0	7.9	43.7	8.1	72.2	14.5	14.3	5.5
<i>panayensis</i>	77.6	66.5	63.4	3.1	42.9	11.3	60.7	16.2	14.9	6.0
<i>albicaudata</i>	80.5	68.8	68.0	.8	45.6	13.7	64.7	18.0	15.2	5.8
<i>indigo</i>	72.3	61.9	58.8	3.1	39.6	10.7	56.3	14.7	13.9	5.5

<sup>a</sup> Longest primary.

<sup>b</sup> Migratory.

<sup>c</sup> Partly migratory.

Benson (1940) and White (1943) have described the behavior of *böhmi* as that of a typical *Muscicapa* but, unlike the species of this genus, much of its food seems to be composed of tree ants which can be caught without flying. The nest of *böhmi* was unknown, until it was recently discovered that this species, like *Muscicapa comitata*, occupies the abandoned nests of weavers. Vincent (1947) has discovered the nest of *böhmi* in the short-funnelled, retort-shaped nest of *Anaplectes*

*rubiceps*, and Benson (1951) in the nest of *Plocepasser rufoscapulatus*.

*Myopornis böhmii* appears to be a somewhat aberrant *Muscicapa*, the nearest relatives of which, though obscure, are probably some of the Ethiopian species of this genus. Chapin (in press) places it next to *Apatema* and *Alseonax*. These last two appear to be typical *Muscicapa*, but *Myopornis* appears to be sufficiently distinct to warrant its retention as a subgenus. In the list of species

under *Muscicapa*, *Myopornis* is placed after the Ethiopian species of the genus and before the Indo-Malayan *Eumyias* which appears to be another subgenus of *Muscicapa* of independent origin.

GENUS **HUMBLLOTIA** MILNE-EDWARDS  
AND OUSTALET

*Humblotia* MILNE-EDWARDS AND OUSTALET, 1885, Compt. Rendus Acad. Sci., Paris, vol. 101, p. 221. Type, by original designation and monotypy, *Humblotia flavirostris* Milne-Edwards and Oustalet.

This monotypic genus, which appears to be very closely related to *Muscicapa*, is restricted to Grand Comoro Island.

*Humblotia flavirostris*, which is lacking in most collections, is illustrated in figure 24. It differs from *Muscicapa* and all the other genera studied in the extremely soft texture of its plumage and in having the feathers of the fore crown squamose and semi-erect, and the rest of the feathers of the crown distinctly elongated.

The tarsus of *flavirostris* is not scutellated or shows but a faint trace of one or two scutes.



FIG. 24. *Humblotia flavirostris*. Natural size.

It is slender, with rather weak claws, and is longer than that of *Muscicapa*, averaging (fig. 26) about 25 per cent of the length of the wing as against 17 in *Muscicapa*, where the length of the tarsus ranges from 13 to 20 per cent except in *M. griseigularis* where the length also averages 25. The bill of *flavirostris* (fig. 25) is a typical flycatcher bill, depressed above and very broad at the base, moderately hooked, feathered over the nostrils, and with long and strong rictal bristles. The wing is well rounded, the formula being  $4 = 5 \text{ slightly} > 3 \text{ slightly} > 6 \text{ (or } 3, 4, 5, 6 \text{ subequal)} > 7 > 2 > \text{or} = 8 > 9 > 10$ . In general *flavirostris* (table 7) fits well in the range of variation of *Muscicapa* (table 6; compare also with *M. gambagae* in table 7).

The coloration of *flavirostris*, which is dull, and its pattern, which is well marked (fig. 24), are similar to those of some *Muscicapa*, *flavirostris* being dark gray-brown above, whitish below, with broad and heavy gray-brown streaks on the sides of the throat, on the breast, and on the flanks. The fore crown is streaked, and the upper wing coverts and secondaries are margined with white, the upper tail coverts with grayish, and the tail feathers, with the exception of the central pair, are narrowly tipped with white. The sexes are presumably alike, although the specimens examined by me were not sexed and, apparently, neither were those studied by Milne-Edwards and Oustalet (1887, 1888). Since these authors had about 20 specimens and I have examined another five, it is likely that some of these are females. The young has not been examined and is unreported, but, since this genus appears to be very closely related to *Muscicapa*, its young are probably spotted.

Although the habits of this species have not been described, its close relationship to *Muscicapa* is clear, an opinion advanced also by Milne-Edwards and Oustalet who call attention to the fact that, with the exception of the fore crown, *flavirostris* is very similar in its pattern and coloration to *Muscicapa sibirica*.

GENUS **NEWTONIA** SCHLEGEL AND POLLEN

*Newtonia* SCHLEGEL AND POLLEN, 1868, Recherches sur la faune de Madagascar, pt. 2, p. 101. Type, by monotypy, *Erythrosterina* (?) *brunneicauda* (sic) Newton.

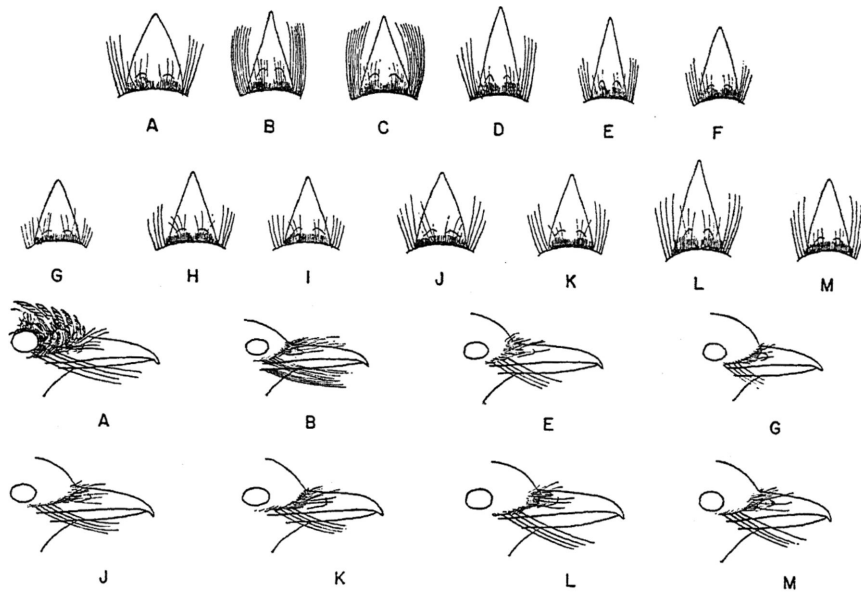


FIG. 25. Bill characters in the genera *Humblotia*, *Newtonia*, *Microeca*, and *Culicicapa*. A. *Humblotia flavirostris*. B. *Culicicapa ceylonensis*. C. *C. helianthea*. D. *Newtonia amphichroa*. E. *N. brunneicauda*. F. *N. archboldi*. G. *Microeca leucophaea*. H. *M. brunneicauda*. I. *M. flavigaster*. J. *M. hemixantha*. K. *M. griseiceps*. L. *M. flavovirescens*. M. *M. papuana*. Natural size.

#### DISTRIBUTION AND CHARACTERS

This genus, which may possibly be distantly related to *Muscicapa* via *Humblotia*, consists of four small species which are restricted to Madagascar. These species differ from *Muscicapa* and related genera in their habits and in some structural characters, chiefly through their long tarsus and very rounded wing, and in the softer texture of their plumage and their unspotted young.

**STRUCTURAL CHARACTERS:** The tarsus, which is booted in two species (*amphichroa* and *brunneicauda*), is scutellated in *archboldi* (the fourth species, *fanovanae*, known only from a single specimen, was not examined) and is very long and slender, averaging (fig. 26) from about 32 to 37 per cent of the length of the wing. The claws, relatively speaking, are moderately strong. The bill (fig. 25), though slender and very attenuated, is somewhat broadened at the base and relatively depressed above; it is well feathered at the base and over the nostrils, and the rictal bristles are long and strong. In *fanovanae*, according to Gyldenstolpe (1933), the bill "is exceptionally thin, even thinner than in all the other hitherto known forms of *Newtonia*.

The rictal bristles are well-developed and quite prominent." The tail and the first and second primaries tend to be long (fig. 26), the tail averaging from about 78 to 93 per cent of the length of the wing.

The wing is exceptionally round, the primaries (table 7) decreasing very little in length from the longest to the tenth, the difference being only 3 to 5 mm. longer, while the second is from 6 to 8 mm. shorter than the tenth. Such a wing is very unusual in the flycatchers, where the second and tenth are very rarely equal, the second being usually slightly longer to much longer than the tenth. The wing formula, which is the same in *brunneicauda* and *archboldi*, is 3, 4, 5, 6, 7, 8 subequal (or  $4=5=6=7$  slightly  $>3=8$ )  $>9 >10 >2$ ; in *amphichroa* the formula is 4, 5, 6, 7, 8 subequal (or  $5=6=7$  slightly  $>4=8$ ) slightly  $>9$  slightly  $>10$  slightly  $>3 >2$ .

A character of interest in *Newtonia*, which may possibly indicate some degree of relationship with *Humblotia*, is the very soft texture of the plumage, the body feathers of *Newtonia* being very long and very silky though somewhat less fluffy than in *Humblotia*.

**PATTERN AND PIGMENTATION:** The pattern

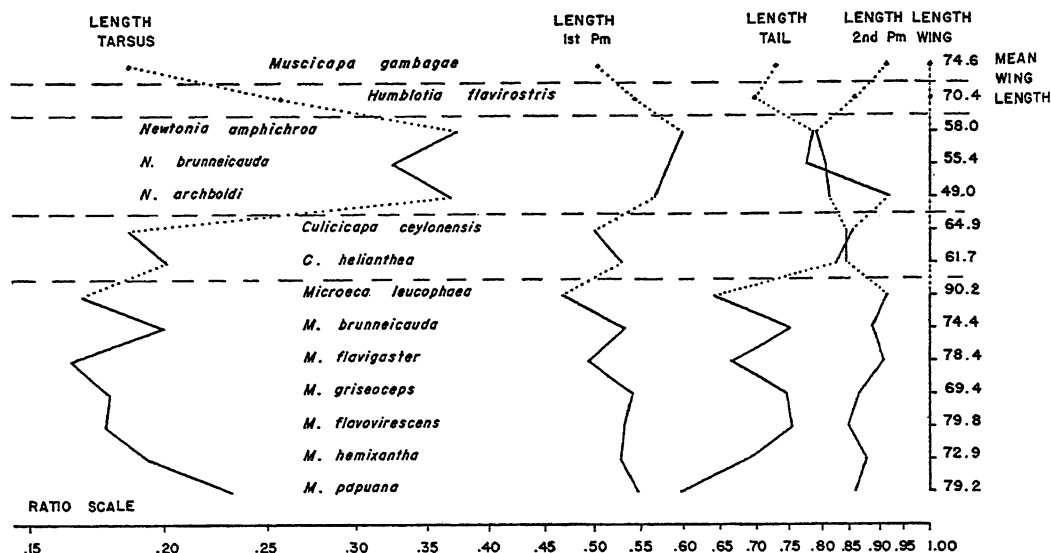


FIG. 26. Comparison through ratio diagram of the proportions in the genera *Humblotia*, *Newtonia*, *Culicicapa*, and *Microeca*. The species of these genera are not migratory, and their proportions are compared to those of *gambagae*, a typical non-migratory *Muscicapa* from the Ethiopian region.

of *Newtonia* is very plain, and its coloration is dull. The four species are dusky olive gray (*amphichroa*) or clay gray, to brownish drab (*fanovanae*) above, more or less tinged with a slight amount of rufous on the crown, rump, and edges of the wing feathers. The tail is colored as on the mantle or, as in *fanovanae*, is rufous. The under parts vary from grayish buff tinged with grayish olive on the breast in *amphichroa*, to creamy buff, slightly tinged with pink in *archboldi*. The chin and the center of the throat, which is said to be pure white in *fanovanae*, are whitish in the other species. The color of the thighs varies. They are said to be whitish in *fanovanae*; they are creamy or buffy in *brunneicauda* and *amphichroa*, with a slight tinge of rufous in the latter, and they are chestnut in *archboldi*. This last species also has a narrow frontal band and eye ring of the same color, and *fanovanae* is said to have a very narrow whitish gray eye ring. In the three species examined the sexes are identical in coloration.

The young of these three species are not spotted. The immature specimens examined show only some indistinct whitish shaft streaks on the crown and have the upper wing coverts margined with buff.

**HABITS:** The habits of *Newtonia*, which

were briefly mentioned by Milne-Edwards and Grandidier (1879), have been described in greater detail by Rand (1936). They are not flycatcher-like. Rand states, "The newtonia [*brunneicauda*] is usually to be found in small parties often associated with other small birds like *Neomixis*, and these very often form part of the big mixed flocks that range through the forest. The newtonia flits from twig to twig, gleaning small insects more in the manner of a titmouse, than of a flycatcher, though occasionally it catches insects on the wing." *N. brunneicauda* [as well as *archboldi*] "commonly frequents the tree tops and the middle spaces, and sometimes even into the ground-cover," while *amphichroa* "frequents the ground-cover and the lower middle spaces, rarely reaching the tree tops." Rand also mentions that *amphichroa* clings to the sides of small branches, and Milne-Edwards and Grandidier state that *Newtonia* "creeps along branches." The song is surprisingly loud and apparently is rich and, as might be expected in such similar species, varies distinctly from species to species. The nest is apparently not described.

#### RELATIONSHIPS

It is obvious that the four species are very

closely related to one another, but the relationship of *Newtonia* to the other Muscicapini is somewhat uncertain. Schlegel and Pollen in their description of *Newtonia* state that this genus "ne saurait faire partie de la famille des Muscicapae" (*sic*). Milne-Edwards and Grandidier (1879) place *Newtonia* in the flycatchers but describe some differences in the shape and proportions of the bones of the skull, but these differences which may be adaptive are not necessarily of phylogenetic significance.

I have retained *Newtonia* in the Muscicapini and place it not far from *Muscicapa*, for *Newtonia*, although aberrant like many other Madagascar genera, seems to be the representative of the tribe and of *Muscicapa* on this island. If further study shows, however, that *Newtonia* should be removed from the flycatchers, it may, perhaps, find a better position in the Sylviinae, not far from *Phylloscopus*.

#### LIST OF THE SPECIES

##### *Newtonia amphichroa* Reichenow

RANGE: Northern and eastern Madagascar.

##### *Newtonia brunneicauda* Newton

RANGE: The whole of Madagascar.

##### *Newtonia archboldi* Delacour and Berlioz

RANGE: Southwestern Madagascar.

##### *Newtonia fanovanae* Gyldenstolpe

RANGE: Fanovana Forest, eastern Madagascar.

#### GENUS MICROECA GOULD

*Microeca* GOULD, 1840 (July, 1841), Proc. Zool. Soc. London, p. 172. Type, by original designation, *Microeca assimilis* Gould [= *Microeca leucoptera assimilis* Gould].

*Kempia* MATHEWS, 1912, Austral Avian Rec., vol. 1, p. 109. Type, by original designation, *Microeca flavigaster* Gould.

*Kempiella* MATHEWS, 1913, Austral Avian Rec., vol. 2, p. 12. Type, by original designation, *Kempiella kempii* Mathews [= *Microeca griseiceps kempii* Mathews].

*Dikempia* MATHEWS, 1920, The birds of Australia, vol. 8, p. 73. Type, by original designation, *Microeca flavovirescens* Gray.

*Devioeca* MATHEWS, 1925, Bull. Brit. Ornith. Club, vol. 45, p. 93. Type, by original designation, *Microeca papuana* Meyer.

#### DISTRIBUTION AND CHARACTERS

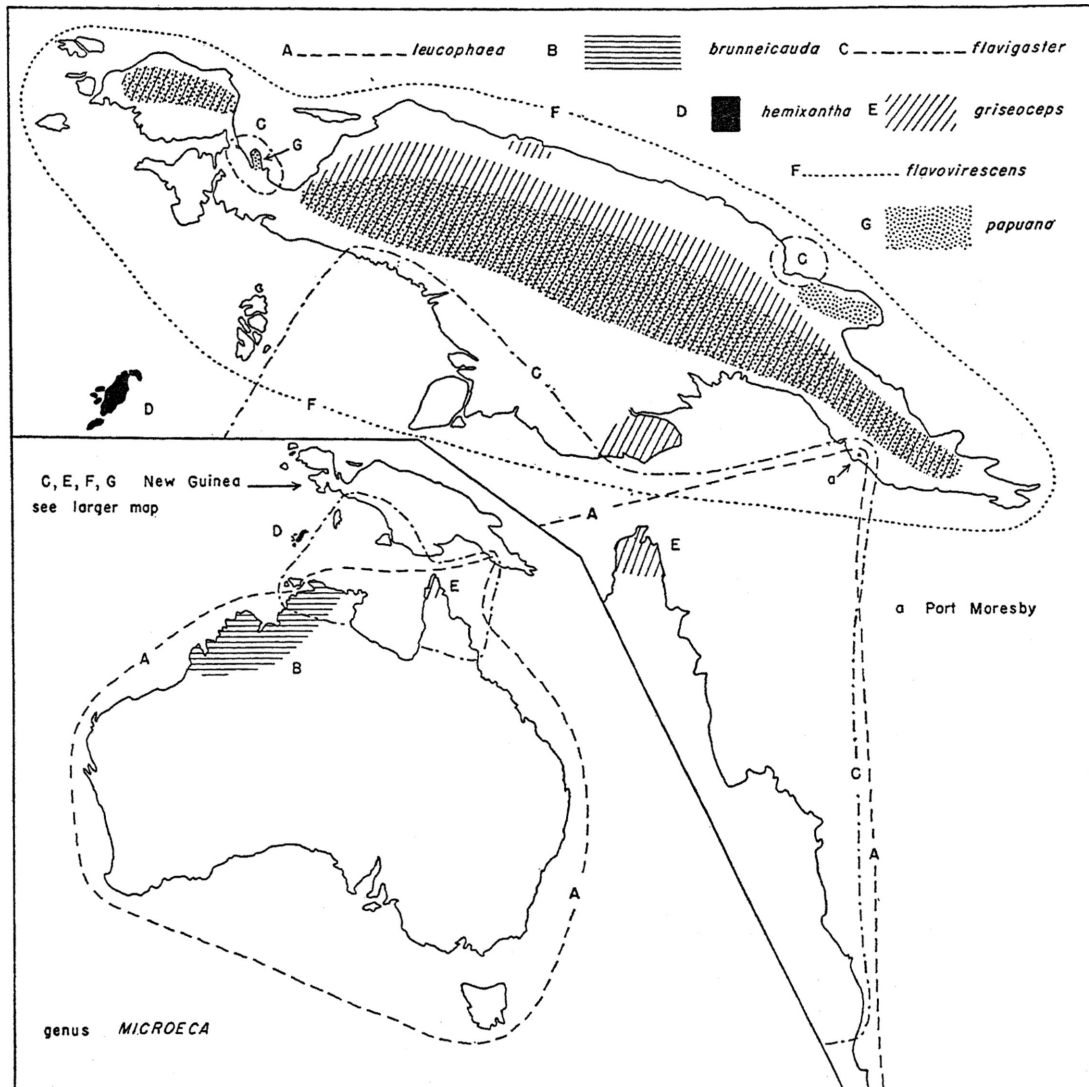
This genus, which has been studied by Mayr (1941b), is the geographical representative of *Muscicapa* in the Australo-Papuan region. It consists of seven small, or medium-sized but rather small, species which are similar structurally and in their habits to *Muscicapa* but different in their pattern or coloration. The distribution of *Microeca* is shown in figure 27.

For reasons given in a preceding study (1952a) I have removed two other species, *addita* Hartert and *oscillans* Hartert (in which I include *stresemanni* Siebers as a subspecies), formerly placed in *Microeca*, to the genus *Rhinomyias*, which seems to be a more primitive group of flycatchers than *Muscicapa* or *Microeca*.

**STRUCTURAL CHARACTERS.** The variation in structural characters is slight. The tarsus of *Microeca* is short, varying (fig. 26) from about 17 to 19 per cent of the length of the wing, except in *papuana* where it averages about 23 per cent. Again with the exception of this species, in which the tarsus is moderately thick and the claws strong, the tarsus is slender and the claws are weak. The scutellation varies. Some species, whether closely related or not, may have a booted tarsus or show one or two scutes. The range of variation in the other proportions is relatively narrow. In the case of the length of the tail the range varies from about 60 to 75 per cent of the length of the wing, *papuana* being again the most distinct with the shortest tail. The shape of the tail varies slightly, from squarish or very slightly forked to slightly or moderately rounded.

The bill of *Microeca* varies very little (fig. 25) and is a typical flycatcher bill, depressed, very well broadened at the base, moderately hooked, well feathered at the base and over the nostrils, and with well- to very well-developed rictal bristles. In *flavovirescens* it is longer and more attenuated, but even in this species it is depressed and well broadened at the base.

The wing is long but not very pointed since the species are not migratory. The formula is similar or varies but slightly. In four species (*brunneicauda*, *flavigaster*, *hemixantha*, and *griseiceps*) it is 3, 4, 5 subequal >6>7< or

FIG. 27. Distribution of the genus *Microeca*.

$=2>8>9>10$ ; *leucophaea* has a very slightly more pointed wing, the formula being 3, 4, 5 subequal (or  $3=4$  slightly  $>5$ )  $>6>2>7>8>9>10$ ; *flavovirescens* and *papuana* vary very little, the formula of *flavovirescens* being  $4=5>3=6>7$  slightly  $>$  or  $=2>8>9>10$ , and in *papuana* 2 may be slightly  $>$  or  $=8$ .

Although, as shown, the variation in structural characters is slight and is no more than one would expect in any group of closely related species (the only well-marked differences consisting of the longer tarsus and stronger claws of *papuana* and its somewhat shorter

tail), Mathews has used these differences to provide a generic name for nearly all the species. Mayr (1941b) has analyzed these so-called genera, but some of the inconsistencies of Mathews and his misleading arrangement (1930) may be briefly discussed.

Mathews (1930) has separated *Devioeca* from *Microeca* on the basis of bill differences, stronger "feet and claws, and different-shaped tail," *Devioeca* consisting of two species, *papuana* (the type species) and *hemixantha*. However, as seen in figure 25 there are no appreciable differences in the shape of the



bill of these two species and the bills of *leucophaea* and *brunneicauda*, the only two species that Mathews places in *Microeca*. The "feet and claws" of *papuana* are stronger but not those of *hemixantha* which are weak and identical with those of *leucophaea* and *brunneicauda*. I cannot appreciate the "different-shaped tail," for it is rounded in both *papuana* and *leucophaea* and squarish or very slightly forked in *hemixantha* and *brunneicauda*. Even if *hemixantha* were to be removed from *Deioeca*, the stated differences in the structural characters of *papuana* do not seem to warrant generic or even sub-generic recognition, for, after all, they are slight, and *papuana* has the same habits as all the other *Microeca* and is virtually identical in coloration with the other green and yellow species of the genus.

Mathews' arrangement (1930) of the various *Microeca* disregards completely the true relationships of some of the species. He places *brunneicauda* and *flavigaster* in different genera, although these two forms are very closely related and are perhaps conspecific. He separates *griseiceps*, a typical *Microeca*, very widely from the other species by many unrelated genera such as *Petroica*, *Gerygone*, and *Poecilodryas*, and so on.

**PATTERN AND PIGMENTATION:** The species vary from gray-brown above and whitish below, with very conspicuous white markings in the tail or well-indicated pale areas, to olive above and yellow below to strong green-olive above and canary yellow below. In *Muscicapa* the tail is uniformly colored, olive pigments are found in only one or two species and are not well developed, and yellow is lacking.

Four species in the following order show a progressive change of pigmentation: *leucophaea*, *brunneicauda*, *flavigaster*, and *hemixantha*. *M. leucophaea* is gray-brown above, whitish below, and has whitish or slightly buffy axillaries. Its inner secondaries are narrowly edged with whitish, and its tail (fig. 2) shows much pure white. The rectrices, with the exception of the central pair, are increasingly tipped with white as they go outward, all of the outer pair and most of the next pair being white. In *brunneicauda* (fig. 2) the distal ends of the rectrices are pale or cloudy white, the tips being white and the

outer edges whitish. In *flavigaster* a trace of the pale areas remains, only the very tips being whitish and the outer edges yellowish. In *hemixantha* only a slight trace of yellowish white persists at the very tips, the outer edges being yellow. The same progressive changes of coloration occur on the edges of the inner secondaries. In *griseiceps* and *flavovirescens* very faint and narrow whitish or yellowish tips are occasionally present on the tail feathers. These pale tips are lacking altogether in *papuana*.

*Microeca brunneicauda* is gray-brown above like *leucophaea* but paler and very weakly tinged with dull olive. It is white or whitish below in the specimens examined, but according to Mathews (1920) may be tinged with yellow on the abdomen. Its axillaries are very pale sulphur yellow. In *flavigaster* and *hemixantha* the yellow pigments increase progressively and are very strongly developed in the latter. In *flavigaster* the upper parts are dull yellowish olive, being grayer in some populations, especially on the crown. The throat is whitish or whitish tinged with yellow. The axillaries and the rest of the under parts are lemon yellow, or pale lemon yellow, being slightly paler in such specimens on the center of the abdomen. In *hemixantha* all of the upper parts are a strong olive, the axillaries and the under parts, with the exception of the throat which is sulphur yellow, being a bright strong canary yellow.

The progressive changes in pigmentation stop with *hemixantha*. *M. griseiceps* is dull slate on the crown and hind neck. The rest of the upper parts are rather dull olive; the cheeks are grayish, the center of the throat grayish white, the upper breast grayish tinged with buff and yellowish, the axillaries and the rest of the under parts dull lemon yellow. *M. flavovirescens* is olive green above, grayish yellow on the throat, and the axillaries and the rest of the under parts are yellow tinged with greenish. *M. papuana* is a strong yellowish olive green above and, as in *hemixantha*, a strong bright canary yellow below, with the exception of the feathers of the center of the throat which are whitish broadly tipped with lemon yellow. All the seven species have, as in the great majority of the *Muscicapa*, a narrow, more or less well-indicated whitish or yellowish eye ring and a spot or small band

of the same color in front of and above the lores. The bill is pure black above and below in *papuana*. The mandible is pale, probably flesh color in life, in *flavovirescens*, *griseiceps*, and *hemixantha*, and horn color in *flavigaster*, *brunneicauda*, and *leucophaea*.

The sexes are identical in coloration. The young are well spotted. They are lacking in *hemixantha* but were examined in the other species. The juvenal plumage has been discussed by Mayr (1941b); it is possible, as this author states, that the first winter plumage of *papuana* may differ from that of the other species.

**HABITS:** The habits of the Australian species have been described by Mathews (1920) and those of the New Guinea species by Rand (*in* Mayr and Rand, 1937). Apparently all the species, with the possible exception of *brunneicauda*, are true flycatchers and very similar in their habits to *Muscicapa*, perching more or less stolidly on some exposed perch from which they make short darting flights after passing insects. However, according to Mathews, *leucophaea* occasionally comes to the ground to feed, and *brunneicauda* conceals itself in mangroves and differs from *leucophaea* by "living entirely on small crabs, and other forms of marine life." The only nests described, those of *leucophaea* and *flavigaster*, are said to be small by Mathews or very small in *flavigaster*. The location and structure of the nest of *flavigaster* are not described. The nest of *leucophaea* is usually placed fairly high in the fork of a tree and is built of grassy materials bound with cobwebs. All the species are said to be good or fairly good singers. The habits of *hemixantha* have not been described.

#### RELATIONSHIPS

As shown by their intergradation, the first four species (*leucophaea*, *brunneicauda*, *flavigaster*, and *hemixantha*) are closely related and seem to form a species group. The first three are obviously very closely related, and one could treat *brunneicauda* and *flavigaster* which are especially close, as conspecific, for they replace each other geographically. However, according to Mathews' check list (1930) their ranges overlap in Northern Territory. This statement cannot be verified from specimens available to me, the Mathews

collection in the American Museum of Natural History containing no specimens of *brunneicauda* from Northern Territory. The only specimens available are from this collection and were collected in northwest Australia at Broome Bay and Point Torment in King Sound.

Concerning the relationships of *papuana*, Mayr (1941b) states "Ogilvie-Grant (1915, Ibis, suppl., p. 161) has . . . placed *M. papuana* in [*Tregellasia*]. This species is intermediate between *Microeca* and *Tregellasia* in the structure of its feet and in its wing formula, but it is better included in *Microeca*, principally on the basis of its bill." It may be added that *Tregellasia* is not flycatcher-like in its habits, whereas *papuana*, according to Rand (*in* Mayr and Rand, 1937), is a typical flycatcher in its habits. The proportions of some true *Microeca* such as *hemixantha*, *brunneicauda*, or *flavigaster* are intermediate between those of *papuana* and the other *Microeca*.

#### LIST OF THE SPECIES

##### *Microeca leucophaea* Latham

**RANGE:** Tasmania, the whole of Australia, and the region of Port Moresby in southeastern New Guinea.

##### *Microeca brunneicauda* Campbell

**RANGE:** Northwest Australia and Northern Territory.

##### *Microeca flavigaster* Gould

**RANGE:** Northern Territory, Melville Island, northern Queensland south to Cardwell, southeastern New Guinea (Port Moresby region), southern and western New Guinea (Wandammen, west coast of Geelvinck Bay), northern New Guinea (Astrolabe Bay).

##### *Microeca hemixantha* Sclater

**RANGE:** Tenimber.

##### *Microeca griseiceps* De Vis

**RANGE:** Mountains of western, northern, and southeastern New Guinea, eastern lowlands, and Cape York in northern Queensland.

##### *Microeca flavovirescens* Gray

**RANGE:** The whole of New Guinea, islands of Japen, Waigeu, Batanta, Misol, and the Arus.

##### *Microeca papuana* Meyer

**RANGE:** Mountains of New Guinea.

GENUS *CULICICAPA* SWINHOE

*Culicicapa* SWINHOE, 1871, Proc. Zool. Soc. London, p. 381. New name for *Cryptolopha auctorum*, nec Swainson. Type, by monotypy, "*Culicicapa cinereocapilla* (Vieill.); Sw. Zool. Ill., pl. 13" [= *Culicicapa ceylonensis* (Swainson)].<sup>1</sup>

*Empidothera* SUNDEVALL, 1872, Methodi naturalis avium disponendarum tentamen, p. 25. New name for *Cryptolopha auctorum*, nec Swainson. Type, by original designation, *Platyrrhynchus ceylonensis* Swainson.

*Xantholestes* SHARPE, 1877, Trans. Linnean Soc. London, ser. 2, vol. 1, p. 327. Type, by monotypy, *Xantholestes panayensis* Sharpe [= *Culicicapa helianthea panayensis* Sharpe].

This genus, which consists of two small and frail species, is Indo-Malayan, the range of one of the species (*ceylonensis*) extending to southern and central China.

These two species, which represent the highest development of the flycatcher type in structure and habits, are small (table 7) and slender. Their tarsus (fig. 26) is short and frail, and the claws are very tiny, smaller even, or somewhat smaller and weaker, than the feet of *Muscicapa epulata* and *seth-smithii*, which are still smaller species than *Culicicapa*. Scutes are not present. The tail and second primaries (fig. 26) are long, proportionately longer than in *Muscicapa*, and are equal in length, unlike those of *Muscicapa*. The wing is round, the formula of *ceylonensis* being  $4=5$  slightly  $>3>6>7>8=2>9>10$  and that of *helianthea*  $4=5>3=6>7>8>$  or  $=2>9$  or  $2=9>10$ .

The chief structural character which, however, separates *Culicicapa* from *Muscicapa* and all other Muscicapini is the large number and very unusual arrangement of its rictal bristles, which are arranged in two rows of five to seven bristles each arising on both sides of the gape, one row in the normal posi-

tion a little in front of and below the eye above the upper half of the bill and the other below the mandible near its base. In the other Muscicapini only the top row, consisting of four to six bristles, is present. The rictal bristles of *Culicicapa* are strong and very long, reaching sometimes to the tip of the bill or beyond. The bill itself (fig. 25) tapers to a very fine point but is very flycatcher-like, being very well broadened at the base, moderately or very well hooked, and unusually flattened, well feathered at the base with antrorse bristles, as distinct from the rictal bristles, extending over the nostrils.

The coloration is a strong yellow-green above and a strong chrome or canary yellow below. The head, throat, and breast of *ceylonensis* is ashy gray, and the upper breast of *helianthea* is slightly tinged with greenish. The first species has a very narrow whitish eye ring and *helianthea* a broader yellow one. The sexes are identical in coloration.

The young are neither streaked nor spotted.

The *Culicicapa*, although typical flycatchers, differ somewhat from the other members of the tribe by being far more gregarious and restless. Ali (1949) describes *ceylonensis* as "an active, restless little bird for ever making lively swoops after winged insects from a base on some exposed twig, turning and twisting in the air with great dexterity and returning to its perch. A couple may invariably be seen amongst the mixed hunting parties of insectivorous birds that rove the forest. The flycatchers act as out-riders to these foraging bands, snapping up tiny flies as they attempt to escape from the concerted hunt." Betts (1951) also states that the members of this species perform "the most vigorous acrobatics . . . and are constant members of the mixed flocks" and describes the song as "short, sweet, and surprisingly loud, which is constantly uttered." The nest according to this author is "built on mossy tree trunks, a moss grown boulder, or a bare earth cutting [and] is a beautiful little half-cup of moss or lichen, felted with cobwebs and is usually composed of the materials of the background . . . the sides of the cup are continued up for several inches to strengthen the support on the vertical face."

According to Heinrich, quoted by Strese-

<sup>1</sup> According to Sharpe (1879, Catalogue of the . . . birds in the . . . British Museum, vol. 4, p. 369, footnote), "Several authors, commencing with Blyth [1849, Catalogue of the birds in the Museum Asiatic Society, p. 205, no. 1238] have attributed a *Muscicapa cinereocapilla* of Vieillot to this species. I have not succeeded in finding this name." I have not found it either. According to Blyth and Swinhoe, *cinereocapilla* Vieillot is based on Swainson (1820, Zoological illustrations, ser. 1, pl. 13), but since Swainson describes the species shown on plate 13 as *Platyrrhynchus ceylonensis*, this name appears to be the correct one for the species and for the generic type.

TABLE 7

AVERAGE MEASUREMENTS OF *Muscicapa gambagae* AND OF THE SPECIES OF THE GENERA  
*Humblotia*, *Newtonia*, *Microeca*, AND *Culicicapa*

	Wing Length <sup>a</sup>	2d Pri- mary	10th Pri- mary	Excess or Defi- cit of 2d Over 10th Primary	1st Pri- mary	Excess of 1st Primary Over Primary Coverts	Tail	Tar- sus	Length of Bill	Width of Bill
Genus <i>Muscicapa</i>										
<i>gambagae</i>	74.6	68.2	59.3	8.9	37.4	6.6	54.5	13.8	14.3	5.5
Genus <i>Humblotia</i>										
<i>flavirostris</i>	70.4	60.2	56.6	3.6	38.0	10.4	48.8	18.0	14.8	6.1
Genus <i>Newtonia</i>										
<i>amphichroa</i>	58.0	45.7	53.8	-8.1	34.6	13.2	45.6	21.6	15.8	4.1
<i>brunneicauda</i>	55.4	44.8	50.6	-5.8	32.1	11.7	42.9	18.0	14.7	4.3
<i>archboldi</i>	49.0	39.9	46.0	-6.1	27.7	10.1	45.0	18.0	14.1	4.1
Genus <i>Microeca</i>										
<i>leucophaea</i>	90.2	82.3	64.6	17.7	41.9	3.7	57.5	15.1	14.5	5.3
<i>brunneicauda</i>	74.4	66.3	58.0	8.3	39.3	9.6	55.6	14.9	14.9	5.7
<i>flavigaster</i>	78.4	71.0	58.8	12.2	38.6	6.7	51.8	12.8	14.1	5.6
<i>hemixantha</i>	72.9	64.1	55.9	8.2	38.5	10.1	50.0	14.1	14.2	5.7
<i>griseiceps</i>	69.4	60.0	54.5	5.5	37.3	10.0	51.5	12.3	13.8	5.2
<i>flavovirescens</i>	79.8	67.7	62.8	4.9	42.3	11.3	60.0	14.1	16.2	5.5
<i>papua</i>	79.2	68.3	62.1	6.2	43.3	13.1	47.2	18.3	14.1	5.2
Genus <i>Culicicapa</i>										
<i>ceylonensis</i>	64.9	54.6	51.8	2.8	32.2	8.5	55.4	12.0	13.9	4.3
<i>helianthea</i>	61.7	51.9	50.8	1.1	32.5	10.0	50.7	12.4	13.2	4.7

<sup>a</sup> Longest primary.

mann (1940), the habits of *helianthea* are similar to those of *ceylonensis*.

#### RELATIONSHIPS

The two species are closely related, but the relationship of *Culicicapa* to the other genera studied is not clear. As stated in the Introduction, further study may show that *Culicicapa* would be better placed in the Rhipi-

durini than in the Muscipapini.

#### LIST OF THE SPECIES

##### *Culicicapa ceylonensis* Swainson

RANGE: Indo-Malaya, southern and central western China.

##### *Culicicapa helianthea* Wallace

RANGE: Philippines and Celebes.

## SUMMARY

THIS PAPER IS A GENERIC STUDY of 113 species of flycatchers of the tribe Muscicapini, about one-third of the species computed for the subfamily Muscicapinae by Mayr and Amadon (1951). Twelve genera with five subgenera are recognized, a list of which is given on page 473 together with a brief synopsis giving the number of species in each genus, its general distribution, and characters.

Of the 12 genera three (*Horizorhinus*, *Newtonia*, and *Culicicapa*) are of uncertain affinities. The first which is monotypic is restricted to Principe Island in the Gulf of Guinea and, though provisionally included in the Muscicapini in this study, is often considered to be a babbler but may possibly be a warbler or a thrush. The second, from Madagascar, although aberrant, is probably a member of the Muscicapini and may be distantly related to *Muscicapa*. The affinities of the third, which consists of two Indo-Malayan species, are perhaps with the Rhipidurini rather than with the Muscicapini. In these three genera the young are not spotted.

The other genera can be divided in two groups, with the Indo-Malayan genus *Rhinomyias* intermediate. The first group which consists of *Bradornis* and related genera is Ethiopian and comprises more primitive species that are usually heavily built and in which the flycatcher habits are not well developed, these species usually dropping down to the ground to feed, though two species (separated as *Fraseria*) are arboreal. The second group consists of *Muscicapa* and related genera and comprises the true flycatchers, the species differing, however, in their feeding or other habits or in the height at which they feed. The main genera recognized in this group are *Ficedula*, *Niltava*, *Muscicapa*, and *Microeca*, these genera ranging widely as a group throughout the Ethiopian, Palearctic, Indo-Malayan, and Australo-Papuan regions.

The variations in the morphological characters and habits are discussed in an introductory section. The large majority of the structural (functional) characters as distinct from the pattern and coloration of the plum-

age appear to be adaptive and are of dubious phylogenetic significance. The feeding habits, however, are not always diagnostic either, for they occasionally vary between species that are obviously closely related. These differences in habits may be correlated with adaptive differences in structure, but in some species, the habits of which vary geographically with changing ecological conditions, the morphological characters do not change. For instance, an arboreal or semi-arboreal species (as in the genus *Niltava*) which occupies open country in a region where exposed hunting perches are available may live in thickets, dense undergrowth, or mangrove in another region where such perches are not available. Or a species may live on the seaboard in one region and in mountains in another. Coloration and pattern are generally far more conservative than the structural characters and feeding habits.

All the characters are weighed together. Functional characters, coloration and pattern, and habits are considered to be equally valid for generic separation, but the emphasis on certain characters, or a complex of characters and habits, must shift in order not to obscure the evident natural relationships of the species. Throughout this study chief consideration is given to the preservation of such relationships.

Most of the genera recognized are quite or relatively homogeneous, but in *Ficedula* a number of more or less closely related subgroups can be distinguished, some of them representing, perhaps, polyphyletic elements.

The Ethiopian genus *Parisoma* is omitted from this study, although this genus is usually placed in the Muscicapini not far from *Muscicapa*. However, as stated in the Introduction, where this genus is briefly discussed, *Parisoma* appears to be a composite and unnatural group made up of species which do not seem to be related to the Muscicapinae, some of them being almost certainly warblers which several authors have suggested should be placed in or near *Sylvia*.

The nomenclatural aspects of this study are listed in the Appendix.

## APPENDIX

### LIST OF RARE OR LESS COMMON SPECIES AND OF SPECIES IN WHICH JUVENAL PLUMAGE WAS NOT EXAMINED

IN THIS LIST the individual specimens examined are indicated together with the locality or regions in which they were collected and the names of the institutions in the collections of which they are present. The nomenclature and order used are those established in this study. The term "no young" indicates that no juvenal specimen is available. The term "type" refers to the type of the species if not polytypic or to the type of the nominate race if polytypic.

A.N.S.P., Academy of Natural Sciences of Philadelphia

A.M.N.H., the American Museum of Natural History

C.N.H.M., Chicago Natural History Museum

M.C.Z., Museum of Comparative Zoölogy

U.S.N.M., United States National Museum

*Bradornis herero*, 1 ♂ (A.M.N.H.); 1 ♀ (type), 1 unsexed adult (A.N.S.P.); all from South West Africa; no young.

*Melaenornis ardesiaca*, 2 ♂, 1 ♀ (A.M.N.H.); west of Lake Edward.

*Rhinomyias addita*, 1 ♂ (type), 1 ♂, 3 ♀ (A.M.N.H.); Buru; no young.

*Rhinomyias oscillans*, no young.

*Rhinomyias umbratilis*, no young, but see text.

*Rhinomyias colonus*, 1 ♂ (type), 2 ♂, 3 ♀ (A.M.N.H.); Sula Mangoli; 2 ♂, 1 ♀ (M.C.Z.); Peling Island.

*Ficedula monileger*, no young.<sup>1</sup>

*Ficedula solitaria*, no young.<sup>2</sup>

*Ficedula rufigula*, no young.

*Ficedula basilanica*, no young.

*Ficedula henrici*, 1 ♂ (type), 4 ♂, 3 ♀ (A.M.N.H.); 1 ♂ (U.S.N.M.); all from Damar Islands.

*Ficedula crypta*, 1 ♀ (A.M.N.H.); Mt. Apo, Mindanao; 1 ♂ (type), 1 unsexed adult (C.N.H.M.); Mt. McKinley, Mindanao; no young.

*Ficedula bonthaina*, no young.

*Ficedula harterti*, 4 ♂, 1 ♀ (A.M.N.H.); Sumba; no young.

*Ficedula nigrorufa*, no young.

*Ficedula (Cyanoptila) cyanomelana*, no nestling, see text for the juvenal plumage.

*Niltava vivida*, no young.<sup>3</sup>

*Niltava sanfordi*, 1 ♂ (type), 3 ♂, 1 ♀ (A.M.N.H.); Ile Ile, Celebes, no young.

*Niltava ruecki*, 1 ♂ (A.M.N.H.); northeastern Sumatra.

*Niltava herioti*, 2 ♂, 1 ♀ (A.M.N.H.); Luzon.

*Niltava superba*, 4 ♂, 1 ♀ (A.M.N.H.); 1 ♂ (U.S.N.M.); 1 ♀ (A.N.S.P.); all Borneo; no young.

*Niltava turcosa*, no young.

*Niltava (Muscicapella) hodgsoni*, no young.

*Muscicapa segregata*, no young.

*Muscicapa olivascens*, 1 ♂, 1 ♀ (A.M.N.H.); eastern Congo; 1 ♀ (A.N.S.P.); Irumu; no young.

*Muscicapa tessmanni*, 2 ♂, 1 ♀ (A.M.N.H.); eastern Congo; no young.

*Muscicapa ussheri*, 1 ♂ (A.M.N.H.); 1 unsexed adult (A.N.S.P.); 1 ♀ (C.N.H.M.); 2 ♂, 1 ♀ (M.C.Z.); 1 ♂ 1 ♀ (U.S.N.M.); all from Sierra Leone or Liberia; no young.

*Muscicapa (Eumyias) albicaudata*, no young.<sup>4</sup>

*Humblotia flaviviridis*, 4 unsexed adults (A.M.N.H.); 1 unsexed adult (M.C.Z.); Grand Comoro; no young.

*Newtonia archboldi*, 2 ♂, 2 ♀, 1 unsexed adult (A.M.N.H.); 1 ♂ (M.C.Z.); Madagascar.

*Newtonia fanovanae*, not examined, known only from a single specimen in the Stockholm museum.

*Microeca hemixantha*, 2 ♂, 1 ♀, 3 unsexed adults (A.M.N.H.); Tenimber; no young.

## NOMENCLATURAL ASPECTS

The generic division proposed in this paper results in the following changes in nomenclature which are listed, within the genus, alphabetically by the specific or subspecific name.

Some changes have already been proposed

<sup>1</sup> According to Baker (1924) the young is streaked with fulvous.

<sup>2</sup> According to Robinson (1928) the young is "streaked and mottled above; irregularly squamated below."

by Deignan (1947) and Wolters (1950). Some of these have been adopted, but most are not followed since, unlike these authors, I do not merge *Ficedula* and *Niltava* with *Muscicapa*. I am very grateful to Deignan for his help in identifying some of the older names.

<sup>3</sup> According to Baker (1924) the young are well spotted.

<sup>4</sup> According to Baker (1924) the young are boldly spotted.

*Alseonax cinereus* [*Eopsaltria cinerea*] Cassin, 1856 = *Butalis* [= *Muscicapa*] *caerulescens* Hartlaub, 1865, as *cinerea* Cassin is preoccupied by *Muscicapa cinerea* Müller, 1776 = *Coracina cinerea*.

*Artomyias fuliginosa* J. and E. Verreaux, 1855 (March) = *Butalis infulcatus* [= *Muscicapa infulcata*] Cassin, 1855 (April), as *fuliginosa* Verreaux is preoccupied by *Muscicapa fuliginosa* Sparrman, 1787 = *Rhipidura fuliginosa*.

*Hemichelidon sibirica fuliginosa* Hodgson, 1845 = *Muscicapa sibirica cacabata* Penard, 1919, as *fuliginosa* Hodgson is preoccupied by *Muscicapa fuliginosa* Sparrman, 1787 = *Rhipidura fuliginosa*.

*Muscicapa amabilis* Deignan, 1947 = *Siphia* [= *Ficedula*] *hodgsonii* Verreaux, 1871.

*Muscicapa solitaria arakanensis* Deignan, 1947 = *Anthipes gularis* [= *Ficedula monileger*] *gularis* Blyth, 1847, not preoccupied by *Muscicapa gularis* Stephens, 1817, which according to Stephens = *Muscicapa superciliosa* Sparrman, 1789 = *Cosyphus caffer* (Linnaeus), 1771; or *Muscicapa gularis* Temminck, 1822 = *Todirostrum plumbeiceps* (Lafresnaye), 1846; or *Muscicapa gularis* Quoy and Gaimard, 1830 = *Eopsaltria griseogularis* Gould, 1838.

*Muscicapa sibirica cacabata* Penard, 1919, see *Hemichelidon sibirica fuliginosa*.

*Muscicapa caerulescens* (Hartlaub), 1865, see *Alseonax cinereus*.

*Muscicapa indigo delicata* Deignan, 1947 = *Stoparola* [= *Muscicapa* (*Eumyias*) *indigo*] *cerviniventris* Sharpe, 1887, not preoccupied by *Digenea* [= *Ficedula tricolor*] *cerviniventris* Sharpe, 1879.

*Muscicapa caerulata deliensis* Deignan, 1947 = *Cyornis* [= *Niltava*] *caerulata albiventer* Junge, 1933, not preoccupied by *Muscicapa albiventer* von Spix, 1825 = *Fluvicola pica albiventer*.

*Muscicapa ervini* Wolters, 1950 = *Siphia* [= *Ficedula*] *hodgsonii* Verreaux, 1871.

*Muscicapa ferruginea* (Hodgson), 1845, see *Muscicapa rufilata*.

*Muscicapa indigo ferrugineiventris* Wolters, 1950 = *Stoparola* [= *Muscicapa* (*Eumyias*) *indigo*] *cerviniventris* Sharpe, 1887, not preoccupied by *Digenea* [= *Ficedula tricolor*] *cerviniventris* Sharpe, 1879.

*Muscicapa fuliginosa* (J. and E. Verreaux), 1855, see *Artomyias fuliginosa*.

*Muscicapa sibirica fuliginosa* (Hodgson), 1845, see *Hemichelidon sibirica fuliginosa*.

*Muscicapa infulcata* (Cassin), 1855, see *Artomyias fuliginosa*.

*Muscicapa rufigastra lepidula* Deignan, 1947 = *Cyornis* [= *Niltava*] *rufigastra longipennis* Chasen and Kloss, 1930, not preoccupied by *Muscicapa longipennis* Lesson, 1831, a synonym of *Colonia colonus* Vieillot, 1818, according to Hellmayr.

*Muscicapa leucomelanura* (Hodgson), August, 1845 = *Digenea* [= *Ficedula*] *tricolor* Hodgson, August, 1845, not preoccupied by *Muscicapa tricolor* Vieillot, 1818 = *Leucocirca leucophrys* (Latham), 1801; or *Muscicapa tricolor* Hartlaub, after December 10, 1845 = *Ficedula zanthopygia* (Hay), beginning of 1845.

*Muscicapa concreta leucoprocta* (Tweeddale), 1877, August, revived by Deignan, 1947 = *Muscitrea cyanea* Hume, 1877 = *Niltava concreta cyanea* (Hume), not preoccupied by *Muscicapa cyanea* Müller, 1776 = *Platysteira cyanea*; or *Muscicapa cyanea* Vieillot, 1818; or *Muscicapa cyanea* Bebbie, 1834 = *Irena puella* (Latham), 1790. Vieillot's *cyanea* appears to be an earlier description of *Muscicapa hyacinthina* Temminck, 1820 = *Niltava hyacinthina* (Temminck), but is invalid as being preoccupied by *Muscicapa cyanea* Müller, 1776. Application to the International Commission to place *cyanea* Vieillot on the list of *nomina rejecta* pending.

*Muscicapa banyumas liga* Deignan, 1947, new name for *Muscicapa cantatrix* Temminck, 1823 = *Niltava banyumas liga* (Deignan), 1947, because *cantatrix* Temminck was preoccupied by *Muscicapa cantatrix* Wilson, 1810 = *Vireo griseus* (Boddaert), 1783, according to Hellmayr.

*Muscicapa melanoleuca* (Blyth), 1843 = *Muscicapula* [= *Ficedula*] *westermanni* Sharpe, 1888, as *melanoleuca* Blyth is preoccupied by *Muscicapa melanoleuca* Forster, 1817 = *Ficedula hypoleuca* (Pallas), 1764.

*Muscicapa migrator* Deignan, 1947 = *Muscicapa parva subrubra* Hartert and Steinbacher, 1934 = *Ficedula parva subrubra*.

*Muscicapa caerulata nigrogularis* (Everett), 1891 = *Cyornis* [= *Niltava caerulata*] *rufifrons* Wallace, 1865, not preoccupied by *Muscicapa rufifrons* Latham, 1801 = *Rhipidura rufifrons*.

*Muscicapa hyperythra olga* Deignan, 1947 = *Dendrobiastes hyperythrus sumatranus* [= *Ficedula hyperythra sumatrana*] Hachisuka, 1926, not preoccupied by *Niltava [vividula] sumatrana* Salvadori, 1879.

*Muscicapa rufilata* (Swinhoe), 1860, revived by Deignan, 1947 = *Hemichelidon* [= *Muscicapa*] *ferruginea* Hodgson, 1845, not to be replaced by *Muscicapa ferruginea* Merrem, 1784, unidentifiable. Application to the International Commission to place *Hemichelidon* [= *Muscicapa*] *ferruginea* Hodgson on the Official List and to place *ferruginea* Merrem on the list of *nomina rejecta* pending.

*Muscicapa rufigastra simplicior* Deignan, 1947 = *Cyornis* [= *Niltava rufigastra*] *simplex* Blyth, 1870, not preoccupied by *Muscicapa simplex* Lichtenstein, 1823 = *Rhytipterna simplex*.

*Muscicapa hyperythra trinitatis* Deignan, 1947

= *Muscicapula luzoniensis* [= *Ficedula hyperythra*] *luzoniensis* Ogilvie-Grant, 1894, not preoccupied by *Muscicapula luzoniensis* Gmelin, 1788 = ? *Parus semilarvatus nehrkoni* (Blasius), 1890. *M. luzoniensis* Gmelin is based on Sonnerat (1776, Voyage à la Nouvelle Guinée, pl. 27, fig. 2), a figure which according to McGregor (1910, Manual of Philippine birds, p. 609) is not identifiable. Blasius suggested that his *nehrkoni* represents perhaps the bird

figured by Sonnerat.

*Muscicapa venusta* Deignan, 1947 = *Cyornis* [= *Niltava*] *superba* Stresemann, 1925, not preoccupied by *Muscicapa superba* Bechstein, 1794 = *Muscicapa superciliosa* Sparrman, 1789 = *Cosypha caffra* (Linnaeus), 1771.

*Muscicapa westermanni* [= *Ficedula westermanni*] (Sharpe), 1888, see *Muscicapa melano-leuca*.

## LITERATURE CITED

- ALI, SALIM  
1949. Indian Hill birds. Oxford, University Press, pp. 74-85.
- AMADON, DEAN  
1950. The Hawaiian honeycreepers (Aves, Drepaniidae). Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 258-259.  
1953. Avian evolution and systematics in the Gulf of Guinea: The J. G. Correia collection. *Ibid.*, vol. 100, pp. 393-452.
- BAKER, E. C. STUART  
1924. The fauna of British India. Birds. London, Taylor and Francis, vol. 2, pp. 199-261.  
1933. The nidification of birds of the Indian Empire. London, Taylor and Francis, vol. 2, pp. 173-231.
- BANNERMAN, DAVID ARMITAGE  
1936. The birds of tropical West Africa. London, Crown Agents for the Colonies, vol. 4, pp. 119-120, 198-245.
- BATES, G. L.  
1926. On the identification of *Eopsaltria cinerea* Cassin. Ibis, pp. 581-585.  
1927. Notes on some birds of Cameroon and the Lake Chad region: their status and breeding-times. *Ibid.*, pp. 32-34.  
1930. Handbook of the birds of West Africa. London, Bale and Danielsson, pp. 321, 325-332.
- BENSON, C. W.  
1940. Further notes on Nyasaland birds (with particular reference to those of the northern province), part 3. Ibis, p. 598.  
1946. Notes on the birds of southern Abyssinia. *Ibid.*, pp. 180-182.  
1951. Breeding and other notes from Nyasaland and the Lundazi district of Northern Rhodesia. Bull. Mus. Comp. Zool., vol. 106, p. 95.
- BERLIOZ, J.  
1936. Étude d'une collection d'oiseaux du Congo belge. Bull. Mus. Hist. Nat. Paris, ser. 2, vol. 8, pp. 329-330.
- BETTS, F. N.  
1951. The birds of Coorg. Jour. Bombay Nat. Hist. Soc., vol. 50, pp. 40-42.
- CHAPIN, JAMES PAUL  
[In press.] The birds of the Belgian Congo, part 3.
- CHASEN, F. N., AND C. BODEN KLOSS  
1929. On some birds of the genus *Cyornis*. Bull. Raffles Mus., no. 2, pp. 23-42.
- DEIGNAN, H. G.  
1947. Some untenable names in the Old World flycatchers. Proc. Biol. Soc. Washington, vol. 60, pp. 165-168.
- DELACOUR, JEAN  
1946a. Les Timaliines. L'Oiseau, vol. 16, pp. 11-12.  
1946b. Notes on the taxonomy of the birds of Malaysia. Zoologica, vol. 31, p. 4.  
1947. Birds of Malaysia. New York, Macmillan Co., pp. 284-293.
- DOHRN, H.  
1866. Synopsis of the birds of Ilha do Principe, with some remarks on their habits and descriptions of new species. Proc. Zool. Soc. London, pp. 326-327.
- FINSCH, O.  
1901. Zur Catalogisirung der Ornithologischen Abtheilung, Note V. Notes Leyden Mus., vol. 23, pp. 33-40.
- GYLDENSTOLPE, NILS  
1933. A remarkable new flycatcher from Madagascar. Arkiv. för Zool., vol. 25B, no. 2, pp. 1-3.
- HARTERT, ERNST  
1907. Die Vögel der paläarktischen Fauna. Berlin, Friedländer und Sohn, p. 493.
- HOESCH, WALTER  
1938. Zur Lebensweise von *Namibornis herero* (M. de Sch.). Ornith. Monatsber., vol. 46, pp. 173-176.
- HOESCH, WALTER, AND GÜNTHER NIETHAMMER  
1940. Die Vogelwelt Deutsch-Südwestafrika. Jour. f. Ornith., vol. 88, Sonderheft, pp. 248-250.



- JACKSON, FREDERICK JOHN, AND W. L. SCLATER  
1938. The birds of Kenya Colony and the Uganda Protectorate. London, Gurney and Jackson, vol. 2, pp. 882-914.
- MATHEWS, GREGORY M.  
1920. The birds of Australia. London, H. F. and G. Witherby, vol. 8, pp. 58-299.  
1930. Systema avium Australasianarum. London, British Ornithological Union, pt. 2, pp. 440-478.
- MAYR, ERNST  
1941a. List of New Guinea birds. New York, the American Museum of Natural History, pp. 122-160.  
1941b. Birds collected during the Whitney South Sea expedition 45. Notes on New Guinea birds 8. Amer. Mus. Novitates, no. 1133, pp. 4-8.  
1944. The birds of Timor and Sumba. Bull. Amer. Mus. Nat. Hist., vol. 83, pp. 136, 160-161.  
1945. In Delacour, Jean, and Ernst Mayr, Notes on the taxonomy of the birds of the Philippines. Zoologica, vol. 30, pp. 113-114.  
1946. In Delacour, Jean, and Ernst Mayr, Birds of the Philippines. New York, Macmillan Co., pp. 207-212.  
1952. Speciation in birds. Proc. Tenth Internatl. Ornith. Congr. Uppsala, Almqvist and Wiksell, p. 108.
- MAYR, ERNST, AND DEAN AMADON  
1951. A classification of recent birds. Amer. Mus. Novitates, no. 1496, pp. 30, 38.
- MAYR, ERNST, AND A. L. RAND  
1937. Results of the Archbold Expeditions, no. 14. Birds of the 1933-1934 Papuan expedition. Bull. Amer. Mus. Nat. Hist., vol. 73, pp. 126-143.
- MEINERTZHAGEN, R.  
1951. Review of the Alaudidae. Proc. Zool. Soc. London, vol. 121, p. 81.
- MILNE-EDWARDS, ALPHONSE, AND A. GRANDIDIER  
1879. Histoire physique, naturelle, et politique de Madagascar. Paris, Imprimerie Nationale, vol. 12, Oiseaux, text, pp. 381-384.
- MILNE-EDWARDS, ALPHONSE, AND E. OUSTALET  
1887. Observations sur quelques espèces d'oiseaux récemment découvertes dans l'île de la Grande Comore. Ann. Sci. Nat. Zool., ser. 8, vol. 2, pp. 229-231.  
1888. Etudes sur les mammifères et les oiseaux des îles Comores. Nouv. Arch. Mus., ser. 2, vol. 10, pp. 261-263.
- MOREAU, R. E.  
1936. A contribution to the ornithology of Kilimanjaro and Mount Meru. Proc. Zool. Soc. London, 1935, p. 877.
- NEUMANN, OSCAR  
1914. Vermeintliche Unica des Philadelphia und des Wiener Museums und ihre systematische Stellung. Jour. f. Ornith., vol. 62, pp. 156-157.
- NIETHAMMER, GÜNTHER  
1937. Handbuch der Deutschen Vogelkunde. Leipzig, Akademische Verlagsgesellschaft, vol. 1, pp. 274-286.
- RAND, A. L.  
1936. The distribution and habits of Madagascar birds. Bull. Amer. Mus. Nat. Hist., no. 72, pp. 429-431.
- ROBERTS, AUSTIN  
1942. The birds of South Africa. Third (revised) printing. London, H. F. and G. Witherby, pp. 279-282.
- ROBINSON, HERBERT C.  
1928. The birds of the Malay Peninsula. London, H. F. and G. Witherby, vol. 2, pp. 136-137.
- ROBINSON, HERBERT C., AND NORMAN B. KINNEAR  
1928. Notes on the genus *Cyornis* Blyth. Novitates Zool., vol. 34, pp. 231-261.
- DE SCHAUENSEE, RODOLPHE MEYER  
1931. A new species of flycatcher from Damaraland. Proc. Acad. Nat. Sci. Philadelphia, vol. 83, pp. 449-450.  
1932. A collection of birds from southwestern Africa. *Ibid.*, vol. 84, p. 188, pl. 20.
- SCHLEGEL, H., AND FRANCIS P. L. POLLEN  
1868. Recherches sur la faune de Madagascar et de ses dépendances. Part 2. Mammifères et oiseaux. Leiden, J. K. Steenhoff, pp. 101-102.
- SCLATER, W. L.  
1930. Systema avium Ethiopicarum. London, British Ornithological Union, pp. 363, 395-417.
- SHARPE, R. BOWDLER  
1879. Catalogue of the Passeriformes or perching birds in the collection of the British Museum, Muscicapidae. London, British Museum, vol. 4, pp. 111-468.
- SIEBERS, H. C.  
1928. Neue Vögel von Sumba. Treubia, vol. 10, p. 402.
- SNOW, D. W.  
1950. The birds of São Tomé and Príncipe in the Gulf of Guinea. Ibis, p. 590.
- STEINBACHER, F.  
1937. Die ostasiatischen Fliegenschnäpper der Untergattung *Zanthopygia* Blyth. Ornith. Monatsber., vol. 45, pp. 166-167.
- STRESEMANN, ERWIN  
1912. Revision einiger Muscicapiden-Gattungen. Novitates Zool., vol. 19, pp. 323-330.

1925. Über einige *Cyornis* Arten. Ornith. Monatsber., vol. 33, pp. 45-53.
1940. Die Vögel von Celebes, Teil 3. Jour. f. Ornith., vol. 88, pp. 73-84.
- STRESEMANN, ERWIN, AND RODOLPHE M. DE SCHAUENSEE
1936. Notes on some South Asiatic species of the genus *Cyornis*. Proc. Acad. Nat. Sci. Philadelphia, vol. 88, pp. 337-351.
- VAURIE, CHARLES
1949. A revision of the bird family Dicruridae. Bull. Amer. Mus. Nat. Hist., vol. 93, p. 209.
1951. A new species of flycatcher from Mindanao, Philippine Islands. Amer. Mus. Novitates, no. 1543, pp. 1-4.
- 1952a. A review of the bird genus *Rhinomyias* (Muscicapini). *Ibid.*, no. 1570, pp. 1-36.
- 1952b. Geographical variation in the Chat Flycatcher (*Bradornis infuscatus*). *Ibid.*, no. 1599, pp. 1-9.
- VINCENT, ALFRED W.
1947. On the breeding habits of some African birds. Ibis, pp. 172-179.
- WHISTLER, HUGH
1949. Popular handbook of Indian birds (new edition). London, Gurney and Jackson, pp. 127-128.
- WHITE, C. M. N.
1943. Field notes on some birds of Mwinilunga, northern Rhodesia. Ibis, p. 129.
- WITHERBY, H. F., F. C. R. JOURDAIN, NORMAN F. TICEHURST, AND BERNARD W. TUCKER
1938. The handbook of British birds. London. H. F. and G. Witherby, vol. 1, pp. 299-314.
- WOLTERS, HANS E.
1950. Ueber die Gattung *Muscicapa*. Krefeld, Goecke und Evers, pp. 34-39.