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Article II.—THE DISTRIBUTION OF THE MOTMOTS OF THE GENUS *MOMOTUS*

By Frank M. Chapman

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INTRODUCTION

The motmots, a distinctively American family of birds, range from the northern limit of the Tropical Zone in northeastern Mexico south to the southern limit of this zone in northern Argentina. The family contains six genera,[1] approximately fifteen species, and some twenty-two subspecies.

All six genera are represented in Central America but, barring the occurrence of *Hylomanes* in northwestern Colombia, only three are present in South America.

Of the fifteen-odd species contained in the family, three are common to South America and Central America, four are exclusively South American, and eight are exclusively Central American. Thus both in genera and species the motmots are more numerously represented in Middle than in South America.

Motmots are sedentary, tree-inhabiting birds. The rufous-crowned species of the genus *Momotus* inhabit semi-arid regions where cacti and mimosas are characteristic growths. The blue and black-and-blue-crowned species of this genus haunt deep forests but are by no means

[1] I see no generic distinction between *Baryphthengus* and "*Urospatha*." On the contrary, both agree and differ from all other members of the group in possessing greatly enlarged auricular tufts, while their pectoral tufts are disproportionately small. Our specimens show no constant difference in tomial serration nor in relative length of tarsus to middle-toe, while east of the Andes "*Urospatha*" *martii* agrees with *Baryphthengus* in having the central rectrices normally non-spatulate.

restricted to heavily wooded areas. Scrubby growth and "gallery" forests bordering streams afford them sufficient cover, a fact which no doubt in a large measure accounts for their wide distribution.

They nest in holes in banks or similar places and lay white eggs, their nidification resembling, therefore, that of their relatives the todies and kingfishers.

In this paper I attempt to show that the motmots originated in Middle America; that they have made at least three invasions of South America, of which the last two have occurred since the elevation of the Andes; that the earlier of these post-Andean invasions was made by a Subtropical Zone bridge over Panama, which has since disappeared; and that the second originated in the Tropical Zone of Panama with a subsequent center of dispersal east of the Andes in Colombia. In order fully to present the facts on which these conclusions rest it will be necessary to review the species of the genus concerned.

THE GENUS *MOMOTUS*

The range of the genus *Momotus* is nearly coëxtensive with that of the family to which it belongs. Its members fall into two distinct groups, in one of which the crown is cinnamon-rufous or chestnut, in the other blue, or black and blue. No two forms of either group are found associated and, in spite of their distinctness, even the rufous-crowned and black-and-blue-crowned species are not known to occur together. Dr. E. W. Nelson, who has had wide field experience in Mexico, writes me in response to my request: "Not one of our many field records shows both of these species from the same locality. We have many records of each of these but always from distinct places, so that the evidence appears to be against their ranges overlapping, unless it may be a very narrow territory along the borders."

The Rufous-crowned Group

On the Pacific slope of Mexico and in Guatemala two species of motmots with reddish-brown heads are found. They are

Momotus mexicanus mexicanus Swains.
Momotus mexicanus saturatus Nels.
Momotus castaneiceps Gould.

Momotus mexicanus mexicanus is found, according to Ridgway, in the states of Sinaloa, Tepic, Durango, Zacatecas, Jalisco, Colima, Michoacan, Mexico, and Puebla; and it is also recorded from Vera Cruz on the authority of Sumichrast, but examination of the page

cited in the work of that author[1] reveals only a reference to "*Momotus lessoni*," the east Mexican species.

Momotus mexicanus saturatus Nels., a closely related, larger race having the brown of the head suffusing the back, represents *mexicanus* in the states of Guerrero, Oaxaca, and Chiapas.

These two birds bear no close relationship to the blue-and-black-crowned group which forms the special subject of this paper, but it is worthy of note that, in spite of their unlikeness, the two are apparently never found associated.

Momotus castaneiceps of Guatemala, though evidently representing *mexicanus*, is specifically distinct from it. Its distribution is given by Salvin and Godman as the "Valley of the Motagua river between the narrow gorge near Guastatoya and La Magdalena, and the denser forest which commences above Gualan. This includes the whole of the plain of Zacapa, which is comparatively open country, large cacti and mimosa trees being the characteristic plants."[2]

The Blue or Black-and-Blue-crowned Group

Our inquiry lies with the blue or black-and-blue, rather than rufous-crowned, species, and the latter are mentioned to show that the southern Mexico-Guatemala[3] region appears to have been a point of origin and subsequent dispersal of two distinct groups of the genus *Momotus*, one of which, in Mexico, is restricted to the Pacific, the other to the Atlantic side; and that in spite of their wide divergence no two species are found associated, and that consequently they bear to each other the relationship of representative species.

In this section of the genus *Momotus* are included the following species and subspecies. I begin with the most northern species and proceed, generally, southward.

Momotus cæruliceps	Eastern Mexico.
Momotus lessoni goldmani	Southeastern Mexico.
" " *exiguus*	Peninsula of Yucatan.
" " *lessoni*	Central America to Subtropical Zone in Chiriqui.
Momotus æquatorialis æquatorialis	Subtropical Zone, Colombia; Ecuador.
Momotus æquatorialis chlorolæmus	Subtropical Zone, Peru.
Momotus subrufescens conexus	Magdalena Valley north to Canal Zone.
Momotus subrufescens reconditus	Eastern Panama, Atrato Valley.

[1] 1869, Mem. Bost. Soc. Nat. Hist., p. 560.
[2] 'Biol. Cen. Amer. Aves,' II, p. 461.
[3] In this connection the restriction of the genus *Aspatha* to the highlands of Guatemala doubtless possesses some significance.

Momotus subrufescens subrufescens	Northern Colombia; northern Venezuela.
Momotus subrufescens osgoodi	Southern Maracaibo region.
Momotus bahamensis	Trinidad; Tobago.
Momotus momota microstephanus	Eastern Colombia; eastern Ecuador.
Momotus momota momota	Between Orinoco and Amazon.
Momotus momota argenticinctus	Western Ecuador.
Momotus momota ignobilis	Eastern Peru.
Momotus momota nattereri	Bolivia.
Momotus momota pilcomajensis	Southern Bolivia; N. W. Argentina; southern Brazil.
Momotus momota simplex	Right side, Lower Amazon, to Santarem; south central Brazil.
Momotus momota parensis	Pará region east of Tocantins.
Momotus momota cametensis	Lower Amazon, west of Tocantins.

From this list it appears that of the some thirty-seven species and subspecies contained in the family Momotidæ more than one-half are contained in the black-and-blue-crowned section of the genus *Momotus*.

Although six of the twenty forms included in this section are ranked as species, no two are found associated. In other words, the various members of the group replace one another in their respective ranges, extending from near the Rio Grande Valley at the north southward to northern Argentina. While in some instances the non-intergradation of a form with its geographic neighbor or neighbors establishes what we term its specific distinctness, it seems evident that, viewed in the broader biologic rather than the narrower taxonomic sense, we have here one widely, almost continuously, distributed, plastic type represented by twenty forms exhibiting various degrees of differentiation. In short, the blue-and-black-crowned group of the genus *Momotus* is apparently now the dominant, most highly developed type of the family.

Before attempting to determine what light the relationships and distribution of these birds may throw on evolutionary and faunal problems, it will be necessary briefly to review their characters, status, and ranges.

The peculiar plumage of motmots occasions the systematist some difficulty in defining their true colors. Seen directly from above, the upperparts of some species appear to be green; viewed at an angle, especially toward the light, the same part is rich brown. Occasionally, however, individuals of one species from the same locality may be either green or brown without regard to the angle from which they are viewed, and species showing this extreme of variation might well be considered dichromatic in color.

It was obviously variation of this kind which led to the description, for example, of *Momotus bartletti*, and the systematist requires, therefore, adequate series of specimens to ascertain the prevailing type of color in a given form.

THE MIDDLE AMERICAN FORMS AND THEIR ANDEAN REPRESENTATIVE

The motmots of Mexico and Central America have been treated by Ridgway[1] so recently that the appended summary of their range and relationships is based chiefly on his work. The conclusions therein presented are supported by a study of our own large series except in the case of *Momotus cœruliceps*, the intergradation of which with *lessoni* is indicated by our material. Since, however, the recognition of such intergradation would involve ranking all the Middle American forms as subspecies of *cœruliceps*, it seems inadvisable to make this nomenclatural change until intergradation of *cœruliceps* with *lessoni* is proven.

Momotus cœruliceps (Gould)

Prionites cœruliceps GOULD, 1836, Proc. Zoöl. Soc., p. 18 (Tamaulipas, Mexico).

CHARACTERS.—Resembling *M. l. goldmani* but pileum wholly blue, forehead tinged with greenish; underparts less tawny; breast-tuft larger.

RANGE.—Tropical Zone of northeastern Mexico from Nuevo Leon south to the state of Vera Cruz.

Ridgway includes Córdova, Vera Cruz, and Rinconada, Puebla, in the range of this species, but does not state whether the Córdova record is based on actual examination of specimens. We have a skin of *goldmani* from Monte de Cuichapa, Córdova, with the crown strongly washed with blue of exactly the same shade as in *cœruliceps*, while the general color of the body is decidedly greener than in a specimen of *cœruliceps* from Valles, San Luis Potosi. In the latter the greenish frontal area is less pronounced than in true *cœruliceps*, but if it were accepted as typical of *cœruliceps*, the Córdovan specimen would certainly be referred to that species rather than to *lessoni goldmani*.

Momotus lessoni goldmani Nelson

Momotus lessoni goldmani NELSON, 1900, Auk, XVII, p. 256 (Motzorongo, Vera Cruz, Mex.).

CHARACTERS.—Differs from *M. lessoni lessoni* of Central America in being greener, in having the breast much less strongly tinged with brown, and particularly in the absence of cobalt-blue in the posterior blue margin to the black pileum. The black margin to the nuchal band appears to be more evident in this race.

[1]1914, Bull. U. S. Nat. Mus., VI, pp. 450–487.

RANGE.—Humid Tropical Zone of southeastern Mexico from the southern limits of the range of *M. cæruliceps* south to Tabasco.

Though much nearer *lessoni*, the characters which separate *goldmani* from *lessoni* mark it as an intermediate between that form and *cæruliceps*. The typical form, with no cobalt-blue in the blue nuchal band, occurs only at the northern limit of the range assigned to the race, and is obviously an approach toward *cæruliceps*.

Fig. 1. Distribution of *Momotus lessoni* Group.

1. *M. cæruliceps.*
2. *M. lessoni goldmani.*
3. *M. lessoni exiguus.*
4. *M. lessoni lessoni.*
5. *M. æquatorialis.*

Note the absence of the group from Panama and its extension southward in the Subtropical Zone.

Momotus lessoni exiguus Ridgway

Momotus lessonii exiguus RIDGWAY, 1912, Proc. Biol. Soc. Wash., XXV, p. 89 (Temax, Yucatan).

CHARACTERS.—Averaging greener than *M. l. goldmani* but agreeing with it and differing from *M. l. lessoni* in having much less or no tawny on the breast; agreeing

with *lessoni* and differing from *goldmani* in having the cerulean blue nuchal band margined posteriorly with smalt-blue.

RANGE.—Tropical eastern Campeche and Yucatan.

While in some respects this form is an intermediate between *lessoni* and *goldmani* in its lighter green color, it differs from them both.

Although traces of smalt-blue are found in the nuchal band of most specimens of *goldmani* from the southern limit of the range of that form, we now encounter this marking for the first time as a constant character and will find it present in variable degrees in all the remaining forms of the group.

Momotus lessoni lessoni Lesson

Momotus lessonii LESSON, 1842, Rev. Zool., p. 174 (Realejo, Nic.).

CHARACTERS.—Foreback and nape suffused with tawny, occasionally traces of chestnut-rufous in the nape; breast with a pronounced tawny wash, throat greenish blue; posterior pileum usually cerulean tipped with smalt-blue, the longer underlying feathers black.

RANGE.—Tropical to Subtropical Zone, from extreme southern Mexico south to Costa Rica and Chiriqui.

This species at the South and *M. cæruliceps* at the North mark respectively the extremes of differentiation of the Middle American forms of this group. Their intergradation as the range of one form passes into that of another is proven in the case of all of them except *cæruliceps* and with that form it is strongly indicated.

Momotus cæruliceps and *Momotus lessoni goldmani* are apparently confined to the Tropical Zone. Sumichrast[1] includes the last-named among the species which characterize the "Hot Region" of Vera Cruz, but from Guatemala southward *lessoni* has a wider altitudinal range.

In Guatemala, Dearborn[2] states that *lessoni* was common on the Pacific slope or San José (sea-level), Mazatenango and Patulul (each 1800 feet). Salvin,[3] however, mentions it as a bird of the "high region."

Of the distribution of *lessoni* in Costa Rica, Carriker writes that it is found throughout the plateau region and the Pacific slope from Nicaragua to Chiriqui. In Chiriqui, Brown records it only from near Boquete at altitudes of from 2500 to 4000 feet.

It appears, therefore, that, whereas in southern Mexico *lessoni* is confined to the Tropical Zone, in Costa Rica and Chiriqui, if not confined to, it is at least characteristic of the Subtropical Zone.

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[1] 1869, Mem. Bost. Soc. N. H., I, p. 560.
[2] 1907, Field Mus. Pub. 125, p. 89.
[3] 1860, Ibis, p. 100.

Chiriqui marks the southern known limit of this species. From Chiriqui to the Canal Zone so little collecting has been done that we do not know what form of motmot inhabits this region. So far as our information goes, therefore, the group next appears in the Canal Zone, where we first encounter *Momotus subrufescens*, which is evidently specifically distinct from *M. lessoni*.

Momotus æquatorialis æquatorialis Gould

Momotus æquatorialis Gould, 1857, Proc. Zoöl. Soc., p. 223 (Archidona, E. Ecuador).
Momotus lessoni gualeæ Lönnberg and Rendahl, 1922, Arkiv für Zool., Band XIV, No. 25, p. 51 (Gualea, Ec.).

Characters.—Most nearly resembling *Momotus lessoni goldmani* but larger, the tawny suffusion of the breast extending to the abdomen, the throat averaging less greenish blue; the blue border to the pileum wider, its black margin above the nape more pronounced; under wing-coverts and wing-lining with no trace of cinnamon. Immature birds have more blue on the crown, the black patch being much reduced and in one female (Salento, Col., September 26, 1911) it is practically wanting, the entire crown being blue.

Range.—Subtropical Zone of all three ranges of the Colombian Andes, and of the eastern slope of the Andes in Ecuador. (Unknown from western Ecuador?)

Momotus æquatorialis is clearly the representative in the Andean Subtropical Zone of the Middle American *M. lessoni*. That it should more closely resemble the Mexican, rather than the geographically nearer Costa Rican form of that species is doubtless due to that type of parallelism which makes *subrufescens* of the Caribbean coast nearest to *simplex* of southern Brazil, and *pilcomajensis* of southern Bolivia almost identical with *argenticinctus* of western Ecuador.

The discovery that a representative of *lessoni* is found in the Andean Subtropical Zone adds another species to the list of between sixty and seventy birds of which the same or obviously representative forms are found in this zone in Costa Rica and in Chiriqui, and in eastern Panama and northwestern Colombia, but are unknown in the low, intervening, tropical area. This subject is discussed in my 'Distribution of Bird-Life in Colombia' (p. 151) and the bearing of the present case on the distribution of the genus *Momotus* in South America will be returned to later.[1]

[1]Since writing the above, I find that Hellmayr (1911, Proc. Zoöl. Soc., p. 1194) has already suggested the possibility of *æquatorialis* being a southern form of *lessoni*, and Lönnberg and Rendahl (*loc. cit.*) have described a specimen, said to have been taken below Gualea, in western Ecuador, as *Momotus lessoni gualeæ*. It seems, however, doubtful if the specimen in question actually came from Gualea. During a visit to Quito in August, 1922, I showed the leading native collectors specimens of *Momotus æquatorialis* and they assured me that this species had never been found by them in western Ecuador. Mr. Ludovic Söderstrom, whose guest I was while in Quito, tells me he is now convinced that the specimen of *Momotus æquatorialis* which he sent to Dr. Lönnberg, and which is the type of *gualeæ*, must have been erroneously labelled. In any event, the characters ascribed to this proposed race are shown by a series from Colombia to be apparently individual rather than geographic.

Momotus æquatorialis chlorolæmus Berlepsch and Stolzmann

Momotus æquatorialis chlorolæmus Berlepsch and Stolzmann, 1902, Proc. Zoöl. Soc., p. 35 (Ocobamba, N. W. of Cuzco, Peru).

Characters.—Similar to *M. æ. æquatorialis* but underparts biscay-green with little or no tawny suffusion; throat more greenish blue.

Range.—Subtropical Zone of eastern Peru south at least to Santo Domingo.

This form is separated on average differences, a specimen from Santo Domingo being essentially like one from Rio Toché, Colombia. Three other specimens, however, are greener below than any I have seen from Colombia.

The South American Tropical Forms

Momotus subrufescens conexus Thayer and Bangs

Momotus conexus Thayer and Bangs, 1906, Bull. Mus. Comp. Zoöl., p. 215 (Sabana de Panama; topotypes examined).

Characters.—An intermediate between *M. subrufescens subrufescens* and *M. s. reconditus;* underparts more nearly resembling, but somewhat darker than in the former; upperparts more like those of the latter, but not quite so dark; blue of the head as in *reconditus.*

Range.—Cauca-Magdalena Fauna in Colombia, northwest, probably on the Caribbean coast region of Panama, at least to the Canal Zone and Savannah of Panama, and doubtless westward toward Chiriqui.

In my 'Distribution of Bird-Life in Colombia' (p. 271) I referred the motmots of the Magdalena Valley to *subrufescens subrufescens.* A broader view of their relationships shows, in my opinion, that, while specimens from the lower, more arid part of the valley are indeed referable to *subrufescens,* those from the more humid central portion of the valley are intermediate between that race and the deeply colored *reconditus;* while those from the semi-arid extreme upper Magdalena Valley are not quite so deeply colored as those from the more heavily forested part of the valley. Considered as a whole, these upper Magdalena birds are not unlike Canal Zone specimens, as Ridgway has already remarked.[1] In other words, they more nearly agree with the form known as *conexus* than with *subrufescens.* So far, therefore, as Colombia is concerned, the three forms of *subrufescens* may each be assigned to an existing faunal area as follows: (1) *M. s. subrufescens,* Caribbean Fauna; (2) *M. s. conexus,* Cauca-Magdalena Fauna; (3) *M. s. reconditus,* northern part of Colombian-Pacific Fauna. Whether the Colombian range of *conexus* is connected with the area this form occupies in Panama, I do not know. No such connection evidently exists on the Pacific side of the Caribbean costal

[1] Bull. U. S. Nat. Mus., L, part 6, p. 462.

range, for this region is inhabited by *reconditus*. Possibly, however, *conexus* may be found on the Caribbean side of this range, though one would imagine that the heavy rainfall that characterizes this region would produce as deeply colored a form as that which exists in the Tuyra and Atrato Valleys.

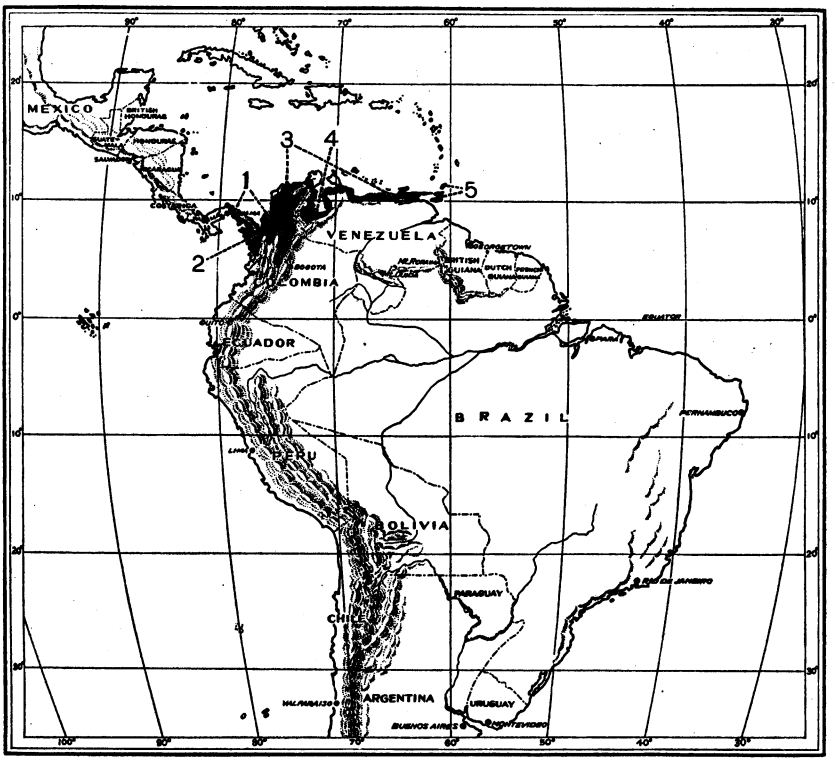

Fig. 2. Distribution of the *Momotus subrufescens* Group.

1. *Momotus subrufescens conexus.*
2. *Momotus subrufescens reconditus.*
3. *Momotus subrufescens subrufescens.*
4. *Momotus subrufescens osgoodi.*
5. *Momotus bahamensis.*

Confined to northern Colombia, the coastal region of Venezuela, Trinidad and Tobago. The form of the lower Orinoco is quite unlike that of Trinidad and northeast Venezuela.

We should, however, regard these variations in color as expressions of environment, chiefly if not wholly climatic, under which the individuals exhibiting them exist.

Considered thus from a biological, rather than nomenclatural, standpoint we have a species, *Momotus subrufescens*, ranging from at least the Canal Zone in Panama to the islands of Trinidad and Tobago. Being apparently continuously distributed throughout this region, it

encounters a wide range of climatic conditions from the semi-arid coastal region of Colombia and Venezuela to the humid districts of the Tuyra, Atrato, upper Magdalena, southern Maracaibo basin and islands of Trinidad and Tobago. In the drier parts of its range this motmot is comparatively light colored (*subrufescens subrufescens*); in the moister areas it is more richly colored (*conexus, reconditus, osgoodi*, and *bahamensis*).

It is of special importance to note that, although northeastern Venezuela is the only place, under existing topographic conditions, where *Momotus* could cross the Andean system without leaving the Tropical Zone, the forms found on the Caribbean slope and in Trinidad are less closely related to *M. m. momota*, the form of the lower Orinoco and the Guianas, the nearest one to them geographically, than to any other one in the group. Whether or not the ranges of *subrufescens* and *momota* come together I do not know, but the available evidence assuredly does not point to their intergradation.

Trinidad forms are usually closely related to those of the lower Orinocan and Guianan region, but in this case it seems quite clear that the Trinidad form has been derived from the Caribbean coast region of Venezuela rather than from the south, and we have further support here, therefore, for our belief that the distribution of *Momotus* has been from the north southward.

Momotus subrufescens reconditus (Nelson)

Momotus conexus reconditus Nelson, 1912, Smiths. Misc. Coll., p. 27 (Marragante, E. Panama; type examined).

Characters.—More richly colored than *M. s. subrufescens*, the underparts nearly, if not quite, as deep as in *M. bahamensis*, but the throat and breast with a greenish caste; upperparts much darker than in *M. s. subrufescens*, parrot-green, suffused with tawny; cerulean blue of the crown deeper.

Range.—Eastern Panama and Valley of the Atrato in Colombia.

The rich colors of this well-marked race express the influence of the exceptionally humid region it inhabits. No species of this group has been found in western Colombia south of the Atrato, and it is especially noteworthy that the form of western Ecuador differs widely from that of northern Colombia.

Momotus subrufescens subrufescens Sclater

Momotus subrufescens Sclater, 1853, Rev. et Mag. de Zool., V, p. 489 (Santa Marta, Col. Topotypes examined).

Momotus venezuelæ Sharpe, 1892, 'Cat. Birds, Brit. Mus.,' XVII, p. 321 (prov. description of "Venezuelan specimens"; no type mentioned; specimens from San Esteban and Puerto Cabello listed).

CHARACTERS.—Underparts rufous-tawny, greener anteriorly, more rufous posteriorly; upperparts varying from parrot-green washed with olivaceous to rufous-tawny nearly as deep as in the underparts of some specimens, but usually with a pronounced tawny suffusion, at least anteriorly, and usually with more or less concealed chestnut on the nape. Differs from *lessoni* in its smaller size, more slender bill, rufous-tawny underparts and more tawny back; tawny instead of greenish or greenish-tawny lower wing-coverts, more cerulean blue of forehead, absence of black margin to the nuchal band, and concealed chestnut on the nape.

RANGE.—Caribbean coastal region of Colombia and Venezuela.

The status and relationship of this race are discussed under *M. s. conexus*. Specimens from northern Venezuela are apparently not separable from true *subrufescens*.

Among forms inhabiting the interior of South America, *subrufescens* is nearest *simplex* of South Central Brazil, from which it differs chiefly in its more tawny upperparts.

Momotus subrufescens osgoodi Cory

Momotus osgoodi CORY, 1913, Field Mus. Pub. 167, p. 285 (El Guayabel, 10 m. east of Cúcuta, Colombia).

CHARACTERS.—Upperparts suffused with tawny as in true *subrufescens*, but much darker; underparts uniform chestnut-rufous as in *bahamensis*.

RANGE.—Humid forests of the southern half of the Gulf of Maracaibo.

Again responding to a more humid environment *Momotus subrufescens* becomes much deeper in color both above and below. Six of the seven specimens examined are indistinguishable below from *bahamensis*, but above are suffused with tawny; the seventh, which has a tinge of greenish on the throat and is greener above, can be closely matched by a specimen of *reconditus* from eastern Panama.

Momotus bahamensis (Swainson)

Prionites bahamensis SWAINSON, 1837, 'Anim. in Menag.,' p. 332 (Trinidad; topotypes examined).

CHARACTERS.—Underparts from bill to vent uniform rich hazel or chestnut-rufous; no green on the throat; upperparts darker green, with much less brownish suffusion than in *subrufescens;* tawny on nape often wanting.

RANGE.—Islands of Trinidad and Tobago.

An island representative of *subrufescens* which, evidently through complete isolation, has become specifically distinct. There is no apparent difference between Trinidad and Tobago specimens.

In spite of the close resemblance usually found among Trinidad, lower Orinocan, and Guianan species, it is noteworthy that *bahamensis* is an evident derivative of the Caribbean coastal form, and differs from *momota momota* more than from any other race in the group.

We now leave the *subrufescens* group, cross the Andes, and find an apparently specifically distinct but representative group in the various races of *Momotus momota.*

Momotus momota microstephanus Sclater

Momotus microstephanus Sclater, 1855, Proc. Zoöl. Soc., p. 135 ("Interior of New Grenada" = region about Villavicencio, east of Bogotá; type examined; a "Bogotá" skin).

Characters.—Prevailing color of underparts greenish when viewed from above, but decidedly medal bronze when seen at a slight angle or on a level with the eye, and this bronze becomes more tawny when the bird is held between the observer and the light; the nuchal band is broadly smalt-blue with little or no cerulean, the chestnut-rufous border more pronounced, as a rule, than in any other form except *momota;* central rectrices of adults not always spatulated; general tone of back much as in *conexus.*

Range.—Colombia (and Ecuador?) east of the Andes.

The only species of *Momotus* definitely known to occur in the "interior" of Colombia (that is, west of the Eastern Andes) are *M. subrufescens* (including its races) and *M. æquatorialis.* Specimens from the Bogotá region on the Rio Meta, east of Villavicencio, agree with the type of *microstephanus,* and are doubtless topotypes of it. While they average slightly greener above than specimens from southeastern Colombia, the two series certainly represent but one form. In a former paper[1] I referred the latter to *M. m. ignobilis,* but the receipt of specimens of this race from the Perené near La Merced, Peru, whence Berlepsch and Stolzmann record typical examples of *ignobilis,* shows conclusively that I was in error. The difference between the two is not, however, so great that it might not be bridged by the range of individual variation and to this fact I attribute the record[2] of *ignobilis* based on an immature specimen from "Mataben, Rio Orinoco," a place I am unable definitely to locate.

The Colombian birds are intermediate between *momota* and *ignobilis* but are nearer to the former in color and to the latter in size. A specimen from Florencia, southeastern Colombia, has more chestnut-rufous on the nape than one from Cayenne. It is also significant that of eight adult specimens of *microstephanus* only four have the central rectrices spatulate, a fact which indicates their close relationship to *momota,* of which only two in twelve adults in our collection have racquet-tipped rectrices. In short, in view of the fact that the ranges of *microstephanus* and *momota* are doubtless connected, there is every reason to believe that the birds themselves intergrade.

[1] 1917, Bull. Amer. Mus. Nat. Hist., XXXVI, p. 271.
[2] 1902, Berlepsch and Hartert, Nov. Zool., p. 106.

To the south there is equally good reason to believe that *microstephanus* intergrades with *ignobilis*, while in western Ecuador it is surprising to find it subspecifically represented by *argenticinctus*.

Fig. 3. Distribution of *Momotus momota* Group.

1. *Momotus momota microstephanus.*
2. " " *momota.*
3. " " *ignobilis.*
4. " " *nattereri.*
5. *Momotus momota pilcomajensis.*
6. " " *simplex.*
7. " " *cametensis.*
8. " " *parensis.*
9. *Momotus momota argenticinctus.*

Note that only the Ecuador form, No. 9, is found west of the Andes. Although apparently derived from No. 1 it most closely resembles No. 5. Although the ranges of Nos. 6, 7, and 8 are separated from that of No. 2 only by the Amazon, the differences between the first three and the last are apparently of specific value, but all are indirectly connected through Nos. 3 and 1.

Momotus momota momota (Linnæus)

Ramphastos momota, Linnæus, 1766, 'Syst. Nat.,' p. 152 (Cayenne; topotype examined).

Characters.—Largest form of the group; central rectrices usually non-spatulate; a large chestnut-rufous post-nuchal band or spot sharply defined from the back, which averages purer green than in *microstephanus;* wing-lining and under wing-coverts with less cinnamon than in *microstephanus;* crown and its border as in that race; underparts yellowish green.

RANGE.—Region between the Orinoco, Rio Negro and Amazon; westward doubtless in Colombia to the district in which it probably intergrades with *microstephanus*; eastward to the Atlantic.

The name of this form, the first race described, has of necessity to be employed as the specific designation of the forms of the group with which directly or indirectly it intergrades.

This race has close relationships only with *microstephanus*, with which, as has been said, it probably intergrades in eastern Colombia.

It is important to observe that to the north its range approaches that of the quite different *subrufescens* and insular *bahamensis*, while on the south the Amazon separates it at Obidos from the quite unlike *simplex* of Santarem. In discussing the relationship of the last-named form, I have given my reasons for the belief that *parensis* and *cametensis* were derived from it rather than direct from true *momota*.

The East Ecuador Form

Unfortunately I have no specimens from eastern Ecuador. Doubtless, however, the bird of that region is between *microstephanus* and *ignobilis* and, in view of the characters shown by specimens from southeastern Colombia, it is probable the east Eucador bird is nearer the former. Whether or not it shows any approach toward the west Ecuador form remains to be determined. Berlepsch (Journ. für Orn., 1889, p. 307), in describing *ignobilis*, refers east Ecuador specimens to it. But he also remarks that La Merced specimens agree with his *ignobilis*. Sharpe describes a bird from the upper Ucayali as *bartletti* and refers Colombian specimens (=*microstephanus*) to it. These facts indicate the close resemblance between northeast Peruvian and east Colombian birds, and lead to the conclusion that the east Ecuadorian bird is *microstephanus*.

Momotus momota argenticinctus Sharpe

Momotus argenticinctus SHARPE, 1892, 'Cat. Birds Brit. Mus.,' XX, p. 323, prov. (Babahoyo, Ec.; type examined).

CHARACTERS.—Nearest to *M. m. microstephanus* but anterior underparts averaging greener, the throat usually tinged with bluish green, much as in *lessoni*, the posterior pileum band usually with more cerulean, less smalt-blue; nuchal region greener less suffused with tawny; rectrices always spatulate in the adult.

RANGE.—Tropical Zone of western Ecuador and northwestern Peru from Esmeraldas to Palambla.

This paper originated in an attempt to determine the affinities of the form of *Momotus* inhabiting Ecuador, and its extent is an indication of the length to which such attempts of necessity sometimes lead one.

It was important, in the first place, to ascertain what races of this group were found in the Tropical Zone of Colombia, where it appears that only *subrufescens subrufescens* and *subrufescens reconditus* are known. Neither of these birds is closely related to *argenticinctus;* and *reconditus*, of the Atrato Valley, the nearest to it geographically, is the least like it of the two. South of the valley of the Atrato no form of *Momotus* has been found in western Colombia; but whether or not one occurs it is not conceivable that *reconditus* intergrades with *argenticinctus* in this area. We must therefore look elsewhere for the ancestor of the west Ecuador bird and we find it, I think, in *microstephanus* of eastern Colombia and (doubtless) eastern Ecuador.

I am not unmindful of certain characters which *argenticinctus* shares with *lessoni*, but the latter is so obviously represented in South America by *æquatorialis* that it is not to be considered as the ancestor of *argenticinctus*. Furthermore, the differences between the last-named form and *microstephanus* are practically bridged by individual variation and in spite, therefore, of their disconnected ranges, I list them as subspecifically related.

Momotus momota ignobilis Berlepsch

Momotus brasiliensis ignobilis Berlepsch, 1889, Journ. für Orn., p. 307 (Yurimaguas, Peru).

Momotus bartletti Sharpe, 1892, 'Cat. Birds Brit. Mus.,' XVIII, p. 321, Pl. x (Upper Ucayali).

Characters.—Described by Berlepsch as smaller than *momota* with less, or without, chestnut-rufous on the nape and with the underparts greener.

Three specimens from the Perené, near La Merced (whence Berlepsch and Stolzmann record *ignobilis*) agree with this description in part but have the abdomen distinctly more rufescent than in *momota* and in this respect agree with Sharpe's description of "*bartletti.*" They have not, however, the amount of chestnut on the nape which he ascribes to that species. Sharpe refers a "Bogotá" specimen to his "*bartletti*" but none of our Colombian birds matches the three very uniformly colored Perené specimens in the greenness of their breast and quite strongly contrasted cinnamon abdomen. The Perené birds further differ from *microstephanus* in the practical absence of cerulean in the postpileum band and of rufescent suffusion on the foreback. Two of them have, however, a trace of chestnut-rufous in the nape.

In the color of the underparts the Perené birds can be exactly matched by one from Todos Santos, Rio Chaparé, Bolivia, but above they are purer green than any of our Bolivian specimens; and in this

respect resemble *simplex*, with which the Peruvian bird doubtless merges. A large series from Chapada, Matto Grosso, includes specimens which are almost identical with the Perené birds, though the latter are less rufescent on the abdomen than the average Chapada examples.

It is clear that with only three east Peruvian birds at hand, and those not topotypical of the bird recognized from that region, I am not in a position satisfactorily and definitely to discuss the relationships of the birds of this area. But it is also equally clear from these birds, and the descriptions of other authors, that *microstephanus* of eastern Colombia and *nattereri* of Bolivia are connected by specimens from the intervening area, but just what part of this area may be allotted to the form known as *ignobilis* I am unable to say.

Momotus momota nattereri Sclater

Momotus nattereri Sclater, 1857, Proc. Zoöl. Soc., p. 251 (Yungas, Bolivia; topotypical specimens examined).

M[omotus] boliviana Reichenow, 1919, Journ. für Orn., p. 335 (La Paz, Bolivia).

Characters.—Underparts (seen from above) uniform rich rufescent olive, the abdominal region not, as a rule, strikingly different from the breast and never as deep cinnamon-rufous as in *simplex;* breast more rufescent than in Perené specimens of *ignobilis;* upperparts dark and more suffused with tawny than in *ignobilis, simplex,* or *pilcomajensis.*

Range.—Tropical Zone at the northeastern base of the Bolivian Andes, doubtless merging with *simplex* toward the east and *ignobilis* toward the north.

The range of *nattereri* has hitherto been applied to all Brazilian specimens south of the Amazon, except those of the Pará region, but it is evident that this name cannot properly be applied to birds from Santarem, and Matto Grosso specimens prove to be nearer to the Santarem than to the Yungas form. Evidently, therefore, the name *nattereri* should be restricted to Bolivian birds. This question is dealt with further under *simplex.*

Momotus momota pilcomajensis Reichenow

Momotus pilcomajensis Reichenow, 1919, Journ. für Orn., p. 334 (Villa Monte, Rio Pilcomayo, S. Bolivia).

Characters.—Greener below than *M. m. nattereri,* with less, or only a tinge of, cinnamon on the abdomen; the throat bluish green; the upperparts green as in *simplex;* differing from *M. m. argenticinctus* only in the absence of a cerulean margin at the back of the pileum.

Range.—Southern Bolivia, northern Argentina, and eastward to Urucum and possibly western São Paulo, Brazil.

Two specimens (one from Vermejo, 3500 ft., Dept. Santa Cruz, Bolivia; the other from Urucum, near Corumbá, Brazil) agree with the description of this form, the most southern of the genus. They agree

minutely in general coloration with average specimens of *argenticinctus* of western Ecuador, even to the greenish blue throat, but the Vermejo bird has the post-pileum band almost wholly smalt-blue with only a trace of cerulean at the bases of some feathers, while in the Urucum bird the cerulean is more evident. The latter and a bird from Santa Rosa, Ecuador, are as nearly alike as two birds can well be.

We have here, therefore, an even more pronounced case of parallelism than is shown by *simplex* and *subrufescens*.

Momotus momota simplex, new subspecies

SUBSPECIFIC CHARACTERS.—Underparts much as in *M. s. subrufescens* but back much purer green (grass-green) without tawny suffusion, except to a limited degree anteriorly, where, in some individuals, there is a trace of chestnut-rufous; abdominal region more rufescent than in *nattereri*, the cinnamon-rufous extending, in most specimens, to the throat, back purer green, size larger; closely resembling *M. m. parensis* but with no or but little chestnut-rufous on the nape.

TYPE.—No. 73,372, Carnegie Museum, ♂ ad. Santarem, Brazil, June 30, 1919; S. M. Klages.

RANGE.—Right bank of the Amazon, from at least the Tapajoz westward probably to near the Peruvian boundary; southward to the head of Amazonian drainage in Matto Grosso, and probably Goyaz.

Specimens from the range ascribed to this race have hitherto been identified as *nattereri*, but in loaning me an excellent series in the Carnegie Museum, from Santarem, Mr. Todd calls my attention to the characters which distinguish the Amazonian from the Bolivian bird. Prior to the receipt of these birds, I had described a large series from Chapada, Matto Grosso, as "greener above and more rufescent below than topotypical Bolivian birds," adding "these characters are most pronounced in two specimens from Santarem."

Until further specimens were received from Santarem, I did not feel convinced of the desirability of separating the Brazilian birds. However, comparison with Bolivian specimens now shows this course to be apparently unavoidable, and the preceding diagnosis is presented with Mr. Todd's kind permission.

To the Santarem form I would refer our Matto Grosso series, as nearer to *simplex* than to true *nattereri*. Specimens from Goyaz should doubtless also be placed with *simplex*, but since a bird from Urucum on Paraguayan drainage agrees with one from Vermejo, Bolivia, which I have identified as *pilcomajensis*, I am uncertain whether a record by von Ihering from Itapura on Paraguayan drainage, in western São Paulo, should be placed under *simplex* or *pilcomajensis*.

In the comparatively pure green color of the upperparts, *simplex* resembles the three specimens from the Rio Perené in the Chanchamayo district of Peru, and it is more than probable that the Amazonian form is a derivative of the Peruvian, rather than of the Bolivian bird.

From *parensis*, *simplex* differs only in being slightly less rufous on the throat, and in having little or no chestnut-rufous on the nape. In other words, *parensis* has the rufous of the underparts as much, or more highly developed than in any other form south of the Amazon. In this respect, therefore, it differs more widely from *momota momota*, which has greenish underparts, than from any other race of this group. In the amount of chestnut-rufous on the nape, on the other hand, it is nearer *momota momota*.

This character, however, is a variable one, even in *momota momota*, and, in my opinion, is of less importance in determining true affinities than is the color of the underparts. Furthermore, *parensis*, so far as my material and the records go, always has the central rectrices in the adult spatulate, while in true *momota* they are usually untrimmed. I feel, therefore, that the relationships of *parensis* are with *simplex* rather than with *momota momota*, and that the Amazon has been an effective barrier to the distribution of *momota momota* south of its left bank.

In this connection, however, we must consider the form from the left bank of the Tocantins described by Dr. Snethlage as *Momotus momota cametensis* (see beyond). Although occurring between the ranges of *simplex* and *parensis*, with no obvious physical or climatic barrier to prevent continuity of range and consequent intergradation, *cametensis* is said to differ from *parensis* in having the chestnut nuchal band of that form extended to the ear-coverts. Thus this geographically intermediate form is less like *simplex* than the latter is like *parensis*.

It should also be observed that in *cametensis* the chestnut-rufous band is even more developed than in *momota momota*. In the intensity of the rufous below, however, it agrees with *simplex* and *parensis* and, as said above, I consider this character of more significance than that of the nuchal band.

Viewed more broadly, it seems evident that we have south of the Amazon one plastic species of motmot which reflects the influences of a widely varying environment chiefly through the amount of cinnamon-rufous in its plumage, mainly of the underparts.

Momotus momota cametensis Snethlage

Momota momota cametensis Snethlage, 1912, Orn. Monatsb., XX, p. 155 (Cameta, left bank of the Rio Tocantins).

Characters.—Described as similar to *M. m. parensis* but with the chestnut-rufous nuchal band extending to the black ear-coverts.

Unfortunately I have seen no specimens of this race, which Dr. Snethlage states is based on five specimens. Its status is briefly commented on under the preceding form.

Momotus momota parensis Sharpe

Momotus parensis SHARPE, 1892, 'Cat. Birds Brit. Mus.,' XVII, p. 320; prov. descr. (Pará, Brazil).

CHARACTERS.—Underparts rich cinnamon-rufous, much as in *subrufescens subrufescens*, but throat without green; closely resembling *M. m. simplex* in general coloration both above and below, but chestnut-rufous nuchal band much as in *momota momota;* differs from that race in being smaller, cinnamon-rufous instead of greenish below, and in having the central rectrices spatulate in the adult.

RANGE.—Pará region east of the Tocantins, to the Parnahyba in the state of Maranhão, Brazil.

The relationships of this form are discussed under *M. m. simplex.*

LIST OF SPECIMENS EXAMINED[1]

Momotus mexicanus mexicanus.—MEXICO, Sinaloa: Manzanillo Bay, 1 ♂; Escuinapa, 1 ♀; Sierra de Armigas, 3500 ft., 1 ♂, 1 ♀; Los Pieles, 3500 ft., 2 ♂; Nayarit; Tepic, 3 ♂; Amatlan de Canas, 2 ♂, 3 ♀; Jalisco; Tuxpan, 2 ♂, 2 ♀; La Pisagua, 1 ♂, 1 ♀; La Laja, 1 ♂; Sal se Puede, 1 ♀; Wakenakili Mts., 3 ♀; Volcan de Nieve, 1 ♀; Colima; Plains Colima, 1 ♂, 2 ♀.

Momotus mexicanus saturatus.—MEXICO, Oaxaca: Tehuantepec, 3 ♂, 3 ♀; Rincon Antonio, 1 ♂.

Momotus cæruliceps.—MEXICO, Nuevo Leon: Soto la Marina, 1 ♀; Tamaulipas: Rio Corona, 1; Victoria, 2 ♂, 2 ♀; Xicotencatl, 1 ♂, 2 ♀; Alta Mira, 1 ♀; Jimenez, 1 ♀; Rio Palone, 1 ♀; San Fernando, 1 ♂; Tampico, 1 ♂.

Momotus lessoni goldmani.—MEXICO: Monte de Cuichapa, 1 ♀; Rio de Givicia, Oaxaca, 800 ft., 1 ♂; Tolosa, 3 ♂, 2 ♀; Chimalapa, Tehuantepec, 3 ♂.

Momotus lessonii exiguus.—YUCATAN: 1 ♂.

Momotus lessoni lessoni.—GUATEMALA: 1 ♂, 1; Central Guatemala (Coban to Clusec), 1. HONDURAS: 1. NICARAGUA: Matagalpa, 3 ♂; Chinandega, 2700 ft., 2 ♂, 3 ♀; Las Sabalos, San Juan River, 1 ♂. COSTA RICA: 1; Heredia, 1; San José, 1 ♀. PANAMA: Boqueron, Chiriqui, 5 ♂, 6 ♀, 1; Chiriqui, 1 ♂, 3; Boquete, Chiriqui, 1 ♂, 1 ♀.

Momotus æquatorialis æquatorialis.—COLOMBIA: La Florida, Cauca, 6600 ft., 2 ♂, 1 ♀; Los Tambos, 1 ♂, 1 ♀; Rio Lima, 2 ♂; Salento, 7000 ft., 2 ♀; La Tigre, 7500 ft., 1 ♂, 1 ♀; above Salento, 9000 ft., 1 ♀; Rio Toché, 6800 ft., 1 ♂, 1 ♀; Sta. Elena, Antioquia, 9000 ft., 1 ♂; El Roble, 7200 ft., 1 ♀; Andalucia, 5000 ft., 1 ♀; Andalucia, 7000 ft., 1 ♀; "Bogotá:" 1. "ECUADOR:" 1; near Baeza, 1 ♂.

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[1] I am indebted to Mr. W. E. Clyde Todd, of the Carnegie Museum, for the loan of 12 specimens of *Momotus momota simplex* from Santarem and vicinity, and for a specimen of *M. m. microstephanus* from Palmar, Colombia, and for 4 specimens of *M. m. parensis* from Pará; to Dr. C. W. Richmond, of the National Museum, for 2 specimens of *parensis* from Pará, and to Dr. W. H. Osgood, of the Field Museum, for 7 specimens of *osgoodi* from the Maracaibo region. The remaining specimens here listed are in The American Museum of Natural History.

Momotus æquatorialis chlorolæmus.—PERU: Tulumayo, 4000 ft., 1 ♀; Santo Domingo, 6000 ft., 1 ♂, 1 ♀; Oconeque, 1 ♂.

Momotus subrufescens conexus.—PANAMA: Canal Zone, 1 ♂, 1 ♀. COLOMBIA: Puerto Berrio, 1 ♀; Malena, 1 ♂, 1 ♀; Honda, 1 ♂, 2 ♀; Chicoral, 1.

Momotus subrufescens reconditus.—EASTERN PANAMA: Boca de Cupe, Tuyra River, Darien, 2 ♂; Cituro, Cupe River, Darien, 1 ♂; Chepigana, 2 ♂. COLOMBIA: Atrato River, Chocó, 1 ♂; River Salaqui, Chocó, 1 ♂.

Momotus subrufescens subrufescens.—COLOMBIA: Sta. Marta, 3?; Bonda, 5 ♂, 1 ♀, 16?; La Playa, near Barranquilla, 1 ♂; Magdalena River, 50–100 ft., 19. VENEZUELA: Barquisimeto, Estado Lara, 2 ♂, 1 ♀; El Cuji, Estado Lara, 1 ♂.

Momotus subrufescens osgoodi.—COLOMBIA: near Cúcuta, 1 ♂ (type), 1 ♀. VENEZUELA: Orope, 3 ♂, 2 ♀.

Momotus bahamensis.—TRINIDAD: 3 ♂, 2 ♀, 1? TOBAGO, B. W. I.: 2 ♂, 3 ♀, 3?

Momotus momota microstephanus.—COLOMBIA: "Bogotá," 4?; Palmar, Boyaca, 1 ♀; Villavicencio, base E. Andes, 1600 ft., 2 ♂; Barrigon, head of Rio Meta, 1 ♀; La Morelia (R. Bodoquera), Caquetá, 600 ft., 1 ♂, 1 ♀; Florencia, Caquetá, 675 ft., 2 ♀.

Momotus microstephanus argenticinctus.—ECUADOR: Esmeraldas, 4 ♀, 1 ♂; Chone, Manaví, 2 ♂, 3 ♀; Naranjo, Prov. Guayas, 1 ♂, 2 ♀; Rio Pindo, Prov. del Oro, 1850 ft., 1 ♂, 1 ♀; Santa Rosa, Prov. del Oro, 2 ♂; Portovelo, Prov. del Oro, 2000–2700 ft., 1 ♂, 1 ♀; Salvias, Rio Salvias, Zaruma-Zaraguro Trail, 3600 ft., 1 ♂, 1 ♀. PERU: Paletillas, Prov. Piura, 1550 ft., 3 ♂, 1 ♀.

Momotus momota momota.—VENEZUELA: Boca de Sina, Cunucunuma River, Upper Orinoco, 440 ft., 2 ♂, 3 ♀; Foot of Mount Duida, Upper Orinoco, 700 ft., 2 ♂; Suapure, 1 ♂, 1 ♀; La Union, Caura, 2 ♂. BRITISH GUIANA: Wismar, Demarara River, 100 ft., 1 ♂. FRENCH GUIANA: Cayenne, 1?

Momotus momota ignobilis.—PERU: Perené, Prov. Junin, 2000 ft., 2 ♂, 1 ♀.

Momotus momota nattereri.—BOLIVIA: Reyes, 1?, Lower Beni, 1; Mission San Antonio, Rio Chimoré, 1300 ft., 1 ♂; Todos Santos, Rio Chaparé, 1300 ft., 1 ♀, 1 ♂.

Momotus momota pilcomajensis.—BOLIVIA: Vermejo, Prov. Santa Cruz, 3,500 ft., 1 ♂. BRAZIL: Urucum, near Corumbá, Matto Grosso, 1 ♂.

Momotus momota simplex.—BRAZIL: Santarem, 3 ♂ (inc. type), 7 ♀, 2? Villa Braza, Tapajos, 1 ♀; Miriituba, Tapajos, 1 ♀; Matto Grosso, Chapada, 12 ♂, 9 ♀.

Momotus momota parensis.—BRAZIL: Pará, 2 ♂, 2 ♀, 2?

CONCLUSIONS

GEOGRAPHIC ORIGIN OF THE MOTMOTS

It appears from the preceding review that the motmots are more numerously represented, both in genera and in species, in Middle than in South America, that the more primitive types of the family (*Aspatha* and *Hylomanes*) are practically restricted to that area, and that certain South American forms have been derived from Middle American ancestors. Furthermore, it may be added that the Todidæ, the only family of birds peculiar to the West Indies, find their nearest known relatives in the early momotine genus *Hylomanes* of Middle America.[1]

[1]In this connection see Murie, 1872, Ibis, p. 394; Miller, 1915, Bull. Amer. Mus. Nat. Hist., XXXIV, p. 139.

These facts indicate that the motmots originated in Middle America. I am aware that the reasons here given for the belief that the motmots were dispersed from Middle America are not in accord with Matthew's[1] views that the most primitive members of a group are not found at its center of dispersal but at the periphery of its range. The more generalized motmots (genus *Momotus*) of South America are, however, clearly of northern origin. This statement applies not only to the numerous and evidently recently evolved forms of the Tropical Zone, but particularly to *Momotus æquatorialis* of the Subtropical Zone in the Andes of Colombia, Ecuador, and Peru. In accordance with the law that all forms of the life zones above the basal Tropical Zone must have originated in a lower zone, we find the ancestral form of *æquatorialis* in the Tropical Zone of southern Mexico. In this instance range extension from what I assume to be the present center of dispersal seems proven.

When to this recent evidence we add the proof of the antiquity of the group in Middle America as evinced by the relationships of the West Indian Todidæ to the Middle American primitive and momotine genus *Hylomanes*, it seems to me that the known facts in the case all support the belief that Middle America is the present center of dispersal of the motmots.

The development in Middle America of the strongly marked generic types which are now found associated there implies the former existence of conditions affording the isolation favorable to such development. Possibly this may have occurred in that period (Oligocene, according to Scott, 'History of Land Mammals,' p. 117) when Middle America was broken into a series of islands.

The Case of *Baryphthengus*

It is true that an isolated species of motmot, *Baryphthengus ruficapillus*, occurs in southeastern Brazil, a region in which we look for ancestral types. But, as I have attempted to show, this bird is generically like "*Urospatha*" *martii*, a species found from Nicaragua southward. It is a far less primitive type than the Middle American genera *Hylomanes* and *Aspatha*, indeed is closely related to the dominant genus *Momotus*. It seems, therefore, more logical to conclude that *Baryphthengus* has been derived from the north than that the northern forms were derived from *Baryphthengus*.

More than a thousand miles now separate the ranges of *Baryphthengus ruficapillus* from that of *B. martii*. A similar hiatus exists in the

[1] 1915, 'Climate and Evolution,' Ann. N. Y. Acad. Sci., XXIV, p. 180.

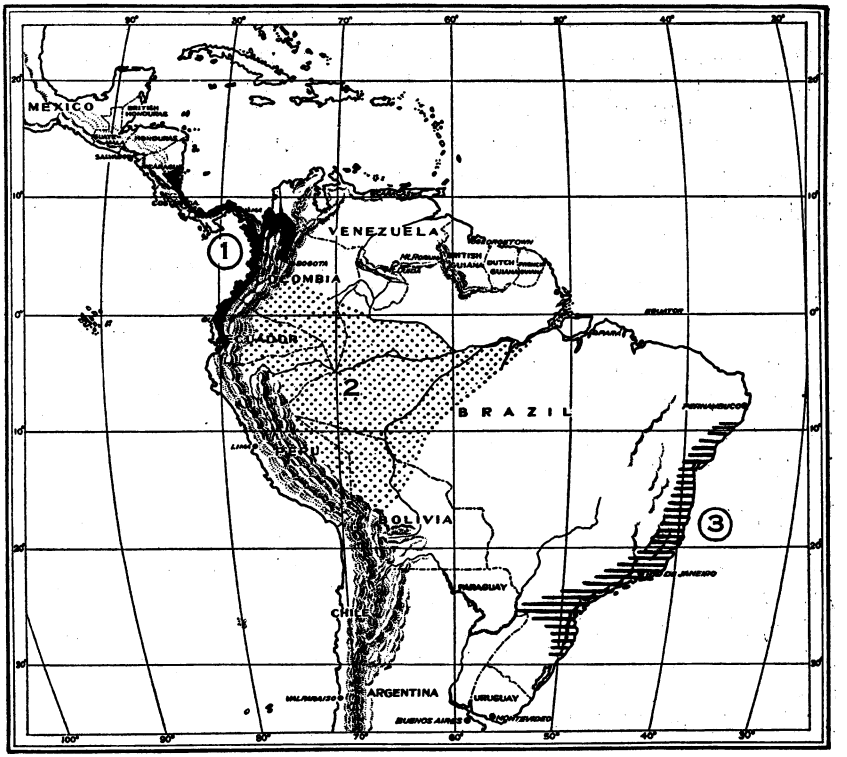

Fig. 4. Distribution of *Baryphthengus*.

1. *B. martii semirufa.*
2. *B. martii martii.*
3. *B. ruficapilla.*

Note the absence of this genus from Venezuela, the proximity of the ranges of *semirufa* and *martii* near the head of the Magdalena, and the wide area separating the range of *martii* from that of *ruficapilla*. The range of *Electron* is essentially like that of *Baryphthengus* excluding that of *B. ruficapilla*.

range of other forms which are represented in the southeastern Brazilian region, but are not again encountered until the Andean region is reached (e.g., *Pyroderus*, *Scytalopus*).

The discovery of marine deposits of Tertiary age in the upper Amazon is, of course, incontrovertible evidence of the existence of an "Amazonian Sea."

Haseman,[1] however, arguing for the reversal of the Amazon, states that this sea is of Pacific not Atlantic origin and hence we should not have that severance in Amazonia of South America into two parts as claimed by some geologists. Whatever may have been the bearing,

[1]1912, Ann. N. Y. Acad. Sci., XXI, p. 32.

if any, of the entrance of the sea into Amazonia on the distribution of *Baryphthengus*, it seems evident that the range of this bird was not developed under existing topographic conditions, and this belief, in connection with the facts that *Baryphthengus* has extended its range farther into South America than *Momotus* and that it is apparently a somewhat more primitive type than that genus, leads to the conclusion that, while *Baryphthengus* is of northern origin, it entered South America at a much earlier period than did *Momotus*.

It is interesting to observe, though I am quite unable to explain the phenomenon, that *Baryphthengus ruficapillus* does not trim its central rectrices into the spatulate form present in most species of this family and thereby agrees with the primitive genera *Aspatha* and *Hylomanes*. But this singular fact loses much of its apparent taxonomic significance when it is learned that east of the Andes *B. martii* has also lost, or at least, lacks the tail-trimming habit, while west of the Andes its tail, normally, is spatulate.

The same inexplicable state of affairs exists in the allied genus *Electron*, in which the forms found east of the Andes (*E. platyrhynchus pyrrholæmus* and *E. p. medianum*) normally have the central rectrices entire, while in those found west of the Andes (*E. p. platyrhynchus*, *E. p. suboles* and *E. p. minor*) these feathers, in the adult, have racquet-shaped tips. Furthermore, in *Momotus momota momota* and *M. m. microstephanus* this habit is subject to individual variation.

Geographic Origin of the Genus *Momotus*

The present center of dispersal in Middle America of the genus *Momotus* appears to be in the Mexico-Guatemala region. Here the two distinct types of the genus are found, and from this point the rufous-crowned species (*mexicanus*) ranges northward into western Mexico, while the black-and-blue-crowned species (*lessoni* and *cæruliceps*) range northward into eastern Mexico. Moreover, it is only in Mexico that *lessoni* is restricted to the Tropical Zone, and it is in this zone that we must look for the ancestors of those species which inhabit altitudinal zones above the Tropical Zone. The chestnut-crowned *Momotus castaneiceps*, according to Salvin and Godman,[1] is found only on the plains of Zacapa in Guatemala, in "comparatively open country, large cacti and mimosa trees being the characteristic plants." If, therefore, the rufous-crowned species prefers haunts of this type, rather than

[1] 'Biol. Cent. Amer.,' II, p. 461.

the denser growth which *lessoni* frequents, it is clear why the former has found a favorable environment in more arid western Mexico, while *lessoni* has been equally at home in humid eastern Mexico.

For the same reason, possibly, *lessoni* has extended its range southward into Central America while the rufous-crowned species is unknown south of Guatemala. We are, therefore, not further concerned with the *castaneiceps-mexicanus* group and may concentrate our efforts on an attempt to trace the history of the black-and-blue-crowned species.

We have seen that as we proceed southward from the assumed place of origin of *lessoni*, in the Tropical Zone of southeastern Mexico, we find this bird extending its range to higher altitudes until in Costa Rica and Chiriqui it becomes a form of the Subtropical rather than of the Tropical Zone. Lack of field experience in Central America denies me that knowledge of topography and environment which comes only from direct observation, and I therefore am not prepared to discuss the causes which have induced *Momotus lessoni* to increase the altitude of its range as it approaches equatorial regions.

It occurs to me, however, that possibly we may have here governing conditions which, in some respects, resemble those that induce birds of the South Temperate Zone to mount to the Andean tableland as they extend their range toward the Equator.

If it could be shown that *lessoni* originated in the northern or subtropical portion of the Tropical Zone of eastern Mexico, we should then have some explanation of why it attempted to remain in this zone by increasing the altitude of its range as it proceeded southward.

Beyond Chiriqui, in western Panama, *lessoni* is unknown, but it is represented in the Subtropical Zone of all three ranges of the Colombian Andes, and southward to Peru by *Momotus æquatorialis*, a distinct species but apparently an unquestionable derivative of *lessoni*.

The Panama Subtropical Bridge

At once we ask: How could a non-migratory, sedentary, cover-haunting bird like the motmot cross the 400-mile gap separating the Subtropical Zone of western Panama from the Subtropical Zone of northwestern Colombia?

Fortunately, our studies of the distribution of bird-life in Colombia[1] furnish an answer to this query. These studies have shown that the ranges of between sixty and seventy species common to the Subtropical Zones of Colombia and Chiriqui-Costa Rica are broken by what I have

[1]1917, Bull. Amer. Mus. Nat. Hist., XXXVI, pp. 151–159.

termed this Panama "fault." A number of them have also been found in the restricted subtropical areas of eastern Panama, but between that point and western Panama they are unknown. The list includes such sedentary species as *Formicarius rufipectus*, *Grallaricula flavirostris* and *Siptornis erythrops*, and species of such specialized habits as the dipper (*Cinclus*) or of such abundance and adaptability as the Andean white-throated sparrow (*Brachyspiza capensis*). In view of the data presented at length in the paper mentioned above, it seems unnecessary to go into further detail here and it may simply be added that the presence in the Subtropical Zones of Chiriqui and Colombia of so large a number of species, many of which are sedentary forms having a limited power of flight, is strong if not conclusive evidence that these regions were at one time connected by a Subtropical Zone bridge which, doubtless through subsidence, has disappeared in comparatively recent geological times.

Once in the Andean region, where it is the only member of its family found above the Tropical Zone, the subsequent extension of range of *Momotus æquatorialis* is an impressive exhibition of the influence of those potent factors which hold a bird to its proper faunal area. Always within the comparatively narrow limits of the Subtropical Zone, or approximately between the elevations of 4500–9500 feet, it has wound its way along the slopes of the Colombian Andes southward and northward until it now is found in all three ranges. It is not recorded from the Santa Marta group nor from Venezuela, and in spite of its presence in the Andes west of Popayan, it is as yet not definitely recorded from western Ecuador.

On the Amazonian slope of the Andes, *æquatorialis* has flowed south, as it were, in that narrow stream of life which so clearly distinguishes the subtropical element from the tropical below it and the temperate above it, at least as far as southeastern Peru near the Bolivian boundary. It has not yet been recorded from Bolivia, and if it does not occur there it has not yet reached the southern limit of the Subtropical Zone in the more eastern part of the Amazonian slope of the Bolivian Andes.

In Peru, *æquatorialis* exhibits some racial variation and is known as *Momotus æquatorialis chlorolæmus*, a form with greener underparts. But the difference between Colombian and Peruvian specimens is slight and bridged by individual variation.

In short, *Momotus æquatorialis*, like numerous other species of the Subtropical Zone, shows, in spite of its wide range, surprisingly little variation and thereby gives expression to the uniform environmental conditions which prevail throughout this remarkable faunal stratum.

To sum up: The evidence in regard to *Momotus æquatorialis* indicates (1) that it was derived from *Momotus lessoni* and thus originated in eastern Mexico; (2) that it entered South America subsequent to the full development of the Andean System; (3) that the subtropical "bridge" on which it crossed Panama has since disappeared; (4) that its subsequent distribution eloquently illustrates the potency of the influences which determine the boundaries of life-zones and (5) that there have been no marked changes of level in the Andes since it reached them.

The Species of the Tropical Zone in South America

Having presented and considered the evidence in regard to the origin and distribution of the *lessoni-æquatorialis* group, we may now turn our attention to the remaining species of the group, all of which, except *subrufescens* which is found in Panama, are confined to the Tropical Zone in South America.

Momotus subrufescens has been found as far west in Panama as the Canal Zone, but there is no reason why it should not be found throughout the Tropical Zone of that country. While not distantly related to, it is apparently specifically distinct from *lessoni* of the Subtropical Zone of western Panama, and with it we enter a new section of the genus *Momotus* and are at once confronted by the problem of its origin.

Since *lessoni* finds its South American representative in *æquatorialis*, we cannot look direct to that species for the ancestral form of *subrufescens*, but possibly we can look indirectly to it and discover the origin of *rufescens* in the pre-*lessoni-æquatorialis* form which once occupied the Panama bridge connecting the Subtropical Zones of Chiriqui and Colombia.

It is true that the survival of this form would be contrary to the rule which has evidently prevailed among the birds with which we assume this connectant, subtropical form was associated. But it is also true that the motmots are with but two exceptions confined to the tropics and that *lessoni* shows its adaptability by inhabiting both the Tropical and Subtropical Zones in Central America. It is not, therefore, beyond the bounds of reason to assume that the connecting, "bridge"-inhabiting form might adapt itself to changing environmental conditions as subsidence gradually lowered its range from the Subtropical to the Tropical Zone.

It is true that *æquatorialis* has extended its range from Colombia to southern Peru without showing as much racial difference as *subrufescens* does from *lessoni*, and hence presumably from its supposedly extinct ancestor. But, as I have attempted to show[1] in comparing the birds

[1] 'The Distribution of Bird-Life in the Urubamba Valley of Peru,' 1921, U. S. Nat. Mus., Bull. No. 117, pp. 30–35.

of the humid Temperate Zone with those of the Puna Zone in southern Peru, it is the extent of environmental change, not time or distance, which supplies the more potent evolutionary factors.

It is therefore to be expected that a change from the Subtropical to the Tropical Zone would be followed by more marked changes in the organism than continued residence in the Subtropical Zone even at widely separated stations.

This theory of the origin of *subrufescens* confessedly rests on a slight foundation of fact, but it is the only one that presents itself, and, since the distribution of this species is apparently from the north southward, we cannot well look for its ancestor in South America.

From Panama the range of *subrufescens* extends eastward into Colombia and the coast region of Venezuela to Trinidad, but it does not extend southward to western Ecuador, where a quite different species of *Momotus* is found.

Specimens from the semi-arid Caribbean coastal region (*rufescens rufescens*), as we have seen, are paler, less intensely colored than those from the more humid, forested areas of Panama, the Atrato and Magdalena Valleys, southern Maracaibo basin, Trinidad and Tobago, but it is evident that we have here but one responsive form, the differentiating characters of which have been derived under existing environmental conditions. When, however, we compare the extreme humidity of eastern Panama and the Atrato Valley with the comparative aridity of the Venezuelan costal region, it is apparent that climatic conditions under which *Momotus subrufescens* lives vary more widely than does the bird itself. Hence we conclude that either the environing conditions have not been in existence for a sufficient length of time fully to express themselves on the bird, or that the bird has not been exposed to them long enough fully to respond to their influences. However, the restriction of the area occupied by *subrufescens* to western Colombia and the Caribbean coast region induces the belief that it is of post-Andean origin (a conclusion supporting our theory of its descent from the pre-*lessoni-æquatorialis* type) and that consequently its range has been acquired under present topographic[1] and hence doubtless climatic conditions.

The response of the various forms of *subrufescens* to the climatic influences which we believe to have produced their distinguishing characteristics not only furnishes an admirable illustration of cause and effect and an indication that the species is in an active state of evolution,

[1]Trinidad, however, was probably connected with northeastern Venezuela and Tobago with Trinidad when the bird entered the territory which has since become insulated.

but gives additional proof of its comparatively late entrance into the region it inhabits.

In western Colombia *subrufescens* is unknown south of the Atrato Valley. Possibly it may occur farther south but it certainly does not reach western Ecuador, where its place is taken by *M. momota argenticinctus*, a close ally of *M. m. microstephanus* of the eastern base of the Colombian (and Ecuadorian?) Andes. This is, however, not the only case where the form of the Tropical Zone of western Ecuador is related to that of the east Ecuador Tropical Zone rather than to that of Panama.[1]

We now cross the Andes and take up the *Momotus momota* group.

The *Momotus momota* Group

The Tropical Zone of the Panama-Caribbean region is connected with the Tropical Zone of that part of South America lying east of the Andes only in northern Venezuela. Whether *subrufescens* enters the interior of Venezuela is unknown.

The bird of the lower Orinoco is *Momotus momota momota*, a form which, whatever its origin or relationships, certainly does not intergrade directly with *subrufescens*. If, therefore, the ancestors of the *momota* group entered the interior of South America through the north Venezuelan Tropical Zone connection, their further progress was presumably not toward the Orinoco, but westward along the base of the Andes toward the region now occupied by *microstephanus*. This question cannot be discussed profitably until we know what form of motmot inhabits the region between the Orinoco and the known range of *subrufescens* in northern Venezuela. Meanwhile we may consider the possibility of an Andean crossing in the comparatively low area at the head of the Magdalena Valley. Our records show the occurrence of *Momotus subrufescens conexus* at Chicoral in the upper part of this valley. If the species could exist in the limited, scrubby growth of this region, there is no reason to doubt its occurrence up to the head of the Valley.

Our explorations in Colombia have shown that the eastern Andes at Andalucia attain an altitude of only 7000 feet. They also show that this elevation has not been great enough to prevent the entrance into the upper Magdalena Valley of several forms from the Tropical Zone at the eastern base of the range. Examples are, *Piaya cayana mesura*, *Conopophaga castaneiceps castaneiceps*, *Myiotriccus phœnicurus*, *Tangara chilensis*, and *Tangara cyaneicollis cæruleocephala*, all of which are known from west of the Andes only in the upper Magdalena Valley. The fact

[1] See 'Distribution of Bird-Life in Colombia,' pp. 106–117.

that neither *Baryphthengus* nor *Electron* is found in northern Venezuela indicates that they have reached the interior of South America by crossing the eastern Andes of Colombia (see the map illustrating the distribution of *Baryphthengus*).

While the frequent occurrence of parallelism in *Momotus* and particularly in *M. subrufescens* (note the recurrence of dark forms in separated humid areas) warns us not to place too great significance on superficial resemblances as indicating sources of derivation, it is nevertheless true that in general coloration the form of *subrufescens* found in the Magdalena Valley shows an approach toward the form inhabiting the Tropical Zone at the eastern base of the Andes. Indeed, the differences between them are obviously not greater than those which distinguish many intergrading forms.

The evidence at our disposal, therefore, makes it within the bounds of probability that the *Momotus* group entered the interior of South America over the Subtropical Zone pass in the eastern Andes of Colombia. The assumption that eastern Colombia has been its point of dispersal finds support in its distribution. In the systematic portion of this paper we have seen that *microstephanus*, the east Colombian form, possesses certain characters which indicate its close relationship with *momota*, with which it is believed to intergrade. In the east, therefore, in the area bounded on the south by the Amazon and on the north by the Valley of the Orinoco, we have but one form which, in its combination of characters of size, markings, and non-spatulate central rectrices, is the most strongly differentiated of the entire group. The lower Amazon has been shown to be an effective barrier to the extension of the range of this species, preventing its contact with the quite different *simplex* at Santarem on the southern side of the river; and I have ventured to express the belief that the races described from the Pará region represent not *momota* but *simplex*.

To the south, *microstephanus*, believed to be the ancestral form of the *momota* group, responds to the widely varying conditions it encounters in the enormous area it now inhabits, and to these expressions of the influences of its environment have been attached the names *ignobilis* in Peru, *nattereri* in Bolivia, *pilcomajensis* in northern Argentina and contiguous Bolivia, *simplex* in central Brazil and *parensis* and *cametensis* in the Pará region. The more important facts revealed by our study of its variations and distribution south of the Amazon are (1) the divergence of the forms of the right bank of the lower Amazon from that of the left bank, which, although they have apparently descended from a common

ancestor, would possibly meet as species. (2) The continuous distribution of the species through the area it inhabits and the evident intergradation of all its forms, as indicating their origin under existing environmental conditions. (3) That, notwithstanding the presumably longer period which *Momotus æquatorialis* of the Subtropical Zone has been in South America, it exhibits far less variation in its range from Colombia to southern Peru than does *momota* in the contiguous Tropical Zone, a fact which is believed to reflect the much higher degree of uniformity prevailing in the Subtropical as compared with the Tropical Zone. (4) That, in spite of the absence of any physical or climatic barrier to range extension, the species has not yet reached the forests of southeastern Brazil and Paraguay, a fact which is believed further to indicate its comparatively recent appearance in South America.

We have seen that the western Ecuador form occupies the Tropical Zone from at least Esmeraldas south to northwestern Peru and that it finds its nearest ally, with which it intergrades by individual variation, not in western Colombia, as might be expected, but in the Tropical Zone at the eastern base of the Andes. We have also seen that the known facts concerning the distribution of *Momotus* indicate that it is of post-Andean origin in South America. From these premises we are forced to conclude that, just as the ancestor of *microstephanus* crossed the Andes from west to east, so the ancestor of *argenticinctus* crossed the Andes from east to west. But we cannot believe in this case, any more than we could believe in that of *microstephanus*, that this presumed transandean passage was made where the mountains attain a sufficient altitude to permit of the development of a Temperate Zone. In Ecuador, therefore, as in Colombia, we look for some lower elevation over which it is conceivable the species might extend its range.

The nearest approach to such a condition is apparently to be found in the cañon of the Rio Zamora, which enters the Loja Valley from the Tropical Zone of Amazonia at an altitude of not more than 7000 feet. From the Loja Valley the Pacific slope may have been reached by following one of the streams having their origin in this valley and flowing into the Pacific. It is true that existing conditions of vegetation in the Loja Valley do not support this theory, but it is also true that in the historic period this valley has been deforested for agricultural purposes and that consequently there was formerly much closer connection between the forested areas of eastern and western Ecuador than is to be found at present.

While this paper is going through the press our collector, Harry Watkins, writes us of his capture of motmots (doubtless *M. m. argenticinctus*) at Palambla on the western slope of the Andes, between Payta and Huancabamba, Peru. This is the most southern point on the Pacific Coast from which motmots have been recorded and also the nearest one to Amazonian drainage. The work of Noble[1] about Huancabamba shows a marked affinity between the avifaunas of that region and southwestern Ecuador, and it is hoped that Watkins' researches will throw much additional light on the possibilty of a faunal connection between the Pacific coast and Amazonia in this region.

SUMMARY

The theories advanced and the principal conclusions reached in this paper may be summarized as follows.

1.—The motmots originated in Central America, where the ancestral forms of the existing genera were possibly developed during the Oligocene when this region consisted of scattered islands which would afford the isolation favorable to differentiation.

2.—The characters and distribution of the genera *Hylomanes* and *Aspatha*, and the relationships of the former with the West Indian family Todidæ, indicate that these genera are the most primitive known members of the family.

3.—The characters and distribution of the genus *Momotus*, which is represented, usually by intergrading forms, throughout the greater part of the area occupied by the family, indicate that it is the most recently evolved member of the family.

4.—Long after the more primitive forms of the group (*Hylomanes* and *Aspatha*) were evolved, on three occasions the family has invaded South America.

5.—The first of these invasions, made by the genus *Baryphthengus*, was possibly pre-Andean or early Tertiary, and extended to southeastern Brazil where the representative of the group was subsequently isolated by causes as yet unknown.

6.—The second invasion was made by the genus *Momotus*, and was subsequent to the elevation of the Andes and not earlier therefore than the later Tertiary, from the Subtropical Zone of the mountains of Costa Rica to the same zone in the Andes of northwestern Colombia over a Panama connection between these zones which, through subsidence, has since disappeared. From northwestern Colombia the species has

[1]Bangs and Noble, 1918, Auk, XXXV, pp. 442–463.

spread southward through the Andean Subtropical Zone to southeastern Peru.

7.—The third invasion was also made by the genus *Momotus* and was subsequent to the period of subsidence which brought the mountains of Panama below the elevation of the lower limits of the Subtropical Zone. It extended from Panama through northern Colombia and Venezuela, north of the Andes, to Trinidad and Tobago when these islands were connected with each other and with the mainland.

The Andes were crossed probably at the head of the Magdalena River and the genus now occupies the greater part of tropical South America, its recent entrance into this region being indicated by the continuity of its distribution, the comparatively slight degree of differentiation it exhibits, and the fact that, although the environment is favorable, it has not yet reached southeastern Brazil.

If, in the main, these conclusions are valid, they will be of much service in our attempt to determine the geographical origin of South American bird-life, and particularly of the highly developed faunas which characterize Andean life-zones.