

TAXONOMY OF THE
CRACIDAE (AVES)

CHARLES VAURIE

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OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 138 : ARTICLE 4 NEW YORK : 1968

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 138, article 4, pages 131–260, text
figures 1–34, plates 15–17, tables 1–4

Issued June 14, 1968

Price: \$5.00 a copy

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INTRODUCTION

THE PRESENT STUDY is restricted to the living Cracidae and to forms that have become extinct recently, and is based chiefly on external morphology and geographical distribution. General habits, broad ecology, and isolating mechanisms were taken into consideration, but I have not enlarged upon these subjects, which, together with the life history, will be contained in a book being prepared by my colleagues Jean Delacour and Dean Amadon.

I discuss phylogeny, but not taxonomic problems at the species or subspecies level; these were considered by me in a series of 10 preliminary papers (Vaurie, 1964, 1965a–1965c, 1966a, 1966b, 1967a–1967d). The geographical variation is described, but not exhaustively, because it was discussed in detail in the preliminary papers, most of which are illustrated by maps which indicate individual records. One of these maps, illustrating the distribution of *Ortalis* in northern South America, is republished in this study (fig. 14). The preliminary papers give also a nearly complete list of the specimens I have examined, and bibliographies in them refer to many papers that are not included in the bibliography of the present publication.

The material studied consists of the collections of the American Museum of Natural History, of those of other institutions listed below in the acknowledgments, and of loans made by museums that I did not visit. The specimens studied reach a total of about 3900 and include 67 types; about 230 additional specimens were seen but were not included in the study because I did not examine them critically.

ACKNOWLEDGMENTS

The museums that I visited are the Academy of Natural Sciences of Philadelphia; British Museum (Natural History), London; Carnegie Museum, Pittsburgh; Field Museum of Natural History, Chicago; Naturhistoriska Riksmuseum, Stockholm; and the

United States National Museum of the Smithsonian Institution, Washington. All these institutions have also lent me selected specimens for further study. The British Museum was visited twice, in 1963 and again in 1966, and the Museum of the Academy of Sciences of Poland, Warsaw, was also visited in 1966 to examine the type of the extinct *Penelope albipennis* which is known from only three specimens. I have also received loans from the Moore Laboratory of Zoology of Occidental College, Los Angeles; the Museum of Comparative Zoology, Cambridge; the Museum of Zoology of the University of Michigan, Ann Arbor; and the Peabody Museum of Natural History, Yale University, New Haven. I am much indebted to the authorities of all these institutions for their cooperation, and for the help and friendly reception that I received.

I have received much help in one form or another from many colleagues, whom I name below, but I am particularly indebted to Dr. Dean Amadon, who read the entire manuscript and made many suggestions, Dr. Jean Delacour and Mr. Eugene Eisenmann for numerous discussions, and Dr. K. C. Parkes, the person who advised me to study the Cracidae. Mr. A. E. Gilbert painted the original of plate 15 and gave me his field notes and photographs.

I am grateful to Messrs. J. P. Angle, L. C. Binford, Emmet R. Blake, Pierce Brodkorb, C. Cordier, Kai Curry-Lindahl, L. Irby Davis, Rodolphe M. de Schauensee, Carl Edelstam, I. C. J. Galbraith, D. Goodwin, John W. Hardy, Thomas R. Howell, Peter P. Kellogg, Wesley E. Lanyon, B. L. Monroe, Jr., S. Parker, William H. Phelps, Jr., S. Dillon Ripley, 2nd, P. A. Schwartz, Lester L. Short, Jr., Charles G. Sibley, Helmut Sick, Robert W. Storer, Alulah Taibel, Melvin A. Traylor, Jr., George E. Watson, 3rd, Alexander Wetmore, and Richard L. Zusi. This study has extended over a period of nearly four years; I apologize to any person who has helped me whom I have overlooked.

GENERAL CONSIDERATIONS AND ANALYSIS

GENERAL DISTRIBUTION AND LIST

SOME AUTHORS BELIEVE the Cracidae originated in North America and retreated to South America when North America became increasingly arid, or when tropical vegetation withdrew southward with the approach of the ice. Such a belief may well be correct, but the question is still open because the fossil subfamilies recognized by Brodkorb (1964) are known from the Upper Eocene to the Lower Miocene of France, and Brodkorb listed also a fossil specimen of the Penelopinae (the Penelopini of my study) from the Middle Miocene of southern Patagonia.

The living genera are, however, most abundant in the forested regions of Neotropical America, although some penetrate into Nearctic America (fig. 1), and three genera, with four species, cross the Tropic of Cancer. *Ortalis vetula* ranges north to latitude 27° 30' N. in the lower Rio Grande Valley of Mexico and Texas, and *O. poliocephala* ranges north to about the same latitude to southern Sonora in western Mexico. *Penelope purpurascens* and *Crax rubra* range north to

about latitude 24° N., or slightly higher, in eastern Mexico, *P. purpurascens* ranging north to about the same latitude in southern Sinaloa in western Mexico, but not *C. rubra*, which does not occur north of the Isthmus of Tehuantepec in western Mexico.

The southern limits of the range extend to the department of Lambayeque in northwestern Peru on the Pacific slope, but, east of the Andes, they extend far south of the Tropic of Capricorn, to Cordoba and Santa Fe in Argentina, and slightly south of latitude 34° S. in southern Uruguay, the species concerned being *Ortalis canicollis* in Argentina, and *Penelope obscura* in Uruguay, the two genera being more widespread than the others.

A list in systematic order is given here to make this study easier to follow:

Subfamily Cracinae

Tribe Penelopini

Genus *Ortalis*

vetula
garrula
ruficauda
erythroptera
guttata
superciliaris
motmot
leucogastra
poliocephala
canicollis

Genus *Penelope*

argyrotis
ortoni
montagnii
superciliaris
marail
dabbenei
obscura
*jacquaçu*¹
purpurascens
albipennis
jacucaca
ochrogaster
pileata

Genus *Pipile*

pipile



FIG. 1. Distribution of the living Cracidae.

¹ I depart from Article 27 of the International Code of Zoological Nomenclature by retaining the original spelling of *Penelope jacquaçu*, because I believe that the retention of the diacritical mark in this case is useful.



Heads of adult males of the genus *Crax*. Upper, left to right: *Crax alector*, *C. globulosa*, and *C. blumenbachii*. Center: *Crax rubra*. Lower, left to right: *Crax daubentoni*, *C. fasciolata*, and *C. alberti*. Painting by A. E. Gilbert.

cujubi
jacutinga
 Genus *Aburria*
aburri
 Genus *Chamaepetes*
unicolor
goudotii
 Genus *Penelopina*
nigra
 Tribe Oreophasini
 Genus *Oreophasis*
derbianus
 Tribe Cracini
 Genus *Nothocrax*
urumutum
 Genus *Mitu*
tomentosa
salvini
mitu
 Genus *Pauxi*
pauxi
unicornis
 Genus *Crax*
alector
globulosa
blumenbachii
daubentoni
fasciolata
alberti
rubra

FEATHER STRUCTURE AND PIGMENTATION

The structure of the plumage varies, but the feathers are moderately firm and compact, generally speaking, and are normally rather broad, with rounded tips. The following description is concerned with the plumage only of the body other than the crest, as the latter and the remiges and rectrices are discussed separately.

The plumage is most compact when most highly glossed, as is true of all birds, but in *Ortalis*, which is not glossy, it seems to be more loose and decomposed than is normal for a bird with a dull plumage. The feathers of the crown, nape, hind neck, and under parts are very soft and "hairy," not at all integrated in most species, but those of the mantle are more compact and, as a rule, are distinctly outlined. The short feathers of the forehead are stiff, however, and those of the malar streak and around the throat are modified also, being more or less elongated, lanceolate in shape, and stiff. This character varies but is characteristic of *Ortalis*, although the feathers of the lower throat tend

to be slightly stiff in *Penelope* and *Pipile* also, and in the male of *Penelopina*.

Ortalis represents one extreme, and the other is best illustrated by *Mitu* which is the most glossy. The feathers of *Mitu* are compact, well integrated, and regularly outlined, except on the head and neck which are pure black and not glossy, the feathers of these regions being completely decomposed, but extremely short and velvety, not "hairy" as in *Ortalis*. This character is shared by *Pauxi* and *Crax*, and also to a certain degree by *Oreophasis*, as far as the feathers on the face and culmen are concerned.

No other feathers (other than the crest) are specialized, but the feathers of the lower flanks, and those that grow from the base of the tibia, are elongated and very loosely integrated in all genera. These feathers are best developed in *Mitu*, *Pauxi*, and *Crax* and form conspicuous tufts which are about equal in length to the length of the tibia.

In forms that have a rufous plumage which is not glossy, such as *Nothocrax* and the female of *Penelopina*, the plumage is soft also, but better integrated than in *Ortalis*.

Some members of the Cracidae are handsome, but the plumage is not highly colored, or very varied, or brilliant, although it may be glossy to a varying degree. All the species, other than the forms that have a strongly rufous plumage, are either black or some shade of brown, with or without white or chestnut areas. The plumage is uniform or patterned, but the pattern is simple. In the Cracini, other than *Nothocrax*, the males and the majority of the females are black, with the exception of the lower abdomen, under tail coverts, and the feathers that grow from the lower flanks and base of the tibia, all of which are either snow-white or chestnut.

In the monotypic Oreophasini, *Oreophasis derbianus* is black and very glossy above, but white on the lower throat and breast which are narrowly streaked with dusky black. The tail of this species is also broadly banded with white a little less than halfway below the base, and the color pattern of this species is unique in the family.

The Penelopini are more variable in color and pattern. *Ortalis* and *Penelope* are chiefly brown, *Penelope* differing from *Ortalis* by being streaked with white. *Pipile* is black,

glossy, and very boldly patterned with white on the upper wing coverts, and is more or less slightly streaked with white below, but not above as in *Penelope*. The plumage of *Aburria*, and of the male of *Penelopina*, is black and glossy, but perfectly uniform, not patterned. The female of *Penelopina* has a brown and cryptic plumage which is heavily vermiculated and barred. One of the two species of *Chamaepetes* is dull black and virtually uniform, but the other is brown and olive above, with a faint pattern, and chestnut below.

The large majority of the species are not sexually dimorphic in coloration. This is true of *Oreophasis*, and of all the Penelopini with the single but very notable exception of the monotypic *Penelopina* in which sexual dimorphism is complete and extreme, at least in adults. Two of the four genera of the Cracini (*Nothocrax* and *Mitu*) are not dimorphic, but all species of *Crax* are dimorphic to some degree, and in some the plumage of the female is very complex and exhibits two or three very distinct color phases. *Pauxi* is intermediate between *Mitu* and *Crax*, as the female of *P. pauxi* has two color phases: one black and white and identical to the coloration of the male; the other, brown with an interrupted pattern. The other species of this genus (*P. unicornis*) is known so far from only one pair, the female being identical with the male in coloration, but possibly the female of *P. unicornis* has another color phase, corresponding to the brown phase of the female of *P. pauxi*.

STRUCTURE AND COLORATION OF THE WING

Generally speaking, the wing is large, strong, very broad, strongly rounded, well arched, and rigid. The secondaries are usually about as long as the primaries, and the distal end of the outer primaries is more or less curved or bowed inward. This type of wing is not adapted for sustained flight, and the Cracidae, though agile climbers, leapers, and gliders, are poor fliers. The large and heavy Cracini are said to be reluctant to take to the wing when threatened and to prefer escape by running.

There are 10 primaries, which I have counted from the outermost throughout my study, because the large and stiff rounded

wing is difficult to examine in any other manner. The wing formula varies somewhat individually, but the basic formulas are as follows: The wing is most rounded in *Nothocrax*, *Mitu*, and *Crax*, with a formula of $1 < 2 < 3 < 4 < 5, 6, 7, 8 > 9 > 10$. The wing is a little less rounded in *Ortalis*, *Penelope*, and *Pipile*; the formula is $1 < 2 < 3 < 4 < 5, 6, 7 > 8 > 9 > 10$. The wing is more pointed in *Chamaepetes*, *Penelopina*, and *Pauxi*, and most pointed in *Aburria* and *Oreophasis*. The formulas are $1 < 2 < 3 < 4 < 5 < 6, 7, 8 > 9 > 10$ in *Chamaepetes*, $1 < 2 < 3 < 4 < 5 < 6 < 7, 8 > 9 > 10$ in *Penelopina*, $1 < 2 < 3 < 4 < 5 < 6, 7 > 8 > 9 > 10$ in *Pauxi*, and $1 < 2 < 3 < 4 < 5 < 6 < 7 > 8 > 9 > 10$ in both *Aburria* and *Oreophasis*.

The wing is less rounded in the genera that are restricted to mountainous regions (*Chamaepetes*, *Penelopina*, *Pauxi*, *Aburria*, and *Oreophasis*), but the correlation with altitude is general only, and the formula fails to express the size of the gaps between the tips of the primaries. The wing can be more rounded or more pointed in birds with the same formula. For instance, the wing is distinctly more pointed in *Aburria* than in *Oreophasis*, although the formula is the same. This difference is apparent when the relative lengths of the primaries are compared, and also when the longest primaries are compared with the secondaries. The gaps between the tips of the middle and inner primaries are greater in *Aburria* than in *Oreophasis*, and the longest primaries project beyond the secondaries (fig. 2), whereas they are slightly shorter or end at the same level in *Oreophasis*.

Aburria and *Oreophasis* are not closely related, but, in the two species of *Chamaepetes* that have the same wing formula, the gaps between the tips are distinctly greater in *C. unicolor* than in *C. goudotii*, and the primaries extend beyond the secondaries to about the same level as in *Aburria*, whereas they end at the same level in *C. goudotii*. These two species have the same altitudinal range (from about 1000 to 3200 meters), but the wing is more pointed in *C. unicolor*, although the formula is the same.

The lack of exact correlation with altitude is shown also by *Aburria* which has a distinctly more pointed wing than *Oreophasis*, although its altitudinal range is significantly lower, from about 750 to 2500 meters, as

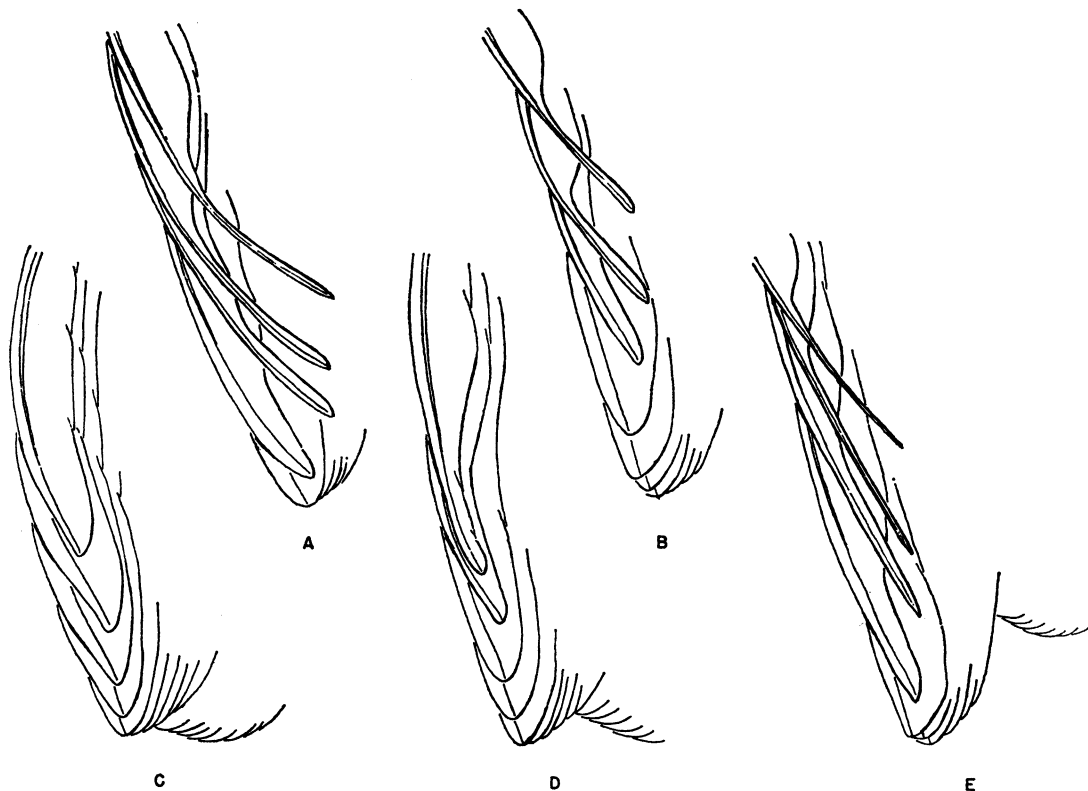


FIG. 2. Shape of the tip of the wing and structure of the outer primaries in some species of the Cracidae. A. *Pipile cufubi*. B. *Chamaepetes unicolor*. C. *Crax globulosa*. D. *Penelope obscura*. E. *Aburria aburri*.

against about 1800 to 3350 meters for *Oreophasis*. Finally, the shape of the wing is apparently not affected by altitude in *Penelope montagnii* which has a rounded wing, although it breeds higher and has a greater altitudinal range than that of any other species of the Cracidae, from about 1060 to 3650 meters.

The lack of correlation in *Penelope montagnii*, *Aburria*, and *Oreophasis*, and the variation noted in *Chamaepetes*, suggest that other factors, such as foraging and feeding habits, are of greater adaptive importance than mere altitude. For instance, *Chamaepetes goudotii* appears to be more terrestrial than *C. unicolor*, which is reflected by the length of its tarsus which is proportionally longer, with a ratio of .25, as against one of .22 in *C. unicolor*, when compared to the length of the wing.

The shape of the outer primaries varies conspicuously, as is shown in figure 2. Some

feathers are normal in shape, such as those of *Crax globulosa*, but others are distally emarginated or excised on the inner web.

The emargination and excision occur only in the Penelopini, but not in *Ortalis* and *Penelopina*, and not in all species of *Penelope*, although the first and second primaries are more or less emarginated in nearly all the species of that genus, but not very deeply. This emargination is best developed in *P. obscura* which is illustrated.

In *Pipile*, the first three primaries are very deeply excised to a great length, and the fourth is emarginated, the excised ends being somewhat stiff and greatly bowed inward. Only the first two primaries are excised in *Chamaepetes*, and the third is emarginated, the excised tips being shorter than in *Pipile*, less bowed, but slightly stiffer. The excision is carried to an extreme in *Aburria*, and the webs have virtually disappeared from the first two primaries, being reduced to only

about 1 mm. in width near the tip, or less in the case of the first primary.

This modification functions to produce sound in display or alarm. The display has been described by Sutton and Pettingill (1942, p. 11) in *Penelope purpurascens* as follows: "... the males sparred, threatening their rivals with harsh, throaty cackles; pursued each other through the tops of the big trees; and *drummed* by flying from perch to perch with wings beating rapidly ... In *drumming* they flew slowly with wings beating furiously, sometimes moving upward, sometimes turning from side to side in mid-air, as if in a daze" (*italics in original*). The tips of the primaries are emarginated in *P. purpurascens*, but less deeply so than in *P. obscura*.

The sound is produced also when the bird is alarmed, at least in *Pipile*, and very probably in all the species, and was described by Olivares (1962) as a very loud wooden rattle in *Pipile*, when it flies off in alarm. The species of *Penelope* "drum," but the drumming is probably replaced by a rattle in *Pipile* and *Chamaepetes*, and possibly by a loud whir in *Aburria* in which the tips of the primaries are so tenuous and excised. This is suggested also by the scientific name, *Aburria aburri*, which is said to be derived from the sound made when the bird flies.

The coloration of the primaries varies and is uniform or not. The primaries are black or brown and are uniform, as a rule, but not in the forms that have a brown or rufous plumage, such as *Nothocrax*, the female of *Penelopina*, and the females of some species of *Crax* and of the brown phase of *Pauxi pauxi*. The primaries are mottled, vermiculated, or barred in these forms, not uniform, on the outer web or on both webs. The eight outer pairs are white in *Penelope albipennis* (see p. 200 and pl. 16, fig. 4) rather than uniformly brown as in the other 12 species of this genus, and are chestnut, rather than brown, in two of the 10 species of *Ortalis*. They are chestnut also in some of the color phases of *Crax*.

STRUCTURE AND COLORATION OF THE TAIL

The tail is composed of six pairs of flat feathers that are very broad in the adult, and have a broadly rounded tip, or are blunt at the end, with well-rounded corners. The

feathers are graduated from the outer to the central pair, and the tip of the tail is usually well rounded, except in most species of *Ortalis*, in which the tip of the tail is more oval than rounded. The shape in *Ortalis* is caused by a more pronounced graduation, the outer tail feathers being, in some cases, only about three-quarters of the total length of the tail or less.

The tail is shorter or longer than the wing, more often shorter. The tail/wing ratio is greater in cases in which the tail is shorter, decreasing to as low as .70, with a mean of about .86, whereas the mean ratio is only 1.06 in birds in which the tail is longer than the wing, the largest ratio being 1.19.

The length of the tail may be correlated with general habits, but the correlation, if any, escapes me. For instance, the mean of the ratio is .85 in the Cracini, as against 1.02 in *Ortalis* and *Penelope* which are more arboreal than the Cracini, but the ratio drops to .78 in *Pipile* and *Aburria* which are the most arboreal of the Cracidae.

The color of the tail is uniform or not. It is bicolored in *Ortalis*, as the tips or distal part of the outer rectrices are conspicuously paler than, or of a color different from, the base of these feathers and also from the central pair. These pale tips are present also in *Penelope argyrotis*, but not in the other species of this genus and other genera of this tribe. In *Oreophasis*, the tail has a single very broad band of white near the center, a pattern that is unique in the family, as stated above. In the Cracini, the outer tail feathers, and in some cases the central pair also, are broadly tipped with white, buff, or chestnut, or the tail is black and uniform. In the forms with the brown or rufous plumage mentioned in the description of the wing, all the rectrices, or the central pair only, are mottled, vermiculated, or barred.

STRUCTURE AND COLORATION OF THE CREST

Many members of the Cracidae have a crest, but *Oreophasis* and *Penelopina* have no crest of any kind. The feathers of the crown are more or less elongated in *Chamaepetes* and *Ortalis*, but do not form a true crest, although a rudimentary one is vaguely suggested in one species of *Ortalis*.

The crest is highly developed in the Crac-



FIG. 3. Structure of the crest and shape of the bill in some species of the Cracidae. A. *Penelope jacquaçu jacquaçu*. B. *Penelope purpurascens purpurascens*. C. *Aburria aburri*. D. *Nothocrax urumutum*.

ini, with the single exception of *Pauxi pauxi* which has no crest, and is very strongly modified in structure and characteristic for each genus. It is composed of very long narrow feathers in *Nothocrax* (fig. 3), which are rather loosely integrated, soft, and not glossy. The crest of *Pauxi unicornis* is extremely short, on the other hand, and composed of stiff and tightly curled feathers that are highly metallic (pl. 16, fig. 1). The crest of *Mitu* is made up of very flat feathers that are slightly rigid and that broaden out distally but do not curl at the tip (fig. 28); and the crest of *Crax* consists of rather long and stiff feathers (pl. 15) which are very gracefully curled at the tip.

The crest of the Penelopini is very generalized, when present, and is best developed in *Pipile* in which the feathers are long, narrow, and attenuated. The crest of *Aburria* is dense, less well developed than that of *Pipile*, and the crest of *Penelope* is rather nondescript, and not well developed in some species. The crest feathers of *Penelope* vary, and are more or less similar to those of *Pipile*, or are short, "bushy," and broad as in *Penelope purpurascens*, or are elongated and similar in most species to those of *Penelope jacquaçu*.

The crests of the latter, and of *P. purpurascens* and *Aburria*, are illustrated in figure 3, and the crest of *Pipile* is shown in figure 20.

The feathers of the crest are uniform in coloration, or not, and are usually margined with white or grayish white in the Penelopini, except in *Aburria* in which the crest is black and uniform. These pale edges vary greatly in width, as shown in *Pipile* (fig. 20) in which the variation is most pronounced, the crest being virtually all white in some forms. The color of the crest varies individually in *Nothocrax* from brown to dull black, the feathers being more or less tipped or edged with chestnut, especially on the front and lower layers of the crest.

The crest is black and glossy in *Mitu*. The feathers are slightly glossy in *Crax* and are uniformly black in the adult male, but spotted or barred with white in the females of all the species. These white markings vary enormously, and are arranged in one, two, or three more or less regular rows, or the rows merge to an irregular degree to form a single and expanded white patch, which invades virtually the whole of the crest in some individuals, only the very base and the curly tip of the feathers remaining black.

The crest appears to be erectile in all instances, with the exception of *Pauxi unicornis* in which it is very stiffly and permanently erect. It is usually decumbent, however, except in *Penelope purpurascens* and some species of *Crax* in which it seems to remain more or less semi-erect at all times.

PLUMAGE SEQUENCE

The molt of the wing and tail has been studied by Stresemann and Stresemann (1966), and the change from the downy to the juvenal plumage has been recorded in birds that were born in captivity (see below), but the full plumage sequence and the schedule of molts are unknown.

Wagner (1953) reported on some young birds that he had collected in Chiapas and stated, in his English summary, that the young "... undergo three incomplete molts before they are fully grown. The male birds of *Crax rubra* acquire the black plumage during the second youth molt, *Penelopina nigra* during the third molt. These species undergo their last juvenile molt at the age of 10-12 months. Only *Oreophasis derbianus* does so at the age of 5-6 months." The age of the birds could only be surmised, and I doubt that *Oreophasis* acquires the adult plumage so rapidly.

Guimarães, Bergamin, and Carvalho (1935), Bronzini (1940, 1943), and Taibel (1940, 1953) who have bred some species in captivity and raised their young, noting the change in the plumage, stated that the downy plumage had been replaced by a plumage similar to that of the adult in about two months, or in less than three. The change took 50 days in *Ortalis garrula*, 70 in *Penelope superciliaris*, and 50 in the young of *Crax fasciolata* raised by Guimarães, Bergamin, and Carvalho, but the change extended into the third month in one young of *C. fasciolata* raised by Bronzini (1940), and in young of *C. rubra* raised by Taibel (1940).

Only one gradual molt seems to be involved, and I find that the plumage that was acquired (the juvenal plumage) is very similar to that of the adult, except in *Penelopina*. It may be indistinguishable from that of the adult, to all intents and purposes, but it is not identical with it.

This plumage can always be identified by

the shape of the primaries and rectrices which differ from those of the adult, even when the rest of the plumage is identical, or virtually identical, with that of the adult. The tips of the juvenal primaries are more acute, narrower, or less regularly and less well shaped than in birds that are unquestionably adult. The outer primaries are also more barbed on the inner web, less emarginated, or less deeply excised in the genera in which these feathers are attenuated or excised (*Penelope*, *Pipile*, *Chamaeptetes*, and *Aburria*). The juvenal rectrices are invariably narrower, more acute, less rounded.

Taibel (1940, fig. 11) has published an instructive photograph which illustrates the replacement of the juvenal rectrices in a young female of *Crax rubra* that was three months old. The first pairs to be replaced by mature feathers are the third and fourth, and this molt, which is protracted, lasts for about four months, as Taibel wrote that the new feathers are not completely grown before the eighth month. A rapid molt would presumably handicap the bird, the long tail being essential for efficient maneuvering through the branches of the trees.

We have accounted for two molts, so far: a complete one from the downy to the juvenal plumage, and a second, but incomplete molt, involving only the rectrices and remiges. A third molt completes the sequence from the downy to the adult plumage. The feathers of the body are replaced at this third molt, and perhaps also the rectrices and remiges, which would make this molt complete. I am not certain, but, as the rectrices are certainly broader in some adults than others, it is possible that this third molt is complete. Only one adult plumage exists, but I do not know whether it is replaced before or after the breeding season.

That birds may be able to breed before assuming the adult plumage, or may occasionally show signs of sexual activity, is suggested by a female of the barred phase of *Crax alberti* that I have seen. Its ovaries were enlarged, according to the collector, but the remiges and rectrices are juvenal feathers. The body plumage is identical with that of the adult, however, and hence the bird is not really "immature" in one sense. It was not full grown, as is shown by the juvenal feathers

and the small measurements, the wing length measuring only 347 mm., as against 364–382 (374.0) of adult females.

To return to the juvenal body plumage, which is said to be similar to that of the adult, the two plumages are very similar (except the plumage of *Penelopina*), and may actually be identical, although most specimens reveal signs of immaturity, which are more or less evident and differ from genus to genus. These concern the crest, wattles, or bony growths, gloss, or color pattern, all of which are less developed than in the adult. The presence of some pale or buffy edges on the feathers, or of some white spots in the crest of the males of *Crax*, is also a sure sign of immaturity.

The juvenal plumage of *Penelopina* is quite different from that of the adult, especially the plumage of the male, which is not pure black or very glossy and uniform, as in the adult, but is dull black and very extensively mottled, vermiculated, or barred irregularly with brown and dark rufous cinnamon. This plumage is more or less intermediate between that of the adult male and that of the adult female, the latter being brown below, dark rufous cinnamon above, and heavily vermiculated and barred with brownish black. The juvenal plumage of the female is less conspicuous, but is much less regularly patterned than the adult plumage, especially on the under parts and head, and also in some cases on the tail.

I have not been able to study the plumage sequence further. Birds of known age are necessary for one to analyze it with certainty, and I may add that I have examined the downy young of relatively few species. They are not common in collections, and I saw a total of only 43 among nearly 3900 specimens examined.

I was concerned chiefly in identifying the juvenal plumage, because birds in this plumage must be eliminated in critical comparisons and from measurements because they are considerably smaller than adults, often much smaller. The fact that they are not adult is shown also by their weight which, unfortunately, was very rarely taken by the collectors. These birds are less heavy. For instance, one juvenal male of *Crax rubra*, collected together with an adult male by Leopold (1959, p. 205) weighed only 2.76 kilograms

as against 4.63 kilograms for the adult, although Leopold wrote that the two birds "looked alike," except that the fleshy knob on the bill was not developed in the juvenal male. Many authors have been misled by the close similarity of the two plumages, but the failure to distinguish between them has led to erroneous conclusions.

FEATHERING OF THE FACE AND THROAT, APPENDAGES, OR BONY STRUCTURES

The skin of the face is bare, except in *Aburria*, *Oreophasis*, *Mitu*, and *Pauxi*, in which it is completely feathered except for the lower eyelid. When present the bare area varies a great deal in extent, and in some cases consists only of a narrow ring around the eye, which usually expands slightly to form a small triangular patch behind the eye. Such is the case with most of the species of *Crax*, but the lores can be bare also and to a varying degree, the bare skin of the lores connecting with the bare skin around the eye. The ring of bare skin is also narrow in *Penelopina*, but the bare area is more extensive in the other genera and can expand over the whole of the face, or virtually so. This character is most highly developed in *Nothocrax*.

The skin of the throat is bare in some of the genera of the Penelopini and in the monotypic *Oreophasini*, but not in the Cracini. The skin is bare in *Ortalis* and divided longitudinally into regular halves by a narrow feathered strip on the median line; there are no wattles. The skin is bare in *Penelope* and *Pipile* and forms a dewlap, or a wattle or caruncle (fig. 20), in all the species, which is attached to the center of the throat; the skin is not feathered, but sparse, hairlike, or bristly short feathers grow from it. The skin of the throat is bare in *Penelopina* also, but only in the male, and forms a very large and broad pendulous wattle, which is more developed than in any other species. *Aburria* has a very long and vermiform caruncle, but the throat is feathered with the exception of this caruncle. The skin of the throat is densely and completely feathered in *Chamaepetes*, and this genus has no wattles or caruncles of any kind.

All the characters so far described, the feathering of the face and throat and the

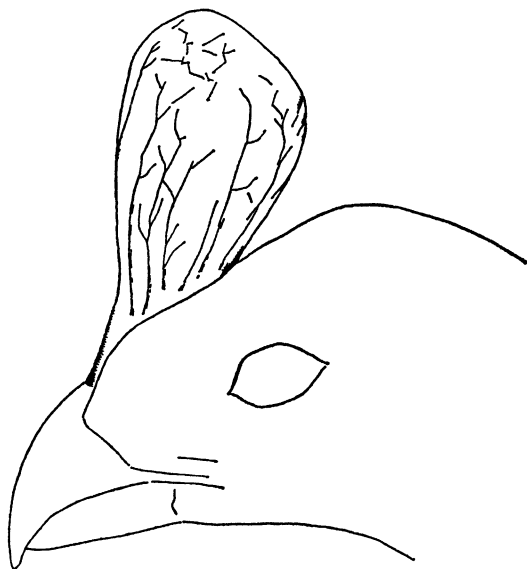


FIG. 4. Profile of *Pauxi pauxi*, illustrating the bony helmet and the shape of the bill.

presence or lack of throat appendages, are not subject to sexual dimorphism (with the single exception of *Penelopina*); they are developed to about the same extent in both sexes. The color of the skin in life is also the same in both sexes, and this lack of sexual dimorphism suggests that these characters probably play no part in courtship, with the probable exception of *Penelopina*. Their function is probably for territorial display, but, as the degree of feathering and color of the skin vary very abruptly from species to species in *Pipile*, I believe that their main function is species recognition in this genus. The same may be true also to some degree in *Penelope*, because, in the case of *P. dabbeni* and *P. obscura*, the ranges of which overlap, the skin is red in *P. dabbeni*, as against dark slaty blue in *P. obscura*.

The center of the lower throat is almost entirely bare in *Oreophasis*, and a wattle is present, according to Wagner (1935, p. 106), but I have found no trace of it in specimens, and I believe it is probably developed only at the onset of the breeding season.

The throat is well and densely feathered, without wattles, in all the Cracini, but in *Crax* the base of the bill is covered by naked fleshy membranes, rather than by horn,

which form a pair of thick fleshy wattles on the mandible and a fleshy knob at the base of the culmen. These appendages are present in the male only (with the exception of *Crax alector*), and their development and color vary from species to species, as is shown in plate 15.

The appendages on the bill of *Crax* probably play a part in courtship, because they increase in size, and their coloration changes or is heightened, with the onset of the breeding season. I believe they also play an important role in species recognition in some cases, because the contrast between the species is especially sharp where their ranges probably come in contact. For instance, in the case of *C. alberti* and *C. rubra*, which seem to come in contact, the bill of *alberti* (pl. 15) has both a knob and wattles that are vivid cobalt-blue in life, whereas the knob is bright yellow in *rubra* and wattles are lacking. These fleshy appendages are not present in the other genera of the tribe.

The base of the premaxillary bone is greatly swollen in *Mitu mitu* and forms a casque (fig. 28), but not in the other two species of this genus, whereas *Pauxi* and *Oreophasis* display some very bizarre bony structures. These take the form of a large and elevated helmet in *Pauxi* (fig. 4) which surmounts the forehead and is analogous to the casque of *M. mitu*, and of a tall "horn" or spike which springs from the vertex of the skull in *Oreophasis* (fig. 5). These bony structures are filled by spongy bone, as shown by X rays which were kindly taken for me by Dr. Richard L. Zusi. The bony core is more finely reticulated in *Oreophasis*.

The integument of these bony structures varies. The casque forms an integral part of the bill in *Mitu mitu* and is completely covered by the horny rhamphotheca, but the latter ends at the base of the helmet in *Pauxi*, and the helmet is covered not by a layer of horn but by skin, which appears to be slightly keratinized but shrinks after death and is blue in life. The helmet of *Pauxi* is much scored by many shallow grooves, some of which are probably occupied by blood vessels. The "horn" of *Oreophasis* is covered by thin skin which is very bright red in life and from which grow short and very thin bristly feathers, especially near the base.

These bony structures are developed to about the same degree in both sexes in the three genera. Their function is obscure.

STRUCTURE AND COLOR OF THE BILL

The bill varies in size, shape, feathering, and coloration, or by being provided with wattles or not, and is clearly different in the three tribes.

It is small, or relatively small, in the Penelopini, rather broad at the base, with the breadth at the base equal to or greater than the height (depth), is depressed, with a gradually decurved tip, not arched, and is not feathered or provided with a cere or wattles. The nostrils are large, fully exposed, more or less narrowly elliptical, slitlike, or comma-like, in shape, with a membrane or operculum overhanging the base. The profile of this type of bill is shown for *Penelope* and *Aburria* in figure 3, and for *Pipile* in figure 20. The bill is dull and dark, not brightly colored, with the single exception of *Penelopina* in which the bill of the male is very bright reddish orange, but not that of the female which is dull and dark brown.

The bill of the monotypic Oreophasini is elongated at the base, but the culmen is very small and short (fig. 5), and the base of the upper bill and that of the mandible are very densely covered with short, velvety, or plush-like feathers. These feathers cover two-thirds or more of the base of the upper bill, conceal the nostril which is rounded in shape, and form a tuft over the base of the culmen, the culmen being pale straw-yellow in life.

The bill of the Cracini is large and heavy, much higher than broad at the base, very strongly compressed laterally, arched, and strongly decurved; but the anterior part of the bill is more elongated in *Crax* than in the other three genera, and the bases of the upper bill and mandible are covered by naked and thick fleshy membranes (the cere) which form wattles on the mandible or a knob on the culmen, or both, in males (pl. 15), but not in females. The nostrils are more or less rounded or elliptical in shape and overhung by an operculum at the base.

The cere and its appendages are lacking in the other three genera. The profile of the bill of *Nothocrax* is illustrated in figure 3; of *Pauxi*, in figure 4, and of *Mitu*, in figure 28.

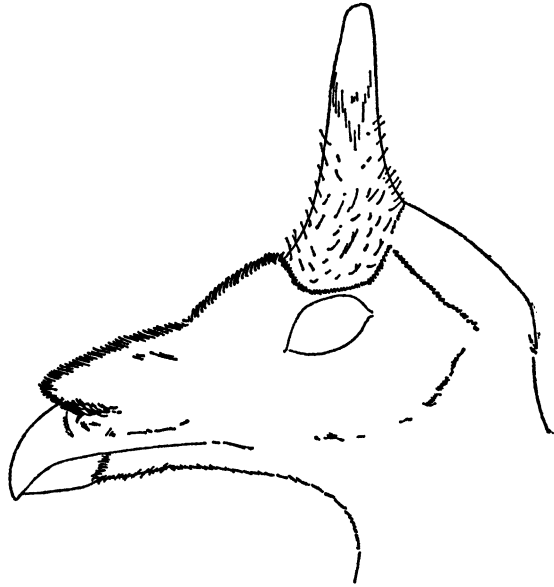


FIG. 5. Profile of *Oreophasis derbianus*, illustrating the denuded vertex of the skull, with its tall bony "horn," and the shape of the bill, with heavy feathering concealing the nostril.

The bill varies in size in *Mitu* and is very swollen at the base in *M. mitu* to form a casque, but the anterior part of the bill is extremely compressed laterally, ending in a very sharp, knifelike keel, hence the name "Razor-billed Curassow" by which *M. mitu* is called in English.

The bill is bright red in both sexes in *Nothocrax*, *Mitu*, and *Pauxi*, but the horny rhamphotheca varies in *Crax* from yellowish, grayish, or bluish, to pure jet black (pl. 15), and the color of the cere varies very conspicuously. The color of the cere varies also sexually in some species; for instance, the cere is red in the male, but blackish in the female, of *Crax blumenbachii*; and bright yellow in the male, but blackish or brown in the female, of *C. daubentoni*. The existence of this sexual dimorphism, which is also shown by *Penelopina*, suggests that it plays a part in courtship. When sexual dimorphism does not exist, the abrupt variations in the color of the cere probably serve for species recognition (as suggested above in the discussion of the appendages).

The Cracidae feed on fruit, buds, tender leaves or tendrils, and occasionally flowers, but they eat insects also or other small in-

vertebrates such as snails when they find them, although they are chiefly vegetarian. The Cracini are more terrestrial than the Penelopini, and their much larger bill no doubt enables them to eat larger and coarser fruit that has fallen to the ground, but the shape of the bill of the Cracidae does not appear to be closely adaptive, as their feeding habits do not seem to be unduly specialized. Animal food has not been reported for *Oreophasis*, but it can be taken for granted, as Salvin wrote (1860) that he was told by his collector that the bird forages frequently on the ground.

STRUCTURE, COLOR, AND PROPORTIONS OF THE TARSUS

The foot is large, with large toes, of which the hallux is exceptionally well developed and long, and the claws are large, moderately or strongly curved, well adapted for grasping limbs, or scratching on the ground in the case of the Cracini. The tarso-metatarsus (tarsus)

is long and varies in length, proportions, coloration, scutellation, and feathering. The range in size is shown in figure 6, the tarsus of *Mitu mitu* representing one extreme and that of *Ortalis superciliaris* the other.

The scutellation varies in some genera, in some cases from species to species, but the front of the tarsus is covered by large, broad, and transverse scutella in all the genera. The back of the tarsus is covered by large scutella on both sides in *Mitu* and *Crax*, and both sides are scutellated in other genera also, such as *Ortalis* and *Nothocrax*, but the scutellation in these genera is irregular on the inner side, or less distinct than in *Mitu* and *Crax*. The back of the tarsus is not well scutellated in *Pipile*, *Aburria*, *Chamaepetes unicolor* (fig. 6), and *Oreophasis*, the scales being small, irregular, or more or less rounded or hexagonal in shape. The scutellation of the back of the tarsus is irregular and varies a great deal individually in *Pauxi*.

The tarsus varies very distinctly in the

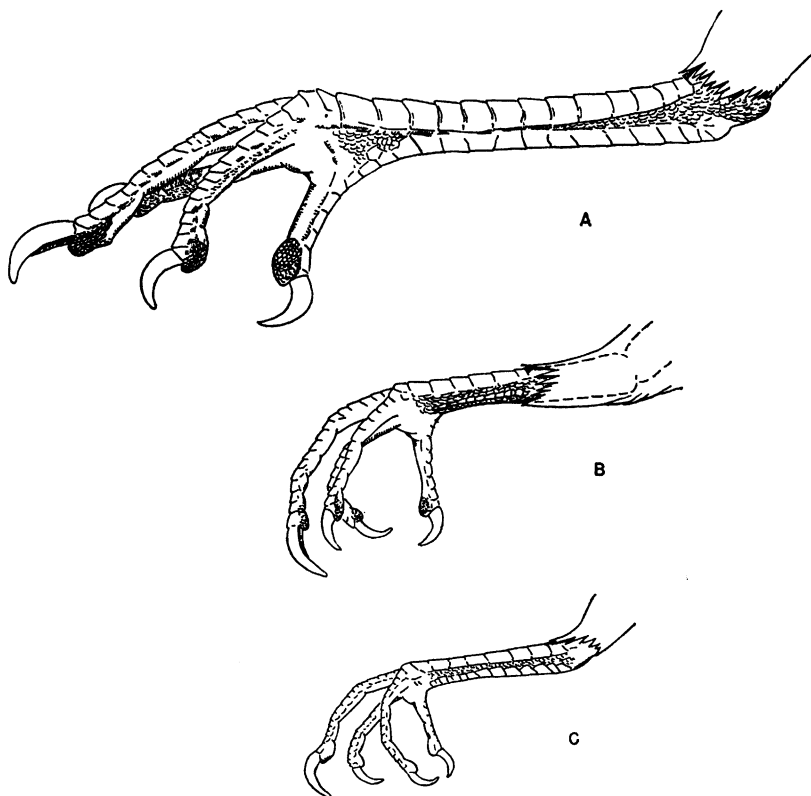


FIG. 6. Size, scutellation, and feathering of the tarsus. A. *Mitu mitu*.
B. *Chamaepetes unicolor*. C. *Ortalis superciliaris*.

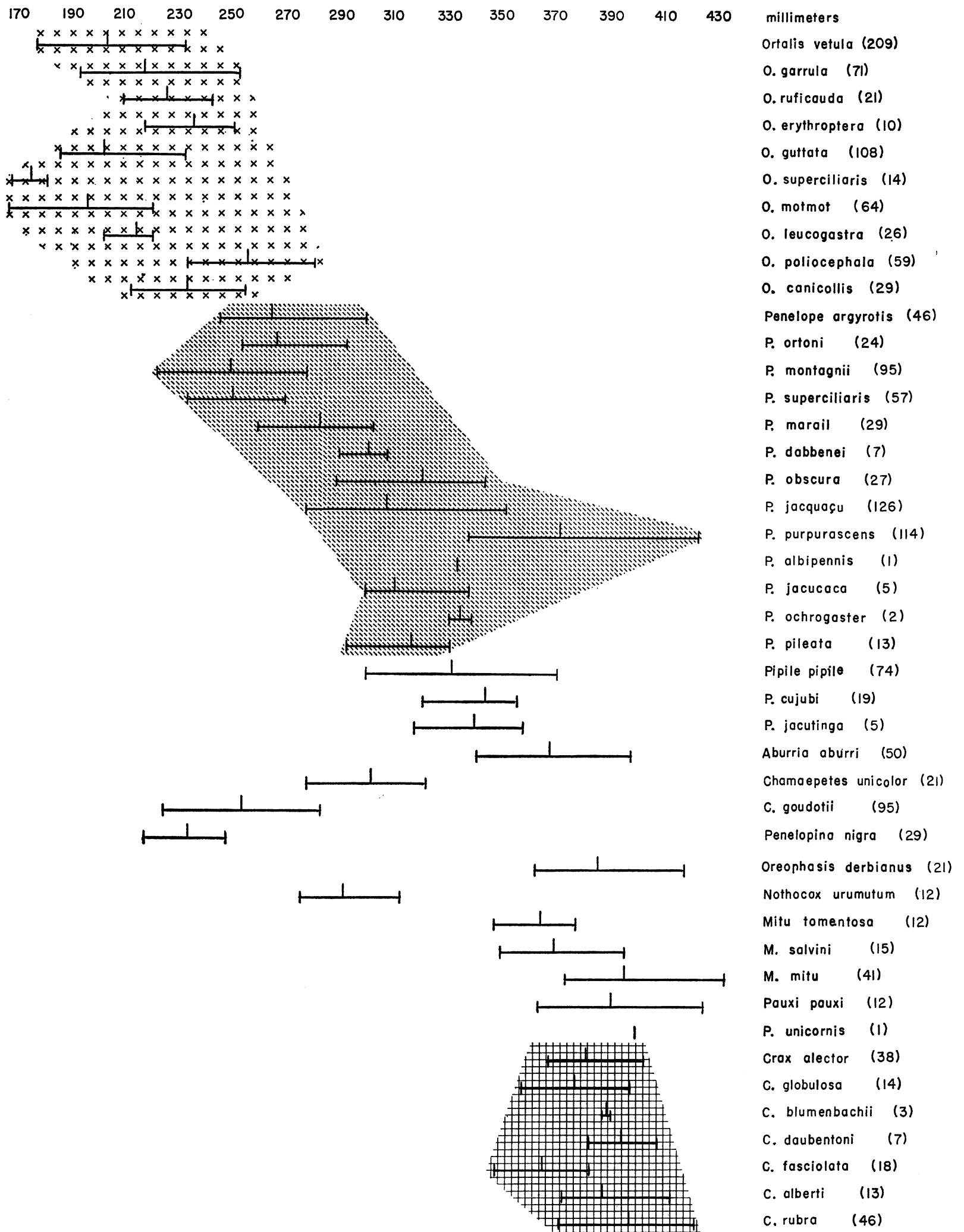


FIG. 7. Variation in the length of the wing in the adult males of the Cracidae. The measurements of the three most highly polytypic genera are encompassed by different patterns. The numbers in parentheses represent the size of the samples.

two species of *Chamaepetes*. It is proportionally longer in *C. goudotii* (see below), scutellated posteriorly on both sides, and only very slightly feathered, whereas the upper third or more is well feathered in *C. unicolor* (fig. 6). The tarsus is entirely bare, or only barely feathered anteriorly, in species that spend much time on the ground, such as those in the Cracini (fig. 6). The correlation is not exact, but the tarsus is less scutellated posteriorly, and is better feathered, as a rule, in the genera or species that are more highly arboreal. The correlation between the length of the tarsus and general habits is more exact and instructive (see below).

The color of the tarsus varies, but is some shade of red in nearly all genera and species; the exceptions are *Ortalis*, in which it is normally bluish or grayish, and some species of *Penelope* and *Crax*. The exceptions provided by these two genera are interesting, because the difference in coloration appears to be an isolating character. The range of *Penelope obscura* (black tarsus) overlaps that of *P. montagnii* (red tarsus), and that of *P. dabbenei* (brown tarsus); *Crax rubra* (grayish or bluish tarsus) comes in contact with *C. alberti* (red tarsus) in Colombia. The color is the same in both sexes except in *Penelopina*, in which the tarsus is very bright reddish orange in the male but brownish in the female.

The variation in the length of the tarsus is best studied by comparing its measurement with that of the wing (table 2), the tarsus/wing ratio being invariably smaller in the genera that are more arboreal, such as *Pipile* and *Aburria*. I have not studied the variation within the genera, but I believe the correlation exists. This is suggested by the relatively great range of variation in *Penelope*, in which the ratios vary from about .19 to .27, and by *Chamaepetes*, as *C. unicolor* has a proportionally shorter tarsus than *C. goudotii* which is known to be less arboreal.

MEASUREMENTS

Four measurements were taken for every species: the length of the wing, the length of the tail, the length of the tarsus, and the length of the exposed culmen. The wing was measured pressed down as flat as possible on

the ruler. The tail, tarsus, and exposed culmen were measured in the standard manner, except that the culmen was measured from the point where the rhamphotheca ends at the base of the helmet in *Pauxi*, and diagonally in *Mitu mitu* from the posterior base of the swelling to the tip of the bill. These measurements are given in table 1. Other measurements, such as those of the crest or of other appendages, are given in the text. The measurements were taken by me with the exception of those of two specimens quoted from the literature, where indicated, and of a very few additional specimens of rare forms that were kindly taken for me by colleagues, following my directions.

I have, as far as possible, excluded individuals that did not appear to be fully adult. These can usually be identified by differences that I describe above in the discussion of the sequence of the plumage. Other possible sources of error are worn or wrongly sexed specimens. The structure of the feathers is not very "hard" in the Cracidae. The large majority of the specimens show some wear, especially the long tail, which is easily abraded, but, by comparing abraded feathers to some that are intact, one can compensate for wear fairly accurately with experience. It is impossible to be certain of the sex in all cases, because males and females are indistinguishable in appearance in most genera, but a "female" that is exceptionally large, or a "male" that is exceptionally small, should be questioned. Undetected errors may have affected the range of variation somewhat in a few instances, but these errors were presumably not frequent enough to affect the mean significantly.

The variation in the length of the wing in adult males is illustrated in figure 7. The measurements shown represent only the range and the mean; the standard deviation for samples of five or more specimens is given in table 1.

The interspecific range of variation is great and varies from 170 mm. in *Ortalis motmot*, and 171 in *O. supercilialis*, to 435 in *Mitu mitu*; the means (in round numbers) vary from 178 in *O. supercilialis* to 400 in *Crax rubra*.

The range in the three genera that are most highly polytypic is covered by a different

TABLE 1

MEASUREMENTS OF ADULT SPECIMENS OF THE GENERA OF THE CRACIDAE
(The standard deviation was not computed for samples of fewer than five.)

	Wing				Tail				Tarsus				Exposed Culmen			
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>Ortalis</i>																
<i>O. v. macalli</i> ^a																
Males	46	209.9	195-230	7.55	46	235.2	215-265	9.45	46	56.8	52-64	2.37	45	22.7	20-25	1.19
Females	30	201.2	187-219	7.66	28	229.7	210-250	9.58	28	54.3	49-60	2.31	29	22.3	20-25	1.10
<i>O. v. vetula</i> ^b																
Males	15	210.2	195-220	7.03	15	233.8	220-253	10.50	15	60.2	53-65	3.12	15	24.2	22-27	1.43
Females	13	208.0	185-218	9.11	13	223.1	209-240	11.04	14	57.0	53-62	2.75	14	23.6	22-27	1.39
<i>O. v. pallidiventris</i>																
Males	17	196.9	184-217	8.51	17	225.0	205-252	12.73	17	59.0	56-62	2.07	17	23.5	22-26	1.36
Females	8	188.9	184-195	3.99	8	217.0	202-235	10.0	8	56.5	53-60	2.69	8	23.5	22-25	1.10
<i>O. v. deschauensei</i>																
Males	7	220.0	213-229	5.54	7	226.0	220-232	4.55	7	59.7	57-63	1.82	7	26.3	25-28	1.01
Females	5	204.4	190-216	9.54	5	219.0	210-230	7.50	5	57.4	56-60	1.65	5	24.1	22-26	1.58
<i>O. g. franzi</i>																
Males	26	208.1	196-225	6.20	25	219.5	204-241	9.16	26	59.1	54-65	2.35	26	24.4	22-27	1.47
Females	18	198.1	189-219	6.86	18	210.0	198-222	6.65	18	55.7	52-62	2.92	18	23.6	22-26	1.34
<i>O. g. cinereiceps</i> ^c																
Males	17	215.9	203-232	6.23	16	233.0	213-250	11.95	17	61.9	55-67	3.66	17	24.8	22-27	1.38
Females	14	205.9	190-214	7.38	14	231.9	212-248	10.46	14	58.7	52-65	3.28	14	24.1	22-27	1.60
<i>O. g. mira</i>																
Males	6	224.0	215-235	4.93	6	235.5	215-252	14.75	6	61.0	57-68	3.76	6	26.5	23-29	2.12
Females	4	211.7	210-214	—	4	223.0	220-225	—	4	59.7	59-60	—	4	25.2	24-27	—
<i>O. g. chocoensis</i>																
Males	3	218.4	216-221	—	3	240.0	235-245	—	3	63.6	62-65	—	3	26.0	25-27	—
Females	4	208.0	205-212	—	4	229.0	223-232	—	4	60.5	57-63	—	4	25.0	24-26	—
<i>O. g. garrula</i>																
Males	19	239.4	223-255	7.46	19	262.1	250-280	8.97	19	66.0	60-72	2.98	19	27.6	23-31	1.90
Females	21	224.1	215-237	5.46	21	248.1	235-262	7.78	21	62.0	59-67	2.08	21	26.2	23-30	1.90
<i>O. r. ruficrissa</i> ^d																
Males	7	224.0	212-241	11.10	7	245.0	225-263	13.95	7	61.7	60-66	2.60	7	25.9	24-28	1.41
Females	4	210.7	201-222	—	4	241.2	230-250	—	4	59.0	56-62	—	4	25.5	24-28	—

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>O. r. ruficauda</i>												
Males	14	230.3	220-245	7.87	14	253.7	234-283	12.28	14	61.9	55-69	3.69
Females	18	220.8	207-245	10.26	18	244.1	230-261	10.52	18	58.6	54-65	2.99
<i>O. erythroptera</i>												
Males	10	237.7	220-253	12.06	9	260.5	232-276	12.27	10	66.0	60-70	3.18
Females	6	225.0	225-230	3.03	6	255.0	244-268	8.29	6	59.3	55-64	3.44
<i>O. g. araucuan</i>												
Male	1	—	193.0	—	1	—	218.0	—	1	—	52.0	—
<i>O. g. squamata</i>												
Male	1	—	213.0	—	1	—	239.0	—	1	—	55.0	—
Female	1	—	215.0	—	1	—	205.0	—	1	—	51.0	—
<i>O. g. subaffinis</i>												
Males	12	204.2	192-218	7.50	12	211.7	196-230	9.32	12	52.1	48-60	3.04
Females	13	196.3	187-204	4.76	13	205.6	198-220	6.47	13	51.1	47-54	1.93
<i>O. g. guttata</i>												
Males	76	199.9	189-211	5.48	76	209.4	192-233	7.95	77	51.0	46-58	2.33
Females	61	192.1	181-208	6.37	62	206.9	189-240	12.72	62	49.0	41-55	2.61
<i>O. g. columbiana</i>												
Males	18	224.6	213-235	6.66	17	250.7	230-265	10.91	18	59.6	56-67	2.54
Females	10	219.5	213-230	5.55	11	240.2	225-258	10.83	13	57.6	54-63	2.32
<i>O. superciliosus</i>												
Males	14	177.6	171-184	3.53	14	190.6	184-208	5.91	14	46.1	42-52	2.41
Females	5	172.8	170-177	3.80	5	187.8	183-192	3.50	5	44.4	43-46	1.50
<i>O. m. molmol</i>												
Males	44	207.1	192-223	7.54	40	242.6	225-270	10.14	43	56.9	51-63	3.75
Females	32	196.5	185-209	5.47	31	232.7	215-253	8.94	32	54.1	48-60	2.53
<i>O. m. ruficeps</i>												
Males	20	181.1	170-190	4.69	20	195.9	183-208	7.42	20	46.7	44-50	1.50
Females	6	175.0	166-185	4.47	6	195.3	185-201	2.65	6	45.0	42-48	2.03
<i>O. leucogastra</i>												
Males	26	217.6	205-223	4.62	26	208.4	198-220	5.42	26	53.5	50-58	2.03
Females	31	209.6	195-225	6.74	30	203.7	191-220	8.26	31	51.2	45-56	2.92
<i>O. p. wagleri</i>												
Males	30	259.3	236-283	12.0	29	274.6	247-295	12.23	30	67.5	62-75	3.14
Females	33	253.2	234-273	9.58	32	268.7	245-290	12.67	33	66.0	61-71	2.71

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>O. p. poliocephala</i> ^a												
Males	28	256.5	240–280	10.2	28	284.5	260–318	16.50	28	69.0	63–74	2.90
Females	15	247.6	230–266	10.83	15	283.0	260–305	13.89	15	67.8	63–72	2.16
<i>O. c. pantanulensis</i>												
Males	6	252.3	245–257	5.27	6	253.9	248–270	4.66	6	65.6	63–68	1.85
Females	6	239.6	222–247	7.49	6	243.5	235–250	5.74	6	60.2	56–64	3.26
<i>O. c. canicollis</i>												
Males	23	232.4	215–246	6.75	22	245.8	230–260	7.83	23	54.2	49–59	2.71
Females	21	221.9	206–236	7.08	21	231.7	213–253	9.68	21	52.4	49–57	2.30
<i>Penelope</i>												
<i>P. a. argyrotis</i>												
Males	21	275.6	254–302	11.56	21	256.6	235–275	10.02	21	53.0	48–57	2.21
Females	20	265.1	254–281	7.04	20	252.7	240–265	6.41	20	53.2	49–59	2.64
<i>P. a. colombiana</i>												
Males	19	263.4	248–281	9.81	19	254.2	240–276	9.95	19	54.5	51–60	2.58
Females	16	254.2	242–268	6.40	16	254.5	230–268	9.53	16	53.3	49–59	2.84
<i>P. a. barbata</i>												
Males	6	261.1	254–267	5.84	5	257.0	242–270	9.87	6	56.8	52–62	3.52
Females	6	251.1	241–256	5.41	5	239.2	230–258	8.63	6	55.8	52–62	3.34
<i>P. ortoni</i>												
Males	24	269.3	256–295	8.50	24	235.8	215–263	11.32	24	55.9	50–60	2.58
Females	23	260.4	244–280	9.02	23	228.1	210–248	9.54	23	53.7	49–57	2.71
<i>P. m. montagnii</i>												
Males	40	255.2	240–280	9.30	39	234.8	212–260	12.81	40	55.5	50–63	2.61
Females	23	247.4	231–261	6.64	24	234.3	210–253	11.98	23	54.2	50–60	2.26
<i>P. m. atrogularis</i>												
Males	11	249.7	235–264	9.32	9	223.6	215–245	9.13	11	56.1	52–59	2.50
Females	9	244.5	232–252	7.38	9	223.0	212–232	8.84	9	55.1	52–59	2.14
<i>P. m. brooki</i>												
Males	10	244.7	225–260	12.34	9	221.0	207–240	11.69	10	54.2	50–59	3.08
Females	11	238.6	223–255	9.17	11	218.2	200–228	9.17	11	53.4	49–57	2.01
<i>P. m. plumosa</i>												
Males	16	240.0	227–250	5.86	16	233.4	222–245	6.27	16	54.0	50–58	2.24
Females	8	232.8	213–245	10.55	8	223.5	212–242	9.91	8	53.1	51–55	1.45

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>P. m. slateri</i>												
Males	19	263.1	246-273	7.21	18	239.8	223-255	9.84	19	57.3	53-63	2.94
Females	16	252.0	240-277	6.99	16	237.8	226-250	6.68	16	56.3	53-59	1.75
<i>P. s. superciliosus</i>												
Males	23	252.2	243-262	5.80	23	270.0	250-285	10.17	23	68.1	63-72	2.57
Females	21	243.4	228-258	7.66	20	267.2	243-290	12.91	21	66.3	63-73	2.39
<i>P. s. jacupemba</i>												
Males	25	251.3	236-272	8.32	25	269.6	240-300	13.46	25	67.0	63-73	3.28
Females	19	244.8	230-260	7.22	19	263.1	240-285	11.98	19	65.0	60-69	2.69
<i>P. s. major</i>												
Males	9	259.2	245-270	9.16	9	275.0	250-300	12.84	9	69.0	67-72	1.83
Females	6	247.0	243-250	2.09	6	262.0	250-270	8.12	6	65.7	63-68	1.89
<i>P. marail marail</i>												
Males	23	286.9	276-305	6.90	23	258.9	245-275	9.48	22	57.5	53-65	2.68
Females	9	273.4	266-280	5.17	9	243.9	230-250	6.96	9	55.2	51-61	3.30
<i>P. m. jacupemba</i>												
Males	6	277.3	262-288	10.27	6	248.6	235-260	10.92	6	56.1	53-60	2.63
Females	8	267.1	241-280	11.71	8	247.3	234-265	10.86	8	56.0	54-58	1.64
<i>P. dabbeni</i>												
Males	7	303.1	292-310	6.81	7	301.0	290-323	11.69	7	67.5	65-70	2.08
Females	4	293.7	285-303	—	4	285.0	270-295	—	4	66.0	65-67	—
<i>P. o. obscura</i>												
Males	3	303.6	301-305	—	2	285.0	280, 280	—	3	72.3	68-77	—
Females	3	290.3	285-301	—	2	277.5	275, 280	—	3	68.0	65-72	—
<i>P. o. bronzina</i>												
Males	5	315.4	304-323	3.96	5	302.8	285-312	4.89	5	75.0	70-81	2.98
Females	8	294.0	270-309	13.27	6	302.0	285-325	13.71	8	74.1	71-79	2.74
<i>P. o. bridgesi</i>												
Males	19	328.1	291-346	12.77	19	330.9	305-345	10.90	19	78.5	72-85	3.49
Females	9	322.0	298-335	12.31	9	333.3	320-365	13.69	9	77.5	72-84	4.24
<i>P. j. perspicax</i>												
Males	11	313.6	302-332	7.64	11	322.8	308-343	8.81	11	76.3	73-80	2.36
Females	7	292.4	285-302	7.10	6	307.4	290-323	14.66	7	72.7	71-75	1.77

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>P. j. jacuacu</i>												
Males	67	303.8	280-330	10.98	60	315.8	292-350	12.57	68	74.7	67-88	4.32
Females	37	290.3	270-312	11.37	33	303.7	273-330	12.62	37	71.9	63-80	3.61
<i>P. j. orienticola</i>												
Males	21	307.2	285-325	8.78	18	323.5	310-343	10.56	22	78.3	72-84	3.16
Females	5	289.0	283-297	6.12	4	304.0	300-310	—	6	77.5	73-83	3.86
<i>P. j. granti</i>												
Males	8	336.8	310-354	13.35	8	345.0	325-375	16.02	8	80.7	75-84	2.85
Females	6	321.1	316-327	3.60	6	327.0	315-345	11.47	6	74.1	70-78	2.92
<i>P. j. speciosa</i>												
Males	19	322.9	290-351	13.25	17	328.4	305-345	11.33	19	77.4	72-85	3.46
Females	11	310.0	302-333	9.03	11	315.7	305-340	11.47	11	76.1	72-82	3.23
<i>P. p. purpurascens¹</i>												
Males	12	399.0	385-425	12.76	12	370.7	340-392	15.66	12	80.0	75-86	3.76
Females	16	391.0	360-428	15.02	17	378.3	350-415	19.18	17	82.5	74-91	3.95
<i>P. p. aequatorialis²</i>												
Males	30	368.7	350-390	10.75	30	333.0	310-370	14.52	30	76.7	71-86	3.20
Females	18	350.1	338-368	8.01	18	325.0	295-350	12.37	18	75.0	65-83	4.20
<i>P. p. brunnescens</i>												
Males	13	359.3	340-374	8.17	13	320.0	290-340	15.36	13	74.0	70-78	2.58
Females	10	345.6	330-353	7.08	10	317.0	280-338	16.32	10	75.0	72-80	2.51
<i>P. albipennis³</i>												
Male	1	—	336.0	—	1	—	325.0	—	1	—	90.0	—
Female	1	—	325.0	—	1	—	325.0	—	1	—	78.0	—
<i>P. jacuaca</i>												
Males	5	312.8	302-340	13.83	5	307.0	280-335	22.49	5	77.4	70-86	5.35
Females	4	287.7	277-302	—	4	283.7	270-305	—	4	74.5	67-80	—
<i>P. ochrogaster</i>												
Males	2	337.0	333, 341	—	2	339.0	338, 340	—	2	79.5	77, 82	—
Female	1	—	327.0	—	1	—	345.0	—	1	—	79.0	—
<i>P. pileata</i>												
Males	13	319.0	295-333	10.89	13	323.0	290-345	14.92	13	81.7	73-89	4.69
Females	9	306.4	292-315	9.04	9	314.5	297-326	10.48	9	78.3	73-87	4.18
<i>Pipile</i>												
<i>P. p. pipile</i>												
Males	2	361.5	360, 363	—	2	286.0	280, 292	—	2	60.5	60, 61	—
Females	1	—	350.0	—	1	—	281.0	—	1	—	61.0	—

TABLE 1—(Continued)

[illegible]

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>C. g. sanctae-marthae</i>												
Males	26	252.0	236–267	7.69	26	256.0	232–275	9.23	26	65.9	61–70	2.46
Females	9	244.2	230–254	8.81	10	246.2	240–262	6.35	10	65.0	61–68	2.21
<i>C. g. goudotii</i>												
Males	35	260.7	236–285	9.28	35	243.0	230–260	8.78	36	62.2	56–70	3.40
Females	27	250.6	228–272	10.82	28	235.6	210–260	11.57	28	60.3	52–68	3.73
<i>C. g. fugani</i>												
Males	16	240.6	227–262	8.65	16	205.3	194–223	7.62	16	58.2	55–63	2.10
Females	5	229.6	225–236	4.38	5	194.6	180–208	11.84	5	56.2	54–60	2.27
<i>C. g. ischudii</i>												
Males	16	263.6	248–277	9.80	16	251.1	230–267	10.29	16	68.6	65–73	2.37
Females	15	251.0	235–268	7.43	15	241.8	220–259	8.61	15	66.6	60–70	3.07
<i>C. g. rufoventris</i>												
Males	2	269.0	265, 273	—	2	255.5	255, 256	—	2	66.5	66, 67	—
Females	5	247.2	241–253	4.60	5	242.6	235–247	5.01	5	67.0	66–70	1.73
<i>Penelopina</i>												
<i>P. nigra</i>												
Males	29	236.2	220–250	8.17	28	263.7	231–290	11.64	29	68.8	60–77	3.41
Females	15	247.1	236–270	8.82	14	270.5	253–290	9.22	15	67.2	60–74	3.34
<i>Oreophaps</i>												
<i>O. derbianus</i>												
Males	21	388.0	365–420	15.28	21	344.5	325–371	11.48	21	81.0	75–86	2.59
Females	9	366.6	353–378	8.84	9	339.5	315–370	18.68	9	79.5	72–83	3.23
<i>Nothocrax</i>												
<i>N. urumutum</i>												
Males	12	294.0	278–315	11.09	12	231.8	220–245	7.05	13	81.7	75–89	3.65
Females	8	280.8	267–287	7.54	8	233.0	225–240	4.67	9	78.9	71–87	5.22
<i>Mitu</i>												
<i>M. tomentosa</i>												
Males	12	367.2	350–380	9.28	12	326.1	305–342	10.43	12	104.1	99–112	4.46
Females	10	349.3	338–363	7.45	9	309.0	290–320	11.64	10	98.8	93–105	4.09
<i>M. subini</i>												
Males	15	372.0	352–398	13.07	14	310.7	285–335	14.14	15	105.0	98–114	4.78
Females	9	354.3	337–375	13.09	7	296.7	280–312	11.49	9	99.7	93–113	6.33

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>M. mitu</i>	41	398.7	376-435	11.47	40	333.7	315-355	11.27	40	110.5	102-122	4.53
Males	30	368.3	348-385	8.30	30	313.1	290-340	12.74	30	103.0	94-112	4.15
Females												
<i>Pauxi</i>												
<i>P. p. pauxi</i>	8	394.3	382-427	12.59	7	336.7	320-362	16.46	8	102.6	97-112	5.28
Males	6	373.6	363-385	8.35	6	319.0	304-335	11.40	6	101.6	90-107	5.98
Females												
<i>P. p. gilliardi</i>	4	394.7	366-410	—	3	330.0	296-355	—	4	103.2	96-112	—
Males	5	372.4	345-390	16.64	4	316.2	305-322	—	5	101.6	89-111	9.66
Females												
<i>P. unicornis</i>	1	—	402.0	—	1	—	335.0	—	1	—	108.0	—
Male	1	—	381.0	—	1	—	310.0	—	1	—	100.0	—
Female												
<i>Crax</i>												
<i>C. alector</i>	38	384.2	370-405	9.71	35	327.1	305-350	12.27	38	103.5	92-111	4.30
Males	31	368.2	350-395	10.34	28	313.5	275-340	14.44	31	98.5	92-105	3.49
Females												
<i>C. globulosa</i>	14	380.0	360-400	11.66	14	328.5	295-350	13.45	14	96.8	88-104	5.14
Males	15	349.5	330-365	9.90	15	305.3	285-330	12.36	15	88.3	82-92	2.86
Females												
<i>C. blumenbachii</i>	3	391.0	390-393	—	3	340.0	330-351	—	3	110.3	105-115	—
Males	3	371.0	350-385	—	3	316.7	310-325	—	3	102.3	98-107	—
Females												
<i>C. dasbentoni</i>	7	397.7	385-410	9.38	7	343.1	325-370	16.03	7	106.4	100-113	4.89
Males	11	374.0	356-390	9.74	10	323.8	306-360	15.35	11	99.3	93-109	4.65
Females												
<i>C. f. pinimaj</i>	1	—	350.0	—	1	—	310.0	—	0	—	—	—
Female												
<i>C. f. fasciolata</i>	16	368.2	350-385	9.25	16	319.2	310-340	8.63	16	96.6	90-102	2.89
Males	20	351.7	337-367	9.71	19	305.2	290-315	6.72	21	89.5	85-95	2.30
Females												
<i>C. f. grayi</i>	2	369.0	368, 370	—	2	325.0	320, 330	—	2	102.5	102, 103	—
Males	10	358.9	346-373	8.53	10	319.2	308-335	5.46	10	92.6	86-103	5.62
Females												

TABLE 1—(Continued)

	Wing			Tail			Tarsus			Exposed Culmen		
	N	Mean	Range	σ	N	Mean	Range	σ	N	Mean	Range	σ
<i>C. alberti</i>												
Males	13	390.3	375-415	11.14	13	340.0	315-350	14.25	13	102.1	95-112	4.82
Females	13	373.6	362-382	6.40	13	320.7	310-330	6.90	13	100.0	96-105	2.92
<i>C. r. rubra</i>												
Males	46	400.0	374-424	12.57	47	333.9	310-380	15.43	47	108.7	98-115	4.61
Females	63	382.0	360-407	13.47	62	320.1	290-350	13.60	63	103.2	94-112	4.37
<i>C. r. griscomi</i>												
Females	4	344.0	332-360	—	4	295.0	285-305	—	4	89.7	85-97	—

^a From the Rio Grande Valley.^b From central Veracruz.^c From southern and central Panama.^d Specimens from the zone of secondary intergradation ("balisus") or of the slightly differentiated local form ("lamprophonia") are not included.^e Specimens from the zone of secondary intergradation ("tajuelae") are not included.^f From Mexico.^g From Colombia.^h Quoted from Taczanowski (1886, p. 271), with the exception of the length of the exposed culmen which was not measured by Taczanowski. The measurement of the exposed culmen given in the table is that of one unsexed specimen that I have seen and is used for the purpose of the ratio diagram of *Penelope* (fig. 18). The male is the type of *P. albigenis* which was measured by Taczanowski soon after it was collected. I have examined it, but do not quote my measurements because the type (pl. 16) is now in bad condition, the wing and tarsus being distorted, and the tip of the culmen broken.ⁱ *Aburria* is monotypic, but its measurements are given separately (as well as combined) because they vary somewhat geographically.^j Wing and tail lengths of the type of *C. f. pinima* quoted from Hellmayr (1906, p. 683).

TABLE 2

RATIO OF THE LENGTH OF THE TARSUS TO THAT OF THE WING IN THE MALES OF THE CRACIDAE^a

Genus	Mean Wing Length	Mean Tarsus Length	Range of Ratios	Mean of Ratios
<i>Ortalis</i>	218	59	.232-.300	.268
<i>Penelope</i>	297	68	.192-.270	.230
<i>Pipile</i>	347	60	.167-.200	.175
<i>Aburria</i>	370	64	.170-.182	.174
<i>Chamaepetes</i> ^b	303	66	—	.216
<i>Chamaepetes</i> ^c	257	64	.238-.262	.249
<i>Penelopina</i>	236	69	—	.290
<i>Oreophasis</i>	388	81	—	.210
<i>Nothocrax</i>	294	81	—	.278
<i>Mitu</i>	379	106	.278-.284	.281
<i>Pauxi</i>	397	104	.260-.268	.263
<i>Crax</i>	385	103	.254-.283	.269

^a Measurements, in round numbers, and samples from table 1.^b *Chamaepetes unicolor*.^c *Chamaepetes goudotii*.

pattern, and it is obvious that *Penelope* (13 species) varies more than *Ortalis* (10 species) and *Crax* (seven species). The smallest individual of *Penelope* measured was 200 mm. smaller than the largest, with a difference of 122 in the means, as against, respectively, 113 and 81 in *Ortalis*, and 74 and 32 in *Crax*. The great range of size in *Penelope* is caused chiefly by *P. purpurascens* which attains a great size, and, if we exclude it, the range is reduced to 129 and the difference between the means to 85. The range of variation of *Penelope* thus becomes about similar to that of *Ortalis*, although the latter is much smaller, averaging 218, as against 289 in *Penelope*, with *P. purpurascens* excluded, or 297 when it is included.

The other genera that are polytypic are *Pipile* and *Mitu* (three species each), and *Chamaepetes* and *Pauxi* (two species each). *Pipile* is very homogeneous, with a difference of only 12 in the means. *Mitu* is not very variable and is comparable to *Crax*. The two species of *Chamaepetes* are quite different in size, as shown by figure 7. *Pauxi unicornis* appears to be similar to *P. pauxi*, but its measurements are not sufficiently known, as only one male and one female have been collected.

All the measurements of the males average larger than those of the females, with the

exception of *Penelopina*, the female of *P. nigra* averaging larger than the male, with a mean wing length of 247, as against 236 in the males.

The sexual dimorphism is slight; it amounts only to about 5 per cent. The female of *Penelopina nigra* is 1.05 larger than the male, the females of the other species varying from .89 to .99 smaller than the males, with an average of .943 in 86 populations.

The coefficients of variation of the four measurements in polytypic genera are given in table 3. *Pauxi* is not included, because the sample was insufficient. The variation is not more pronounced in one sex than the other, but the length of the tail appears to be slightly more variable than the length of the wing, and the lengths of the tarsus and exposed culmen are more variable than the length of the tail. The reasons for this increased variability are not clear to me, but the difference in the case of the tail is probably valid because such a difference is quite general in birds, as Amadon (1950, p. 186) has remarked. Greater coefficients in the case of the tarsus and culmen are shown also by several statistical studies of completely unrelated birds. It is probable that the length of the wing is more "critical," and is therefore less variable, and that the greater coefficients for the tarsus and culmen are

TABLE 3
COEFFICIENTS OF VARIATION^a FROM MEASUREMENTS IN TABLE 1

Genus	No. of Coeffi- cients	Males		No. of Coeffi- cients	Females	
		Range	Mean		Range	Mean
<i>Ortalis</i>						
Wing length	22	1.98-5.07	3.25	18	1.34-4.64	3.16
Tail length	22	1.83-6.26	4.30	18	1.35-6.14	3.95
Tarsus length	22	2.82-6.59	4.16	18	3.18-5.80	4.66
Culmen length	22	3.84-8.0	5.93	18	4.68-8.65	6.08
<i>Penelope</i>						
Wing length	25	2.23-5.03	3.23	24	0.84-4.52	2.94
Tail length	24	2.69-5.45	4.12	23	2.54-5.14	4.03
Tarsus length	25	2.65-6.17	4.43	25	2.42-5.96	4.29
Culmen length	25	3.51-7.58	5.70	25	3.80-8.91	5.59
<i>Pipile</i>						
Wing length	4	3.23-4.32	3.49	4	2.76-5.00	3.98
Tail length	4	2.60-4.04	3.76	4	2.64-7.37	5.70
Tarsus length	4	3.03-6.06	3.95	4	4.68-5.62	5.32
Culmen length	4	4.41-4.97	4.84	4	3.75-5.68	4.99
<i>Chamaepetes</i>						
Wing length	5	3.05-3.71	3.44	4	2.96-4.31	3.58
Tail length	5	3.05-4.09	3.61	4	2.57-4.91	3.84
Tarsus length	5	3.45-5.46	4.01	4	3.40-6.18	4.69
Culmen length	5	4.14-7.44	5.80	4	5.85-6.84	6.30
<i>Mitu</i>						
Wing length	3	2.52-3.51	2.96	3	2.13-3.69	2.69
Tail length	3	3.19-4.55	3.70	3	3.76-4.06	3.89
Tarsus length	3	4.09-4.55	4.30	3	4.02-6.34	4.83
Culmen length	3	4.45-5.86	5.00	3	4.35-4.81	4.67
<i>Crax</i>						
Wing length	6	2.35-3.14	2.73	7	1.17-3.52	2.65
Tail length	6	2.70-4.67	4.00	7	1.71-4.74	3.38
Tarsus length	6	2.99-5.30	4.33	7	2.56-4.68	3.88
Culmen length	6	4.51-7.35	5.62	7	3.63-6.77	5.32

^a Computed for samples of five specimens or more.

affected to some extent by errors in measurements. I find it difficult to measure the tarsus with accuracy in any bird, and the difficulty is increased in the Cracidae by the fact that the skin does not dry evenly and that the tarsus is often distorted also by the dissection of the tendons. The exposed culmen is relatively short, and the results are, no doubt, affected to some extent by the loss of a few feathers and the wear of the tip of the bill.

PROPORTIONS

The four measurements that were taken for each species were analyzed by means of

logarithmic ratio diagrams which are easy to construct and provide a method for comparing the proportions graphically and clearly. These diagrams compare the ratios only, not measurements, and the ratios would form a straight vertical line when the proportions of two birds are identical whether these are of the same absolute size or not. The ratio between the length of the wing and that of the tarsus is discussed above in the description of the characters of the tarsus.

The ratio diagrams used in this study are of two types. A standard of comparison is used in the diagram that compares the proportions of the genera (fig. 8) and also those of

some polytypic genera (figs. 15, 18, 21, 33, and 34). The standard corresponds to the ratio of 1.0, and its logarithms represent zero, the differences above or below being plotted on ordinary graph paper with a suitable scale. This method was first proposed by Simpson (1941), and was adopted by Amadon (1950), and by me in other papers on the Cracidae or other birds. Simpson and Amadon gave directions for the construction of this type of ratio diagram.

The proportions shown are relative, and the resulting pattern is affected, of course, by the selection of the standard. If one or more of the measurements of the standard are aberrant, the pattern of the connecting lines will be more or less skewed.

A standard of comparison is not used in the other type of diagram, which illustrates the variation in the Penelopini (fig. 11) and that in the Cracini (fig. 27). The wing length of each species corresponds to the ratio of 1.0, and its logarithm to zero, and the differences are plotted in the same manner as in the other type of diagram. The ratios are absolute, because no standard of comparison is used, but the pattern can be continuous for only one ratio. This second type of diagram, which is useful for comparing a large number of forms, was devised by Amadon and me for my study of the Muscicapini (1953). It does not seem to have been used by anyone else, or again since 1953 until the present study.

The standard of comparison that I selected is *Penelope marail*, because I believe that the ancestor of the modern Cracidae was very probably a form that resembled it—a bird of medium size, not highly specialized, with a long tail, which was arboreal but not extremely so, and not terrestrial to the extent that some members of the modern Cracidae have become. Its tarsus was intermediate in length, not so short as in *Pipile* and *Aburria*, and probably not so long as in the Cracini. *Penelope* meets all these requirements, and *Penelope marail* seems to be an excellent choice because it occupies a central position in *Penelope*, intermediate in size between the small and large species, and is not primitive or specialized in any other character.

The genus *Procrax* that Tordoff and Macdonald (1957) have described from the Lower Oligocene of South Dakota seems to

be essentially similar to *Penelope*, although its tarsus was shorter, measuring 101 mm., as against 136 in *Penelope marail*, according to Tordoff and Macdonald who wrote that *Procrax* "most resembles *Pipile* among modern genera." *Pipile* and *Penelope* are, however, certainly related, and it seemed best not to select *Pipile* for the standard for comparing the proportions of the modern genera, because its legs are too short, and it represents (with *Aburria*) one extreme among the modern genera.

The proportions of all the modern genera diverge. The tail of the Cracini (fig. 8) is somewhat shorter than that of *Penelope*, the tarsus is very much longer, and the culmen varies from short in *Pauxi* to much longer in *Crax* and *Mitu*. The tail and tarsus of *Ortalis* and *Penelopina* are longer than in *Penelope*, but the reverse is true in *Pipile* and *Aburria*. The proportions of the culmen are, however, identical, or virtually so, in the five genera. The proportions of the tail and tarsus are nearly identical in *Oreophasis* and *Penelope*, but the culmen of *Oreophasis* is very short, much shorter than in *Penelope* or any other genus. The proportions of *Chamaepetes* differ least from those of *Penelope*.

It is shown, in the discussion of the tarsus, that it decreases in the genera that are more arboreal, as is illustrated by the ratio diagram (fig. 8), which shows also the increase in the genera that are more terrestrial. The pattern of *Chamaepetes* in figure 8 is ambiguous, because the measurements of its two species were averaged for the purpose of the diagram, but the tarsus is proportionally shorter also in *C. unicolor* which is more arboreal than *C. goudotii* (table 2).

It is interesting to note that the decrease or increase in the tail ratios is correlated with the ratios of the tarsus, the tail, as well as the tarsus, being shorter in the genera that are more arboreal. This correlation exists also in *Chamaepetes*, the wing/tail ratio of *C. unicolor* being only .85, as against .94 for *C. goudotii*. This correlation of the ratios of the tail and tarsus is true only of the Penelopini, not of the Cracini.

The proportions of the culmen are not affected, or only very slightly so, except in *Oreophasis*, in which two-thirds or more of the base of the bill is very heavily feathered,

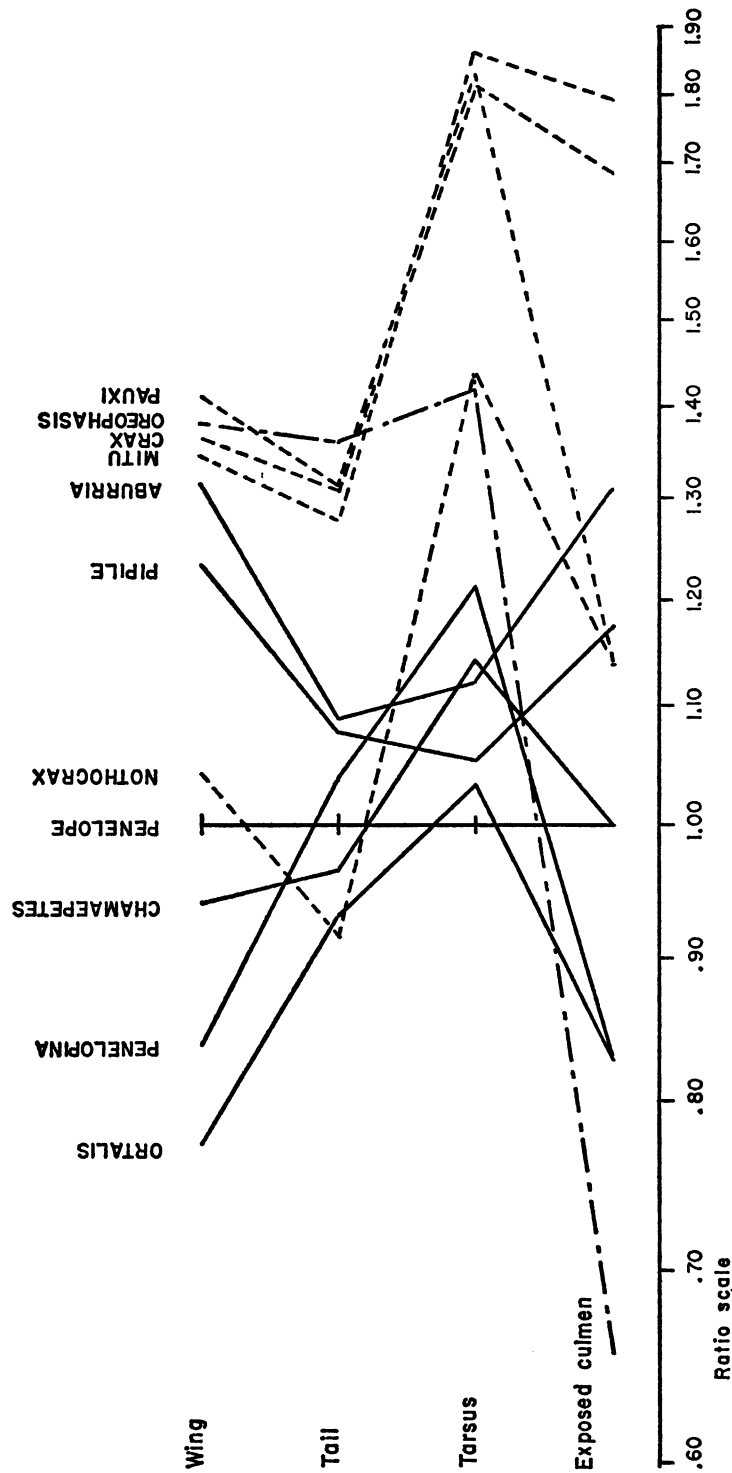


FIG. 8. Comparison by ratio diagram of the proportions of the genera of the Cracidae. The standard of comparison is *Penelope marail*. The proportions of the Penelopini are shown by solid lines; of the Oreophasini, by a line of long and short dashes; and of the Cracini, by short dashes.

and in *Pauxi*, in which the development of the helmet has apparently caused a general decrease in the size of the bill.

DISTRIBUTION AND ISOLATING MECHANISMS

The distribution of the Cracidae is briefly outlined above, and the distribution of the genera and species is discussed in detail in the Systematic List and is illustrated by maps.

Some species have a very restricted range, whereas the range of some others is enormous and encompasses more than one climatic region. The range of *Pauxi unicornis* is probably quite small, because this bird is known so far from only one locality in the Yungas de Cochabamba which have been visited by more than one collector. *Penelope albipennis* is extinct and is known with certainty from only two localities, about 200 kilometers apart in northwestern Peru. *Oreophasis derbianus* is local in the upper levels of the cloud forest of the Sierra Madre of Chiapas, south to the Volcan de Fuego in Guatemala, a total range of only about 240 kilometers.

On the other hand, *Penelope purpurascens* is widely distributed from about the twenty-fourth parallel in both eastern and western Mexico, south to the delta of the Orinoco, and about the fourth parallel south of the equator in western Ecuador. *Penelope superciljaris* blankets the whole of Brazil, south of the Amazon, west to the Guaporé and Madeira, and spreads also to eastern Paraguay, and Misiones in Argentina. The ranges of *Ortalis guttata*, *Penelope jacquacu*, *Pipile pipile*, *Mitu mitu*, and *Crax fasciolata* are also immense.

The ecology of the very widely distributed species undoubtedly varies a great deal; for instance, *Ortalis guttata* inhabits north-eastern Brazil from the Rio Doce north to Pernambuco, extreme southeastern Brazil, and the foothills of the Andes from Colombia to Bolivia. These regions have a very different climate, and the rainfall, which also varies locally, creates very important changes in the vegetation and its distribution. *Ortalis vetula* inhabits regions that are extremely humid, and others that are arid, such as the

valley of the Rio Grande where the annual rainfall varies from about 400 to 700 mm., and eastern Guatemala in a region where it exceeds 5600 mm.

Some genera, such as *Nothocrax*, *Oreophasis*, *Penelopina*, and *Aburria*, are restricted to regions where physiographic and phytogeographic conditions are uniform, or probably do not vary significantly. These genera are chiefly montane, as is true of individual species, such as *Penelope montagnii*, but the ecology varies with the altitudinal range. For instance, *P. montagnii* is distributed from about 1060 to 3650 meters, ranging from the humid tropical zone up through the subtropical to the temperate zone. *Crax* is restricted chiefly to the lowlands or low elevations but breeds from the coast up to 1900 meters, or from the tropical to the subtropical zone.

The distribution of the polytypic genera shows two very distinct patterns: one in which all the species overlap partially or completely, and the other in which they are allopatric or virtually so. The first pattern is shown only by *Penelope*, in which 12 of the 13 species overlap. The only species that does not overlap any other is *P. albipennis*, but the original range of this bird is really unknown, as it was discovered on the extreme verge of extinction. *Penelope superciljaris* overlaps five species, as does *P. montagnii*, if not six.

All seven species of *Crax* are perfectly allopatric. The overlap is very slight in *Ortalis* (figs. 13 and 14) and *Mitu* (fig. 30), but it is more extensive in *Pipile* (fig. 19), although its three species are essentially allopatric. *Chamaepetes* and *Pauxi* have two species each that are isolated by enormous gaps: about 600 kilometers for *Chamaepetes* and about 2900 for *Pauxi*.

The ranges of some of the allopatric species come in contact, or approach closely, but reproductive isolation is maintained because hybrids are unknown, although the species of *Penelope*, *Mitu*, and *Crax* that have been tested in captivity are interfertile, as was shown by Taibel (1954, 1958, 1964). Taibel succeeded also in breeding hybrids of the second generation in *Crax* (1958), and of *Mitu* and *Crax* (1961b) that he had inter-

bred (1961a). Vuilleumier (1965) listed successful hybridization experiments conducted by other investigators.

Nevertheless, interbreeding does not occur in nature, as the isolating mechanisms seem to be perfectly effective. These mechanisms are of various sorts, and in some instances more than one probably operates. The isolation may be ecological or geographical. As far as the latter is concerned, it is noteworthy that all the Cracidae are very sedentary, and a large river may form a perfect barrier, as is very evident in *Ortalis* and *Crax*. For instance, *Ortalis ruficauda* and *Crax daubentoni* replace *O. motmot* and *C. alector* on opposite sides of the Orinoco. The Amazon, or some of its large tributaries, form similar barriers.

In *Penelope*, in which there is so much overlap, the most important isolating mechanism seems to be differences in ecology, because the species that overlap, as a rule, differ very clearly in general size. Such differences are very probably reinforced by differences in behavior, consisting of vocalizations, or of sound produced by the modified outer primaries during display. The differences in vocalization are probably the most important mechanism in *Ortalis*; the birds of this genus are noted for being very vocal and raucous. Vocalizations undoubtedly operate in other genera, as suggested by the modification of the trachea. The trachea is looped and convoluted in some species of *Penelope* and *Crax* but is straight in others. A convoluted trachea seems to be found in the males only of *Ortalis*; it has been reported also in the males of *Nothocrax*, of some species of *Mitu*, and in *Pauxi pauxi*.

I have shown in one of my preliminary papers (1965a), as also by Davis (1965), that the vocalizations of *Ortalis vetula* and *O. poliocephala* are very different. These two species come in contact and appear to overlap slightly on the Isthmus of Tehuantepec and probably differ in their ecology as well as in their vocalizations. These two isolating mechanisms seem to operate also between *O. vetula* and *O. garrula* which approach each other very closely in Nicaragua.

Finally, the very sharp morphological differences, which are so obvious in *Pipile*, *Mitu*, and *Crax*, must be very important isolating

mechanisms. These involve the plumage in *Mitu*, as *M. tomentosa*, the range of which appears to overlap slightly that of *M. salvini*, is chestnut below and at the tip of the tail, whereas *M. salvini* is snow-white below and at the tip of the tail. In the case of *Pipile*, the color of the face or the throat, or both, differs abruptly in all three species, and the fleshy appendages at the base of the bill differ very strikingly in *Crax*, as is shown in plate 15.

DECLINE AND EXTINCTION

All the Cracidae, with the possible exception of *Ortalis*, have decreased in number and receded from many areas with increasing settlement. Overhunting, and the spread of roads into regions that were formerly not easily accessible, have played their part, and the birds have been eliminated by the destruction of the forest. The regions that have been most seriously affected are eastern Brazil, Central America, northern Venezuela, Trinidad, and some parts of Mexico.

Penelope albipennis did not inhabit these regions but disappeared very soon after it was discovered in northwestern Peru in the 1870's. The reports of its discoverer show very clearly that it was then on the verge of extinction, and only three birds were collected.

A very well-characterized subspecies of *Crax fasciolata*, named *pinima*, appears also to be extinct. *Pinima* was apparently restricted to northeastern Para and northern Maranhão. It has not been collected or reported from Para since 1842, and from Maranhão since 1907. It is also very rare in collections and seems to be known from a total of only seven specimens, two of which may have been destroyed during World War II.

Mitu mitu is abundant in the Amazon Basin, but has very probably disappeared from northeastern Brazil where it seems to have always been very rare. Marcgrave (1648) reported it from northeastern Brazil, but more than 300 years elapsed before it was rediscovered in this region in 1951. The only bird that was seen and shot has been discussed by Pinto (1952), who stated that the survivors were doomed by the rapid destruction of the last remnants of the forest.

Burmeister (1856) may have seen a specimen from northeastern Brazil.

Crax blumenbachii, also of eastern Brazil, is very gravely threatened and has disappeared from nearly all the localities from which it was known. It may never have been abundant, as it seems to be known from only about 10 specimens.

The nominate subspecies of *Pipile pipile* (which could be considered to be a separate species, depending on one's concept) is restricted to one or two remote localities in the mountains of northern Trinidad. It seems to be very rare and gravely threatened. The population of *Crax rubra* from Cozumel Island, which represents a distinct subspecies, is probably also quite small.

Oreophasis derbianus has become very rare during the last 30 years and has disappeared from a number of localities of its relatively small range. This regal game bird may survive on a few remote and inaccessible mountaintops but must be protected rigidly in the parts of its range that are more accessible.

The record is not very good, and it is possible also that some species of the Cracidae

decline for reasons that are unknown, but not caused by human disturbance. Extinction seems to be the only way to account for the greatly disjunct ranges of *Chamaepetes* and *Pauxi*, but the morphological characters of the birds show that the separation is ancient; no explanation comes to mind.

PHYLOGENY

The living Cracidae were divided by Huxley (1868) into two subfamilies, the Penelopinae and the Cracinae, a division he based on a clear-cut difference in the proportions of the pelvis. The postacetabular area is short and broad in the Penelopinae, long and narrow in the Cracinae (fig. 9). Vuilleumier (1965) did not recognize subfamilies or tribes because the difference appears to be adaptive, but all the characters of an organism are adaptive, unless proved otherwise. We can judge only whether the difference is of phylogenetic importance or not. I believe it is important because it certainly corresponds to a natural division of the living genera, and is accepted by paleontologists, or

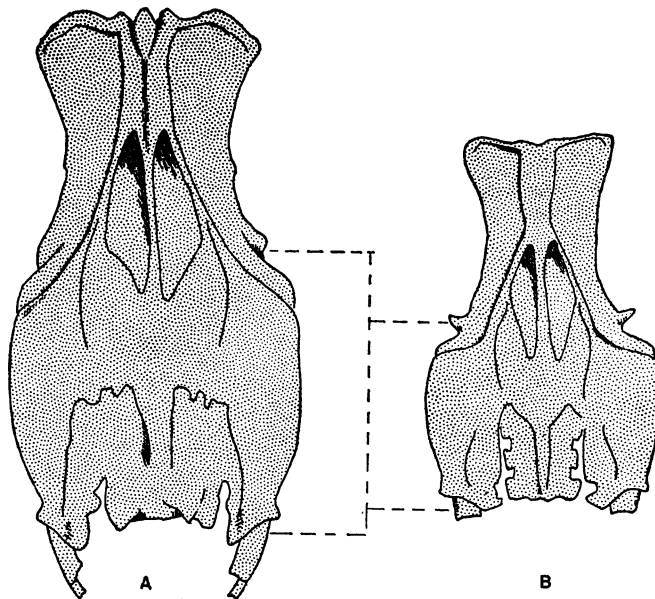


FIG. 9. Proportions of the postacetabular area in the living Cracidae. A. Cracinae. B. Penelopinae. The dorsal aspect of the pelvis is shown, and the area included between the broken lines constitutes the postacetabular area. Adapted from Huxley (1868), with his nomenclature and terminology.

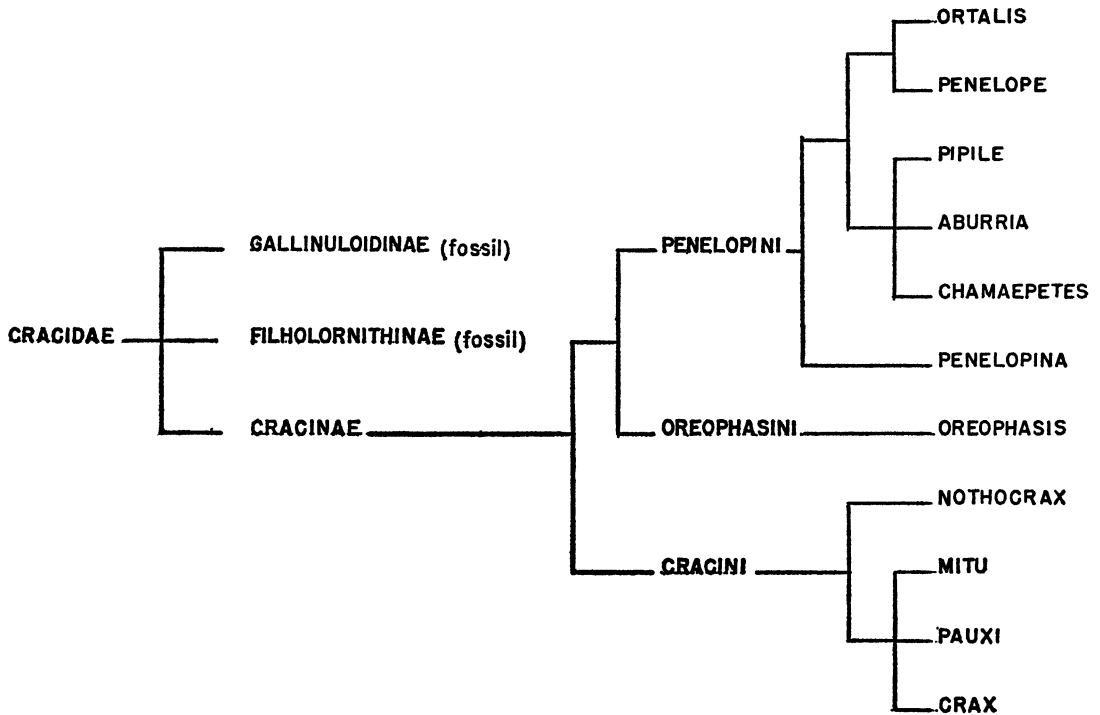


FIG. 10. Phylogenetic diagram of the Cracidae.

other authors such as Ridgway and Friedmann (1946).

Sclater and Salvin (1870) and G. R. Gray (1870) adopted the division proposed by Huxley, but modified it by recognizing an additional subfamily, the Oreophasinae,¹ for *Oreophasis* which Huxley had included in the Penelopinae. *Oreophasis* differs from the Penelopinae by being bare, not feathered, on the vertex of the skull from which a tall bony "horn" grows; by being very densely feathered at the base of the bill, the feathers covering the nostril, whereas the base of the bill is nude and the nostrils are exposed in the Penelopinae; and by its unique color pattern, which differs from that of the Penelopinae and from that of all other members of the Cracidae.

Tordoff and Macdonald (1957) have recog-

nized the fossil subfamily Gallinuloidinae and the three living subfamilies of Sclater and Salvin. Brodkorb (1964) has recognized the Gallinuloidinae, the Filholornithinae (also fossil), and the Penelopinae and the Cracinae. I am not qualified to discuss the fossil subfamilies, but I am convinced that the arrangement of the living Cracidae in three groups is a quite natural division. It may be too important to accord them subfamily rank, and I prefer to recognize three tribes, the Penelopini, the Oreophasini, and the Cracini, which correspond to the subfamilies of Sclater and Salvin, although I have reversed the sequence of these authors, by starting with the Penelopini which are the least specialized. Verheyen (1956) has subdivided the Penelopini by recognizing an additional tribe, the Pipilini, for *Pipile*, *Aburria*, and *Chamaepetes*, which seems unnecessary.

My concept of the phylogeny is shown here diagrammatically (fig. 10). I believe that *Ortalis* and *Penelope* are very closely related, as no line can be drawn between them that is not breached by one character or another.

¹ G. R. Gray called the subfamily Oreophasidinae, but this name was probably published later than Oreophasinae. Sclater and Salvin's paper is dated June 9, 1870, but was actually published in November, 1870. The day is not known, but it is probable that it was earlier than November 9, 1870, which is the date of the preface of Gray's book.

When all the characters are assessed as a unit, however, it is quite evident that it would be an error to merge these two genera. *Pipile* is related to *Penelope* also, but is more distinct from *Penelope* than *Penelope* and *Ortalis* are from each other. *Aburria* seems to be related to *Pipile*; and *Chamaepetes*, to *Aburria* and *Pipile*. These three genera form a distinct radiative group, best adapted to a highly arboreal mode of life, but the adaptation is less perfect in *Chamaepetes*, as one of its two species is less arboreal than the other. The characters of *Chamaepetes* are simplified, and *Aburria* is more simplified than *Pipile* in some respects, but possibly this simplification represents secondary modifications.

Penelopina is aberrant in virtually all characters and occupies a position apart. I certainly do not agree with Vuilleumier (1965) that *Penelopina* is intermediate be-

tween *Ortalis* and *Penelope* and that this "intermediate" position "must be emphasized." *Penelopina* is a true member of the Penelopini, but a very strange one.

The characters of *Oreophasis* are sufficiently distinct to warrant its isolated position as a separate tribe. Nevertheless it is a guan, not a curassow, hence is related to the Penelopini.

Three genera (*Mitu*, *Pauxi*, and *Crax*) of the curassows are closely related. They represent different evolutionary lines, however; *Mitu* is the least evolved, *Pauxi* is intermediate, and *Crax* is the most specialized. *Nothocrax* is a strongly aberrant curassow, not closely related to the other three genera. The phylogeny of the species of the polytypic genera is discussed below in the Systematic List.

SYSTEMATIC LIST

KEY TO THE TRIBES

1. Vertex denuded, with tall bony tubercle; basal two-thirds of upper bill densely feathered, feathers concealing nostril . . . *Oreophasini*
Vertex completely feathered, without tubercle; base of upper bill not feathered, nostril exposed 2
2. Postacetabular area narrow; bill large and heavy, distinctly arched and compressed laterally, much higher than broad at base *Cracini*
Postacetabular area broad; bill small or relatively small, not arched but depressed, not compressed laterally, broad at base, with breadth at base equal to height, or more often greater *Penelopini*

TRIBE PENELOPINI

KEY TO THE GENERA

1. Throat completely feathered 2
Throat not completely feathered 3
2. Pattern of plumage interrupted, barred and mottled *Penelopina* (female)
Pattern of plumage not interrupted *Chamaepetes*
3. Inner web of outer primaries narrowly falcate, very deeply excised distally 4
Inner web of outer primaries not falcate, normal in shape, or more or less slightly emarginated 5
4. Upper wing coverts very boldly patterned with white *Pipile*
Upper wing coverts uniform, not patterned *Aburria*
5. Plumage totally uniform *Penelopina* (male)
Plumage not uniform 6
6. Tail uniform¹. *Penelope* (in part)
Tail not uniform 7
7. Mantle and upper wing coverts streaked with white to varying degree; forehead, face, and malar streak variegated with white *Penelope argyrotis*
Mantle and upper wing coverts not streaked with white; forehead, face, and malar streak not variegated with white *Ortalis*

MORPHOLOGICAL VARIATION

The Penelopini are not homogeneous and vary in many characters, which are enumerated below.

¹ The tail is brown and uniform in 12 of the 13 species of *Penelope*, but is tipped with dull chestnut in *P. argyrotis*, which, however, differs from all the species of *Ortalis* as stated in the key.

ated in the analysis of the family. The characters of this tribe, and the phylogeny of its genera, are also mentioned in the discussion of the phylogeny of the family and are briefly summarized in the key to the three tribes.

The morphological variation affects the structure of the plumage, the juvenal molt, the shape and structure of the wing and tail, the development of the crest, the feathering of the face, throat, and head of the tarsus, the pigmentation, color pattern, measurements, proportions, and sexual dimorphism.

Sexual dimorphism in coloration exists only in *Penelopina*, in which it is extreme, the male being uniformly deep black and very glossy, whereas the female has a concealing plumage which is brown, mottled and heavily barred, and shows a general similarity to the coloration of the females of other Galliformes, especially among the Tetraonidae. It is noteworthy also that females of *Penelopina* average larger than the males, whereas the reverse is true for the rest of the family.

The narrowly falcate outer primaries of *Pipile*, *Aburria*, and *Chamaepetes*, and the presence of throat wattles, are peculiar to the Penelopini.

The variation in size and proportions is shown in figure 11, where only the mean wing length is given; the absolute range of the length of the wing is illustrated in figure 7. The measurements and proportions of the Penelopini are far more variable than those of the Cracini (fig. 27), the highly arboreal habits of some Penelopini causing a very distinct decrease in the ratios of the tarsus and tail.

A diagnosis is given below for each genus, in which it is compared to the genus or genera to which it is related.

GENUS ORTALIS

DIAGNOSIS

This genus is composed of 10 species that are very widely distributed from the lower Rio Grande Valley of Texas, south to northern Argentina. All the species are small, or relatively small, and include all the smallest

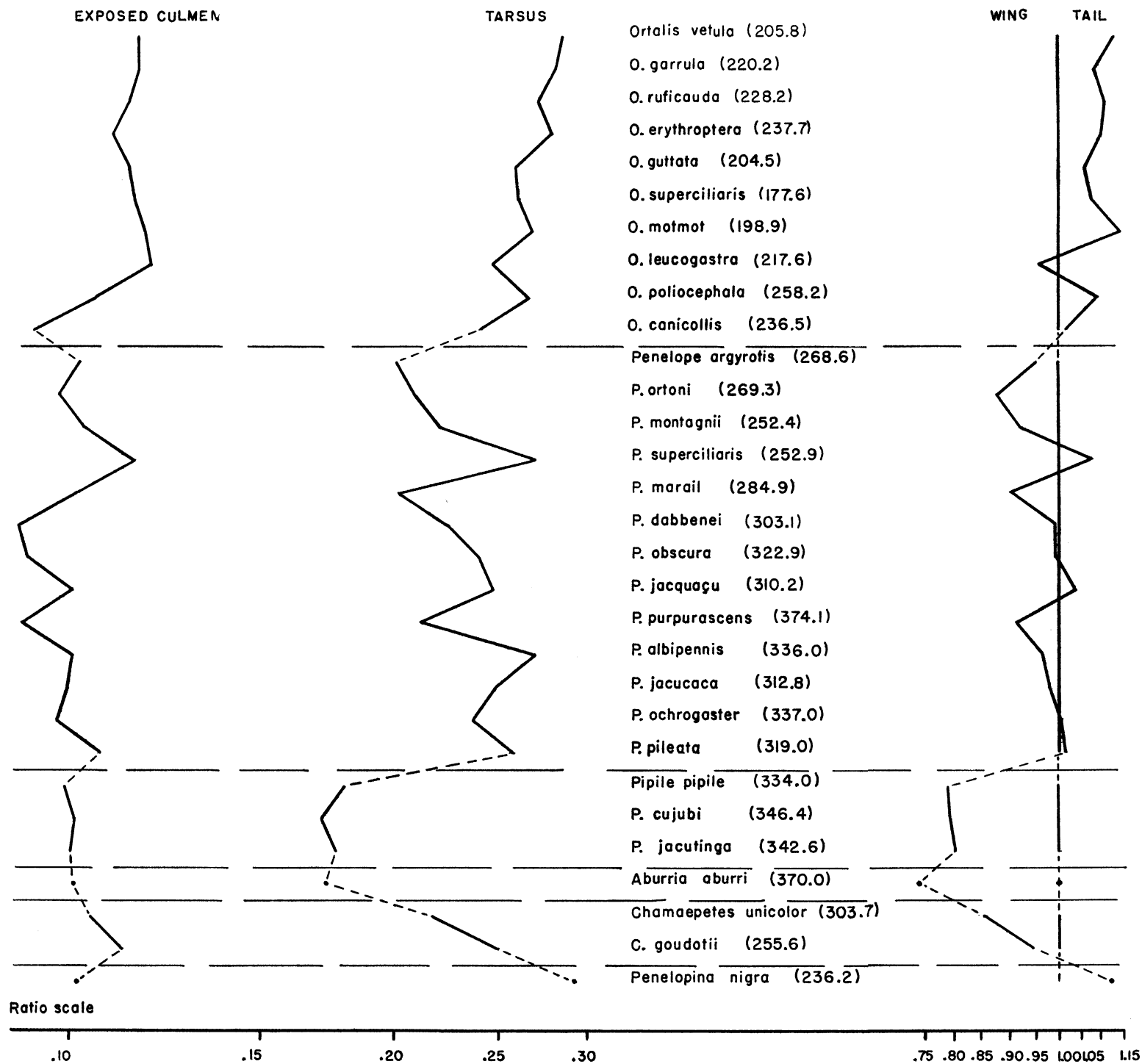


FIG. 11. Comparison by ratio diagram of the proportions of the adult males of the Penelopini.
 The numbers in parentheses denote the mean wing length.

members of the family. The plumage is loose and soft in most species, more decomposed than in any other genus of the family. The feathers of the crown are more or less elongated, integrated, or decomposed, but they do not form a true crest. The tail of some species is more graduated than in any other genus of the family, and is in no instance uniform in coloration, the tips or distal part of the outer tail feathers being distinctly paler, or of a different color than the base, with which they contrast most conspicuously. The rest of the plumage is predominantly plain "brown," paler below. The lores and most of the face and upper throat are bare, with the exception of a narrow feathered strip which divides longitudinally and sharply into halves the bare area of the throat, and the bare skin of the throat does not form a dewlap or wattle.

KEY TO THE SPECIES OF *Ortalis*

1. Primaries chestnut 2
Primaries brown 3
2. Tips of tail chestnut *O. erythroptera*
Tips of tail buffy white or grayish white, not chestnut *O. garrula*
3. With a superciliary streak which is buffy, cinnamon, or whitish *O. superciliaris*
Without a superciliary streak 4
4. Crown, nape, and feathers bordering bare areas on face and throat reddish chestnut, and confluent with broad band of reddish orange encircling base of throat *O. motmot*
Crown, nape, and feathers bordering bare areas on face and throat not reddish chestnut, lacking band of reddish orange at base of throat 5
5. Lower breast and abdomen chestnut *O. poliocephala wagleri*
Lower breast and abdomen white, buffy, grayish, or brownish, not chestnut 6
6. Feathers of breast rounded and normal in shape, not decomposed, and with pale tips, or pale edges 7
Feathers of breast decomposed, without pale tips, or pale edges 8
7. Tips of tail white *O. leucogastra*
Tips of tail chestnut *O. guttata*
8. Tips of tail chestnut 9
Tips of tail creamy or buffy white, grayish or dingy white, not chestnut 10
9. Chestnut tips restricted to first and second outer rectrices, also to third, in one subspecies *O. canicollis*

- Chestnut tips present on all outer rectrices (lacking only on central pair of rectrices) *O. ruficauda ruficauda*
10. Vent, and under tail coverts chestnut *O. ruficauda ruficrissa*
Vent, and under tail coverts varying from creamy or buffy white to paler ocher, buffy, or isabelline brown, not chestnut 11
11. Breast olive-brown; vent and under tail coverts buffy or isabelline brown; lanceolated feathers at base of throat short and soft; very much smaller, wing length of 150 adults measuring 176–235 (201) mm. *O. vetula*
Breast grayish; vent and under tail coverts pale ocher, or creamy or buffy white; lanceolated feathers at base of throat long and stiff; very much larger, wing length of 53 adults measuring 234–283 (255) mm. *O. poliocephala*

DISTRIBUTION

The 10 species of *Ortalis* represent one another geographically (figs. 12 and 13), with only one exception; in southern Mexico *O. vetula* and *O. poliocephala* come together on the Isthmus of Tehuantepec and appear to overlap slightly. These two species occur also in the region of Pijijiapan, Chiapas, together with *O. leucogastra* (for a detailed discussion of the distribution in these regions, illustrated by maps, see Vaurie, 1965a).

In that preliminary paper (1965a) and in another (1956b), I mentioned that the ranges of *Ortalis vetula* and *O. garrula* met or overlapped slightly, in Nicaragua in the region of Matagalpa. These statements were based on specimens of the two species that I had examined and that were labeled "Matagalpa." Dr. Thomas R. Howell, who is most familiar with the birds of Nicaragua, has since written to me that he doubts very much that the two species overlap in Nacaragua. He wrote that the mere mention of "Matagalpa" as a locality is misleading, because very distinct types of habitat, namely, "Cloud Forest, Montane Pine Forest, Caribbean Slope Rain Forest, and Pacific Slope Thorn Forest . . . can be found within a few kilometers of the town." *Ortalis garrula* inhabits more humid regions than *O. vetula*. Howell concluded: ". . . it is safe to say that all records of *O. garrula* [in Nicaragua] are from the humid Caribbean Slope and all records of *O. vetula* are from the relatively dry

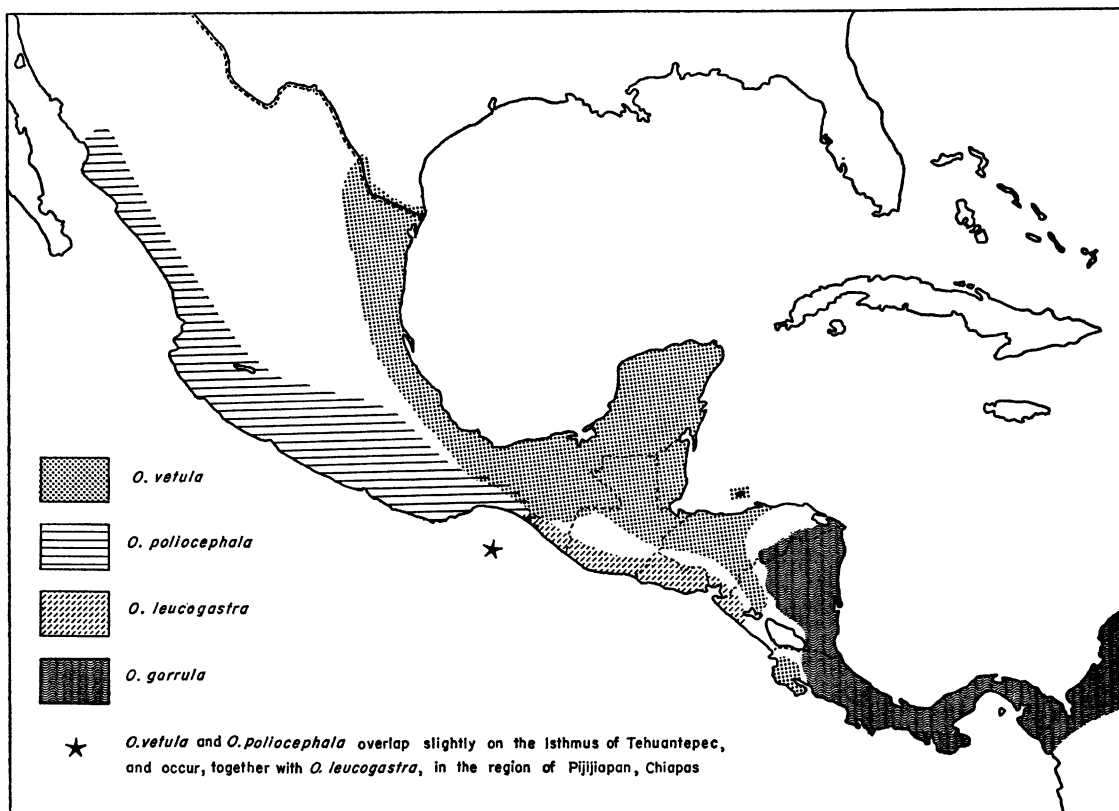


FIG. 12. Distribution of the genus *Ortalis* from Mexico to northern Colombia.

Pacific Slope. The ranges of the two forms doubtless approach closely in the Matagalpa area as well as in other less well-studied regions along the Pacific and Caribbean Slope divide, but I do not believe that there is any significant overlap, if any at all between the two forms."

The range of *Ortalis garrula* extends to the Santa Marta Massif in northern Colombia, but the remaining species of the genus (*ruficauda*, *guttata*, *superciliaris*, *motmot*, *erythroptera*, and *canicollis*) are restricted to South America and are strictly allopatric (fig. 13). In some instances, the ranges are separated only by a very large river which evidently forms a complete barrier. The Orinoco divides *O. ruficauda* and *O. motmot*, and the latter replaces *O. guttata* north of the Amazon and east of the lower Tapajoz. The eastern limits of the range of *O. motmot* south of the Amazon are uncertain, but *O. motmot* and *O. superciliaris* are probably separated by the Araguaia and the Tocantins. Present

evidence shows that *motmot* reaches only to the left bank of the Araguaia and that *O. superciliaris* is not found west of the lower Tocantins. To be sure, one specimen of *O. superciliaris* has been collected on the left bank of the Tocantins at Santo Antonio, but this locality is above its junction with the Araguaia. The range of the latter may therefore extend west of the Tocantins (at least above its junction with the Araguaia), but, if so, an overlap does not result.

In Ecuador, the Andes separate the ranges of *Ortalis erythroptera* and *O. guttata*. The Andes have not, however, always been a barrier, because *O. guttata* inhabits also the western slopes of the Eastern Andes in Colombia and the valleys of the Magdalena and Cauca rivers (fig. 14; Vaurie, 1965b).

Some narrow or very broad gaps in distribution are shown in figure 13. The narrow gap in Bolivia between the range of *Ortalis guttata* and that of *O. canicollis* may be more apparent than real, but in northern Colom-

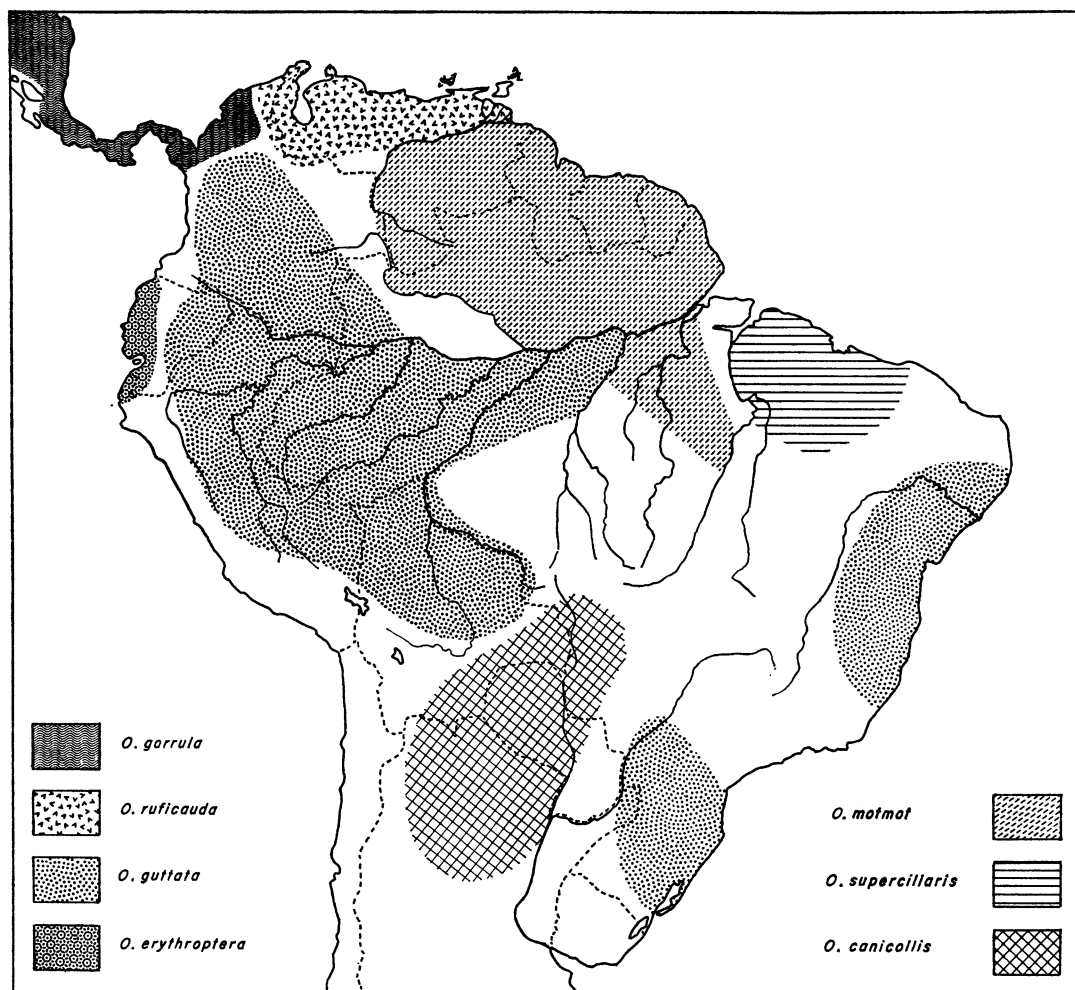


FIG. 13. Distribution of the genus *Ortalis* in South America.

bia, where the distribution is much better known because of extensive collecting, there is no evidence that the ranges of *O. garrula*, *O. ruficauda*, and *O. guttata* overlap or even come into contact.

On a more detailed map (fig. 14), reproduced from my study of *Ortalis garrula* and *O. ruficauda* (1965c) and which shows individual records, it is instructive to note that the range of *O. ruficauda* extends west only to the northeastern, eastern, and southeastern foothills of the Santa Marta Massif (the localities shown are Dibulla, the region west of Fonseca, Valledupar, and Camperucho), whereas the range of *O. garrula* extends east only to the northwestern, western, and southwestern foothills of the Massif (or to Mamatoco

which is 7 kilometers east of the city of Santa Marta, to the mouth of the Rio Aracataca, and to Fundacion).

In the south, the range of *Ortalis ruficauda* extends west to the region north of Cucuta (or about latitude 8° N.), and to the Rio Bojaba in Arauca (or about latitude 7° N.), whereas *O. guttata* ranges north to about latitude $7^{\circ} 20'$ N. in the region northwest of Bucaramanga, but, as the latter lies west of the range of *O. ruficauda*, there is no actual overlap.

The ranges of *Ortalis garrula* and *O. guttata* approach rather closely in the valleys of the Cauca and Nechi rivers, but do not come into contact as far as is known. *Ortalis garrula* has been collected near Caceres in the Cauca

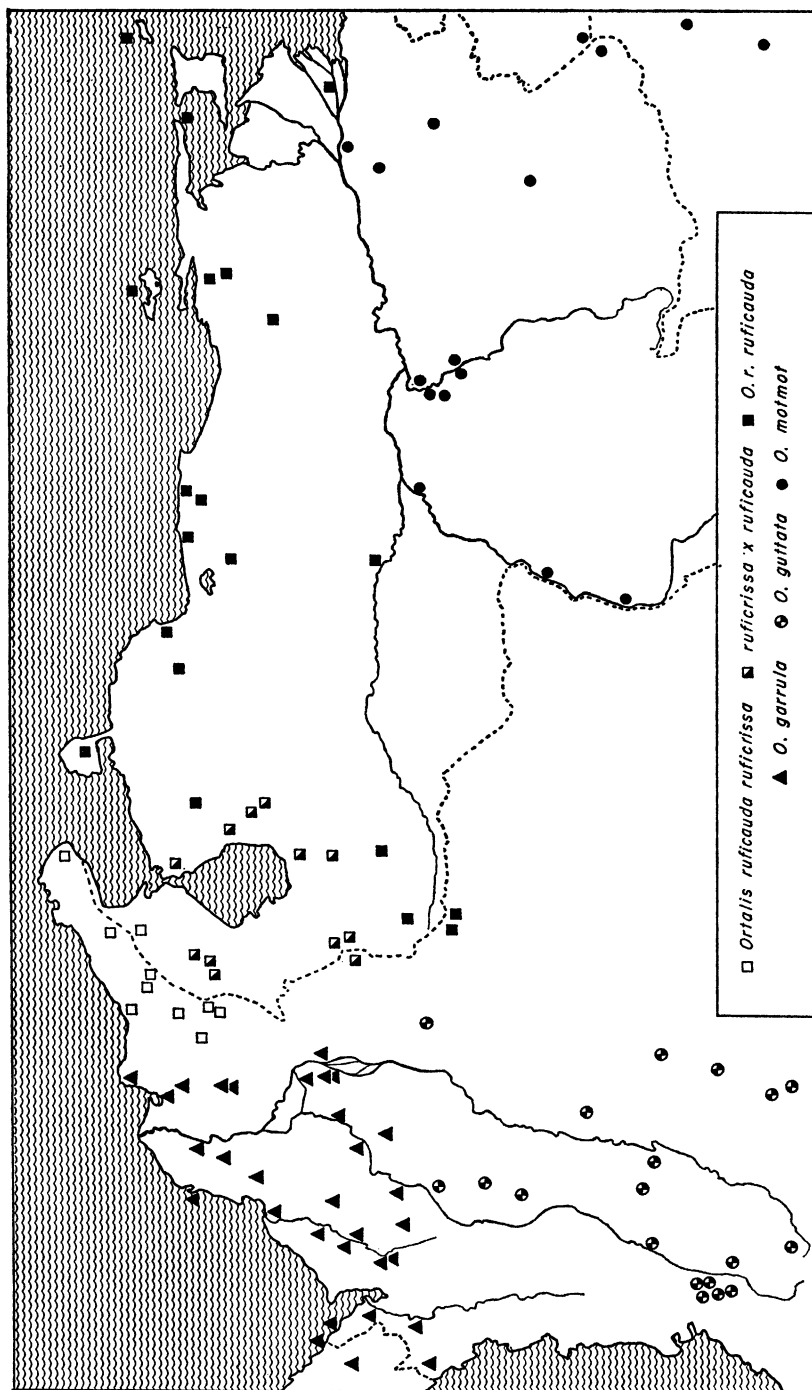


FIG. 14 Distribution of the genus *Ortalis* in northern South America.

Valley (or about latitude 7° 35' N.) and at Cuturu (7° 45' N.) on the Rio Nechi, but, to my knowledge, *O. guttata* is not found north of Valdivia in the Cauca Valley. The specimen of *O. guttata* that seems to have been collected farthest north, which I have seen, was taken 4 kilometers south of Valdivia, or at latitude 7° 08' N.

The ranges of *Ortalis guttata* and *O. canicollis* approach in Bolivia and may come into actual contact, and it is possible that the gaps between the range of *O. guttata* and that of *O. motmot* in eastern Colombia and between the Amazon and Rio Negro may be narrowed by future collecting, but it is difficult to account for the very broad gaps in central and eastern Brazil where, apparently, *Ortalis* is not present. A possible explanation may be that these gaps are inhabited by *Penelope superciliaris* (fig. 17), a small and relatively unspecialized species, which may compete with *Ortalis*.

VARIATIONS IN PIGMENTATION AND STRUCTURE

The coloration is plain, with a restricted range of variation. The crown and nape vary from ashy, slaty, or sooty gray to brown, red-brown, or chestnut and are concolorous, as a rule, contrasting to a greater or lesser degree with the color of the back which is usually olive-brown, but may be sepia, or rufous brown and more grayish or rufescent in some species than others. The rump and upper tail coverts match the color of the back but in some cases are more rufescent or somewhat paler. The tail feathers are brown also, but they are darker than the back and their upper surface has an "oily" and more or less bronzy sheen. The central tail feathers are invariably uniform in coloration, but the other pairs are very broadly tipped with white, buffy or grayish white, cinnamon, chestnut, or reddish chestnut, the pale or rufous tips varying in extent from feather to feather, especially in the species in which they are rufous. In these species, the rufous area may be very extensive, invading all or most of the visible part of the feather, or it decreases inwardly to such an extent that it is lacking on the two or three innermost pairs of feathers. The primaries are also brown, with the exception of two species (*Ortalis garrula* and

O. erythroptera) in which they are chestnut.

The coloration of the under parts is more variable. The lower breast and abdomen are paler than the upper breast and throat, the difference as a rule being quite distinct. The throat (below the bare gular area) and the upper breast vary from gray to more or less brownish olive, or to rufescent or dark brown, whereas the lower breast and abdomen vary from pure white, buffy or creamy white, to drab-gray or fulvous gray, or to chestnut in one subspecies (*wagleri*) of *Ortalis poliocephala*. The "thighs" and flanks are usually darker than the abdomen, the crissum is tinged with buff or rust, and, in all species, the under tail coverts are more or less rufous.

In one group of four species (*Ortalis guttata*, *O. superciliaris*, *O. motmot*, and *O. leucogastra*), the feathers of the lower throat and upper breast are tipped or edged with pale gray, buffy white, or white, the pale markings being faint or conspicuous. This character is important taxonomically, and the pattern is invariably associated with the structure of these feathers which are more compact and integrated, more rounded in shape, than in the other species in which they are more or less decomposed and "hairy." In this group, the feathers of the crown and mantle are also better integrated than in the other species, and, in some of its forms, they also have faint pale borders.

The feathers on the median strip of the upper throat, of the malar region, and of the throat below the bare area vary also in structure. Those on the median strip are completely decomposed in most species, forming true bristles which are more or less stiff, but in the other species they are partially webbed and are more or less lanceolate in shape. The feathers of the malar region and around the bare throat are lanceolate in all the species, or they tend to be, but this character varies from species to species. It is best developed in *Ortalis poliocephala* in which these feathers are elongate and stiff, but it is not well developed in such species as *O. vetula*, *O. garrula*, and *O. ruficauda*, and least of all in *O. erythroptera* in which these feathers are chiefly "hairy." In *O. canicollis*, the feathers of the median strip are more webbed than in the other species, and those of the malar region and around the throat are soft and not

distinctly lanceolate, although elongate.

I have not been able to find information on the labels or in the literature about the color of the bare skin of the face, throat, and tarsus in life for all the species, and no information at all for *Ortalis superciliaris*. In the other nine species, the tarsus was said to have been blue, bluish, ashy, gray, slaty, plumbeous, or "pardusco" (which may be interpreted as either grayish or brownish) in life. But in some individuals of *O. guttata*, *O. motmot*, and *O. canicollis* the collectors also noted that the tarsus had been pinkish, reddish, or red. Hazel was also mentioned for *O. canicollis*.

In the nine species, the bare skin of the throat was said to be pinkish yellow, reddish, red, or carmine, although "grayish flesh" was mentioned also for *Ortalis vetula*. The bare skin of the face was said to be blue or blue-gray in *O. ruficauda* and *O. erythroptera*, carmine or blue in *O. poliocephala*, and yellowish in *O. canicollis*. No information was found for the other species, although the skin of the face is certainly dark in life in *O. vetula* and probably some shade of gray.

The significance of the variations in the color of the soft parts is not clear to me, because the face may be red or blue in *Ortalis poliocephala*, and the tarsus red or bluish in *O. guttata* and *O. motmot*. I suspect that the coloration probably reflects physiological changes, including differences in age, but in *O. canicollis* the skin of the face and tarsus is very distinctly pale in all the skins that I have examined and still somewhat pinkish on the face on some specimens. Delacour writes to me that in his captive birds obtained from South America, which he believes are *O. canicollis*, the color of the bare skin of the face and tarsus is grayish pink. He also says that the bare patches on the throat of these birds are red but very narrow and scarcely visible, an observation that can be accounted for by the fact that the feathers of the median strip of the throat are better developed and more webbed, less decomposed, in *O. canicollis* than in the other species (see above).

VARIATIONS IN SIZE AND PROPORTIONS

The measurements of *Ortalis* are given in Table 1, and the relative proportions of the males are compared in a ratio diagram (fig.

15) in which *O. vetula* is used as the standard of comparison. This species was selected because it is not specialized in any respect, and all its measurements are about average.

General size, as expressed by the length of the wing (generally assumed to be a sound index to general size), varies in round numbers from a mean of 177 in the males and 172 in the females of *Ortalis superciliaris* to, respectively, 258 and 250 in *O. poliocephala*. One subspecies (*ruficeps*) of *O. motmot* is almost as small as *O. superciliaris*, and one (*pantanalensis*) of *O. canicollis* is almost as large as *O. poliocephala*, but in the other species of *Ortalis*, the mean wing length of males fluctuates between about 200 and 235, with an average of about 217, and that of the females between about 190 and 225, with an average of about 208. The females are therefore somewhat smaller than the males, but the difference in proportions is slight, as the ratios vary from .92 to .99 in the females, with a mean of .95, which is a difference of only 5 per cent.

The tarsus is proportionally shorter than that of *Ortalis vetula* in all the species, although the difference is very slight in the case of *O. garrula*. The tarsus of *O. canicollis* (represented by a dotted line in fig. 15), and its bill also, are disproportionately shorter than in the other species, the ratio of the tarsus being about .90 and that of the bill about .92, as against a wing ratio of about 1.10. All the other morphological characters of *O. canicollis* differ markedly from those of *O. superciliaris*, *O. guttata*, *O. motmot*, and *O. leucogastra* (represented by lines of short dashes), which form a group apart in *Ortalis*, characterized by having the feathers more integrated and edged or tipped with pale gray, buffy white, or white. The similarity in the proportions of these four species is clearly evident, except that the tail of *motmot* is longer.

Four other species (represented by a solid line) form another group (*Ortalis vetula*, *O. garrula*, *O. ruficauda*, and *O. erythroptera*) which differs only slightly in proportions, although *O. ruficauda* and *O. erythroptera* are appreciably larger; the only significant variation is the shorter tarsus of *O. ruficauda*. The proportions of *O. poliocephala* are about similar to those of these four species, but

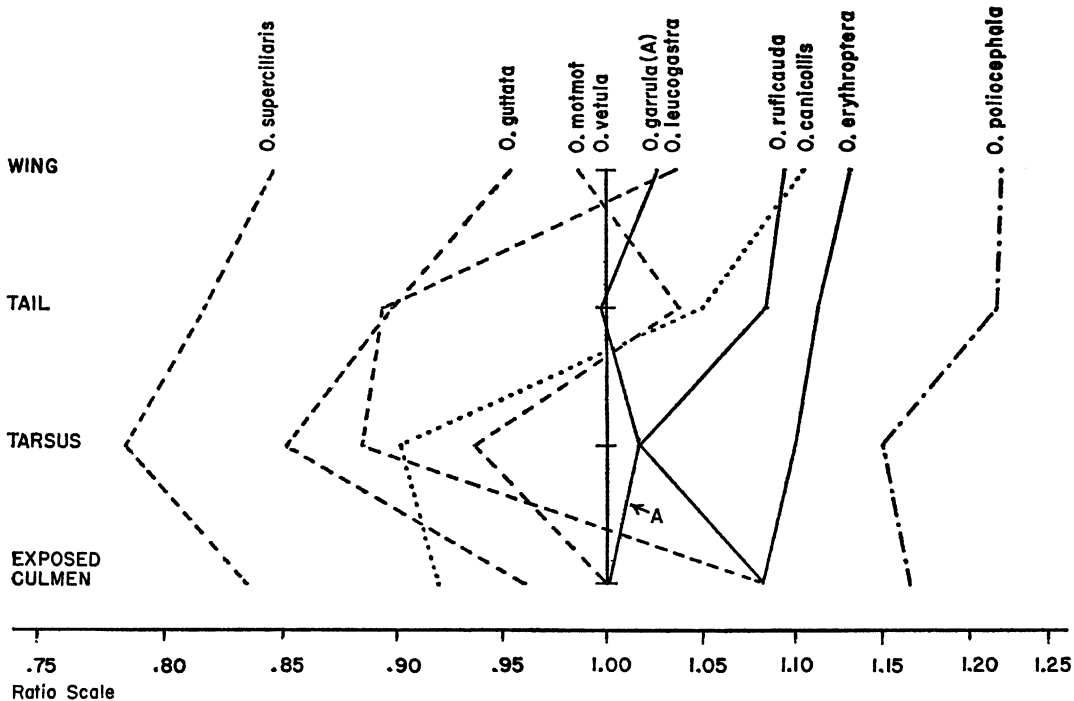


FIG. 15. Comparison by ratio diagram of the proportions of the adult males of the genus *Ortalis*. A identifies *O. garrula*.

other characters indicate clearly that it is not related to them.

PHYLOGENY

Four species (*Ortalis guttata*, *O. superciliaris*, *O. motmot*, and *O. leucogastra*) form a group that is characterized by similarities in proportions and in the structure and color pattern of some body feathers. The first three inhabit South America and are probably more closely related to one another than they are to *O. leucogastra* which is restricted to Central America. The latter differs from the other three species by having the tail feathers tipped with white as against reddish chestnut, and from *O. superciliaris*, *O. motmot*, and all but one subspecies of *O. guttata* by being white on the lower breast and abdomen, as against gray or brownish. The differences are certainly conspicuous, but the color of the abdomen and tail varies intraspecifically in *Ortalis*, and this variation is therefore quite misleading at the species level.

This variation occurs in species that may be related or not. For instance, the lower

breast, abdomen, and the tips of the tail are chestnut in *Ortalis poliocephala wagleri*, whereas they are buffy white in nominate *poliocephala*; the tail is tipped with chestnut in one of the two subspecies of *O. ruficauda*, but with white in the other; in *O. guttata*, the lower breast and abdomen are white in one subspecies, but are fulvous brown or fulvous gray in the other subspecies. The very conspicuously distinct subspecies of *O. poliocephala* and *O. ruficauda* are connected by intermediate populations which do not exist in the case of *O. guttata*, because the subspecies with a white belly (*araucuan*) is isolated geographically from the other populations of the species. The three species mentioned are not related, but *O. guttata* appears to be related to *O. leucogastra*, as mentioned above.

If the similarity between *Ortalis guttata*, *O. superciliaris*, *O. motmot*, and *O. leucogastra* denotes relationship and their integrated and patterned feathers are interpreted as an instance of specialization, it is evident that *O. vetula*, *O. garrula*, *O. ruficauda*, and *O. erythroptera* form another and more "primitive" group in which the species are very

plain in appearance. The two groups are also clearly separable by the proportions of the tarsus. In fact, *O. vetula*, *O. garrula*, and *O. ruficauda* are essentially but one "Caribbean" superspecies to which *O. erythroptera* appears to be related, as suggested by its lack of specialized characters, similarity in general appearance and proportions, and also the color of its primaries which are chestnut as in *O. garrula*.

The remaining two species (*Ortalis poliocephala* and *O. canicollis*) inhabit the opposite extremes of the range: *O. poliocephala*, western Mexico north to Sonora; and *O. canicollis*, the Chaco. They are clearly not closely related to each other or to the other eight species. *Ortalis canicollis* is aberrant in several respects (primitive feathering of the throat, color of the soft parts, and "abnormal" proportions), whereas *O. poliocephala* is the most specialized species of the genus. To be sure, it lacks the integrated and patterned feathers of the four species of the *O. guttata* group, but the specialized feathers of the throat are more highly developed in *O. poliocephala* than in any other species, and the feathers of its crown are longer, coming closest to forming a true crest. It is also the largest species and the one that exhibits the most striking geographical variation, the two extremes in the color variation.

LIST OF THE SPECIES

Ortalis vetula

DIAGNOSIS: Crown and nape varying from mouse gray or brownish gray to sooty gray, not contrasting strongly with color of back which varies from brownish to grayish olive; lower throat and upper breast olive-brown or ashy olive but paler than back; lower breast and abdomen paler than lower throat and upper breast and varying from fulvous white, drab or pale smoky gray, to ochraceous white or pale rufescent brown; flanks more fulvescent than center of abdomen, and under tail coverts buffy brown; outer tail feathers tipped with dingy, grayish, or buffy white, or with grayish buff or pale dull cinnamon, extent of pale area varying from feather to feather; lanceolated feathers of malar region and of throat below bare gular area not well developed.

RANGE: Lower Rio Grande Valley in

Texas and Mexico west to the region of Laredo, south through eastern Mexico (Nuevo Leon, Tamaulipas, southeastern San Luis Potosi, northeastern Puebla, Veracruz, and eastern Oaxaca) to the Isthmus of Tehuantepec (west to the regions of Matias Romero and Chimalapa where it meets *Ortalis poliocephala* and appears to overlap it slightly), Tabasco, Chiapas (but not along the Pacific coast except in the region of Pijijiapan), Yucatan Peninsula, Guatemala (but not reported from the western highlands, and not occurring along the Pacific coast where it is replaced by *O. leucogastra*), and Honduras (including Utila Island) to northern Nicaragua to the region of Matagalpa, re-occurring in northwestern Costa Rica where it replaces *O. garrula*.

GEOGRAPHICAL VARIATION: The geographical variation was discussed by me in detail in a preliminary paper (1965a) and consists of slight and predominantly clinal variations in color saturation and in size and proportions.

Color saturation increases clinally from the Rio Grande Valley south to central Veracruz where the cline ends. All the other populations are essentially similar to those of central Veracruz in coloration except those of the northern Yucatan Peninsula and Utila Island which are paler and similar to those of northeastern Mexico and Texas but differ from them in some details. The birds of northwestern Costa Rica may be more rufous than those from the rest of the range but require further investigation, as they are now known from only a single specimen.

The populations vary in size, but all the measurements overlap although the birds of Utila Island are the most distinct. They have the longest bill and wing, but, as the tail is distinctly short, a difference in proportions results, the wing and tail ratio being .98 in the birds of Utila as against .87 to .90 for those of the mainland. On the latter, the largest birds are not found on the northern border of the range (Rio Grande Valley), but farther south, in Nuevo Leon, Tamaulipas, and San Luis Potosi. The lengths of the wing and tail decrease clinally from these regions southward to the Caribbean lowlands, to increase again in northern Yucatan, Honduras, and Nicaragua, and slightly so on the highlands of Chiapas and Guatemala.

Four subspecies can be admitted: *mccalli* from the Rio Grande Valley south to northern Veracruz and southeastern San Luis Potosi, *pallidiventris* in northern Yucatan, *deschauenseei* on Utila Island, and nominate *vetula* in the rest of the range. *Ortalis vetula deschauenseei* differs from the other subspecies by having a larger bill and in size and proportions. It is a pale race, but it is more uniform in coloration below, more drab and ochraceous, than *pallidiventris* and *mccalli*, both of which are paler than nominate *vetula*, the darkest and most richly colored subspecies. *Ortalis vetula mccalli* is paler, duller, more olive above and less fulvescent below, than nominate *vetula*, and the tips of its tail are also more whitish. *Ortalis vetula pallidiventris* shows some similarity to *mccalli*, but it is brighter, less dull above, the pale area on its abdomen is purer white and invariably more extensive, and the tips of its tail are darker. The population from the more central and southern parts of the Yucatan Peninsula is intermediate in coloration between *pallidiventris* and nominate *vetula*, but speaking generally only, as it is not homogeneous.

The only specimen of *Ortalis vetula* that has been collected to date in northwestern Costa Rica has been examined by me and differs from all the other specimens of *O. vetula* that I have seen by being more rufous brown on the back, rump, upper tail coverts, and wings, with scarcely a trace of olive anywhere, although it is similar to nominate *O. vetula* below. The fact that its wings are more rufous suggests, perhaps, that *O. vetula* (brown wings) and *O. garrula* (chestnut wings) are not perfectly isolated reproductively in northwestern Costa Rica. If this interpretation is correct, this specimen would represent the only hybrid cracid on record taken "*in natura*," but, as we may be dealing instead with an individual variant or an undescribed and isolated subspecies, the situation in northwestern Costa Rica requires further investigation.

Ortalis garrula

DIAGNOSIS: Differing from *Ortalis vetula* by having chestnut rather than brown primaries, and by showing greater range of variation in color of crown, nape, ear coverts, sides of neck, and lower throat, these parts

varying from gray to reddish brown in *O. garrula*, whereas they are gray in *O. vetula*.

RANGE: Southeastern Honduras and northeastern and central Nicaragua, south and east through Costa Rica (with the exception of the northwest where it is replaced by *Ortalis vetula*) and Panama to northern Colombia, east to the northwestern, western, and southwestern foothills of the Santa Marta Massif, and south to the northern Choco, and to latitudes 7° 35' N. in the Cauca Valley and 7° 45' N. in the valley of the Rio Nechi.

GEOGRAPHICAL VARIATION: The geographical variation is better marked than in *Ortalis vetula* and has been discussed by me in detail in a preliminary paper (1965c). The populations belong to two distinct groups. In one (the *cinereiceps* group), which is polytypic and ranges from Nicaragua to the Atrato River in Colombia, the birds have a gray head, whereas the head is reddish brown in the second group which is monotypic, consisting of nominate *garrula* only. The latter ranges from the Rio Sinu eastward and, in addition to the color of the head, differs from the birds of the *cinereiceps* group by being, on average, very distinctly larger (table 1), and by being somewhat paler, less brownish, more olive above, and more whitish below.

The conspicuous difference is the color of the head (which did not seem to be bridged by intermediates), and the well-marked difference in size suggested that the two groups might not be conspecific. After investigating this question, however, I concluded that they were (1965c), because all the measurements and proportions of the easternmost populations of the *cinereiceps* group converge with those of nominate *garrula*, whereas the reverse would have been expected if the two groups were not conspecific. Moreover, the two groups interbreed, at least occasionally, because the color of the crown was intermediate in one specimen, which I have examined, from the Rio Sinu. They do not grade smoothly into each other, however, which suggests that they are probably connected by a zone of secondary intergradation which probably follows the head of the Gulf of Uraba.

In the *cinereiceps* group, virtually perfect clines run southeastward from Honduras and

Nicaragua, one of increasing size in all measurements to western Colombia, and one of decreasing color saturation to central Panama. The second cline is reversed somewhat farther east, as specimens from eastern Panama are darker than birds from central Panama, and those of the Choco are the darkest and about as saturated as the birds of Honduras and Nicaragua, or slightly more so.

In view of this clinal variation it would be most constructive not to recognize subspecies in the *cinereiceps* group, dividing *Ortalis garrula* only into its two well-differentiated phylogenetic units: nominate *garrula* with a reddish brown head and *cinereiceps* with a gray head. The *cinereiceps* group has been divided, however, into four subspecies which, ranging from Honduras and Nicaragua south-eastward, are. *frantzii*, *cinereiceps*, *mira*, and *chocoensis*.

Ortalis ruficauda

DIAGNOSIS: Very similar to *Ortalis vetula*, but outer tail feathers tipped with reddish chestnut, or with white, and distinctly more rufous, less brownish, on crissum and under tail coverts. In form in which tail feathers tipped with white, pale area more extensive than in *O. vetula* and purer white.

RANGE: Northern Venezuela, north of the Orinoco and the Rio Arauca, west to north-eastern Colombia to the region of Cucuta, the region of Codazzi in eastern Magdalena, and the southeastern, eastern, and north-eastern foothills of the Santa Marta Massif to the base of the Guajira Peninsula. Also the Serrania de Macuire at the tip of the Guajira Peninsula, the northwestern corner of the Comisaria de Arauca of Colombia on the lower Rio Covaria and lower Rio Bojaba, Margarita Island, and Tobago, but not Trinidad. Introduced in the southern Lesser Antilles on some of the Grenadines.

GEOGRAPHICAL VARIATION: This species has been reviewed by me (1965c) and the map that illustrated its distribution and geographical variation in that paper is reproduced here (fig. 14).

The populations belong to two groups: nominate *ruficauda* in the eastern part of the range, in which the tail is tipped with chestnut, and *ruficrissa* at the western extremity of the range, in which the tips of

the tail are white; the two groups are connected by a zone of secondary intergradation around Lake Maracaibo. The birds of the second group (*ruficrissa*) are also somewhat smaller and are paler throughout, more olive-brown on the back, less brownish, have a paler gray head, and are much less rufescent on the under parts.

The two groups were considered to be separate species until recently, but Phelps and Phelps (1958, pp. 82, 83) decided they were conspecific after Phelps (1943) had reported that the color of the tail was intermediate in specimens collected south and southeast of Lake Maracaibo in Venezuela and north of Cucuta in Colombia. The extent of the zone of secondary intergradation is shown in figure 14. A form (*baliolus*) that was described from this zone, where the coloration of the population is not stable, was synonymized by me (1965c) with *ruficrissa*. In the same paper, I also synonymized another form (*lamprophonia*) with *ruficrissa*, because it represents merely an isolated local population from the tip of the Guajira Peninsula, which differs from *ruficrissa* only in minor characters. It seemed more meaningful to me to recognize only two subspecies, nominate *ruficauda* and *ruficrissa*, which represent the two phylogenetic units of this species and are well differentiated by a number of characters.

The range of nominate *ruficauda* extends (fig. 14) from Tobago and eastern Venezuela, including Margarita Island, westward to the states of Falcon, Lara, Barinas, Tachira, and Apure in Venezuela, and the northwestern corner of the Comisaria de Arauca in Colombia. It is replaced farther west by the populations ("*baliolus*") that are more or less intermediate between it and *ruficrissa*. The latter (including "*lamprophonia*") ranges from the region of Codazzi in Colombia, north to the Guajira Peninsula, including neighboring northwestern Zulia in Venezuela, and west to the southeastern, eastern, and northeastern foothills of the Santa Marta Massif.

Ortalis erythroptera

DIAGNOSIS: Crown, nape, feathers of face and at sides of neck russet or dull reddish chestnut, and very decomposed; upper parts

dull olive-brown; lower throat and upper breast olive-brown but paler than back; lower breast and center of abdomen varying individually from creamy white to buffy white; flanks and "thighs" fulvescent, with crissum and under tail coverts also fulvescent but more "rusty"; outer tail feathers and primaries chestnut; lacking lanceolated feathers on malar region or throat as a rule, but, if present, obsolete or very vaguely indicated.

RANGE: Western Ecuador from Esmeraldas south to the department of Tumbes in neighboring Peru.

This species, which has a very restricted range, does not vary geographically.

Ortalis guttata

DIAGNOSIS: Crown and nape varying from ashy gray, sooty or brownish gray, to brown, rufous brown, or reddish brown, uniform in coloration or becoming paler on fore crown; feathers well integrated, slightly elongate, and rounded or attenuated at tip, with or without faint and narrow pale edges. Feathers of face and sides of neck integrated and similar in structure to those of crown and nape, but in some cases paler or having clearer pale markings. Upper parts below nape varying from dark olive-brown to rufescent brown, with feathers integrated and, as a rule, faintly and narrowly edged with gray or buff. Lower throat and upper breast varying from dull grayish or rufescent brown, to dark olive-brown or dark brown, feathers well integrated and very conspicuously edged or tipped with white, cloudy white, or buffy white. Lower breast and abdomen varying from pure white, or virtually pure white, to relatively pale or dark drab-gray, brownish or cinnamon gray, or ferruginous ocher, feathers somewhat integrated or decomposed, and, if integrated, more or less faintly edged with buff. Flanks, "thighs," crissum, and under tail coverts darker than abdomen, fulvescent brown or rufous in forms that have a dark abdomen, or chestnut on crissum, in some cases slightly so on rump. Primaries brown, outer tail feathers reddish chestnut or chestnut, rufous areas varying in extent. Lanceolate feathers of malar region and throat moderately well developed. Tarsus and tail proportionally shorter than wing (fig. 15).

RANGE: Colombia from latitudes 7° 08' N. in the Cauca Valley and about 7° 20' N. in the Magdalena Valley, southward and along the eastern slopes of the Andes and their foothills from Colombia south to central Bolivia, and east in the Amazon Basin to the Guaporé and Mamoré rivers and the left bank of the lower Tapajoz, but (fig. 13) not found north of the Amazon in Brazil except on the upper Solimões and upper Rio Uaupes; also eastern Brazil from the state of Pernambuco south to eastern Minas Gerais and Espírito Santo, and, after a very broad gap, from extreme southeastern Mato Grosso to Santa Catarina and Rio Grande do Sul.

GEOGRAPHICAL VARIATION: This species has the widest distribution of any and is the most variable geographically. Its geographical variation, which has been discussed by me in detail (1965b), consists of differences in coloration, relative development of the whitish markings at the tip or along the edge of the feathers, especially those of the lower throat and upper breast, and of differences in size (table 2). The geographical variation is clear cut.

Five subspecies are recognized: *araucuan* in northeastern Brazil, *squamata* in southeastern Brazil; *subaffinis* in eastern central Bolivia east to the Guaporé River in Brazil and south to about latitude 18° or 19° S.; nominate *guttata* in the Amazon Basin of Brazil, Peru, Ecuador, and Colombia; and *columbiana* in the valleys of the Cauca and Magdalena rivers and their surrounding slopes but not to the higher elevations of the Eastern Andes which form an ecological barrier between it and nominate *guttata*. The northern limits of the range of *subaffinis* cannot be defined with certainty, because it intergrades with nominate *guttata* in Bolivia at about latitude 15° S. on the Rio Mamoré and also along the base of the Andes in the department de la Paz.

The geographical variation is complex, and some of the characters are best visualized in tabular form (table 4).

Ortalis guttata araucuan differs sharply from all the other subspecies by being much paler below and white or whitish on the abdomen. It is also reddish brown on the head, and the feathers of the crown and nape are more elongate than in the other subspecies,

TABLE 4

SUBSPECIFIC VARIATIONS IN THE COLORATION OF THE ABDOMEN AND HEAD, SHAPE OF THE TIPS OF THE CROWN FEATHERS, AND PATTERN OF THE PALE MARKINGS ON THE LOWER THROAT AND UPPER BREAST OF *Ortalis guttata*

Subspecies	Color of Abdomen	Color of Head	Shape of Tips	Pattern of Markings
<i>araucuan</i>	Very pale (white or whitish)	Reddish brown	Attenuated	Not sharply defined
<i>squamata</i>	Dark (grayish brown)	Brown	Rounded	Sharply defined (shallow crescentic bars)
<i>subaffinis</i>	Dark (grayish brown or ochraceous)	Sooty gray	Rounded	Diffused
<i>guttata</i>	Variable, but dark	Sooty to brownish gray	Rounded	Sharply defined ("spotted")
<i>columbiana</i>	Dark (brownish gray)	Ashy gray, paler on forecrown	Rounded	Sharply defined ("scaloped")

being also slightly attenuated at the tip rather than rounded as in the other subspecies. The whitish markings on the lower throat and upper breast of *araucuan* are conspicuous, as in all forms of *guttata*, but less sharply defined.

Ortalis guttata squamata is dark below, has a brown head and upper throat, and is more rufescent (virtually chestnut) on the rump, upper tail coverts, crissum, and under tail coverts than the other subspecies. Its whitish markings are sharply defined but are restricted chiefly to the edges of the feathers, thus forming shallow crescentic bars.

Ortalis guttata subaffinis is much more similar to *squamata* than the latter is to *araucuan*, but it is paler and duller than *squamata*, has a sooty gray rather than brown head, and its whitish markings are diffused.

Ortalis guttata guttata is dark below but varies individually, and is best characterized by the shape of its whitish markings which are sharply defined and are restricted chiefly to the tips of the feathers at the end of the shaft, thus giving it a characteristic "spotted" appearance.

Ortalis guttata columbiana is larger than the other subspecies (table 1) and is a dark race, although its head is ashy gray, paler and less uniform in coloration than that of *subaffinis* or the gray head of some individuals of nominate *guttata*. Its whitish markings are sharply defined, but, although they are restricted to the edges of the feathers (as in *squamata*), they ascend much farther up on the sides,

giving to the upper breast and throat a "scaloped" appearance.

Ortalis superciliaris

DIAGNOSIS: Differing from *Ortalis guttata* and all other species by having well-indicated superciliary streak which varies individually from buffy white or buff to pale cinnamon, and extends from region above lores or base of bill on forehead to region behind eye. Body feathers integrated and patterned as in *Ortalis guttata*, but pale edges of feathers relatively faint or much less conspicuous. General coloration similar to that of dark subspecies of *O. guttata*. Smaller than all other species.

RANGE: Eastern Brazil from the eastern estuary of the Amazon and the right bank of the lower Tocantins, eastward through eastern Para and the state of Maranhão to the Parnaíba River in Piauí, and south to extreme northern Goyaz where it occurs on the left bank of the Tocantins above its junction with the Araguaia River.

This species, which has a relatively restricted range, does not vary geographically.

Ortalis motmot

DIAGNOSIS: Head reddish, crown and nape and feathers of face and sides of the neck varying from chestnut to bright reddish chestnut, reddish pigment elongated as broad band of reddish orange encircling base of throat. General coloration, other than that of head, similar to that of dark subspecies of

Ortalis guttata, and structure of body feathers also similar, although feathers less integrated, and, as a result, pale edges faint and disappearing, or tending to disappear, with wear, especially on back.

RANGE: Southern Venezuela, south of the Orinoco, and Guianas, south to the left bank of the Rio Negro and the north bank of the Amazon to the level of the mouth of the Tapajoz, but present south of the Amazon from the right bank of the lower Tapajoz southeast to the left bank of the Araguaia where it reaches Conceição do Araguaia, or about latitude 8° 15' S. The range of *Ortalis motmot* is uncertain east of the lower Tapajoz but probably extends beyond the Rio Xingu (fig. 13).

GEOGRAPHICAL VARIATION: This species consists of two subspecies which differ very markedly in size (table 1) and are divided by the lower Amazon: nominate *motmot* (the larger subspecies) north of the Amazon, and *ruficeps* south of it. The reddish pigment of the head, throat, and tail of *ruficeps* is paler and brighter, and the base of its outer tail feathers is somewhat more invaded with brown, especially on the outer web, but only on an average, and the difference is slight.

Ortalis leucogastra

DIAGNOSIS: Crown and nape ashy gray, contrasting well with back which is sepia or rufous brown, rump and upper coverts slightly paler than back and slightly tinged with olive. Sides of face and lower neck, and lower throat, ashy gray, grading into pale olive-brown on upper breast, brown of upper breast grading in turn into pure white on lower breast, abdomen also pure white, but rest of under parts less pure white than abdomen, and more or less slightly tinged with buff on flanks, "thighs," crissum, and under tail coverts. Primaries brown, outer tail feathers brown, tipped broadly with pure white. Lanceolated feathers of malar region and throat moderately well developed. Body feathers very well integrated, except on abdomen, and with distinct pale grayish edges, relatively faint as compared with conspicuous markings of *O. guttata*.

RANGE: Western Mexico, from the region of Pijijiapan in Chiapas, south through the coastal districts, Pacific plain and slopes of

Chiapas and Guatemala, to El Salvador and northwestern Nicaragua in Chinandega and Leon.

This species, which has a restricted range, does not vary geographically.

Ortalis poliocephala

DIAGNOSIS: Crown and nape ashy, slaty, or brownish gray, with feathers of crown, especially of fore crown quite elongate, more so than in other species, but not forming true crest; crown and nape contrasting with rest of upper parts which are grayish olive, umber, or pale brownish olive. Lower throat and upper breast brownish or grayish olive, but paler than back; rest of under parts either reddish russet (or dull reddish chestnut), or whitish, more or less washed with buff or pale ochraceous buff, flanks, crissum, and under tail coverts more heavily and darkly tinged with buff or pale ocher. Primaries brown, outer tail feathers very broadly tipped with chestnut or buffy white. Body feathers more or less decomposed, not integrated, but lanceolated feathers of malar region and throat very well developed, more than in any other species, and stiff. Larger than all other species.

RANGE: Western Mexico, from the region of Alamos in southern Sonora, south to the region of Pijijiapan in coastal Chiapas where its range meets that of *Ortalis leucogastra* and *O. vetula*; east to northwestern Durango near the border of Sinaloa, central Jalisco, southern Guanajuato (probably), state of Mexico, Distrito Federal, Morelos, central and western Puebla, and western Oaxaca, east on the Isthmus of Tehuantepec to the regions of Matias Romero and Chimalapa where its range meets and overlaps slightly that of *O. vetula*.

GEOGRAPHICAL VARIATION. The geographical variation, distribution, and relationships of this species to the other two species of Mexico (*Ortalis leucogastra* and *O. vetula*) were discussed by me in detail (1965a). Its populations form two subspecies that are sharply differentiated by the color of the abdomen and tail, which is chestnut in *wagleri*, but whitish in nominate *poliocephala*. The former inhabits the northern part of the range, or from Sonora to western Jalisco, and is connected to nominate *polio-*

cephala by a zone of secondary intergradation in western Jalisco and in Colima which extends from the region of Puerto Vallarta to the Rio Armeria. *Ortalis poliocephala wagleri* differs also from nominate *poliocephala* by being more brownish, less grayish, above, and by having longer feathers on the crown.

Moore and Medina (1957) were the first to show that *wagleri* and nominate *poliocephala* are connected by intergrades. Prior to the work of these authors, the two birds were considered to be separate species, although such treatment had been questioned before Moore and Medina.

Ortalis canicollis

DIAGNOSIS: Head and neck varying from ashy or slaty gray to brownish gray, not contrasting strongly with color of back and breast which varies from grayish to brownish olive, breast paler than back. Rest of under parts varying from drab or brownish gray to pale ochre brown, more or less fulvescent; flanks, "thighs," crissum, and under tail coverts darker than abdomen, crissum and under tail coverts more or less heavily tinged with russet, or dull pale reddish chestnut, extent of rufous area varying individually and geographically. Body feathers decomposed; specialized feathers or malar region and base of throat usually soft and not distinctly lanceolate, less developed than in other species; feathers on median strip dividing bare gular area also partially webbed, usually not modified into bristles.

RANGE: Marshy lowlands of southeastern Mato Grosso, and Chaco in Bolivia and Paraguay, south to about latitude 31° S. in the Argentine Chaco, west to the foothills and lower slopes of the Andes from Jujuy south to Catamarca.

GEOGRAPHICAL VARIATION: The geographical variation is clinal and was discussed by me in a preliminary paper (1964). Two subspecies can be recognized: one (*pantanalensis*) in the marshy and humid lowlands of the Mato Grosso, and the other (nominate *canicollis*) in the rest of the range. *Ortalis canicollis pantanalensis* is distinctly larger than nominate *canicollis* (table 1), and much darker, being browner and more rufescent

throughout, less grayish. The population from the western limits of the range of nominate *canicollis* from the regions along the Andes, or not far from them (Oran, Salta, Tucuman, western Santiago del Estero, extreme western Paraguay, and the region of Vila Montes in Bolivia), is paler and more grayish than the birds of the Chaco.

The rufous tips of the tail vary individually and geographically in extent, but, generally speaking, the rufous area decreases clinally from the Mato Grosso southward. For instance, the rufous area was present on the first three outer pairs of rectrices of 11 from 12 specimens that I examined (1964) from the Mato Grosso, with a trace of it on the fourth pair in the twelfth, but in 25 birds from Paraguay, it was restricted to the first and second pairs in only 11 specimens, and this area appears to decrease further in birds from Argentina. The decrease in the rufous area seems to be accompanied by a decrease in the size of the birds, as shown by the measurements of the wing and tail (for details on the variations of the rufous area and in size, see Vaurie, 1964).

GENUS *PENELOPE*

DIAGNOSIS

This genus is richest in species, with 13 that, as a group, are very widely distributed from about the twenty-fourth parallel in Mexico south to northern Argentina and southern Uruguay. *Penelope* is closely related to *Ortalis* but is more arboreal and has a shorter tarsus, with a mean ratio of .23 as against a mean of about .27 in *Ortalis*, a difference that seems slight but is quite apparent in life. All species of *Penelope* are larger than those of *Ortalis* with only two exceptions, and *P. purpurascens* attains a great size; it is slightly exceeded only by a very occasional specimen of *Pauxi* and *Mitu*. All species of *Penelope* have a crest, and the throat is less feathered than that of *Ortalis*, the skin forming a dewlap or wattle in all species. *Penelope* is "brown," more or less streaked with white, but the tail is uniform in coloration, not bicolored as in *Ortalis*, except in *P. argyrotis*, in which the tips of the tail are dull chestnut and contrast with the rest of the tail which is dark brown.

KEY TO THE SPECIES OF *Penelope*

1. Primaries white *P. albipennis*
Primaries brownish, brown, or brownish black 2
2. Inner secondaries, scapulars, and greater upper wing coverts edged with chestnut *P. superciliaris*
Inner secondaries, scapulars, and greater upper wing coverts not edged with chestnut 3
3. Tail feathers tipped with buffy white, cinnamon-buff or cinnamon *P. argyrotis*
Tail feathers uniform in coloration, not tipped with buffy white, cinnamon-buff, or cinnamon 4
4. Hind neck and upper mantle chestnut, not concolorous with back *P. pileata*
Hind neck and upper mantle not chestnut, but concolorous with back 5
5. Ground color of lower throat and breast maroon and chestnut *P. ochrogaster*
Ground color of lower throat and breast various shades of brown or olive, but not maroon and chestnut 6
6. Supraorbital region pure white, or virtually so, separated from bare skin of face by narrow and sharp line of pure black, contrasting completely with top of head which is dark sooty brown *P. jacucaca*
Supraorbital region brown, or not pure white, not separated from bare skin of face by band of black (or, if present, band not well defined), and not contrasting strongly with top of head 7
7. Supraorbital region pure brown and uniform in coloration 8
Supraorbital region more or less variegated with pale whitish gray or grayish white, not uniform in coloration 9
8. Size small (mean wing length, 260–269) *P. ortonii*
Very large (mean wing length, 345–399) *P. purpurascens*
9. Feathers at sides of neck behind ear coverts conspicuously edged with grayish white, and malar stripe conspicuously variegated with silvery or grayish white 10
Feathers at sides of neck behind ear coverts lacking pale edges (or, if present, edges very faint), and malar stripe brown and concolorous, or only slightly variegated with gray¹ 11
10. Upper parts dark olive-green, including rump, and with well-defined bronzy gloss *P. marail*
Upper parts rufous brown, with brighter, more auburn or chestnut rump, and not highly glossed *P. montagnii*
11. Feathers of crest broad, rounded at tip, semi-erect, and broadly edged with pale whitish gray *P. dabbeni*
Feathers of crest narrow, or relatively so, attenuated at tip, decumbent, and less broadly edged with pale gray or dull white 12
12. Chin feathered, bare area of throat relatively restricted, and tarsus dark (blackish or black in life) *P. obscura*
Chin bare or less feathered, bare area of throat very extensive, and tarsus pale (red or reddish in life) *P. jacquaçu*

DISTRIBUTION

The distribution of *Penelope* is shown in figures 16 and 17. It presents a very different pattern from that of the other polytypic genera of the Cracidae. In the latter, the species are allopatric, or essentially so, as any overlap that exists is very slight and involves few species, but in *Penelope* 12 of the 13 species overlap to a varying degree, from slight to complete.

The only species of *Penelope* that apparently does not overlap another is the extinct *P. albipennis* which is known from only three specimens taken when it was on the verge of extinction. The first was collected by Stolzmann on December 18, 1876, in inaccessible mangroves in the delta of the Rio Tumbez in northwestern Peru. The second is a female that was shot near her nest about a month later on January 10, 1877, by Jelski at the Hacienda de Pabur which is situated near the town of Piura and apparently in the valley of the Rio Piura, or about some 200 kilometers south of the delta of the Rio Tumbez. This female had two chicks with her which appeared to be scarcely two days old. One was captured alive and was raised in captivity and probably represents (Vaurie,

¹ In the species that remain in the key, the malar stripe is conspicuously variegated in *Penelope montagnii* and *P. marail*, slightly variegated in *P. dabbeni* and three of the five subspecies of *P. jacquaçu*, and brown

and uniform (not variegated) in *P. obscura* and the other two subspecies of *P. jacquaçu* (n nominate *jacquaçu* and *perspicax*). The three subspecies of *P. jacquaçu* in which the malar stripe is more or less variegated are *orienticola*, *granti*, and *speciosa*.

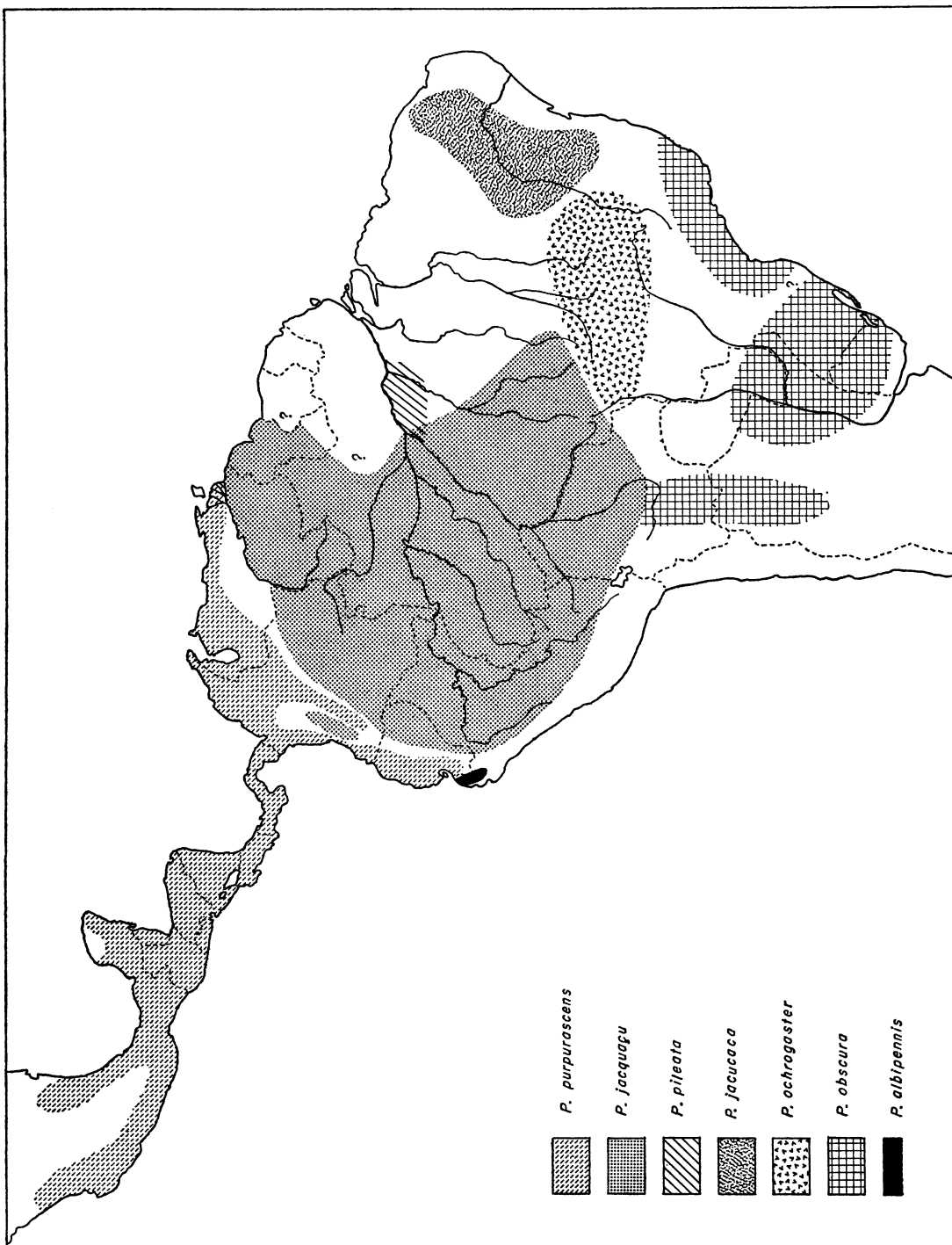


FIG. 16. Distribution of seven species of the genus *Penelope*.

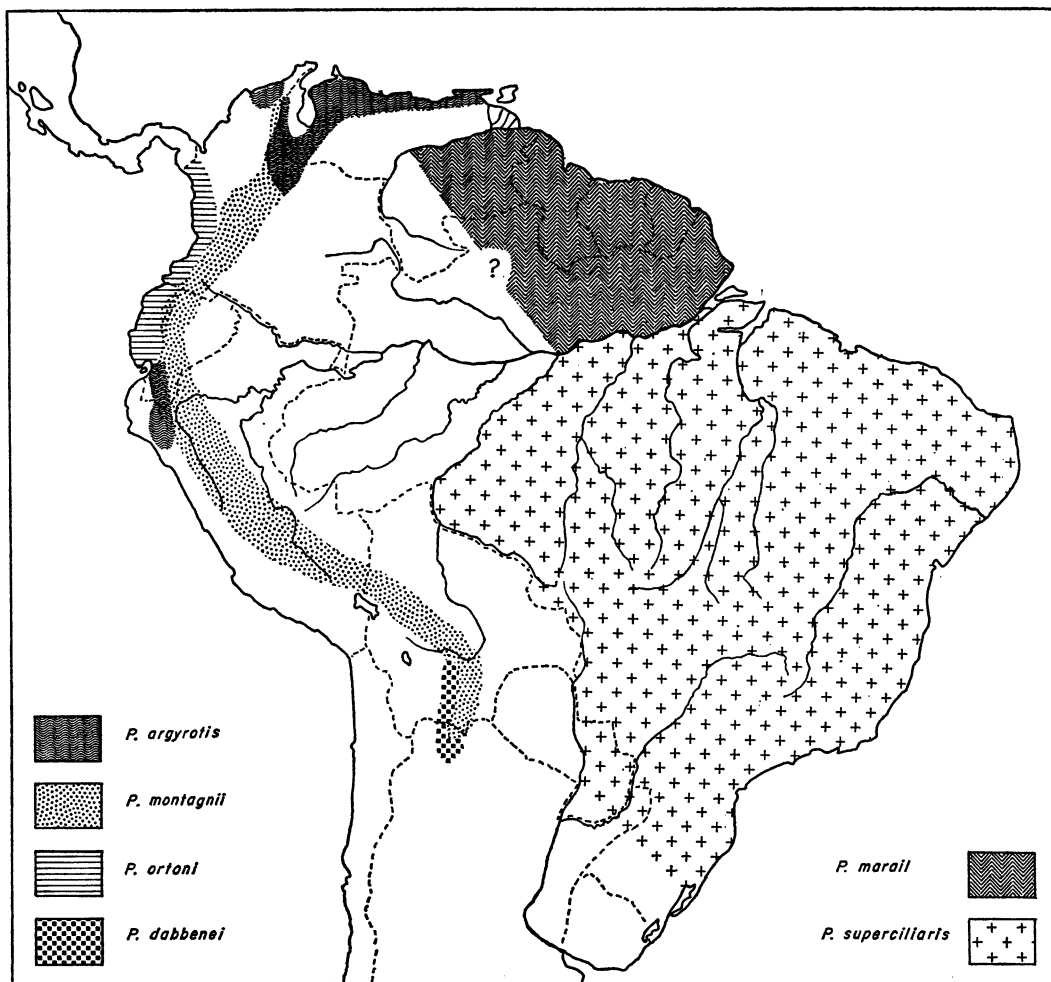


FIG. 17. Distribution of six species of the genus *Penelope*.

1966b) the third specimen of *P. albipennis*. It is also labeled Hacienda de Pabur but has no date nor the name of the collector. It is probable, however, that the range of *P. albipennis* was more extensive than these three specimens indicate, because Stolzmann stated (1886, p. 271) that *P. albipennis* had been reported to him from the mouth of the Rio Zurumilla, which forms the frontier between Ecuador and Peru, and that other information led him to suppose that *P. albipennis* still existed in the river valleys of northern Peru south to the Rio Chicama north of Trujillo.

Stolzmann may have been wrong, but, as *Penelope albipennis* seems to have inhabited only the lower course of the coastal rivers

and their deltas, we can conclude that its range probably did not come into contact with that of other species of *Penelope* of southwestern Ecuador and northwestern Peru. These are *P. purpurascens*, which ranges south to southwestern Ecuador, and *P. argyrotis*, found in both southwestern Ecuador and northwestern Peru, but, as these two species seem not to descend below 5000 feet in these regions, it seems unlikely that they would have overlapped *P. albipennis*. The probability that *P. albipennis* was restricted to low river valleys and mangroves seems to be confirmed by the great length of its tarsus which implies an adaptation to a habitat along streams and in mangroves.

The overlap in *Penelope* is too complex and involves too many species to be illustrated clearly on a single map of small scale, and to describe it in detail would be confusing. It is best made clear, I believe, by listing below the species that overlap and the regions where overlap occurs.

The fact that two or more species overlap does not necessarily imply that specimens have been collected at the same locality or in identical habitat. Very little information on the habitat is provided by the literature or by the labels of the specimens that I have examined, and relatively few of the birds seen had been taken at the same locality, although others had been taken not far apart in regions where the habitat may be more or less homogeneous.

The species that overlap differ, as a rule, very clearly in size. For instance, *Penelope purpurascens*, which is a large species, overlaps in northern Colombia *P. argyrotis* and *P. montagnii*, which are small. The factor that permits this overlap is probably a difference in ecology, a large species presumably exploiting a partly different food supply and frequenting different types of trees from those by a small one. The small species, in which the mean wing length of the males varies from 240 to 275 mm., are *P. argyrotis*, *P. ortonii*, *P. montagnii*, and *P. superciliaris*; the large species, in which the mean wing length of the males varies from 303 to 399 mm., are *P. dabbenei*, *P. obscura*, *P. jacquacu*, *P. purpurascens*, *P. jacucaca*, *P. ochrogaster*, and *P. pileata*; *P. marail*, with a mean wing length of 277 and 287 in its two subspecies, is intermediate in size.

There are some exceptions to this "rule," but a difference in ecology probably exists, because the species of the same size that overlap tend, on the whole, to replace one another altitudinally. For instance, *Penelope argyrotis* and *P. montagnii*, which are both small and restricted to mountains, overlap in northern Colombia, western Venezuela, and southwestern Ecuador. The altitudes indicated on the labels of the specimens that I have seen show, however, that *P. argyrotis* was collected in northern Colombia and western Venezuela between about 915 meters, or somewhat lower, and 1830 meters, whereas *P. montagnii* was taken between at about

1676 and 3353 meters. In southwestern Ecuador the altitudinal segregation is not sharp but exists to some degree, as *P. argyrotis* was collected in this region from about 1524 to 3048 meters, and *P. montagnii* from about 2438 to 3048 meters.

It is of interest to note that *Penelope montagnii* descends lower in regions where *P. argyrotis* is not present, as in northwestern Ecuador where it has been collected at Paramba and Mindo; the first locality is at an elevation of 1067 meters, and, at Mindo, *P. montagnii* was taken at 1200 meters, the town itself being about 30 meters higher. *Penelope montagnii* apparently slightly overlaps *P. ortonii*, which has been taken at the same localities, but, although *P. ortonii* is also small, this case is not a true exception to the "rule" because the two species are essentially allopatric. *Penelope montagnii* is a species of the mountains, but *P. ortonii* is restricted chiefly to the coastal lowlands, Paramba and Mindo being, apparently, the highest localities at which it has been taken.

Another apparent and interesting exception consists of *Penelope dabbenei* and *P. obscura*, which are both large species that overlap along the slopes of the eastern Andes in southern Bolivia and northern Argentina. Both species have been taken at the same altitudes and at the same locality one day apart by the same collector, Carriker, on the Rio Azuero on November 25 and 26, 1936. They differ in size, however, *P. dabbenei* being appreciably smaller than *P. obscura bridgesi*, which it overlaps, but it is of interest to note that the difference in size is not present where the species do not overlap. The mean wing length of males in nominate *obscura*, which ranges from Paraguay and northeastern Argentina to Uruguay and southeastern Brazil, and also in *P. dabbenei*, is 303 mm., increasing to 328 in *P. obscura bridgesi*.

Altitude cannot be invoked in regions that are low and flat or where the relief is not great, as in the greater part of Brazil south of the Amazon which is occupied by *Penelope superciliaris*. The latter overlaps completely the ranges of *P. pileata*, *P. jacucaca*, and *P. ochrogaster*, the entire range of *P. jacquacu* which extends east of the Guaporé and Madeira, and virtually the whole range of *P.*

obscura in Brazil, but all these species are large, whereas *P. superciliaris* is very small. To be sure, *P. pileata* and nominate *jacquaçu* overlap slightly near the mouth of the Rio Madeira (fig. 16), but they are essentially allopatric, and *P. pileata* is considerably larger. The mean wing lengths, 319 in *P. pileata* and 303 in nominate *jacquaçu*, do not make this difference very evident, but the tarsus of *P. pileata* is considerably longer (81 mm. as against 74) and about twice as thick as in nominate *jacquaçu*, and its bill is also much thicker. *Penelope pileata* appears to be notably heavier, judged by skins of comparative make, and in coloration and the modification of its crest, it is also very different from *P. jacquaçu*. Wagler placed it in a separate genus (*Salpiza*), of which it is the type.

In short, all but one of the species of *Penelope* overlap one or more other species, but those that are sympatric very probably differ in their ecology.

LIST OF OVERLAPPING SPECIES

- Penelope argyrotis* overlaps *P. montagnii* and *P. purpurascens*
Penelope ortonii overlaps *P. montagnii* and *P. purpurascens*
Penelope montagnii overlaps *P. argyrotis*, *P. ortonii*, *P. obscura*, *P. jacquaçu*, *P. purpurascens*, and perhaps *P. dabbenei*
Penelope superciliaris overlaps *P. obscura*, *P. jacquaçu*, *P. jacucaca*, *P. ochrogaster*, and *P. pileata*
Penelope marail overlaps *P. jacquaçu*
Penelope dabbenei overlaps *P. obscura* and perhaps *P. montagnii*
Penelope obscura overlaps *P. montagnii*, *P. superciliaris*, and *P. dabbenei*
Penelope jacquaçu overlaps *P. montagnii*, *P. superciliaris*, *P. marail*, and *P. pileata*
Penelope purpurascens overlaps *P. argyrotis*, *P. ortonii*, and *P. montagnii*
Penelope jacucaca overlaps *P. superciliaris*
Penelope ochrogaster overlaps *P. superciliaris*
Penelope pileata overlaps *P. superciliaris* and *P. jacquaçu*

OVERLAP BY REGIONS

- Santa Marta: *P. argyrotis* and *P. purpurascens*
 Sierra de Perija and Andes of Venezuela: *P. argyrotis*, *P. montagnii*, and *P. purpurascens*
 Northeastern Andes of Colombia: *P. argyrotis*, *P. montagnii*, and probably *P. purpurascens* at lower altitudes (I have seen also a specimen of

- P. purpurascens* that was said to have been collected near Bogota)
 Central Andes of Colombia: *P. montagnii* and *P. jacquaçu*
 Pacific coast of Colombia: *P. ortonii* and *P. purpurascens*
 Venezuela south of the Orinoco, Guianas, and northeastern Brazil north of the Amazon: *P. marail* and *P. jacquaçu*
 Western Ecuador: *P. argyrotis*, *P. ortonii*, *P. montagnii*, and *P. purpurascens*
 Eastern Ecuador and eastern Peru: *P. montagnii* and *P. jacquaçu*
 Eastern slopes of the Andes of Bolivia: *P. montagnii*, *P. dabbenei*, *P. obscura*, and *P. jacquaçu*
 Northwestern Argentina: *P. montagnii*, *P. dabbenei*, and *P. obscura*
 Eastern Paraguay and Misiones: *P. superciliaris* and *P. obscura*
 Brazil between the Madeira and the Tapajoz: *P. superciliaris*, *P. jacquaçu*, and *P. pileata*
 Northeastern Brazil south of the Amazon: *P. superciliaris* and *P. jacucaca*
 Central Brazil: *P. superciliaris* and *P. ochrogaster*
 Southeastern Brazil: *P. superciliaris* and *P. obscura*.

VARIATIONS IN PIGMENTATION AND STRUCTURE

The coloration is plain and, generally speaking, varies only slightly. Nearly all the species are similar and some shade of brown on the back and the upper surface of the wings and tail, the feathers of the hind neck, mantle, scapulars, and upper wing coverts being more or less narrowly edged with white, buffy white, or grayish white. The pale edges are normally restricted to the sides of the feathers and interrupted at the tip, and thus form streaks. The only exceptions to the streaked plumage are *Penelope ortonii* and *P. superciliaris*. The former is uniform in coloration above, without streaks, whereas the pale edges are continuous around the tip of the feather in *P. superciliaris*, not interrupted. In *P. superciliaris*, the edges are pale gray, and, in specimens in very fresh plumage the gray edge is normally bordered terminally with a very faint and narrow blackish band. These gray edges are replaced by chestnut on the middle and greater coverts, scapulars, and inner secondaries, the width of the chestnut edge becoming progressively broader posteriorly. In *P. superciliaris*, the outer web of the other secondaries and the webs

of the central two or three pairs of rectrices are more or less faintly edged also with chestnut.

The species, or subspecies, that are not brown above are more or less olivaceous brown, olive-green, or dull bluish olive-green. The plumage of the upper parts has a faint or slight bronzy sheen in all the species which is somewhat more pronounced in the forms that are olive-green.

The ground color of the crown and hind neck is more grayish, sooty, or blackish, less brown or olive-green, than the back, but usually does not contrast strongly with the ground color of the mantle and back. In *Penelope pileata*, however, the upper parts are dichromatic, as the coloration is maroon and chestnut on the hind neck and upper part of the mantle and dark olive-green on the rest of the back. The feathers of the crown are almost entirely dull white anteriorly and cinnamon posteriorly, and *P. pileata*, with its pale crest, chestnut neck and upper back, and maroon and chestnut under parts, is the most colorful species in an otherwise very plain genus.

In the other species, the feathers of the crown are brown and are either uniform or more or less narrowly edged with dull white or grayish white. These pale edges are invariably broader on the feathers of the fore crown, and, in some species, outline or invade to a greater or less degree the feathers of the supraorbital region, forming a superciliary streak which extends posteriorly to the region behind the ear coverts or farther back. In *P. jacucaca*, the feathers of the supraorbital region are virtually all pure white and form a broad and very conspicuous superciliary band which rejoins across the forehead. This white band is bordered at the edge of the bare skin of the face by a narrow band of pure black which ends posteriorly with the white band. This narrow band of black is also present but is less sharply defined in *P. pileata* and *P. ochrogaster* in which, however, it continues along the edge of the bare skin to the sides of the neck and around the base of the throat. A suggestion of this band is found also in *P. dabbenei*, but it is more brownish, less well indicated, and ends behind the ear coverts.

The feathers of the malar band are more or

less variegated with gray white, or they are brown and uniform, not variegated.

The rump and upper tail coverts are usually paler and more rufescent than the back and upper surface of the tail and, in some forms, more or less chestnut, auburn, or coppery.

The ground color of the under parts is brownish also, but paler, duller, more grayish, or more rufescent, than the upper parts. The contrast between the color of the upper parts and that of the under parts is much less pronounced than in *Ortalis*, except in *Penelope pileata* and *P. ochrogaster* in which the whole of the under parts is chestnut, brighter below the upper breast. In the other species, the lower neck and upper breast may or may not be darker than the lower breast and abdomen, or are more grayish or olivaceous, less rufescent, the contrast being best indicated in *P. superciliaris* in which the ground color of the lower neck and upper breast is grayish, much less rufescent than the lower breast and abdomen. The crissum and under tail coverts are of the same color as the lower abdomen or are more rufous.

In all the species, the feathers of the lower neck, breast, and abdomen are edged or bordered with white, buffy white, or grayish white to a varying degree and extent, these pale markings being much better indicated than on the upper parts and more abundant. The pale edges do not meet at the tip of the feather, being more or less broadly interrupted, and this forms streaks, or they are continuous around the tip, forming "scallops." This pattern varies geographically in *Penelope montagnii*, the populations from the northern end of its range being "scalloped"; those from the southern end, streaked.

The tail feathers are brown or olivaceous above and are somewhat darker than the back or of the same color, and are more blackish brown below. They are uniform in 12 species, but in *Penelope argyrotis* they are broadly tipped with auburn, cinnamon, or dingy white more or less tinged with cinnamon, a pale tip being present also on the central pair but more vaguely defined than on the outer pairs. This character is reminiscent of *Ortalis* in which the tips or distal part of the outer tail feathers are paler, or of a different color from that of the base of the

feathers, in all its 10 species, but the pale tips of *P. argyrotis* are less extensive and less sharply defined than in *Ortalis*, and the central rectrices of the latter are brown and uniform, without pale tips.

The primaries are brown in 12 species, but in *Penelope albipennis* the eight outer pairs are white, more or less dusky at the base and tip, the ninth primary being brown except at the center which is whitish. In the populations of *P. jacquacu* from the northeastern part of its range, the primaries, though still brown, are much paler than in its populations from the central and western end of its range.

The feathers of *Penelope* are well integrated, compact, and moderately firm. They vary less in structure than those of *Ortalis*, in which they are more or less decomposed in some parts of the plumage in some species, or modified into bristles on the throat or stiff around the throat. Those of the crest are fully webbed except in *P. pileata*, in which they are partly decomposed. All the species have a crest, but it is better developed in some species than others, and the feathers vary in shape, being relatively broad or narrow, more rounded or more attenuated at the tip. The crest is erectile but is decumbent at rest, with the exception of *P. purpurascens* in which the crest is very bushy and apparently remains semi-erect. In *P. dabbenei* the crest has also a tendency to remain semi-erect.

The face and throat are bare, and all species have a dewlap, a few hairlike feathers growing from the skin of the throat, but the dewlap is not evident in most dried skins. The bare area of the throat is usually very extensive, reaching from the base of the throat to the point of the chin and well up onto the sides of the neck, but it is restricted in some species, in which the chin and upper throat may be feathered. The degree of feathering and the extent of the bare patch vary geographically to a very marked degree in *Penelope montagnii*.

The tarsus is red or some shade of red in life in all species, except in *Penelope obscura* in which it is blackish brown or black, and in *P. dabbenei* in which it is brown. The bare skin of the throat is probably red in all species, although I have found no information for *P. montagnii*, but it is very probably

red also as it is very pale and yellowish in skins. The bare skin of the face is said to be slaty blue in 12 species, or lead-blue, livid violet, violaceous blue, blackish, or black. The only exception is *P. dabbenei*, in which the only color that has been noted is red. I found this information on the label of only one specimen, but it seems to be correct because the skin is pale and yellowish in skins.

The color of the iris has been noted as red, garnet, reddish brown, or brown in both sexes of all species, but a sexual difference probably exists, because brown, rather than red, was usually mentioned in the case of females. The iris probably becomes red in males during the breeding season.

VARIATIONS IN SIZE AND PROPORTIONS

The measurements of *Penelope* are given in table 1, and the relative proportions of the males are compared in a ratio diagram (fig. 18) in which *P. marail* is the standard of comparison. This species was selected because it is intermediate in size between the small and large species, and its other characters are neither primitive nor specialized. It is the most "typical" species of *Penelope* and, by chance, is also the type of the genus. The small species are *P. argyrotis*, *P. ortonii*, *P. montagnii*, and *P. superciliaris*; the large ones are *P. dabbenei*, *P. obscura*, *P. jacquacu*, *P. purpurascens*, *P. albipennis*, *P. jacucaca*, *P. ochrogaster*, and *P. pileata*. The species are listed here in systematic order, not progressively by size.

Penelope is larger than *Ortalis*, and the mean wing length in round numbers varies from 252 mm. in the males and 243 in the females of *P. montagnii*, to 374 in the males and 362 in the females of *P. purpurascens*, with a mean for the genus of 303 in the males and 290 in the females. Some subspecies of *P. montagnii* and *P. superciliaris*, which are the smallest species, are slightly smaller than some subspecies of *O. poliocephala* and *O. canicollis*, the two largest species of *Ortalis*, but the mean measurements of the two genera show very little overlap (fig. 7).

The proportions of the large species show very little variation except those of *P. purpurascens* and the unusually long tarsus of *P. albipennis* which represents, I believe, an adaptation to its habitat, as I mention

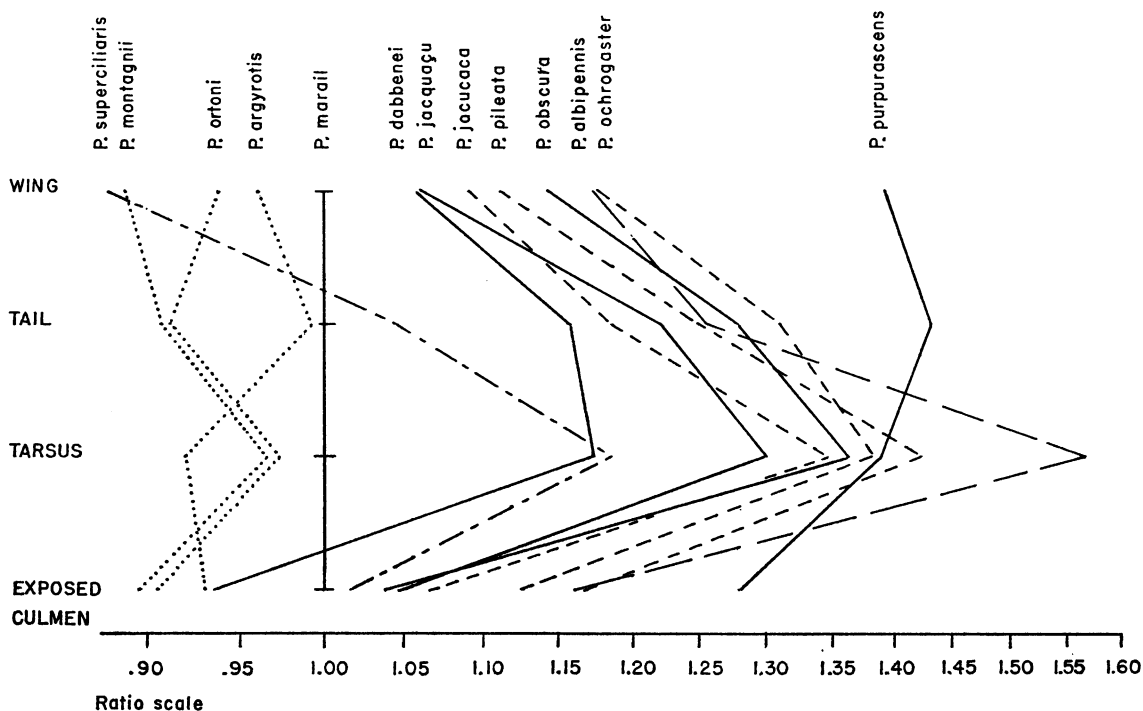


FIG. 18. Comparison by ratio diagram of the proportions of the adult males of the genus *Penelope*.

above in the discussion of the distribution.

The proportions of *Penelope dabbenei*, *P. obscura*, and *P. jacquaçu* (represented by an unbroken line in fig. 18) are remarkably similar and furnish another and convincing argument that *P. dabbenei* is related to *P. obscura*, but not to *P. montagnii*, a question that I discussed in one of my preliminary papers (1966b) before I had completed my study of the genus and compared the proportions.

Penelope obscura is related in turn to *P. jacquaçu*, and the latter to *P. purpurascens*; these three form a single complex which includes *P. dabbenei*, but it is evident that *P. purpurascens* is the most aberrant member of this complex. The latter has often been said to be conspecific with *P. jacquaçu*, but the proportions of the two birds differ, and they are differentiated also by other very sharp morphological differences (Vaurie, 1966a) which show that they are certainly not conspecific.

The proportions of *Penelope jacucaca*, *P. pileata*, and *P. ochrogaster* (represented by short dashes in fig. 18) are similar, and they

are similar also to those of *P. dabbenei*, *P. obscura*, and *P. jacquaçu*, but clear-cut differences in the plumage and crest show that the two groups are not very closely related.

The proportions of three of the four small species (*Penelope montagnii*, *P. ortoni*, and *P. argyrotis*, represented by a line of dots in fig. 18) do not vary significantly, and tend to be similar to those of *P. marail*, with the exception of the tarsus which is proportionally somewhat longer or shorter. However, the proportions of the small *P. supercilialis* are strongly aberrant, and it is noteworthy that its coloration is aberrant also.

PHYLOGENY

The 13 species form two dissociated groups, composed of the small species in one, and of the large species in the other, with the intermediate *Penelope marail* as the "pivot." The small species do not appear to be closely related to one another (see below), but it seems best to place them first in the linear sequence, not only because they are small (a marked increase in size presumably

denoting a greater degree of specialization), but also because they include the three species (*P. argyrotis*, *P. ortonii*, and *P. montagnii*) that appear to be the most primitive. *Penelope marail* is not demonstrably related to either the small or the large species.

All the large species can be divided into two groups, *Penelope albipennis* being omitted. One of these groups is composed of *P. jacucaca*, *P. ochrogaster*, and *P. pileata* which form a very clear superspecies. These three birds have been considered conspecific, but they have become sharply differentiated morphologically, and it is highly probable that they are separate species (Vaurie, 1966b). These three species, which represent one another geographically, are the most specialized in *Penelope*, as demonstrated by the elaborate pattern of the head, modified and highly developed crest, and the colorful plumage of *P. ochrogaster* and *P. pileata*, the latter being the only species of *Penelope* that is dichromatic above.

The second group of large species is composed of *Penelope dabbeni*, *P. obscura*, *P. jacquaçu*, and *P. purpurascens*, the last three being geographically representative. These three have been considered to be conspecific, but I believe this decision is incorrect (see Vaurie, 1966a). *Penelope dabbeni* and *P. obscura* overlap, but this overlap does not contradict their relationship, and it is possible that it represents a secondary expansion of *P. obscura* forced by a recent deterioration of its former habitat in the Chaco. This second group of four less-specialized species shows no evidence of close relationship to the first group of three species.

The position of *Penelope albipennis* is more doubtful, but it seems best listed between the two groups, because its white primaries are an instance of specialization, although its other characters are more similar to those of the four species of the second group.

To return to the small species. It seems logical to start the systematic list with *Penelope argyrotis* on the ground that it retains the tail pattern of *Ortalis*, but *P. ortonii* is actually more primitive than *P. argyrotis*. The crest of *P. ortonii* is more poorly developed than that of any other species, and its upper parts, wing, face, and sides of

the neck are uniform, whereas they are streaked or patterned in all the other species. Hellmayr and Conover (1942, p. 145) have remarked that *P. ortonii* is an isolated species. This is quite correct (Vaurie, 1966b), and one could rank it lowest, but I have given more systematic weight to the *Ortalis*-like tail pattern of *P. argyrotis*.

The nearest relative of *Penelope ortonii* is not clear to me, but it is not *P. montagnii*. The latter is less primitive, but the fact that some of the subspecies of *P. montagnii* are heavily feathered on the throat and that their bare gular patch is very reduced, much more so than in any other species of *Penelope* argues for a certain degree of primitiveness.

Penelope superciliaris is strongly aberrant in coloration and proportions (fig. 18). The edges of its greater upper wing coverts, scapulars, and inner secondaries are chestnut, rather than white or whitish as in the other species, and the gray edges on its mantle, neck, lesser upper wing coverts, and breast form very regular scallops, rather than streaks as in the other species of *Penelope*. The unusual color pattern and proportions of *P. superciliaris* suggest that it is less primitive than the other small species and also occupies a position apart.

The systematic sequence that I have adopted is therefore as follows: *Penelope argyrotis*, *P. ortonii*, *P. montagnii*, *P. superciliaris*, *P. marail*, *P. dabbeni*, *P. obscura*, *P. jacquaçu*, *P. purpurascens*, *P. albipennis*, *P. jacucaca*, *P. ochrogaster*, and *P. pileata*.

LIST OF THE SPECIES

Penelope argyrotis

DIAGNOSIS: Crown varying from raw umber to dark olive-brown, similar to or contrasting slightly with color of back which varies from auburn brown to dark brown with a slight olivaceous cast; rump and upper tail coverts more rufescent than back, varying from umber to dull chestnut. Under part, paler than back, varying from grayish or olive-brown to dull chestnut brown, feathers of abdomen more or less faintly vermiculated with blackish brown. Tail feathers, including central pair, more or less broadly tipped with auburn, cinnamon, or dingy white tinged faintly with cinnamon to varying extent; pale tip on central pair more

vaguely defined and restricted than on other pairs. Primaries brown and uniform. Feathers of crest varying in shape, from relatively short, broad, and rounded at tip, to relatively long, narrow, and more attenuated, and more or less edged with buffy or grayish white; these pale edges restricted chiefly to feathers of fore crown, or present on all feathers, extending along their entire length, or not. Superciliary streak and malar stripe more or less variegated with buffy white or grayish white. Whitish edges of feathers of mantle, upper wing, sides of neck, breast, and abdomen more or less sharply defined, abundant or reduced in number. Bare gular patch extensive, extending to chin, or much reduced, chin and upper throat being fully feathered.

RANGE: Disjunct, consisting of three groups of populations inhabiting mountainous districts, from low to moderate elevations (from about 450 to about 3050 meters). One group is restricted to southwestern Ecuador and northwestern Peru, another to the Santa Marta Massif of northern Colombia, and the third ranges from the Sierra de Perija on the border of Colombia and Venezuela, south in the Eastern Andes of Colombia to at least the region of Cachiri in Santander and that of the Rio Negro in northern Boyaca, and east through the Andes and cordilleras of northern Venezuela to Monagas.

GEOGRAPHICAL VARIATION: The geographical variation is very well marked and has been reviewed by Hellmayr and Conover (1932) and by me (1966b). Three subspecies, one for each of the three isolated groups, can be recognized. *Barbata*, which inhabits Ecuador and Peru, differs from *colombiana* of the Santa Marta Massif and from nominate *argyrotis* of the Sierra de Perija and the Andes of northern Colombia and Venezuela by being fully feathered on the chin and upper throat, with the consequence that its gular patch is restricted, whereas the chin and upper throat are bare, or virtually so, and the bare gular patch is very extensive in the other two subspecies. *Barbata* is also darker above and below and has fewer pale streaks on the back and upper wing coverts. The general coloration of *colombiana* and nomi-

nate *argyrotis* is similar, but the feathers of the crest are narrower in *colombiana*, more attenuated at the tip, less rounded, and they are edged with grayish white along their entire length, whereas the pale edges are interrupted in nominate *argyrotis* and restricted chiefly to the feathers that spring from the fore crown. The superciliary streak and malar stripe of *colombiana* are also much less distinct than those in nominate *argyrotis* in which the streak and stripe are pale silvery gray and very conspicuous, and all the pale edges of the rest of the plumage are duller in *colombiana*, more buffy, less pure white, than in nominate *argyrotis*. The three subspecies also vary in size, the wing length of nominate *argyrotis* averaging distinctly longer than that of *colombiana* and *barbata* in which it is about similar (table 1).

After the review of Hellmayr and Conover (1932), with which I am in complete agreement, four additional forms were named which I do not recognize as they are all based on trivial differences, or on a single character of minor importance, and serve only to obscure the geographical variation of the species as a whole (see the synonymy and my review, 1966b).

Penelope ortonii

DIAGNOSIS: Top and sides of head dark umber-brown, contrasting slightly with back, rump, and upper surfaces of tail and wings which are dark bronzy brown with slight vinaceous cast; lower throat and breast dark brown, not bronzy or vinaceous, abdomen grayish brown, "thighs" and under tail coverts umber-brown. Head, including superciliary and malar regions, back and sides of neck, and whole of upper parts, including wings, uniform in coloration, without pale markings of any kind. Feathers of lower throat having narrow white edges, these white edges becoming broader and more abundant on breast and abdomen, forming streaks or coalescing to varying degree. Tail and primaries brown and uniform.

RANGE: Pacific coast of Colombia, from the Rio Jurado near the border of Panama, and lower (Pacific) slopes of the Western Andes, south through western Ecuador to about the valley of the Rio Chimbo; ascend-

ing to 1554 meters in Colombia and about 1250 in Ecuador.

This species does not vary geographically.

Penelope montagnii

DIAGNOSIS: Ground color of crown and hind neck dark umber or olivaceous brown, similar to or contrasting slightly with back and upper surface of wing which vary from dark auburn-brown to olivaceous brown with faint bronzy sheen; rump and upper tail coverts dark chestnut or more rufescent than back. Under parts paler than back, more olive on breast, more grayish brown or more rufous on abdomen. Feathers of crest, hind neck, mantle, and lesser upper wing coverts more or less narrowly edged with grayish white or buffy white to varying degree, greater coverts and feathers of back below mantle more or less faintly bordered with dull gray or reddish brown. Feathers of breast and abdomen well or rather poorly edged with dull white, these edges continuous around tip of feather, as a rule, and forming "scallops" in forms in which they are well developed, but interrupted and forming streaks which vary in width and abundance in forms in which they are not well developed. Feathers of superciliary streak, malar stripe, and at sides of neck edged or variegated to varying degree with dull pale gray, or with bright silvery grayish white. Tail and primaries brown. Bare gular patch varying in size, being extensive or very restricted, chin and upper throat more or less well feathered in forms in which it is restricted.

RANGE: Sierra de Perija, and the Andes, from the State of Trujillo in Venezuela, south to extreme northern Salta in Argentina. The specimens that I have examined were collected from about 1067 to about 3657 meters, *Penelope montagnii* ascending higher than any other species.

GEOGRAPHICAL VARIATION: The geographical variation is well marked, and five subspecies can be recognized which form two groups. Those of the first group (nominate *montagnii*, *atrogularis*, and *brookii*) differ from those of the second (*plumosa* and *sclateri*), by being less rufescent below, by having the pale edges of the feathers of the head, mantle, and wing coverts less well

developed, those on the under parts being, on the other hand, much better developed. On the under parts of nominate *montagnii*, *atrogularis*, and *brookii*, the pale edges are broad and continuous around the feather, forming "scallops," but they are interrupted at the tip in *plumosa* and *sclateri*, forming streaks. The geographical variation is strongly clinal in both groups, and these are presumably connected by intermediate populations, although I did not find a specimen that is truly intermediate.

Nominate *montagnii* inhabits the Sierra de Perija and ranges from the Andes in the state of Trujillo in Venezuela, south through the Eastern and Central Andes of Colombia to Nariño, but the southern limits of its range are difficult to define because it intergrades with *atrogularis* in the Central Andes from Caldas to Nariño, and with *brookii* in the eastern Andes of Nariño. In this subspecies, the throat is heavily feathered except for a very restricted area on the center of the throat, which is bare, the feathers of the throat being fully webbed and well edged with pale gray. *Atrogularis*, which ranges from the southwestern slopes of the Andes of Nariño southward through western Ecuador to Azuay, is less heavily feathered on the throat than nominate *montagnii*, with the result that the bare gular area is more extensive. Moreover, the feathers of its throat are nearly all decomposed and are blackish, with only a faint trace of gray. *Atrogularis* is also darker below than nominate *montagnii*, more brownish, less russet. Typical *brookii* seems to be restricted only to eastern Ecuador, but the intermediate population of the eastern slopes of the Andes of Nariño is best referred to *brookii* to which it appears to be more similar than to nominate *montagnii*. The bare gular area is about as extensive in *brookii* as it is in *atrogularis*, but the feathers of its upper throat are even more blackish and decomposed than those of *atrogularis*. The pale edges of the feathers are well developed in *brookii*, better than in *atrogularis*, and about as well developed as in nominate *montagnii* on the crest, superciliary streak, sides of the neck, and malar stripe, but they are somewhat broader and more conspicuous than in nominate *montagnii* on the hind neck, upper

mantle, breast, and abdomen. The general coloration of *brookii* is also distinctly duller and darker above and below than that of the other two subspecies.

The two subspecies of the second group range from eastern Peru southward through the yungas of Bolivia, to the department of Santa Victoria in extreme northern Salta, Argentina. They intergrade in southeastern Peru where the cline is pronounced, but specimens that I have seen taken from the region northeast of Paucartambo south to the region southeast of Marcapata are much more similar to *plumosa* from central and northern Peru than they are to *sclateri* from Bolivia. *Plumosa* is much better feathered on the upper throat than *sclateri*, which is feathered very scantily only on the chin, and its superciliary streak and malar stripe are much less conspicuous than in *sclateri*, in which they are silvery white. On the other hand, the pale edges of the feathers of the under parts, mantle, and hind neck are much better developed in *plumosa*, the hind neck of *sclateri* being uniformly brown, not streaked, and the mantle virtually uniform, with only a few faint streaks. *Plumosa* is also more rufous below than *sclateri*, more brownish above, less bronzy green.

It is of interest to note that the upper throat of *plumosa* is well feathered, less so than in nominate *montagnii*, but much better than in *atroglaris* and *brookii*, its feathers being better integrated, less decomposed, than those of *atroglaris* and *brookii*, and well edged with gray.

The geographical variation of the species also affects size (table 1) and the color of the bill. The wing length averages shorter in *atroglaris* and *brookii* than in nominate *montagnii*. The smallest subspecies is *plumosa*, and the largest is *sclateri*. The bill is dark and uniform in coloration in the last two, has a pale tip in nominate *montagnii*, the tip becoming progressively paler and more conspicuous in *atroglaris* and *brookii*.

Penelope superciliaris

DIAGNOSIS: Ground color of upper parts and upper surface of wings olive-brown, except for rump and upper tail coverts which are dark russet or chestnut, under parts paler, more grayish brown on lower throat

and breast, more rufescent brown on abdomen. Feathers of back and sides of neck, mantle, lower throat, breast, and lesser upper wing coverts bordered narrowly with pale gray or grayish white, and, terminally, with very narrow and faint blackish band evident only when feathers are not worn; pale edges regular and continuous around entire contour of feather, not interrupted at tip, scalloped pattern being very regular, as a rule, especially on lower throat, breast, and mantle. On middle and greater wing coverts, scapulars, and inner secondaries, gray borders replaced by rusty buff, rufous ocher, or chestnut edges which become progressively broader and more interrupted at tips distally. Outer web of other secondaries and webs of central two or three pairs of rectrices more or less faintly edged with chestnut. Crest dark brown and virtually uniform, except for faint grayish or ochraceous edges on feathers that spring from forehead. Superciliary streak moderately well defined, varying in color from grayish or buffy white to ochraceous white. Malar stripe brown and uniform, or very slightly and faintly variegated with brownish gray. Tail and primaries brown and uniform.

RANGE: Very extensive, extending from the right bank of the Guaporé and Madeira rivers eastward through Brazil, south of the Amazon, to northeastern Para and south to eastern Paraguay, Misiones in northeastern Argentina, and Rio Grande do Sul in southeastern Brazil.

GEOGRAPHICAL VARIATION: The geographical variation is slight, despite the enormous range, and affects chiefly the width and shade of the rufous edgings, although the superciliary streak, general coloration, and size also vary somewhat. Individual variation is more or less pronounced. Three rather poorly differentiated subspecies can be recognized. Nominate *superciliaris* inhabits western and northern Brazil from the Guaporé and Madeira eastward to Para, and differs from *jacupemba* by being darker, less grayish, above, by having darker rufous edges on the coverts, scapulars, and inner secondaries, and by having a somewhat less well-defined superciliary streak which varies from grayish white to buffy white, whereas it varies from grayish or buffy white to ochraceous in

jacupemba. The latter replaces nominate *superciliaris* from Maranhão southward through eastern and central Brazil, but not south to the states of Santa Catarina and Rio Grande do Sul where it is replaced by *major*, the range of *major* extending westward through Misiones to eastern Paraguay east of the Paraguay River. The rufous edges are narrower in *major* than in *jacupemba* and nominate *superciliaris*, and *major* also differ from the other two subspecies by being darker above, more olive, and by averaging a little larger (table 1).

Penelope marail

DIAGNOSIS: Upper parts, including crown, upper surface of wing, rump, and upper tail coverts, dark olive-green, with distinct but not very highly developed gloss. Lower throat and upper breast also olive-green, but more brownish than back, not glossed or only very faintly so, contrasting to greater or lesser degree with lower breast and abdomen which are more or less dull burnt sienna, feathers being slightly mottled with dark brown. Crest feathers very narrowly edged with pale gray, edges restricted chiefly to feathers of front and sides of crest; feathers of hind neck, upper mantle, and lesser upper wing coverts edged laterally, but not at tip, with grayish white, edges becoming broader and purer white on mantle; feathers of lower throat and upper breast more broadly edged laterally with white than those of mantle, but resulting streaks relatively short. Superciliary streak not sharply defined, but its feathers, and those at sides of neck and of malar stripe well edged with grayish white. Tail and primaries brown and uniform.

RANGE: Southern Venezuela, south of the Orinoco west to the Rio Caura, and the Guianas, south to the north bank of the Amazon. The western limits of the range (fig. 17) are not well known, but on the Amazon the range extends west to at least the region of Itacoatiara, or to about longitude 58° 30' W.

GEOGRAPHICAL VARIATION: The geographical variation is slight and has been discussed by me in a preliminary paper (1964). The birds of Brazil, at least those along the Amazon, are paler, more grayish brown, below than those of the Guianas, the dark

area of the breast is more restricted, not extending so far down, and the ground color of the feathers is somewhat paler, with the result that the white edges of the feathers are less conspicuous than in the birds of the Guianas. The wing and the tail average shorter in the birds of Brazil (table 1). Two subspecies can be recognized: *jacupemba* for the birds of the Amazon, and nominate *marail* for those of the Guianas. The subspecific status of the other populations, including the population of Venezuela, is not clear, and the range of the two subspecies requires further investigation.

Penelope dabbenei

DIAGNOSIS: Upper and lower parts warm olivaceous umber-brown, somewhat paler and more grayish below, faintly glossy above but not below. Rump, upper tail coverts, lower abdomen, and under tail coverts somewhat more rufescent, less olivaceous, but, with these exceptions, ground color of entire plumage virtually uniform. Feathers of mantle, upper wing coverts, lower throat, and breast having rather narrow dull white edges broadly interrupted at tip and forming relatively poorly developed streaks. Feathers of crest semi-erect, broad, rounded, and well developed, and except for those growing from rear of crown, broadly or very well edged with pale grayish white or dull white, white area of crest merging with superciliary streak, latter not distinct except toward rear of crown; superciliary streak bordered at edge of bare skin of face by narrow band of brownish black extending to region behind ear coverts. Anterior part of malar stripe slightly variegated with dull gray. Tail and primaries brown and uniform. Bare skin of face pale and yellowish in skins and red in life. Tarsus brown in life.

RANGE: Lower slopes of the eastern Andes, between about 1524 and 2042 meters, from the departments of Chuquisaca and Tarija in southern Bolivia, south to the region above Calilegua in eastern Jujuy in Argentina, or to about latitude 23° 47' S.

This species, which has a restricted range, does not vary geographically. It is poorly known and is represented by relatively few specimens in collections.

Penelope obscura

DIAGNOSIS: Crown and hind neck varying from sooty olivaceous black to olivaceous brown or warm dark brown, somewhat darker than back and upper surface of wing which are bronzy to some degree and varying from olivaceous black to olive-brown or warm brown; rump and upper tail coverts a little paler than back. Under parts having same general coloration as back but paler and less bronzy. Feathers of hind neck, mantle, upper wing coverts, lower throat, and breast moderately well edged with grayish or dull white, or with white, pale edges being interrupted at tip and forming streaks which are more or less conspicuous, varying in abundance, and may be much reduced on lower throat, breast, and hind neck. Feathers of anterior and middle parts of crest edged with grayish white, or pale edges obsolete, very faint, and restricted to front of crest. One subspecies having a well-defined superciliary streak which is relatively conspicuous, but superciliary streak absent or virtually so in other subspecies. Malar stripe brown and uniform. Tail and primaries brown and uniform. Tarsus blackish brown or black in life.

RANGE: Disjunct, consisting of three groups of populations (fig. 16): one in eastern Brazil from the states of Espírito Santo, Rio de Janeiro, and southeastern Minas Gerais south through São Paulo and Parana to Santa Catarina; the second distributed from extreme southeastern Brazil (Rio Grande do Sul) west to northeastern Argentina (Misiones, Corrientes, and eastern Chaco to northern Santa Fe) to southern Paraguay, and south to Uruguay; and the third from central Bolivia south through northwestern Argentina in the subtropical zone of Jujuy, Salta, and Tucuman to neighboring Catamarca.

The gap between the ranges of the last two groups probably represents (as mentioned above in the discussion of the phylogeny) a secondary modification of the range caused by an increase of aridity in the Chaco which has forced the species to expand westward. A gap in southern Brazil may occur, because the two populations of Brazil are quite distinct and show no evidence of intergradation.

GEOGRAPHICAL VARIATION: The three groups form three very distinct subspecies: *bronzina* in eastern Brazil, nominate *obscura* in Rio Grande do Sul, Uruguay, northeastern Argentina, and southern Paraguay, and *bridgesi* in Bolivia and northwestern Argentina. The coloration of *bridgesi* is warm brown, and this subspecies is less streaked than nominate *obscura* and *bronzina* on the lower throat, breast, hind neck, and mantle, but more so on the scapulars and wing coverts, its streaks also being purer white. Nominate *obscura* is very dark, olivaceous black, whereas *bronzina* is paler, olive-brown, and the most bronzy subspecies. The pale edges of the feathers of the crest are well developed in *bridgesi* and *bronzina*, but are very faint in nominate *obscura* and restricted to the anterior feathers. The superciliary streak is well developed in *bronzina*, but is obsolete and absent, or virtually so, in *bridgesi* and nominate *obscura*. The three subspecies vary also in size (table 1), nominate *obscura* being the smallest, *bridgesi* the largest, and *bronzina* being intermediate.

Penelope jacquaçu

DIAGNOSIS: Color of upper parts varying from olive-brown on hind neck and mantle, reddish brown, somewhat "coppery," on inner secondaries and upper surface of tail, and chestnut on rump and upper tail coverts, in one subspecies, to bronzy olive-brown, brownish olive-green, bluish olive-green, and dark dull bluish green, with more or less pronounced gloss, best developed in most greenish and bluish forms; upper parts virtually uniform except for rump and upper tail coverts which are usually slightly paler. Lower throat and breast about same color as back, but paler, and grading into rufescent brown, russet, or dull chestnut on abdomen, abdomen sooty brown, however, in form which is dark bluish green above. Feathers of hind neck, mantle, scapulars, upper wing coverts, lower throat, and breast edged with grayish white or buffy white, pale edges interrupted at tip and forming streaks that are well or rather poorly developed. Feathers of crest slightly or well edged with whitish gray, feathers distinctly longer and narrower in one form, more attenuated at tip, less rounded. Superciliary streak very faintly



1, 2. Top of the head, nape, and hind neck. 1. *Pauxi unicornis* (with crest). 2. *P. pauxi* (no crest)
 3, 4. Type of *Penelope albipennis*. 3. Collector's labels (for translation, see text). 4. Type specimen



Side views of the skull in some species of the Cracini. 1. *Nothocrax urumutum*. 2. *Crax globulosa*. 3. *Mitu mitu*. 4. *Pauxi pauxi*

indicated or not well developed and inconspicuous. Malar stripe brown and uniform, or virtually so, or variegated to slight degree with pale gray. Tail and primaries brown and uniform, but primaries becoming progressively paler in populations from northeastern part of range, buffy brown or fawn, less dark seal-brown.

RANGE: Partly disjunct; an isolated population (*perspicax*) inhabits the Cauca Valley, the west slopes of the Central Andes, and both slopes of the Western Andes of Colombia. The range of the other populations is continuous and consists of the Amazon Basin from the eastern slopes of the Andes in Colombia, Ecuador, Peru, and Bolivia south to the region of Buena Vista in Santa Cruz or about latitude 17° 21' S., east to the headwaters of the Rio Tapajoz and very probably those of the Rio Xingu, and the region east of and near the mouth of the Rio Madeira, north to northwestern Brazil, Venezuela south of the Orinoco, and Guyana (former British Guiana). The eastern limit of the range in northern Brazil and the Guianas is not well known, however, and may extend farther (fig. 16).

GEOGRAPHICAL VARIATION: The geographical variation, which was reviewed by me in a preliminary paper (1966a), is very well marked, consisting of variations in size, coloration, and the development of the crest, and is or appears to be clinal in the four subspecies that have a continuous range (nominate *jacquaçu*, *orienticola*, *granti*, and *speciosa*).

The isolated *perspicax* is more similar to nominate *jacquaçu* of the Amazon Basin than it is to the other subspecies, but is distinctly more rufous above, although not below, and averages a little larger (table 1). The crest is similar in both subspecies, as is also the malar stripe which is brown and uniform, or virtually so, but the pale streaks on the scapulars and mantle are usually a little narrower and less conspicuous in *perspicax*, whereas those of the under parts are better developed. *Orienticola*, which replaces nominate *jacquaçu* north of the Solimões and Amazon, is intermediate in size and coloration between nominate *jacquaçu* and *granti*, darker above than nominate *jacquaçu*, greener, much less bronzy, and darker, less rufous, on the rump

and under parts. The development of the crest and the shape of its feathers are similar in *orienticola* and nominate *jacquaçu*, but the pale edges of its feathers are less well developed in *orienticola*. The streaks are also less well developed on the scapulars and mantle, but the malar stripe is slightly variegated with gray in *orienticola*, and its primaries are distinctly paler. *Orienticola* intergrades with nominate *jacquaçu* in southeastern Colombia (the range of nominate *jacquaçu* extending west to the Eastern Andes of Colombia), and with *granti* in the east over a very broad zone in southern Venezuela and probably western and southern Guyana (former British Guiana). *Granti*, which is restricted to Guyana and the northeastern part of the state of Bolívar in Venezuela, is larger and darker than *orienticola*, more bluish throughout, has a similar crest, and, in some individuals, is better variegated with gray on the malar stripe. The streaks on the scapulars and mantle are usually less developed in *granti*, and the primaries average paler brown. *Speciosa* has a much better-developed crest than the other subspecies, its feathers being longer, narrower, more attenuated at the tip, and better edged with grayish white. Its superciliary streak is also better developed. The malar stripe is variegated with gray. The general coloration of the rest of its plumage is about the same as the coloration of nominate *jacquaçu*, but *speciosa* is usually somewhat darker above, a little less streaked above and below, and a little darker rufous below. *Speciosa* replaces nominate *jacquaçu* in Bolivia, apparently intergrading with it in the north on the lower Rio Beni.

Penelope purpurascens

DIAGNOSIS: Upper parts warm brown, varying from warm sepia-brown to dark auburn or dark russet-hazel, with slight greenish bronzy or vinaceous sheen; crown and hind neck darker, more fuscous than back, and less bronzy; rump and upper tail coverts somewhat paler than back, more rufous or chestnut; upper surface of tail bronzy olive-brown, reddish brown, or "coppery" auburn. Under parts dark fuscous brown, becoming more rufescent, auburn, or russet on lower abdomen. Feathers of hind

neck, mantle, scapulars, upper wing coverts, lower throat, and breast edged narrowly and laterally with dull white, pale edges forming streaks which are lacking altogether in some forms on hind neck, mantle, scapulars, and coverts. Feathers of crest very broad and rounded, relatively short, usually semi-erect, forming "bushy" crest; brown and uniform, or a few feathers of fore crown very faintly edged with gray near base. No superciliary streak, and malar stripe brown and uniform. Tail and primaries brown and uniform.

RANGE: Mexico, from southern Sinaloa in the west and the region of Ciudad Victoria in Tamaulipas in the east, south through Central America to Colombia, northern Venezuela to the delta of the Orinoco, and southwestern Ecuador to the cordilleras north of Zaruma in El Oro. In Colombia the range extends from the north, south to Antioquia and the Magdalena Valley to its headwaters (the species has been collected also "near Bogota"), and in the west follows the Pacific coastal region.

GEOGRAPHICAL VARIATION: The geographical variation is relatively slight and consists chiefly of clinal variations in size and coloration. The size decreases gradually southward from Mexico to Ecuador, as shown by the measurements in my preliminary paper (1966a). Three subspecies can be recognized, two of which (nominate *purpurascens* and *aequatorialis*) are reasonably well differentiated. Nominate *purpurascens*, which ranges from Mexico south to Honduras and Nicaragua where it grades into *aequatorialis* in size and coloration, differs from the latter by being less rufescent throughout, and by having the hind neck, scapulars, mantle, and wing coverts streaked. A very few faint traces of streaks persist on the scapulars and mantle in an occasional specimen of *aequatorialis*, but such a bird is rare. In nominate *purpurascens* the short feathers of the fore crown are usually very faintly edged with grayish white, but not in *aequatorialis*. Some of the populations of *aequatorialis* are not constant, as the studies of Blake (1955) and myself (1966a) have shown. Some individuals from the range of *aequatorialis* in Colombia and Venezuela are very similar to or even identical in coloration with the third subspecies (*brunnescens*) which differs from

aequatorialis by being only somewhat more rufous. On the whole, however, it is desirable to restrict the range of *brunnescens* to the Santa Marta Massif and the basin of Lake Maracaibo where this subspecies, which is not very well differentiated at best, is reasonably constant. The range of *aequatorialis* extends from Costa Rica south to Colombia and Venezuela (with the exceptions noted) and to Ecuador.

Penelope albipennis

DIAGNOSIS: General coloration brownish olive, with very faint bronzy sheen above, duller and more rufescent; below with feathers of abdomen slightly mottled with dark brown.

Taczanowski (1886, p. 271) compared *Penelope albipennis* to *P. marail*, stating that the upper parts of *P. albipennis* are dark olive, with a rather pronounced gloss, more or less similar to that of *P. marail*, "*La couleur générale des parties supérieures du corps est olive foncé avec un éclat verdâtre métallique assez fort, à peu près comme celui de la P. marail de la Guyane.*" The plumage of *P. marail* is not truly "metallic," however, even in birds in fresh plumage collected recently, and the two specimens of *P. albipennis* that I have seen do not resemble *P. marail*. They are more brownish, less greenish, and are not glossy, or are only very faintly so. To be sure, they were mounted birds which were exposed to light for many years and have probably faded badly, especially the unsexed specimen in the collection of the British Museum which, moreover, is in extremely worn plumage. The third specimen of *P. albipennis* in existence is also a mounted bird and therefore is probably faded.

The true general coloration of *Penelope albipennis* can no longer be ascertained, but the pale grayish white edges of the feathers of the crest were better developed, and those of the upper mantle, lower throat, and upper breast were less developed, than in *P. marail*. *Penelope albipennis* had no superciliary streak, and its malar stripe was dark brown and uniform, not variegated with grayish white. The most important and very conspicuous difference in coloration that distinguishes *P. albipennis* from *P. marail* and all other species of *Penelope* is the color

of the primaries which are not brown and uniform, but white, the eight outer pairs being white, with a more or less dusky tip and base, and the ninth brown except at the center which is whitish.

The white primaries are conspicuous in the photograph of the type of *Penelope albipennis* (pl. 16, fig. 4) which shows the upper surface of the edge of the folded wing, as well as the under surface of some of the tips of the outer primaries on the opposite side. Note also the lack of a superciliary streak, the dark and uniform coloration of the malar stripe, and the very long and strong tarsus. The bill is not normal, as the tip of the culmen has been broken off.

Plate 16, figure 3 shows also the original collector's label and the museum label attached subsequently. The collector, J. Stolzmann, wrote after his field book number ("299") a name ("*Penelope albiblanca*") that was never published (and therefore has no standing in nomenclature), the date ("d. 18 December 1876"), and the color of the soft parts, in Polish, followed by the sex, and the locality where the bird was collected ("Sa. Lucia"), in northwestern Peru. The color of the soft parts, as translated, is: iris pale brown, color of bare face livid violet, gular patch orange. I am indebted for the photographs to the authorities of the Instytut Zoologiczny, Polskiej Akademii Nauk, Warsaw, who had them prepared for me at the time of my visit to that institution.

RANGE: The range of this species is discussed in detail above, in the discussion of the distribution of the genus. *Penelope albipennis* is extinct and known from only three specimens taken in 1876 and 1877 in northwestern Peru when it was on the verge of extinction, one in the delta of the Rio Tumbes, and the other two in the valley of the lower Rio Piura, about 200 kilometers south of the first locality. It is possible that the range of *albipennis* was once more extensive, but would seem to have been too restricted to foster geographical variation.

Penelope jacucaca

DIAGNOSIS: Crown and hind neck sooty brown, grading into warm brown on mantle, and into auburn-brown on scapulars and upper wing coverts, scapulars and coverts

having a slight greenish bronzy sheen. Lower throat and upper breast dark maroon-brown, grading into dark chestnut-brown on lower breast and abdomen, some feathers of lower breast and abdomen more or less variegated near edge with russet. Feathers of mantle, scapulars, upper wing coverts, lower throat, and breast well edged laterally with white, white edges forming conspicuous streaks. Feathers of crest very long, narrow, fully webbed, and decumbent; short feathers at front of crest white on mesial half, those at sides of crest and feathers of superciliary region white, except at very base which is brown and concealed, forming two broad and very conspicuous bands which extend posteriorly well behind ear coverts, contrasting very boldly with blackish center of crown. White band separated from bare skin of face by narrow band of pure black which joins across forehead and reaches posteriorly to region behind ear coverts. Malar stripe brown and virtually uniform, showing only a very few tiny whitish feathers. Tail and primaries brown and uniform.

RANGE: Interior of northeastern Brazil, from Piahy, Ceara, and Paraiba south to southern Piahy, and central and southern Bahia.

This species does not vary geographically.

Penelope ochrogaster

DIAGNOSIS: Hind neck and ground color of crest dark auburn or dark dull reddish brown, grading into olive-brown on nape, scapulars, and mantle, upper wing coverts auburn-brown, these, and mantle and scapulars, having slight bronzy sheen; rump and upper tail coverts rufous brown verging on chestnut and contrasting with color of back. Lower throat maroon, grading into chestnut which becomes progressively paler and brighter on breast and abdomen. Feathers of mantle, scapulars, upper wing coverts, lower throat, and breast well edged laterally with white, streaks conspicuous. Feathers of crest long, very narrow, fully webbed, and decumbent, with faint buffy or grayish edges. Superciliary streak present but dingy and not well indicated. Band of brownish black separating feathers of superciliary region from bare skin of face (as in *P. jacucaca* in which it is black) but better developed than

in *P. jacucaca* and continuing along edges of bare skin to sides of neck and around base of bare throat. Malar stripe similar to that of *P. jacucaca*. Tail and primaries brown and uniform.

RANGE: Central Brazil, from the region of Descalvados in central eastern Mato Grosso east to the Rio São Domingos in central eastern Goyaz and to western Minas Gerais.

This species does not vary geographically.

Penelope pileata

DIAGNOSIS: Closely related to *Penelope ochrogaster*, resembling it in being maroon and chestnut below, well streaked with white, having same band of brownish black along edges of bare skin, and in color of malar stripe, tail, and primaries. Differing from *P. ochrogaster* by being much darker, olive-green above, rather than olive-brown, including rump and upper tail coverts which do not contrast with back, and by being much more glossy, especially by being maroon and chestnut on hind neck, nape, and upper border of mantle, thus being dichromatic above. Structure of crest and color also quite different. Crest feathers longer and broader than those of *P. ochrogaster*, less decumbent, and less integrated, those arising from front of crown almost wholly decomposed. Crest feathers from front, sides, and center of crown also almost completely buffy white (with the result that the superciliary streak has vanished), only shaft remaining brown, tips are more or less slightly tinged with cinnamon or pale auburn, feathers from rear of crest chiefly bright pale russet.

RANGE: Brazil on the south bank of the middle and lower Amazon, from the lower Tapajoz River west to the right bank of the lower Madeira River in the region near its mouth.

This species, which has a restricted range, does not vary geographically.

GENUS *PIPILE*

DIAGNOSIS

This genus consists of three species that are widely distributed in South America from Trinidad, Venezuela, and Colombia to Bolivia, Paraguay, Misiones, and southeastern Brazil. *Pipile* is more highly arboreal than *Ortalis* and *Penelope* and has a much shorter

tarsus, with a mean ratio of about .17, as against .23 in *Penelope* and about .27 in *Ortalis*. *Pipile* differs also from *Ortalis* and *Penelope* by being black and very glossy, not brown as are the two other genera; by having a different color pattern, the upper wing coverts of *Pipile* being very boldly patterned with pure white; by having the inner webs of the outer primaries very deeply excised distally, narrowly falcate in shape, these primaries being also very strongly bowed inward; and by having a more rounded, less graduated, tail. The crest and the wattles of *Pipile* are also more developed than in *Penelope*.

KEY TO THE SPECIES OF *Pipile*

1. Face fully feathered (except for bare narrow eye ring which is bluish white in life) and pure black; anterior feathers of crest pure black at base, forming broad black band across forehead *P. jacutinga*
Face completely bare (skin slaty in specimens but bright cobalt-blue in life); without black band across forehead, base of anterior feathers of crest white, or feathers broadly edged with white 2
2. Bare skin of whole throat dark, slaty in skins, but bright cobalt-blue in life *P. pipile*
Bare skin of anterior part of throat dark (slaty in skins, but dark blue in life), contrasting very strongly with color of skin of center and posterior part of throat which is pale and flesh-colored in skins, but bright red in life *P. cujubi*

DISTRIBUTION

The distribution of *Pipile* is shown in figure 19. The three species are essentially allopatric, but *Pipile pipile* overlaps *Pipile cujubi* in the Mato Grosso, and *Pipile jacutinga* in eastern Paraguay. The zone of overlap in the Mato Grosso appears to be fairly extensive, as it seems to extend between the fifteenth parallel and the eighteenth parallel from Bolivia to about the border of Goyaz. Within this zone, the two species have been taken in July, 1930, at about latitude 17° 38' S. on the Rio Piquiry by Lima.

The zone of overlap in Paraguay appears to be much narrower. *Pipile pipile* and *P. jacutinga* were both taken in October, 1938, at Cerro Amambay by Schulze, but, to my knowledge, *P. jacutinga* is not found north of

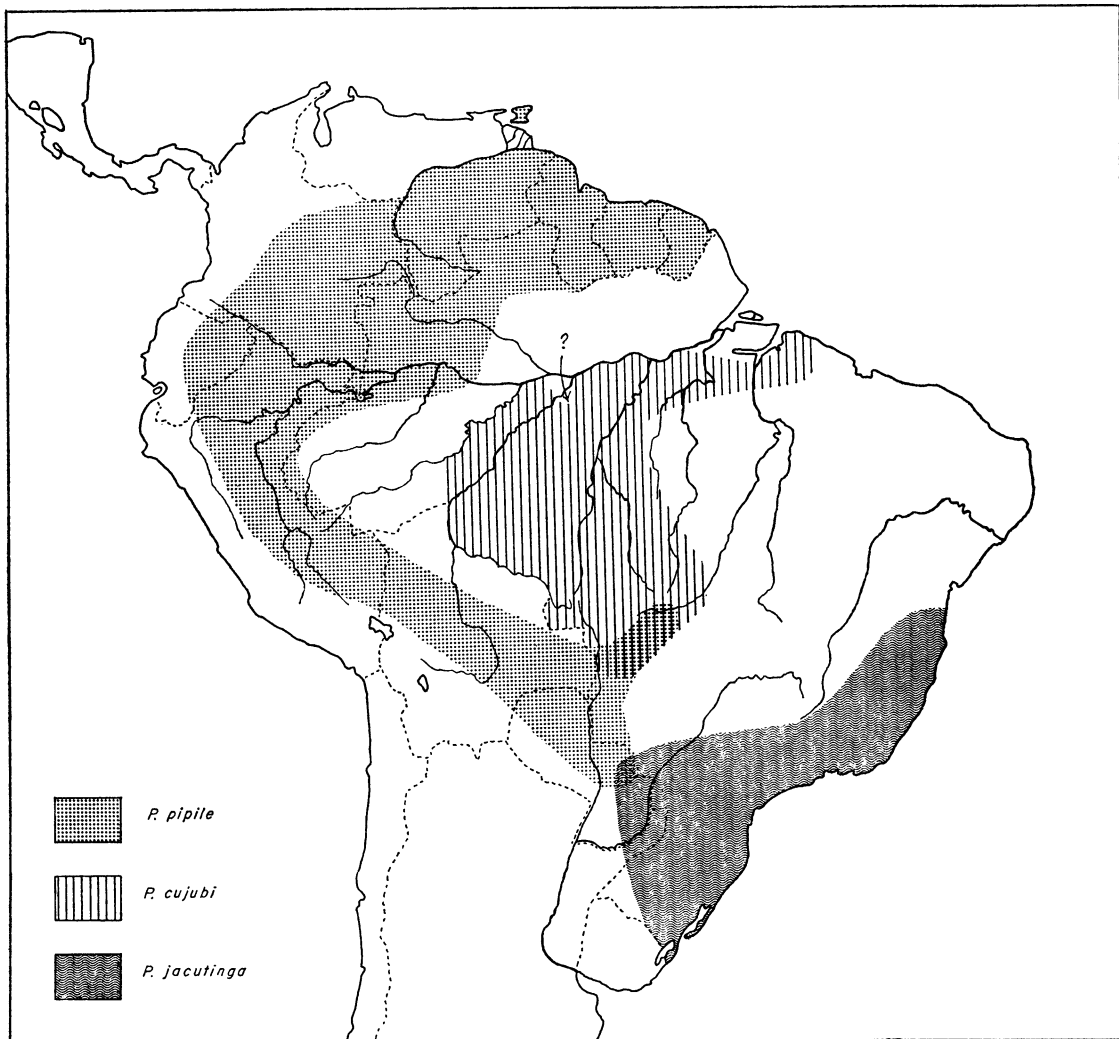


FIG. 19. Distribution of the genus *Pipile*.

this locality, and *P. pipile* is not found south of it. Cerro Amambay is in the southern part of the Departamento de Amambay, and the birds were collected 40 kilometers southwest of Capitan Bado, according to Schulze, Capitan Bado being situated at latitude $23^{\circ} 10' S$.

Pipile kujubi and *P. jacutinga* are broadly allopatric.

The distributional pattern of *Pipile* is therefore similar to that of *Ortalis*, although not quite so perfectly allopatric, but very different from that of *Penelope*, in which 12 of the 13 species are partly or completely sympatric.

I have placed a query on my map (fig. 19) on the right bank of the lower Rio Madeira, because this region is of critical importance in determining whether or not the two forms (*P. kujubi* and *nattereri*) that I have combined in one species are subspecies or species. From this region, Gyldenstolpe (1945, p. 65) and Pinto (1964, p. 112) have both reported specimens of *P. kujubi* from Lago do Batista, and I have seen one specimen of *nattereri* from Igarapé Auara. The two localities are 183 kilometers apart, a gap that seems to be considerable, but, taking into consideration the fact that the region is very uniform and does not seem

to offer any geographical, climatic, or ecological barriers, we cannot assume that the two localities represent the boundaries of the ranges of the two birds. In other words, it is quite possible that they meet and perhaps overlap without interbreeding, which would imply that they are not conspecific.

Pipile pipile has not been collected north of the Orinoco in Venezuela, but Mr. William H. Phelps, Jr., tells me that it may be present also in the delta. Such an occurrence would bring it not far from Trinidad. The population of Trinidad has probably been isolated for a long time, because it is morphologically very distinct, but it was clearly derived from Venezuela, and, I believe, from the same parental stock as present-day *cumanensis*.

VARIATIONS IN PIGMENTATION AND STRUCTURE

This genus is very homogeneous. Some of the six forms that compose it (divided by me into three species) differ in proportions, or in the color of the bare skin of the throat, the feathering of the face and upper throat, or the shape of the throat wattle, but, with these exceptions, all the other differences are only a question of degree. The variation in the characters of the head is shown semi-diagrammatically in figure 20.

The color pattern is uniform. All the forms are black, with a large white area on the upper wing coverts, have a "white" crest which overlies partly a small "white" area on the nape, and are streaked with white on the under parts, but the extent of the white and black areas varies from form to form and on the individual feathers.

The back is well glossed, but the gloss varies in intensity and color, the latter varying from purplish brown in the form on Trinidad, to olive-green, greenish blue, bluish, or violet-blue in the continental forms.

The variations of the white area on the lesser, median, and upper wing coverts are difficult to describe. The base, tips, and shaft streaks of the individual feathers are black, generally speaking, and the rest of the feather is pure white, but the size of the black areas varies in the different rows of coverts and from form to form. The black area at the base of the feather is also prolonged distally to a very irregular degree along the shaft of the

feather. In one form (*Pipile cunjubi*), the white area is very considerably reduced by being restricted rather narrowly only to the edges of the lesser and median coverts on both webs of the feather, and is lacking entirely along the inner web of the greater coverts, although it is very broad along the edge of the outer web. Individual variation is very marked.

The crest and patch on the nape may be virtually all white or buffy white. The shafts of the feathers are so pale and faint that they scarcely contrast with the webs, or the crest and patch appear to be more black than white because the white is restricted rather narrowly to the edges of the feathers, especially on the feathers from the posterior part of the crest. The white extreme is represented by *cumanensis* and the black one by *Pipile pipile* from Trinidad, the color of the crest and nape being intermediate to a varying degree in the other four forms, but mostly white. In *P. jacutinga*, however, the base of the feathers of the anterior part of the crest is pure black, and the feathers lack white edges altogether and form a broad band which varies from about 10 to 15 mm. in width.

The white streaking on the under parts varies, the streaks being nearly obsolete in *Pipile pipile* from Trinidad, but conspicuous and abundant in *P. jacutinga*. The other forms vary between these two extremes.

The crest is very well developed in all forms, and its feathers are either integrated and normal in structure, or somewhat disintegrated at the edges and tips. The feathers are most disintegrated in *grayi* in which the posterior part of the crest is hirsute.

The skin of the face and throat is completely bare in five forms, but in *Pipile jacutinga* the face is feathered, with the exception of a ring of bare skin around the eye which varies individually in width but is relatively narrow. In *P. jacutinga*, the chin and upper throat are also fully feathered, or virtually so.

In five forms (including *Pipile jacutinga*), the bare skin along the median line of the throat forms a conspicuous dewlap or wattle, more developed in some forms than others, which is attached to the throat along its entire length, or nearly so. In *grayi*, however,

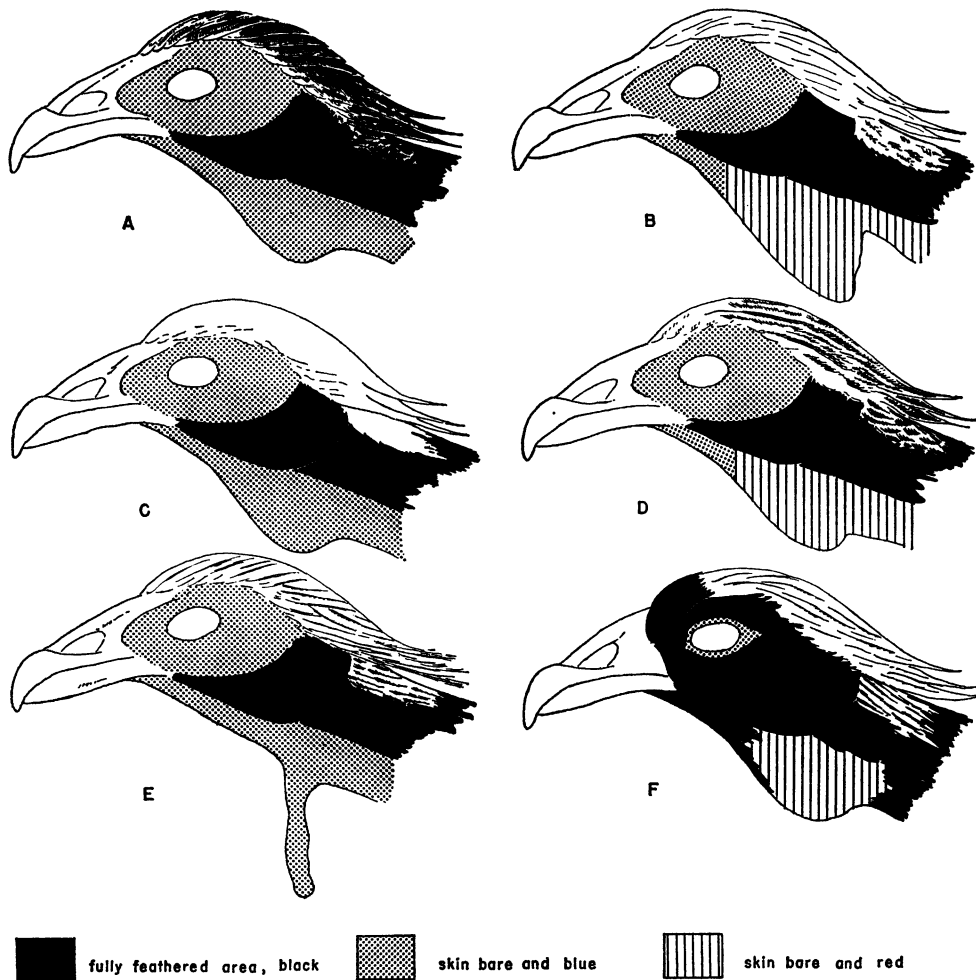


FIG. 20. Variations of the feathering of the face, upper throat, and chin; color of the bare skin of the throat, crest, and pale patch on the nape; and development of the appendages of the throat, in the six forms of the genus *Pipile*. A. *P. pipile*. B. *P. nattereri*. C. *P. cumanensis*. D. *P. cuzubi*. E. *P. grayi*. F. *P. jacutinga*.

this wattle is strongly modified to form a long, slender, and pendulous caruncle which is attached only to the center of the throat (fig. 20). This caruncle varies in length from about 18 to 45 mm. in adults, averaging about 30, but the length of the caruncle and the relative size of the wattle are, no doubt, modified by the physiological state of the bird. These appendages presumably become more conspicuous before and during the breeding season, but they do not appear to be secondary sexual characters as they are present in both sexes. I suspect that they probably play an important role in species

recognition as they differ very conspicuously in coloration (see below).

A few hairlike feathers, which are scattered or arranged in more or less well-defined rows, grow from the bare skin of the throat, wattle, or caruncle in all six forms. They are not shown in figure 20.

The tarsus seems to be red or bright red in all forms. I did not find any information for *grayi*, but, as its color in skins is similar to that of the skins of the other forms, it also is most probably red in life.

The iris is probably some shade of brown in all forms, but I did not find any informa-

tion for *grayi*, *nattereri*, and *jacutinga*. In the other three forms, the collector reported that it had been brown, chestnut, or red-brown.

The colors of the bare skin of the face and throat are the most important taxonomic characters, because they permit a division of the six forms into three species when taken in consideration with the feathering of the face and upper throat, the color of the anterior part of the crest, and distribution. In *Pipile pipile*, *cumanensis*, and *grayi*, which can be combined in one species, the skin of the face and of the whole throat is bright blue in life, cobalt-blue being the shade most often mentioned, but in skins this color has vanished and the skin is slaty or dull black.

In *Pipile cujubi* and *nattereri*, which can be combined in a second species, the face is also bright blue in life, but the color of the throat is not. In the latter, the chin and upper throat are said to be "dark blue" or "bluish black" in life, contrasting very strongly with the color of the center and posterior part of the throat (i.e., the wattle) which is bright red. This contrast is very evident, even in skins, the anterior part of the throat being blackish, whereas the center and posterior part are pale and flesh-colored or faded orange.

In *Pipile jacutinga*, which forms the third species, the ring of the bare skin around the eye is said to be very pale in life, "bluish white," and is gray in skins. The skin of the rest of the face is fully feathered, but, as these feathers are pure velvety black, the color of the face differs conspicuously from that of the other two species which is bright blue. The contrast is emphasized by the broad band of pure black at the base of the anterior part of the crown, this region being pure white or nearly so in the other species (fig. 20). The color of the skin of the throat in *P. jacutinga* is similar to that of the second species (*cujubi* and *nattereri*), being bright red where the skin is bare, and dark blue under the feathers of the chin and upper throat.

VARIATIONS IN SIZE AND PROPORTIONS

The three species are large and nearly uniform in size, the mean wing length in round numbers varying from only 328 to 361 mm. in males, and from 310 to 350 in females. The mean is 347 in the males and

329 in the females. The difference between the mean wing length of the smallest and that of the largest males is only 33 in *Pipile*, as against 82 (mean 218) in *Ortalis*, and 159 (mean 295) in *Penelope*, and the range of variation relative to general size (expressed as a ratio of the mean) is therefore only .10 in *Pipile* (three species), as against .38 in *Ortalis* (10 species), and .54 in *Penelope* (13 species). One expects less variation in a small genus than in a large one, but it is clear that the three species of *Pipile* are very uniform in general size.

The narrow range of the measurements would lead one to believe that the proportions of the three species (and their subspecies) are quite similar, but an analysis of the proportions by means of a ratio diagram (fig. 21) shows that the proportions of the three subspecies of *Pipile pipile* (nominate *pipile*, *cumanensis*, and *grayi*) are not homogeneous. The tarsus and bill of nominate *pipile* are proportionally very much shorter than those of *P. pipile cumanensis* (the standard of comparison). The tail of *P. pipile grayi* is proportionally shorter, and the bill very much shorter, but the proportion of the tarsus is identical with that of *P. pipile cumanensis*.

It is difficult to account for these intra-specific differences, but they may reflect the isolation of nominate *pipile* on the island of Trinidad where it seems never to have been numerous, judged by the very few specimens that have been collected. In this connection, it is noteworthy that nominate *pipile* is an exception to the well-known rule that the bill is usually larger in insular forms.

The proportions of the other three forms are not similar to those of the three subspecies of *Pipile pipile*, but the proportions of *P. jacutinga* do not vary significantly from those of the two subspecies of *P. cujubi* (nominate *cujubi* and *nattereri*).

PHYLOGENY

The discussion of the distribution, and of the color of the bare skin of the face and throat, shows that *Pipile pipile* is a separate species which overlaps both *P. cujubi* and *P. jacutinga*. It can be argued that *P. pipile* from Trinidad is not conspecific with *cumanensis* and *grayi* because it is an insular form

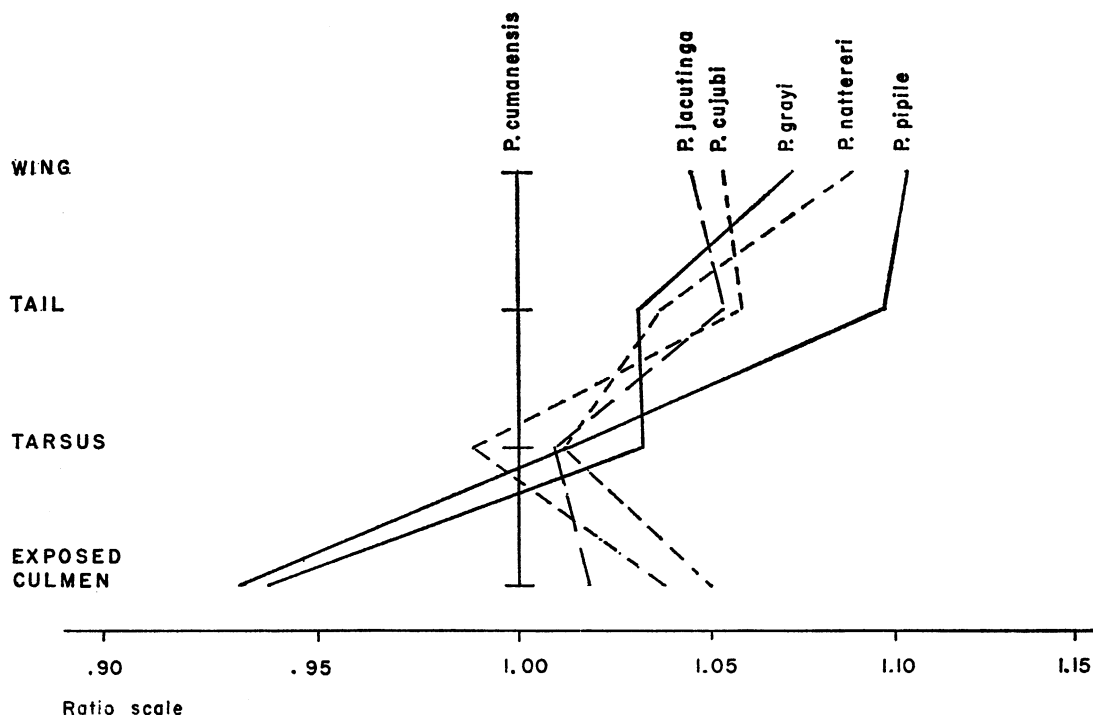


FIG. 21. Comparison by ratio diagram of the proportions of the adult males of the six forms of the genus *Pipile*.

which is very distinct from the other two. We cannot ever be certain, but it is reasonable to believe that it is conspecific with the other two, because it was clearly derived from Venezuela which is inhabited by *cumanensis*, and the color of the bare skin of the face and throat is the same, the character to which I accord the greatest taxonomic importance.

The difference in the shape of the throat appendage which forms a wattle in *cumanensis*, as against a caruncle in *grayi*, is very conspicuous but apparently is not of specific importance. Some specimens are more or less intermediate, in respect to this character and coloration, between *cumanensis* and *grayi*. I have seen two from the mouth of the Rio Inambari in southeastern Peru which are intermediate to some degree, although more similar to *cumanensis* on the whole, and Gyldenstolpe (1945, pp. 63-66) has reported that in his series of *grayi* from Bolivia some specimens have a wattle rather than a caruncle.

Nominate *cujubi* and *nattereri* certainly

seem to be more closely related to each other than to *Pipile jacutinga* and *P. pipile*. I believe they are conspecific, but their range on the right bank of the lower Rio Madeira is imperfectly known, and it is possible they come into contact, and perhaps even overlap, without interbreeding. If they overlap, it would prove that they are not conspecific, and that other isolating mechanisms operate in addition to the color of the skin, but it would not contradict their close relationship.

Pipile jacutinga replaces *P. cujubi* geographically and seems more closely related to it than to *P. pipile*, as suggested by similarities in the color of the skin of the throat, in the color of the gloss of the upper parts, and in proportions. *Pipile pipile* overlaps both *P. cujubi* and *P. jacutinga*, but the three species are essentially allopatric and constitute but one superspecies.

LIST OF THE SPECIES

Pipile pipile

DIAGNOSIS: Gloss of upper parts varying from purple-brown to greenish blue, or

olive-green. Feathers of crest very broadly streaked with black, white area restricted to edges of feathers and becoming progressively narrower posteriorly on center and back of crown, or black streaks narrow and restricted to shaft, or virtually lacking altogether, with result that whole crest appears to be white or buffy white, pale area on nape being also much mixed with black or virtually all white. White area on upper wing coverts broadly developed, but white streaks on under parts poorly developed, narrow and few in number, or obsolete and reduced to a few faint traces. Skin of face and throat completely bare, slaty or blackish in skins, but bright cobalt-blue in life. Throat appendage forming broad wattle attached to throat along entire length, or virtually so, or strongly modified to form long, slender, and pendulous caruncle attached to center of throat only.

RANGE: Trinidad, the Guianas, and Venezuela south of the Orinoco (but occurring perhaps also in the delta), west to the foothills of the Eastern Andes of Colombia, north to the region of Villavicencio (also "Bogota"), and northern Brazil (upper Rio Branco, Rio Catrimani, upper Rio Negro, and upper Amazon east to the region of Tefé), south through eastern Ecuador and eastern Peru, to central Bolivia, northern and eastern Paraguay (south to the southern part of the Departamento de Amambay in the east), and east from Bolivia to the Mato Grosso, between the fifteenth parallel to the eighteenth parallel, to about the border of Goyaz.

GEOGRAPHICAL VARIATION: This species consists of three strongly differentiated subspecies: nominate *pipile*, *cumanensis*, and *grayi*.

Nominate *pipile*, which is restricted to Trinidad, differs from the other two subspecies by being glossed with purple-brown above, as against greenish blue in *cumanensis* and olive-brown in *grayi*, and by having a very much darker crest and patch on the nape, the white area being restricted only to the edges of the feathers. The feathers at the sides of the crest are virtually pure white in nominate *pipile*, however, and form a conspicuous supraorbital streak which extends from the forehead and region above the

lores posteriorly to the region behind the ear coverts. Nominate *pipile* is known from only a very few specimens and always seems to have been rare; it is said to be reduced to only a few individuals now, which are in danger of extirpation.

Pipile p. cumanensis, which inhabits the rest of the range with the exception of Bolivia, Paraguay, and the Mato Grosso where it is replaced by *grayi*, differs from nominate *pipile* in the color of its gloss, as stated, and in having a very much whiter crest and patch on the nape. In *cumanensis*, the shaft streaks of the feathers of the crest and nape patch are extremely narrow and pale brown, or are only faintly darker than the rest of the feather which varies from nearly pure white to dingy white or buffy white. The white streaks on the under parts are also better developed than in nominate *pipile*, in which they are obsolete and reduced to a few faint traces.

Pipile p. grayi differs from the other two subspecies by being glossed with olive-brown above, as stated, and, most conspicuously, by lacking a wattle on the throat which is replaced by a long and pendulous caruncle. The feathers of its crest are also more decomposed, more hirsute, especially those that grow from the center and posterior part of the crown, but they have a distinct, though narrow, black shaft streak which is very sharp.

Pipile kujubi

DIAGNOSIS: Gloss of upper parts bluish. Feathers of crest and patch on nape streaked with black, streaks varying from rather heavy to slight. White area on upper wing coverts moderately well developed, or reduced and much interrupted with black, and white streaks on under parts moderately or only slightly developed. Skin of face and throat completely bare, skin of face slaty or blackish in skins, but bright cobalt-blue in life as in *P. pipile*, skin of chin and upper throat blackish in skins but dark blue in life, contrasting very strongly with color of skin of center and posterior parts of throat which is bright red in life, pale and flesh-colored in skins. Throat having a broad and large wattle.

RANGE: Central and eastern Brazil, south

of the Amazon,¹ from the right bank of the lower and probably middle Rio Purus, east to northeastern Para in the region east of Belem, south to the right bank of the Rio Guaporé and the Mato Grosso (where it overlaps *Pipile pipile*; fig. 19) to the upper Rio Paraguay and Rio Piquiry, east to the upper Rio Araguaya and the region of Cachimbo at the headwaters of the Rio Curua.

GEOGRAPHICAL VARIATION: This species consists of two very well-differentiated subspecies: nominate *cujubi* and *nattereri*. The latter inhabits the range west and south of nominate *cujubi* (which ranges from the right bank of the Rio Madeira at its mouth, east, along the Amazon, to the region east of Belem) and differs from nominate *cujubi* by having the white area on the upper wing coverts much better developed and the crest much less heavily streaked. The gloss of the upper parts is also somewhat duller and less bluish in *nattereri*, and its throat wattle, as a rule, is larger. In nominate *cujubi*, the white area on the upper wing coverts is very much smaller than in any of the other forms of the genus, consisting of rather narrow edges on both webs of the lesser and median coverts, and of broad edges on the greater coverts, which, however, are restricted to the mesial edge of the webs, the distal edge being black.

Pipile jacutinga

DIAGNOSIS: Gloss of upper parts highly developed and rich violet-blue. Feathers of crest and patch on nape sharply and well streaked with black, but less heavily so than in *P. cujubi* and, especially, nominate *pipile*. Base of feathers on anterior part of crest pure black, forming broad band of black across forehead, whereas bases of these feathers white, or have very broad white

edges, in all other forms of genus. White area on upper wing coverts very broadly developed, more extensive than in any other form, and white streaks on under parts also more developed and much more abundant. Skin of face fully feathered (not completely bare as in all other forms) except for rather narrow eye ring which is bare and gray in skins, but very pale, whitish blue, in life. Feathers of face pure velvety black. Chin and upper throat fully feathered, or virtually so (not completely bare as in all other forms), skin below these feathers dark blue in life, as in *P. cujubi*, bare skin of rest of throat bright red in life, as in *P. cujubi*. Area of bare skin on throat more restricted than in all other forms because upper throat is feathered and wattle smaller.

RANGE: Eastern Brazil, from southern Bahia south to southern Rio Grande do Sul, west to eastern and southern Minas Gerais, São Paulo and Parana, eastern Paraguay (north to the southern part of the Departamento de Amambay where it overlaps *Pipile pipile*), and Misiones in Argentina.

This species shows no evidence of geographical variation.

GENUS *ABURRIA*

DIAGNOSIS

This monotypic genus is restricted to the mountains of western South America from Venezuela and Colombia south to southern Peru. *Aburria aburri* is the most highly arboreal of all the Cracidae and has the most pointed wing and a very short tarsus, comparable with that of *Pipile*, or slightly shorter. Its outer primaries are extremely excised on the inner web (fig. 2), more so than in *Pipile*, and its plumage is black and very glossy, but differs from that of *Pipile* by being completely uniform, without a trace of white anywhere. The face of *Aburria* is feathered, as is also most of the throat, from which grows a very long vermiform caruncle.

Aburria shows some similarity to *Pipile* and is probably related to it, but some of the similarity (such as the short tarsus) may be due to adaptive convergence.

DISTRIBUTION

The distribution of *Aburria aburri* is

¹ Pinto (1938, p. 102) reported a specimen of nominate *cujubi* from Lago Cuipeva [= Cuipeua] that was collected by [A. M.] Olalla [or his party] in June, 1933. This locality is about 30 kilometers north of the main channel of the Amazon at about latitude 1° 53' S. by longitude 54° 55' W. This is the only record north of the Amazon, but I believe it is not valid and that this species does not occur north of the Amazon. I do not accept this record for reasons that I have stated in detail in another paper on the Cracidae (1965b, p. 16), namely, that the authenticity of some of the Olalla's records from Lago Cuipeua is strongly suspect.

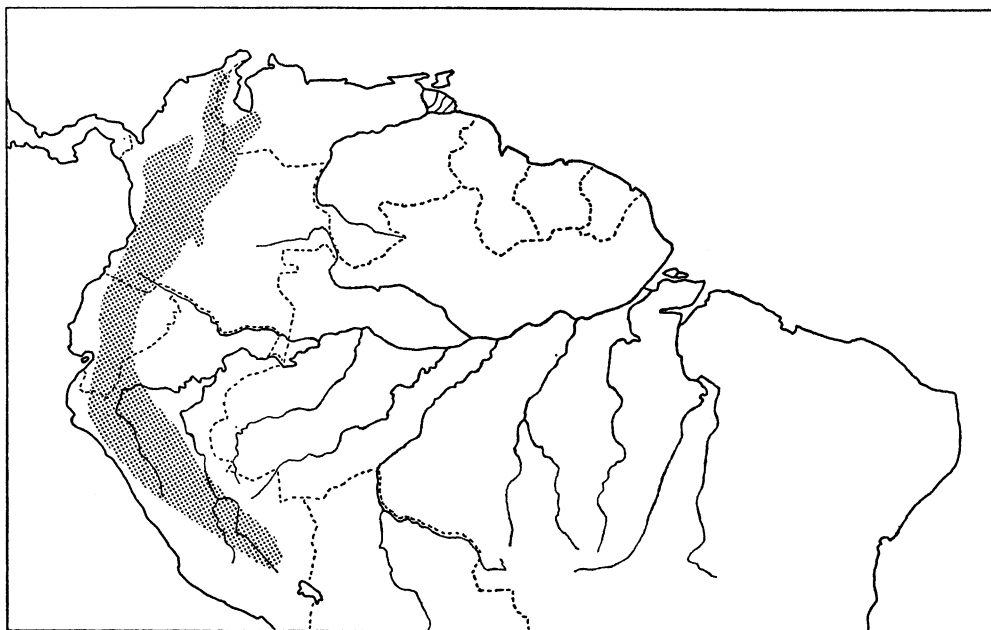


FIG. 22. Distribution of the genus *Aburria*.

shown in figure 22. It inhabits the upper tropical and the subtropical zone, between about 750 and 2500 meters, from the north-eastern lower slopes of the Santa Marta Massif, the Sierra de Perija in Colombia and Venezuela, and the Cordillera de Merida in the western Andes of Venezuela, south through the Eastern, Central, and Western Andes of Colombia (including the Cordillera de la Macarena), eastern Ecuador, and Peru to the upper Urubamba Valley and the region of Marcapata. The normal (or usual) lower limits of the altitudinal range seem to be about 750 meters, but I have seen a few specimens that had been collected lower, at about 610, and at about 428 meters in southern Colombia.

DESCRIPTION OF *Aburria aburri*

The entire plumage is black and glossy, the gloss being much stronger on the upper parts and varying geographically from a strong bronzy olive-green to Prussian blue. The lores and face are completely and densely feathered with the exception of the eyelids, the upper lid being more feathered than the lower and back, whereas the skin of the lower lid is pale and denuded to a width which varies from about 2 to 3 mm. This

narrow line of bare pale skin below the eye is not well indicated in some specimens, but may be more evident in life.

The chin and throat are also densely feathered, except for a bare area at the base of the lower throat which is about 1 cm. in size and from which grows a long and very slender vermiform caruncle. This caruncle is present in both sexes and varies in length from about 25 to 65 mm., with an average of about 40, in the specimens I have examined. The caruncle is bare, except for a small tuft or two of short black feathers at its base, and also has, as a rule, two or three thin and inconspicuous pale bristles at its tip.

The feathers of the crest are dense and recumbent, normal in structure and rather broad, and are relatively short, not very elongate except at the rear.

The information that I have found on the color of the soft parts in life is scanty and not very satisfactory, because some of it seems to be contradictory. The only character on which all the collectors agreed is the color of the bill which was said to be blue at the base and black at the tip. The legs were described as brown, cream, flesh-colored, pinkish, or yellow and are pale in all the specimens. The iris was said to have been

brown, hazel, dark red, or blood red, but blue was mentioned also; and the "eye lids" (probably the lower one only) as were either pale blue or dull yellow. I found only a single observation concerning the color of the caruncle which was said to have been bright yellow, although, judging by the specimens, I would have expected it to be pinkish or flesh-colored.

GEOGRAPHICAL VARIATION

The geographical variation of this species was discussed by me in a preliminary paper (1967b) and consists of variations in coloration and average size. The upper parts are glossed with bronzy olive-green in the populations of Venezuela and Colombia, as against Prussian blue in those of Ecuador and Peru, but the variation appears to be clinal. The wing length averages also distinctly shorter in the birds of Peru (table 1), but the individual measurements and those of birds from the rest of the range overlap greatly. A division of *Aburria aburri* into subspecies has never been attempted, and it would be misleading to propose one, but this species varies geographically to a greater extent than has been suspected.

GENUS CHAMAEPETES

DIAGNOSIS

This genus is composed of two montane species that are widely separated: *Chamaepetes unicolor* in Costa Rica and western Panama, and *C. goudotii* in western South America. They are less highly arboreal than *Aburria* and *Pipile*, especially *C. goudotii*, in which the ratio of the tarsus is about .25. The tarsus of *C. unicolor* is shorter, with a ratio of about .21, and is more feathered than in *C. goudotii* or than in nearly all the other Cracidae (fig. 6). The two species are also dissimilar in size and coloration, but they differ from other members of the Penelopini by being completely and densely feathered on the throat and consequently have no wattles or caruncles of any kind. The outer primaries of *Chamaepetes* are falcate, but much less so than in *Aburria* and *Pipile* (fig. 2), and *Chamaepetes* differs also from these two genera by having no crest.

KEY TO THE SPECIES OF *Chamaepetes*

- Upper parts brownish or olive, contrasting with under parts which are chestnut or strongly rufous *C. goudotii*
- Upper parts black, not contrasting with under parts which are black and brownish black *C. unicolor*

DISTRIBUTION

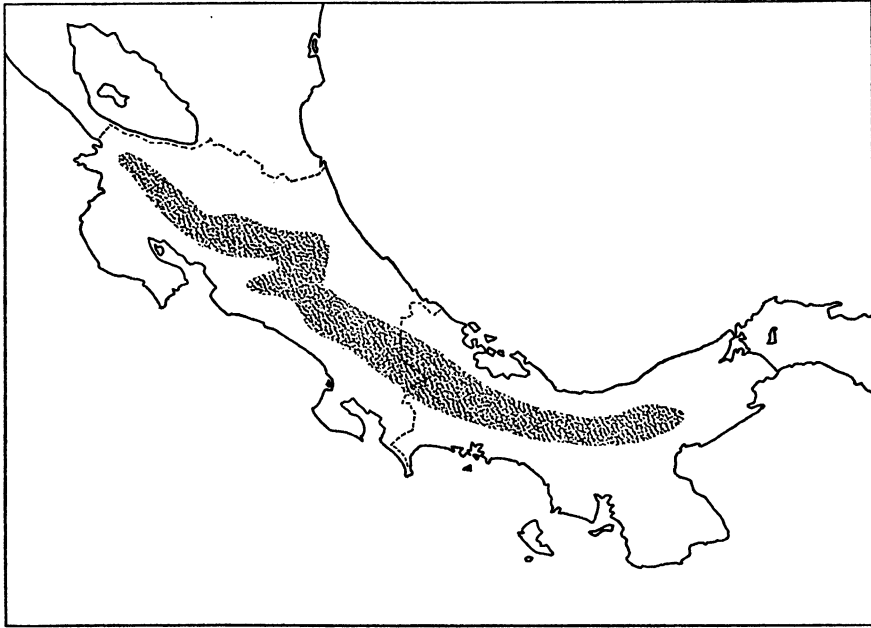
Chamaepetes unicolor inhabits the mountains of Costa Rica and western Panama (fig. 23) and has a more restricted range than *C. goudotii*, which inhabits the mountains of western South America from Colombia south to the department of Junin in central Peru (fig. 24). The range of *C. unicolor* is continuous, but that of *C. goudotii* is interrupted in northern Colombia. The altitudinal range of the two species is similar and varies normally from about 1000 to 3200 meters, but both species occur lower occasionally; *C. unicolor* has been reported at 450 meters in Panama, and *C. goudotii* at 700 in southern Colombia.

VARIATIONS IN STRUCTURE AND COLORATION

The two species are not homogeneous. The difference in the proportions and feathering of the tarsus is mentioned above, but *Chamaepetes unicolor* is also considerably larger than *C. goudotii* and has a more pointed wing. The wing length of the males averages about 303 mm. in *C. unicolor*, as against a mean of 257 in *C. goudotii*, and its primaries project well beyond the secondaries, whereas the primaries and secondaries end at about the same level in *C. goudotii*.

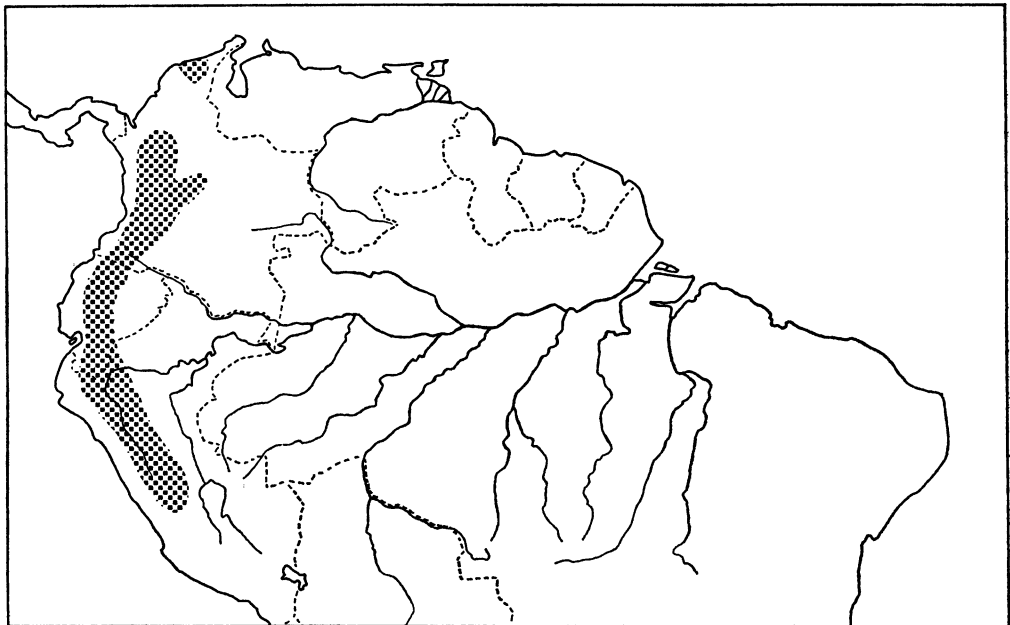
The proportionally shorter tarsus and the more pointed wing of *C. unicolor* are probably adaptations to more highly arboreal habits, but these do not explain the heavy feathering of the tarsus; the tarsus is less feathered in *Aburria* and *Pipile* which are probably more highly arboreal than *C. unicolor*. The shape of the wing tip is also usually correlated with altitude, rather than with arboreal habits, but the variation in the length of the wing is very abnormal in *C. goudotii* (see below).

The coloration of *Chamaepetes* is very plain; *C. unicolor* is black above and below, *C. goudotii* olive above and chestnut below, but the plumage has a slight pattern in both

FIG. 23. Distribution of *Chamaepetes unicolor*.

species. This pattern is created by the faint grayish or brownish margins of the feathers of the under parts, head, mantle, and lesser upper wing coverts, which give to the feathers

a rounded appearance. These pale margins are restricted to the under parts in *C. unicolor*, but their distribution varies geographically in *C. goudotii*, in which they may be

FIG. 24. Distribution of *Chamaepetes goudotii*.

absent or present on the feathers of the head, neck, mantle, and coverts, as well as on the under parts.

The anterior part of the face is not feathered in *Chamaepetes*, the bare area extending from the sides of the forehead, lores, and anterior part of the malar region to the orbital region which it encompasses. The skin is some shade of blue in life, and the colors that are most often mentioned are bright cobalt or azure. As a rule, the orbital region is apparently darker, because the collectors have usually noted that the bright blue of the anterior part of the face shaded posteriorly into ultramarine or violet-blue around the eye. The extent of the bare area and its coloration in life are the same in the two species, as are also the colors of the iris and tarsus. Some variation has been noted between the two species, but it is only of degree.

The color notes that I have found for the iris are reddish brown, red, or wine-purple, although hazel and brown were also mentioned. The tarsus was said to be some shade of red, the shades noted varying from pink or rose to carmine, crimson, lake, or brick-red. No doubt, the shades in the color of the tarsus and iris, and probably the face also, vary to some degree according to physiological condition.

The skin of the face has invariably become blackish in specimens of both species, but the skin of the tarsus differs appreciably. It had faded to the color of horn, with dusky toes, in the specimens of *Chamaepetes unicolor* that I have examined, but to dull orange, with darker toes, in *C. goudotii*, which suggests that the tarsus is brighter red in life in *C. goudotii*. Red was mentioned for both species by the collectors, but pink or rose were noted only for *C. goudotii*, whereas lake or brick-red were noted only for *C. unicolor*.

LIST OF THE SPECIES

Chamaepetes unicolor

DIAGNOSIS: Upper parts uniformly black, well but not highly glossed with dull greenish blue; throat and upper breast duller black than back, less glossy, feathers faintly edged with dull gray. Blackish color of upper breast grading into brownish black or drab

on lower breast, feathers of latter and abdomen faintly edged with pale brown.

RANGE: Mountains of Costa Rica and western Panama east to Veraguas and probably neighboring Coclé.

GEOGRAPHICAL VARIATION: The geographical variation is very slight and not of taxonomic importance, but the wing length averages slightly longer in the birds of Costa Rica, probably because the mountains of Costa Rica are higher than those of Panama. The measurements of the two populations are combined in table 1. In my preliminary paper (1967b), I reported that the wing length in the specimens I measured was 293–321 (309.2) in eight males, and 280–308 (293.6) in six females from Costa Rica, as against 280–315 (300.1) in 13 males, and 280–301 (288.6) in five females from Panama. The specimens from Costa Rica had been collected between 1219 and 3048 meters; those from Panama, between 1097 and 2011 meters.

Chamaepetes goudotii

DIAGNOSIS: Upper parts varying from brownish olive to olive and dark bronzy green, under parts, below throat or upper breast, varying from chestnut to dusky chestnut and bright ferruginous rufous. Color of throat and upper breast similar to that of lower breast, although more dusky, or throat brown, this pigment more or less sharply restricted to throat or invading upper breast. Feathers may or may not have grayish margins, and, to a varying degree, pale margins also present on all feathers of head, including crown and neck, upper breast, nape, mantle, and lesser upper wing coverts.

RANGE: Santa Marta Massif of northern Colombia, and, after a gap in distribution, from the departments of Antioquia and Cundinamarca in Colombia, south through Ecuador, to about latitude 11° 30' S. in the department of Junin in central Peru.

GEOGRAPHICAL VARIATION: The geographical variation is well marked, and five subspecies can be recognized: *sanctae-marthae*¹ which is restricted to the Santa Marta Massif; nominate *goudotii* in the Eastern, Central, and Western Andes of Colombia

¹ I depart from Article 27 of the International Code of Zoological Nomenclature and retain the original form of this name because I believe that the hyphen is useful.

south to Nariño; *fagani* which replaces nominate *goudotii* on the western slopes of the Andes of southern Nariño and ranges south through western Ecuador; *tschudii* which replaces nominate *goudotii* on the eastern slopes of the Andes of southern Nariño and ranges south through eastern Ecuador to about the eighth parallel in the departments of La Libertad and San Martín in Peru, south of which it intergrades with *rufiventris* which ranges south to the department of Junín.

The geographical variation has been discussed in another paper (Vaurie, 1967b) and consists of variations in coloration, size, and proportions.

The variation in coloration can be briefly summarized as follows: *sanctae-marthae* is the palest subspecies above, but the most chestnut below, with only a slightly brownish throat; nominate *goudotii* is darker above, but paler below than *sanctae-marthae*, except for the throat which is brown; *fagani* and *tschudii* are both darker above than nominate *goudotii*, and are the darkest subspecies above, *fagani* differing from *tschudii* by being browner on the throat, the brown area being restricted in *tschudii*, but very extensive in *fagani*, invading the upper breast; *rufiventris* is relatively pale, but the pale margins are best developed and better defined in *rufiventris* than in any other subspecies. These pale margins are lacking in *sanctae-marthae*, and, generally speaking, this character varies clinally from Colombia south to Peru.

The variations in the length of the wing and proportions are very curious. The wing length is not correlated with altitude, as is normal; it is longer in the subspecies with the lowest altitudinal range. The mean wing length of the males that I have measured, and the average altitude (in parentheses) at which these specimens were taken, are as follows: *sanctae-marthae*, 252 mm. (2229 meters); nominate *goudotii*, 261 (1954); *fagani*, 241 (1901); *tschudii*, 264 (1566); and *rufiventris*, 269 (1546). These measurements and altitudes show that *rufiventris* and *tschudii* have the longest wing, although the specimens measured were taken at the lowest altitude; and that the wing length of *fagani* is very considerably shorter than that of nominate *goudotii*, although the specimens

concerned of these two subspecies were taken at very nearly the same altitudes.

The tail ratios of the males are 1.01 in *sanctae-marthae*, .95 in both *tschudii* and *rufiventris*, .93 in nominate *goudotii*, and only .85 in *fagani*.

The variations in the length of the wing and in the proportion of the tail are presumably adaptive, but no explanation comes to mind without an investigation of the ecology and habits of the birds.

GENUS *PENELOPINA*

DIAGNOSIS

This monotypic genus is restricted to the humid highland forest from southern Mexico to northern Nicaragua, and differs from the other genera of the Penelopini in being more terrestrial; the tarsus is proportionally longer, with a ratio of .28. *Penelopina nigra* is strongly aberrant and differs from the other species of the Penelopini, and from the other two tribes of the family, in many characters, which are mentioned above in the analysis of the family. The most notable differences are the distinctness of the juvenal plumage of the male and the fact that the female is larger than the male; in all other members of the Cracidae the juvenal plumage of the male is very similar to that of the adult male, which is larger than the female. It differs from other species of the Penelopini in its extreme degree of sexual dimorphism; the other members of the Penelopini are sexually dimorphic only in size. *Penelopina nigra* has no crest, its face is well feathered, except for a narrow eye ring of bare skin, and the male has a more highly developed wattle than the other species of the Penelopini; the wattle is present only in the male. The outer primaries are normal in shape, not falcate.

The nesting habits of *Penelopina nigra* are also important. It appears to be the only species of the Cracidae that nests on the ground as well as in trees.

DISTRIBUTION

Penelopina nigra inhabits cloud or very humid highland forest from the Sierra Madre in southeastern Oaxaca (where it is reported north of Niltpec) and the mountains of northern Chiapas east through those of

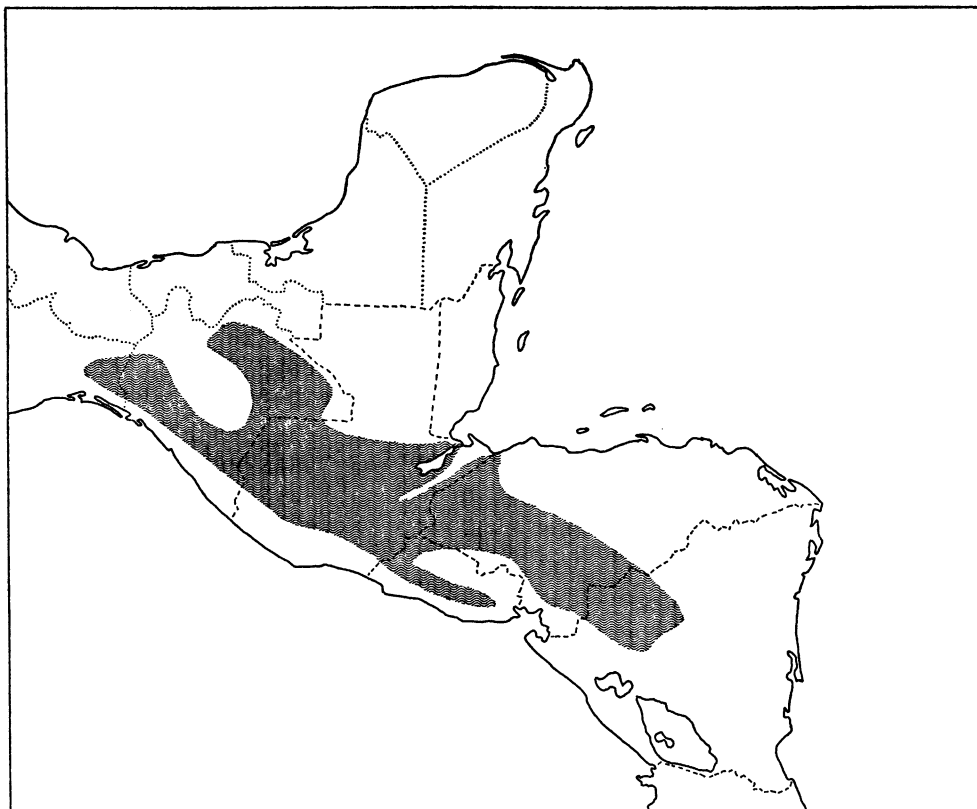


FIG. 25. Distribution of the genus *Penelopina*.

Guatemala, El Salvador, and Honduras to the region of Matagalpa in Nicaragua (fig. 25). The range in El Salvador has receded from the area shown on the map, and *P. nigra* probably exists now only in the mountains of the northwest near the border of Guatemala and Honduras. It formerly ranged in the coastal cordillera east to the Volcan de San Miguel. *Penelopina nigra* has been reported as low as 457 meters in Oaxaca, but the normal altitudinal range seems to be from 1000 to 2600 meters, although I believe the bird probably ascends higher in the Cuchumatanes Mountains of Guatemala, to perhaps 3000 meters.

DESCRIPTION OF *Penelopina nigra*

The plumage of the adult male is pure black, with a dark blue or greenish gloss which varies individually and is highly developed on the upper parts with the exception of the rump, the lower abdomen

being sooty, rather than pure black, and not glossy.

The adult female has a brown concealing plumage which is strongly interrupted. Individual variation is rather great, but this plumage can be described as follows: the ground color of the feathers of the upper parts varies from pale brown to dark fuscous brown on the head, and from buffy brown to ochraceous cinnamon, or pale russet on the back and wings, the ground color of the tail being more rufous than the color of the back. The feathers of the head are dark brown at the center, the dark center contrasting with the pale edges; the feathers of the back and tail are very heavily vermiculated, or barred with dark fuscous brown, the pale bars being narrower than the dark interspaces, except on the tail where the dark and pale bars are of about the same width. The bars of the tail are not invariably regular, as the dark bars are in some cases more or less wavy and

irregular. The under parts are paler than the upper parts and are chiefly grayish buffy brown, less rufous than the back, and are less heavily vermiculated and barred, the dark bars being paler and more irregular, especially on the upper breast which in some is more mottled than barred.

The plumage of the juvenal male is very distinct. It is blacker than that of the adult female, but is not uniformly black as in the adult male. The head is dull black, but not perfectly uniform, as the feathers are more or less edged with reddish brown. The feathers of the back and tail are chiefly black, but are interrupted by bars or heavy vermiculation which varies from dull pale chestnut to rufous cinnamon, the pale bars being more regular and broader on the upper tail coverts, and the tail being vermiculated rather than barred. The under parts are grayish buffy brown, but darker than in the adult female, and more or less regularly barred with very dark buff. The juvenal plumage of the female is less distinct and resembles that of the adult female but is much less regularly and distinctly patterned.

The color of the soft parts in life is affected also by sexual dimorphism. The bill and the bare skin of the throat and of the wattle, and the tarsus are bright red-orange, or coral-red in the male, whereas the bill is brown and the tarsus brownish red in the female. The fact that the female has a dark bill and a darker tarsus is evident even in old specimens, and the throat of the female is completely feathered and consequently has no wattle. The color of the iris, however, is reddish brown in both sexes.

The eye ring of the male, which is prolonged into a small triangular patch behind the eye, is brownish red or reddish brown in the male, but is said to be "dusky" in the female. The skin of the circumocular region of the male was said to be "purplish or bluish purple" by van Rossem (1934b) in one form, which he described as a new subspecies on that account, but his evidence was indirect, and it is not clear whether this color was noted in life or after death. The difference between brownish versus purplish is only one of degree (of hue) which, moreover, can easily be modified by an increase or decrease in vascularization.

Penelopina nigra was studied by van Rossem (1934b), who divided it into three subspecies, but I have found no evidence of geographical variation. I have discussed this question in another paper (1967b).

TERRESTRIAL AND NESTING HABITS

Alvarez del Toro (1952), who is familiar with *Penelopina nigra* in its natural habitat, wrote that it spends much time on the ground scratching among the litter of the forest floor for insects, fruits, and tender leaves. This behavior is confirmed by Wagner (1953) who characterized *Penelopina nigra* as "*keine unbedingten Baumbewohner*," which can be translated as not by any means strictly arboreal. The only nest that has been described in the literature was found by Wagner who said that it was on the ground, dug in humus, and that the coloration of the female, which was reluctant to fly, matched perfectly the color of the ground. However, among several nests that have been observed very recently, only one was on the ground; the others were in trees up to 40 feet from the ground.¹ This last report does not necessarily contradict the fact that *Penelopina nigra* nests regularly on the ground, as well as in trees, because its concealing plumage is certainly not fortuitous.

TRIBE OREOPHASINI

GENUS OREOPHASIS

Oreophasis derbianus

The tribe, genus, and species are monotypic.

DISTRIBUTION

Oreophasis derbianus inhabits cloud forest and is locally distributed, between about 1600 and 3350 meters, in the Sierra Madre of Chiapas, from the region above Mapastepec, east through the coastal cordillera of Guatemala to the Volcan de Fuego, and through the Cuchumatanes to the region of Coban. It is found also in the mountains above and near Tecpan in the department of Chimaltenango, very probably in the Alto Cuchumatanes of Huehuetenango, and perhaps in

¹ This report came from J. S. Rowley to Dean Amadon, and I am indebted to Drs. Amadon and Rowley for this information, which will be published eventually by Rowley.

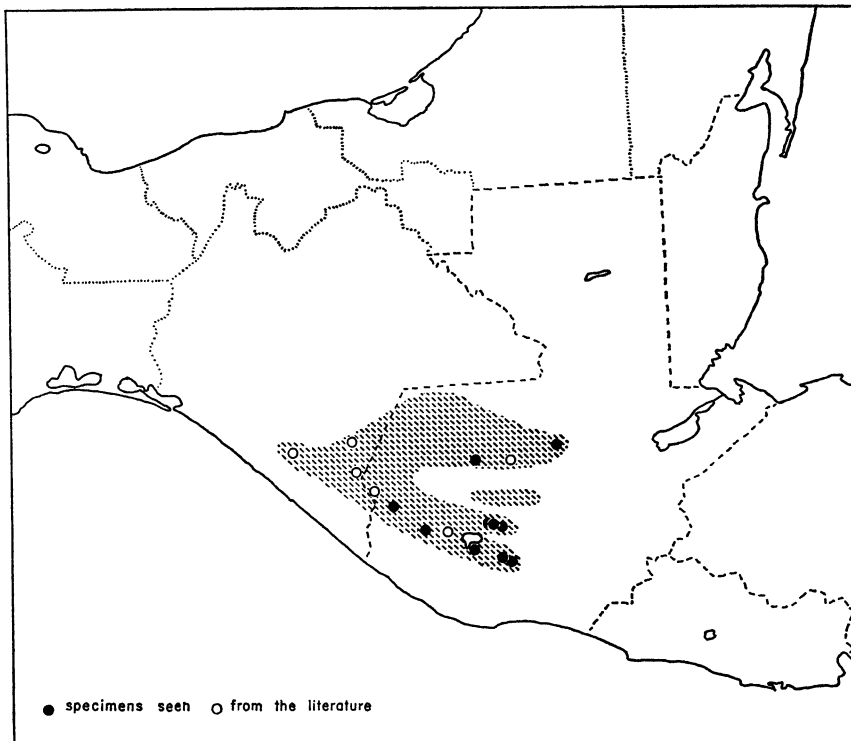


FIG. 26. Distribution of the genus *Oreophasis*. See also footnote on page 217.

the Sierra de Chuacus in southern El Quiche and Baja Verapaz. I have included the Sierra de Chuacus and the Alto Cuchumatanes in the range (fig. 26), but without evidence; all the records obtained by me from specimens or from the literature are shown on the map. This species has disappeared, however, from the more accessible parts of the range, a decline that had started before Griscom (1932b) published his report on the birds of Guatemala and that is said to have been greatly accelerated since.¹

DESCRIPTION

The head is very bizarre; the profile is

¹ Andrie (1967) published a very instructive paper on *Oreophasis* after my study was completed. He wrote that its survival is now threatened by increasing deforestation and hunting. He also mentioned the fact that Alvarez del Toro had received information from the natives that *Oreophasis* occurs in the Sierra Madre above Tonala, near Cintalapa, and in the Sierra Madre in extreme eastern Oaxaca. These records, which are probably reliable, extend very considerably the range shown on figure 26 and suggest that *Oreophasis* occurs along almost the entire length of the Sierra Madre.

illustrated in figure 5. *Oreophasis derbianus* has a "snout", but the part of the bill that is exposed is very short, as the culmen averages only about 20 mm. in length. It is much shorter than that of any other species of the Cracidae (fig. 8). The basal two-thirds of the bill, including the mandible, is very densely feathered with short velvety feathers which are pure black and erect over the culmen, forming a tuft over its base and concealing the nostril. These velvety feathers also cover the forehead, the front of the crown, and the whole of the face with the exception of the lower eyelid, but are extremely short, tight, and plushlike on the face.

The vertex is denuded. A tall, erect, bony tubercle, or "horn," grows from it, which tapers upward and is more or less inclined backward. The horn rises to a maximum height of about 60 mm., but its anterior slope is more gradual and starts considerably lower than in the rear. The vertex and horn are covered by a thin skin which is scarlet-vermilion or bright coral-red in life, and from

which sparse and scattered, very short, hair-like feathers grow. These feathers are not conspicuous as they are very thin and soft, usually pale, and wear off toward the top of the horn. The latter is somewhat shorter in the female, averaging about 42 mm., as against about 48 in the male.

The chin and upper throat are completely and densely feathered with short, glossy black feathers, but the center of the lower throat is almost completely bare, with only a few decomposed black feathers. This area is restricted and measures about 25 mm. in well-prepared skins and shows no trace whatever of a wattle, or even a dewlap, in the specimens that I have seen, but Wagner (1953) stated that a wattle is present. The fact that specimens have no wattle, and that it is not mentioned in the literature other than by Wagner, suggests that the wattle is not well developed and becomes evident only at the onset of the breeding season.

The lower throat below the bare area, the breast, and the upper abdomen are covered by tapering oblong feathers, which become progressively more elongated, and are white, with the exception of the shaft which is black or dusky, the dark shafts creating a finely streaked appearance. The white feathers become cloudy with brown on the flanks, and the rest of the under parts, including the thighs and under tail coverts, are dull black, or sooty brownish black, a few of the feathers of the lower abdomen having disintegrated white tips.

The feathers of the rear of the crown behind the horn, back and sides of the neck, and nape are glossy ivy green, the feathers being short and tight, tapering at the tip, but becoming progressively longer and broader, and less flattened, posteriorly. The rest of the upper parts, including the wings and tail, are black, strongly glossed with Prussian blue or dark blue-green on the upper wing coverts, scapulars, and mantle. The rectrices are very broadly interrupted by a single band of white, a little less than half-way down from the base, which averages about 40 mm. in width. The upper border of this band is regularly defined, but the distal border is more or less interrupted, the white impinging on the black.

The skin of the vertex and horn is very

bright red in life, as stated above, and Wagner (1953) wrote that the bare skin of the throat is also bright red. The tarsus and toes are red, but more carmine, less bright, than the skin of the vertex and horn; the iris is white; and the bill is pale straw-yellow.

The sexes are alike, the female differing from the male only by averaging somewhat smaller (table 1). Specimens in juvenal plumage resemble the adult very closely, but their plumage is duller, less sharply patterned, and the horn is shorter or only slightly developed.

The tarsus of *Oreophasis derbianus* is very short, relatively speaking, (its ratio is only .21), which implies that this species is arboreal, although it has been reported from the ground by Salvin (1860) and Wagner (1953). Salvin wrote that he was informed by his collector that individuals of *Oreophasis* feed chiefly on fruit that they obtain "in the upper branches of the forest trees" in the morning, but descend later to the ground. Wagner found individuals of *Oreophasis* along the paths in the forest made by coffee workers, and stated that the bird is "probably terrestrial, unlike the other Cracidae" (my translation) because it breeds along running streams above the timberline. He wrote that he had observed it there, but he did not find the nest, and his belief that it nests on the ground was based on information received from the natives. His supposition may be correct, but it is best to reserve opinion because the nest has not, up to the present time, been discovered and described by an ornithologist. The habits of *Oreophasis* are scarcely known, in spite of the observations of Wagner, and I believe it is mainly arboreal (as suggested by its short tarsus), and that the nest will probably be found built in a tree.

TRIBE CRACINI

KEY TO THE GENERA

1. With a large, elevated, bony helmet, horn-shaped or fig-shaped, surmounting forehead *Pauxi*
Without helmet 2
2. Base of upper and lower bill covered by fleshy membranes forming wattles or not; crest feathers curly at tip *Crax*
Base of upper and lower bill wholly covered with horn, not by fleshy membranes; crest

- feathers rudimentary or well developed, but not curly at tip 3
3. Much smaller (mean wing length of males, 294 mm.); face wholly bare; crest highly developed, feathers very long and narrow, not glossy *Nothocrax*
- Much larger (mean wing length of males, 379 mm.); face fully feathered, with exception of lower eyelid; crest rudimentary or well developed, feathers broadening distally and very glossy at tip *Mitu*

MORPHOLOGICAL VARIATION

Mitu, *Pauxi*, and *Crax* are all very large birds which differ only slightly in size (figs. 7 and 27) and are much larger than *Nothocrax*, the mean wing length of the males, expressed in round numbers, measuring 294 mm. in *Nothocrax*, as against an average of 379 in *Mitu*, 395 in *Pauxi*, and 385 in *Crax*.

The proportions of all the species are compared in figure 27 and are very similar, except for the size of the bill, as expressed by the length of the culmen. The bill is much smaller proportionally in *Pauxi* than in the other genera, and is distinctly larger in *Mitu* than in *Mitu tomentosa*. The development of the bony helmet in *Pauxi* has caused a general reduction of the bill, but in *Mitu* the bill increases in direct proportion to the enlargement of the base of the premaxillary bone.

The other proportions differ only very slightly. The ratio between the length of the tarsus and that of the wing is virtually identical (.28 in *Nothocrax*, .26 in *Pauxi*, and .27 in *Crax* and *Mitu*), in contrast to the Penelopini in which the ratios vary significantly.

The wing is arched and very strongly rounded. The basic formula is $1 < 2 < 3 < 4 < 5$, $6, 7, 8 > 9 > 10$ in *Nothocrax*, *Crax*, and *Mitu*, but the wing is slightly more pointed in *Pauxi* and the basic formula is $1 < 2 < 3 < 4 < 5 < 6, 7 > 8 > 9 > 10$, a difference that is probably correlated with the fact that *Pauxi* normally inhabits higher elevations.

The bill is arched and compressed laterally, but is modified in all the genera (pl. 17). It is higher, more compressed laterally, and has a sharper keel in *Mitu* than in *Nothocrax*, and is more swollen at the base in two of the three species. The bill is completely covered by a horny sheath in these two genera. The

bill of *Pauxi* is relatively small, displaced forward by the development of a very large and elevated bony helmet, which is covered by skin, but not by the rhamphotheca which ends at the base of the helmet. The bill is most strongly modified in *Crax*, the basal half of both the upper and lower bill being covered, not by horn, but by naked fleshy membranes which form a knob or wattles, or both, in all the species except *C. alector* (pl. 15).

The feathering of the face varies. In *Nothocrax*, the lores and the whole of the face are bare and vividly colored with bright yellow, blue, and purple in life. In *Mitu* and *Pauxi*, the lores and face, with the exception of the lower eyelid, are fully and densely covered by pure black velvety feathers. In *Crax*, the lores are feathered or not, and, when bare, the naked skin connects with the skin of the orbital region which is also bare, the ring of skin expanding posteriorly to form a small triangular patch behind the eye. The size of the naked area varies from species to species (pl. 15), but is usually quite restricted except for *C. fasciolata* in which a large part of the face may be bare, the extent of the bare area varying greatly individually.

The crest is very different in all the genera. It is composed of soft and loosely integrated feathers in *Nothocrax*, which are narrow and very long and project well beyond the nape onto the neck. These feathers are dark brown, sooty, or blackish brown, more or less margined with chestnut, not glossy anywhere. The crest is decumbent but erectile. The crest is very much shorter in *Mitu* and composed of flat and well-integrated feathers which broaden distally to end in a well-rounded tip (fig. 28); they are very glossy and never curled at the tip. This crest is best developed in *M. mitu*, but is very poorly developed in *M. tomentosa* and rudimentary in some individuals. *Pauxi pauxi* has no crest, but *P. unicornis* has a very strange one, composed of very short but erect and stiff feathers, which grow also on the nape and hind neck, are highly metallic at the tip, and very tightly curled forward (pl. 16, figs. 1, 2). In *Crax*, the feathers are long and grow in rows, and are rather stiff except at the tip which is very gracefully curled (pl. 15), the crest remaining more or less erect at all times. The crest is

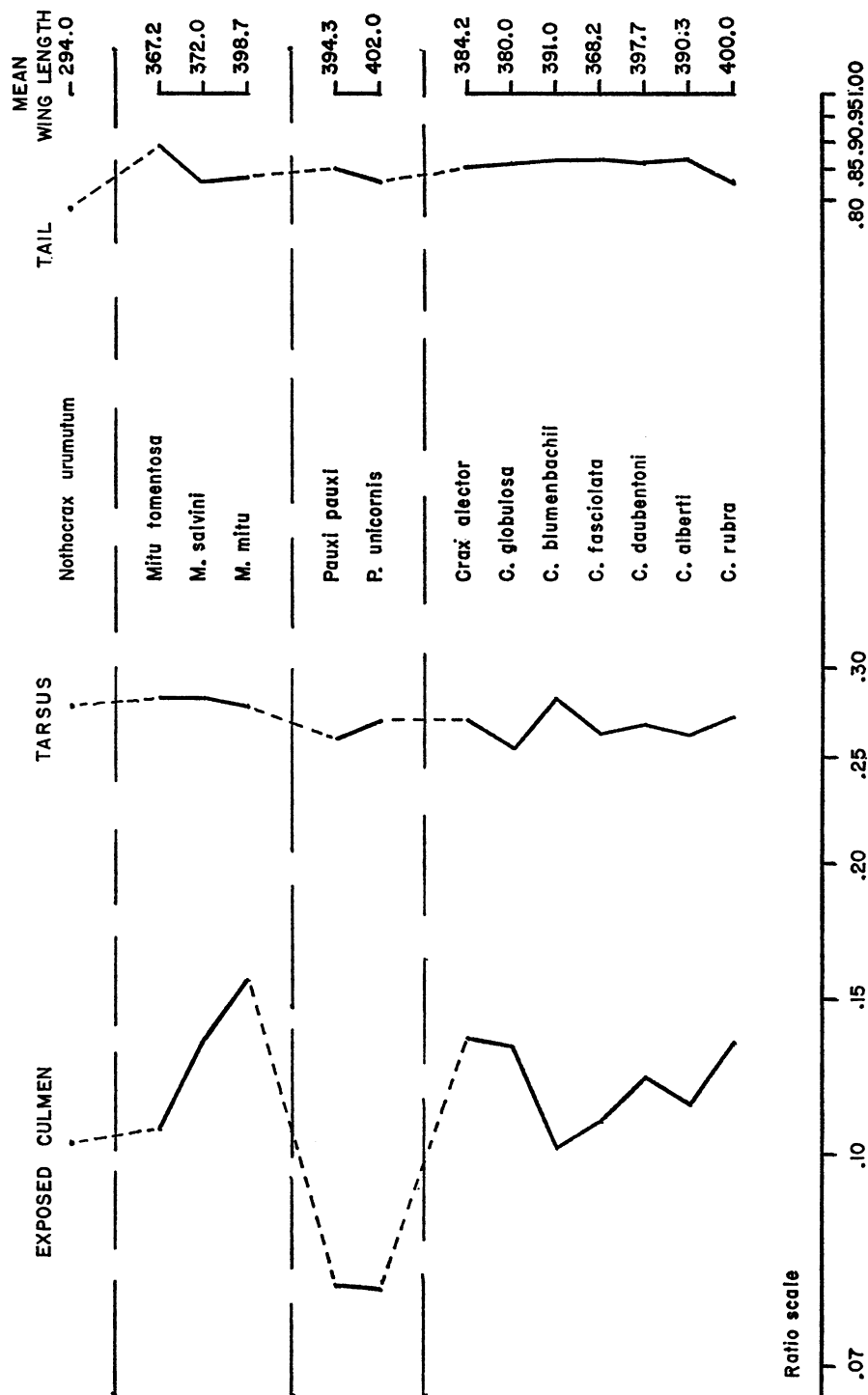


FIG. 27. Comparison by ratio diagram of the proportions of the adult males of the Cracini.

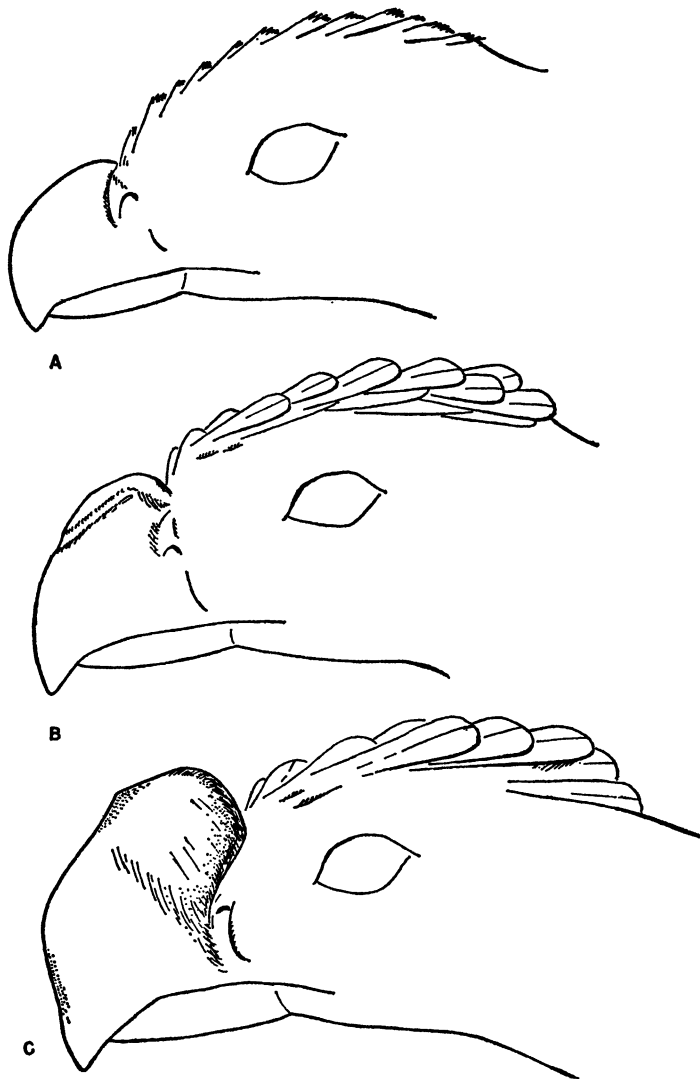


FIG. 28. Shape of the bill and relative development and structure of the crest in the genus *Mitu*. A. *M. tomentosa*. B. *M. salvini*. C. *M. mitu*.

black and glossy, barred with white in all the females to a varying degree, the color of the crest being identical in the two sexes of the other genera.

The coloration and the pattern of the plumage show two types; one in *Nothocrax*, and the other common to *Mitu*, *Pauxi*, and *Crax*. *Nothocrax* is chestnut and very rufous, finely vermiculated with brown above, and is not glossy anywhere. Its crest and malar stripe are blackish in some individuals,

brown in others, but true black is lacking in its plumage.

The males of *Mitu*, *Pauxi*, and *Crax* are black and glossy, generally speaking, and the lower abdomen, the under tail coverts, the long tufts of feathers that grow from the base of the thighs, and the tips of the outer rectrices (in some species) are white or chestnut.

The plumage is glossy, but the gloss is not uniformly distributed. The head and most of

the neck are pure velvety black, with a slight sheen, but not glossy except on the crest. The feathers of the rest of the body, including the upper wing coverts and upper tail coverts, are glossy, but not at the edge which is dull black, the basal half of the feather being also dull black in *Mitu*. These dull edges contrast with the glossy part of the feather and create a scalloped or squamated pattern which is sharp in *Mitu* and *P. pauxi* but not very evident in *P. unicornis* and *Crax*, the dull edges being narrow and faint, especially in *Crax*, in which they disappear very quickly with wear.

The coloration and the pattern of the females vary in the three genera. *Mitu* is not sexually dimorphic, except slightly in size, and the coloration of the female is therefore identical with that of the male. *Pauxi pauxi* has two color phases; one brown, and the other black and white and identical with the male. Color phases may exist also in *P. unicornis*, but the only female that has been collected so far is black and white and identical with the male. *Crax* is sexually dimorphic. The females of all species differ from the males in having white markings in the crest, but the degree of dimorphism varies very greatly. The female of *C. alector* differs from the male only in these white markings, but the dimorphism is greater in the other species and becomes very complex, reaching a climax in *C. rubra* which has three color phases. Some females of *C. rubra* have some brownish areas in the plumage which are more or less vermiculated and mottled, and one of the two color phases of *P. pauxi* is brown, with an interrupted plumage, but the color pattern is quite different from that of *Nothocrax*.

Nothocrax differs also from *Mitu*, *Pauxi*, and *Crax* by being nocturnal (see below), rather than diurnal, and it appears to have a larger eye. The orbit of *N. urumutum* appears to be proportionally larger (see the skulls illustrated in pl. 17); this difference is confirmed by measurements. The ratio between the width of the gaps between the tips of the two processes at the base of the orbit and the length of the skull measured from the suture at the anterior border of the lacrimal bone is .27 in *M. mitu*, .34 in *C.*

globulosa, .42 in *P. pauxi*,¹ and .50 in *N. urumutum*.

PHYLOGENY

The morphological differences that are described above, and the difference between nocturnal versus diurnal habits, show that *Nothocrax* is much less closely related to *Mitu*, *Pauxi*, and *Crax* than these are to one another. It is a very distinct genus. The other three genera are closely related but they differ in the structure of the bill (wattles in *Crax*, helmet covered with skin in *Pauxi*), and in having completely different crests. *Mitu* is not sexually dimorphic, but *Pauxi* and *Crax* are. The three genera are polytypic and, in my opinion, represent different evolutionary lines, *Mitu* being the least evolved, and *Crax* the most.

GENUS NOTHOCRAX

DIAGNOSIS

This genus is monotypic. *Nothocrax urumutum* differs from the other three genera of the Cracini by being a much smaller bird, which is nocturnal rather than diurnal, and by having a completely different coloration, brown and vermiculated, not glossy or true black anywhere. The crest is also very different, composed of very long, narrow, and loosely integrated feathers, and no wattles or elevated bony helmet is present. It differs also by having the whole of the face completely bare and vividly colored in life.

DISTRIBUTION

The distribution of *Nothocrax urumutum* is shown in figure 29. This species inhabits the dense forests of the upper Amazonian Basin from Mt. Duida, the Casiquiare River, and the Rio Guainia in southern Venezuela, westward through Vaupés and Caqueta in southeastern Colombia to the foothills of the Andes, north to the region of Morelia, and south through eastern Ecuador to north-eastern Peru, and Brazil from the upper Rio Negro south to the Rio Purus to the region of Labrea, the Rio Madeira to São Carlos,

¹ The anterior process of the lacrimal bone is broken and missing from the left side of the skull, which was the side photographed. The gap was measured on the right side where this process was intact.

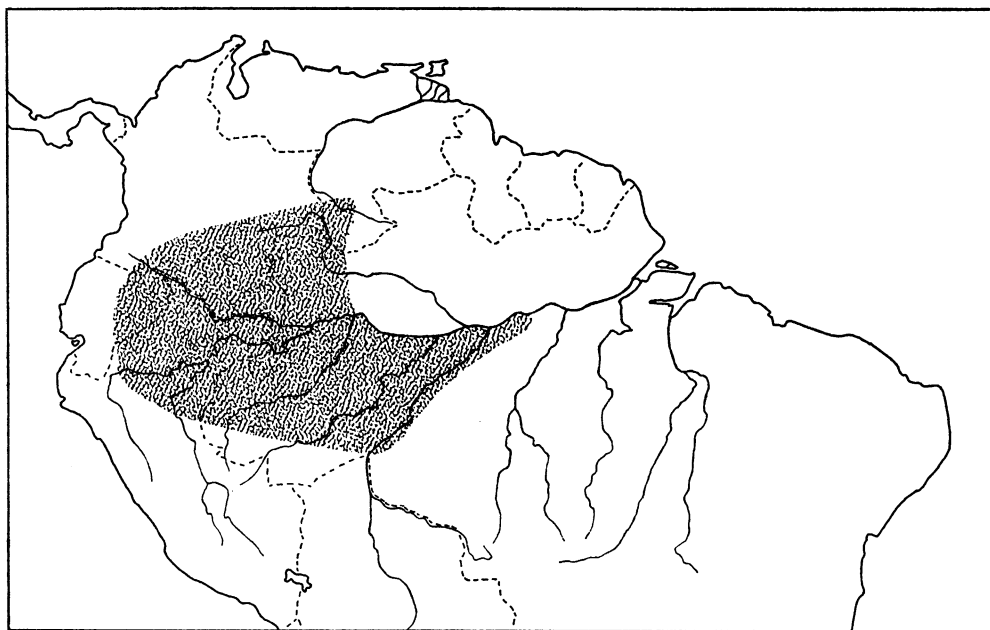


FIG. 29. Distribution of the genus *Nothocrax*.

and from the right bank of the lower Rio Madeira east, along the south bank of the Amazon, to at least Lago Andira, or to longitude $56^{\circ} 55' W$.

DESCRIPTION

The throat, upper breast, nape, hind neck, and upper part of the mantle are reddish chestnut, grading posteriorly into brownish chestnut; the upper surface of the wing and tail are colored like the back, and, with the rest of the upper parts from the level of the upper border of the mantle down, are very finely vermiculated with dark brown. On the under parts, the chestnut of the upper breast grades into dark rufous cinnamon on the lower breast and upper abdomen, and cinnamon-buff on the lower abdomen and under tail coverts, the sides of the breast and the flanks being more or less slightly mottled with dark brown. The primaries are brown, the rectrices dull brownish black, broadly tipped with dark buff, with the exception of the central pair which lacks the buffy tips and is similar to the back in coloration, most of the outer web of the next two pairs of rectrices being also mottled with brown.

The crest is very long, projects well beyond the nape onto the neck, and is composed of

narrow, soft, and loosely integrated feathers which vary in coloration from dark brown to sooty brown, or dull brownish black, and are more or less faintly and narrowly edged or tipped with chestnut. These chestnut markings are usually restricted to the front of the crest and to its lowest layers and are much more conspicuous in birds that are probably not fully adult, but persist to a much-reduced degree in many adults.

The lores and the whole of the face are completely bare. The malar stripe is feathered and varies from dark chestnut to blackish. The bill is compressed laterally, highly arched and strongly decurved, ending in a prominent hook. It is bright coral-red in life.

In life, the skin of the face is very vividly colored, bright yellow in front of, above, and behind the eye, but blue below the eye, grading into purplish; the iris is brown: the tarsus is pale carmine or rose.

The females of *Nothocrax urumutum* average smaller than the males (table 1), but are identical in all other respects, with the slight exception that they are a little more mottled with brown on the under parts.

Nothocrax urumutum does not vary geographically.

NOCTURNAL HABITS

The habits of *Nothocrax urumutum* are very poorly known, but this species appears to be nocturnal in its native forests. Its eye seems to be larger (see above) than that of the other curassows, which are all diurnal, and *N. urumutum* has been reported in the literature as active at night. Sick (personal communication) says he has heard it calling during the night, and Wetmore (personal communication) told me that he collected a specimen at night on the Rio Guainia after he had been informed by his native assistants that the bird was nocturnal.

Natterer (1869, p. 288) wrote that *Nothocrax urumutum* feeds at night and is vocal from midnight to daybreak, and he has described the manner in which it is hunted by the Indians. The latter light torches and follow its calls during the night until daybreak when the bird is found and shot. Bartlett (1873, p. 307) has described this hunt in almost the same words, saying that he had obtained this information from reliable persons in Peru, but he wrote also that *N. urumutum* lives "in holes and burrows in the ground," which seems to be very doubtful and was not mentioned by Natterer. Bartlett was probably reporting only on hearsay, because his personal acquaintance seems to have been only with a captive bird, and with others that "I have often heard . . . in the middle of the night near Nauta," which is on the lower Marañon in Peru.

GENUS MITU

DIAGNOSIS

This genus is composed of three species of large size with a glossy plumage which is black and white or black and chestnut. The bill is massive and completely covered by the horny rhamphotheca; wattles or an elevated bony helmet is not present. The crest, when well developed, is composed of flat feathers, which broaden distally but do not curl. The sexes are not dimorphic in coloration.

KEY TO THE SPECIES OF *Mitu*

1. Lower abdomen, under tail coverts, and long tufts of feathers growing from base of thighs white *M. salvini*
- Lower abdomen, under tail coverts, and long

- | | | |
|---|---------------------|---|
| tufts of feathers growing from base of thighs | chestnut | 2 |
| 2. Tips of tail chestnut | <i>M. tomentosa</i> | |
| Tips of tail white | <i>M. mitu</i> | |

DISTRIBUTION

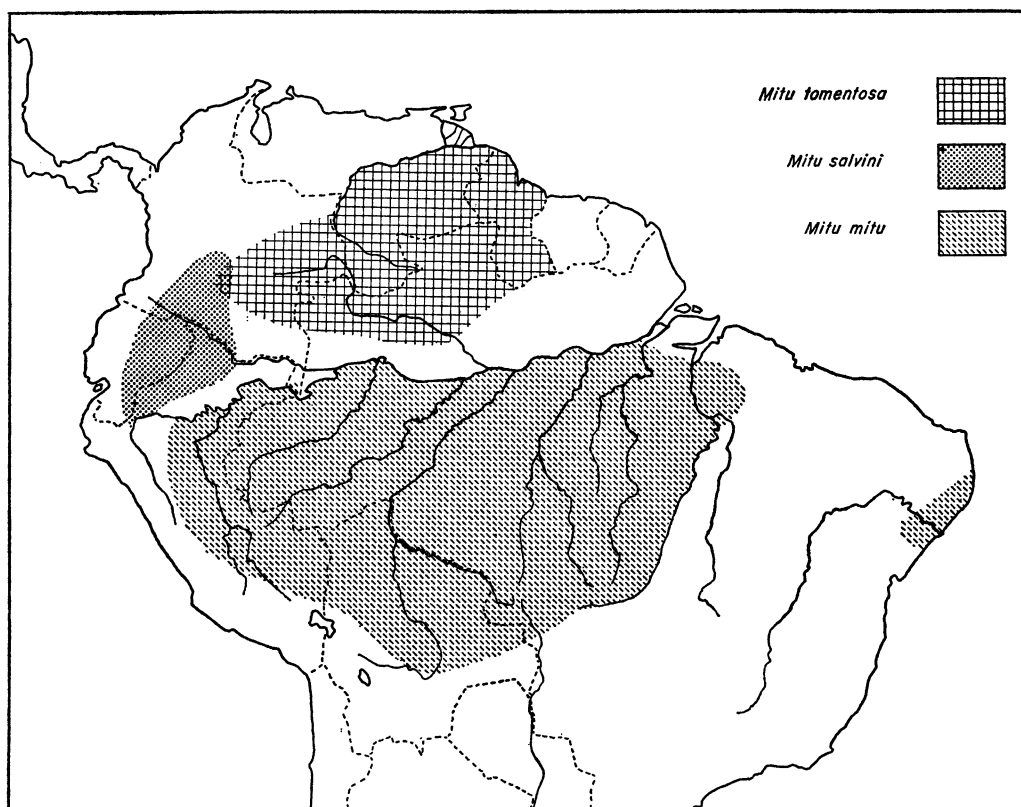
The distribution of *Mitu* is shown in figure 30. The three species are virtually allopatric, except in southeastern Colombia where the ranges of *M. tomentosa* and *M. salvini* appear to overlap slightly on the Rio Guayabero south of the Cordillera de la Macarena. The range of *M. salvini* is relatively small, but the other two species are widely distributed, especially *M. mitu* which replaces *M. salvini* and *M. tomentosa* south of the Amazon. One specimen of *M. mitu* has been collected, however, on the north bank of the Amazon west of Leticia, but this record is probably abnormal (see Vaurie, 1967d). The gap shown between the range of *M. tomentosa* and that of *M. mitu* may be closed by future collecting, but I believe the two species will be found to replace each other north and south of the Amazon.

Mitu mitu formerly inhabited northeastern Brazil from perhaps Pernambuco south to northern Bahia (fig. 30), but is probably extinct now in this region. Marcgrave (1648) reported its presence in this region in the middle of the seventeenth century, but no specimen was known until Pinto (1952) reported one that was collected on October 5, 1951, at São Miguel dos Campos in eastern Alagoas. It is possible that Burmeister (1856) knew that the species existed in northeastern Brazil, because he included the region north of Bahia and near Pernambuco in its range, but he did not mention any specimen, and his statement may have been pure conjecture.

VARIATIONS IN COLORATION AND STRUCTURE

The three species are quite homogeneous, but differ in the shape of the bill, the relative development of the crest, and in alternate differences in coloration, although the color pattern remains unchanged.

The three species are black and glossy, with the exception of the lower abdomen, under tail coverts, long tufts of feathers that grow from the base of the thighs, and the

FIG. 30. Distribution of the genus *Mitu*.

tips of the tail, including the central rectrices, which are either chestnut (*M. tomentosa*), or white (*M. salvini*). *Mitu mitu* resembles *M. tomentosa*, with the exception of the tips of the tail which are white as in *M. salvini*.

The gloss is highly developed on the upper parts and varies from greenish blue in *Mitu salvini* and *M. mitu*, to purplish blue in *M. tomentosa*, but is not evenly distributed. The head (except the crest), neck, and throat are pure velvety black, with a slight sheen in some lights which is more apparent on the hind neck and lower throat. The edges of the individual feathers and their basal half are dull black, contrasting with the glossy part of the feather and creating a sharp scalloped or squamated pattern.

The face, except the lower eyelid, is fully and densely feathered.

The crest (fig. 28) is very well developed in *Mitu salvini* and *M. mitu* and is composed of flat and well-integrated feathers which broaden out distally to end in a well-rounded

tip, but these feathers are not stiff and in no case are curled like those of *Pauxi* and *Crax*. The crest is glossy, but the gloss is more intense near the tip, the very edge of the feather being dull black. This black averages about 2 mm. in width and wears off rapidly. The longest feathers average about 45 mm. in length in the two species, but are broader in *M. mitu*, averaging about 14 or 15 mm. in width, as against about 10 or 11 in *M. salvini*. A similar crest is present in *M. tomentosa*, but it is much more poorly developed, at best, and is rudimentary or scarcely evident in some individuals. The longest of its feathers reach about 20 mm. in length, but they are "shaggy," not well integrated as in the other two species, and are poorly glossed.

The shape of the bill varies conspicuously (fig. 28). It is massive in *Mitu tomentosa*, strongly compressed laterally, and has a rounded blunt keel, but it is not swollen at the base and is "normal" in shape. The bill of *M. salvini* is larger, decurved at a different

angle, and is usually slightly swollen at the base, with, as a rule, an additional ridge at the top. It is also more compressed anteriorly than the bill of *M. tomentosa* and has a sharper keel. The bill of *M. mitu* is considerably larger than that of *M. salvini*, much more swollen at the base in front of the nostril, and especially above the nostril, this bulbous base rising to form a sort of "casque," but not a true helmet as occurs in *Pauxi*. The anterior part of the bill is highly compressed laterally, however, and has a very sharp keel, hence the name "Razor-billed Curassow," by which this species is known in English.

The females are identical to the males in all respects with the only exception that they average somewhat smaller (table 1). The three species differ only slightly in size, but they differ in proportions (fig. 34), although the difference is caused chiefly by the fact that *Mitu mitu* has a disproportionally much larger bill. The tail of *M. tomentosa* is, however, slightly longer proportionally than that of *M. salvini* and *M. mitu*, the tail/wing ratio being .89 in *M. tomentosa* as against .83 in *M. salvini* and .84 in *M. mitu*.

The colors of the soft parts in life appear to be the same in both sexes and in the three species. The tarsus is some shade of red, and "flesh," reddish pink, orange-red, red, and dull red have been noted. The iris is brown or reddish brown. The bill is also some shade of bright red, but it grades into vinaceous toward the base in *M. tomentosa* as a rule, and the tip is usually much paler than the rest of the bill in *M. salvini*.

PHYLOGENY

The three species are closely related and form a superspecies, but *Mitu salvini* and *M. mitu* are more closely related to each other than they are to *M. tomentosa*. Such a close relationship is suggested by several characters: the swelling at the base of the bill, which is only slightly developed in *M. salvini* but completely lacking in *M. tomentosa*; the similarity in the tail/wing ratio; the similarity in the color of the gloss (greenish, as against bluish in *M. tomentosa*); and the fact that the crest is well developed in *M. salvini* and *M. mitu* but not in *M. tomentosa*. We may add also the fact that the ranges of *M. salvini* and *M. tomentosa* overlap slightly,

whereas *M. salvini* and *M. mitu* are perfectly allopatric.

LIST OF THE SPECIES

Mitu tomentosa

DIAGNOSIS: Differing from *Mitu salvini* by being chestnut, where latter is white, from *M. mitu* by having tail tipped with chestnut, as against white. Gloss more bluish, crest much less well developed, and bill smaller, less modified.

RANGE: Guyana (formerly British Guiana), and Venezuela, south of the Orinoco, south to northern Brazil to the upper and middle courses of the Rio Branco and Rio Negro, westward through southeastern Colombia to the Rio Guayabero, south of the Cordillera de la Macarena, where the range of *Mitu tomentosa* meets and appears to overlap slightly the range of *M. salvini*. The range in Colombia is scarcely known: the only other record, besides the Rio Guayabero, is a locality about 60 kilometers west of the border of Brazil on the lower Rio Apaporis. The record of *M. tomentosa* from San Fernando de Apure in Venezuela north of the Orinoco is erroneous.

This species shows no evidence of geographical variation.

Mitu salvini

DIAGNOSIS: Differing from *Mitu tomentosa* by having lower abdomen, under tail coverts, long tufts of feathers growing from base of thighs, and tip of tail white rather than chestnut; from *M. mitu* by being white below where the latter is chestnut. Crest very well developed, but feathers narrower than in *M. mitu*. Bill smaller, much less swollen than that of *M. mitu*.

RANGE: Southeastern Colombia along the base of the Eastern Andes, north to at least the Cordillera de la Macarena, and south through eastern Ecuador to about the Rio Curaray in northern Loreto in northeastern Peru.

This species shows no evidence of geographical variation.

Mitu mitu

DIAGNOSIS: Differing from *Mitu tomentosa* by having tail tipped with white, rather than chestnut, from *M. salvini* by having lower

abdomen, under tail coverts, and long tufts of feathers growing from base of thighs chestnut rather than white. Crest very well developed, but feathers broader. Bill very massive and greatly swollen at base (fig. 28).

RANGE: Brazil, south of the Amazon, from eastern Para west to eastern Peru, south to central Bolivia, and about the fifteenth and sixteenth parallels in the Mato Grosso; also formerly northeastern Brazil from perhaps eastern Pernambuco south to northern Bahia. One specimen has been collected on the north bank of the Amazon in Colombia west of Leticia, a record included in figure 30, but I do not believe this species occurs normally north of the Amazon.

This species shows no evidence of geographical variation, but it is possible that the population of northeastern Brazil may have been distinct. Pinto (1952, 1964) believed that it was, basing his opinion on the specimen that was collected in 1951 in Alagoas, but this bird appears to me (1967d) to be immature and does not seem to differ from young birds from the Amazon Basin.

GENUS PAUXI

DIAGNOSIS

This genus is composed of two species which differ from those of *Mitu* and *Crax* by having a large, elevated, bony helmet on the forehead, and by lacking the wattles of *Crax*. The crest is lacking or present; when present it is composed of very short and very tightly curled feathers. The females are very strongly dimorphic in coloration or are identical with the males.

KEY TO THE SPECIES OF *Pauxi*

- Feathers on top of crown, nape, and hind neck very highly glossed and very tightly curled *P. unicornis*
- Feathers on top of crown, nape, and hind neck velvety black and not glossy, not curled *P. pauxi*

DISTRIBUTION

The distribution of *Pauxi* is shown in figure 31. The two species inhabit very dense and wet forest in mountainous regions and are extremely isolated, *P. pauxi* in northern Venezuela and neighboring Colombia, *P. unicornis* in the Yungas de Cochabamba in Bolivia. The gap that separates the two

species is enormous—nearly 3000 kilometers. It will probably be narrowed somewhat by future discoveries, but it is evident that the two specimens have been isolated for a long time. *Pauxi unicornis* is known so far from only one male and one female which were taken near El Palmar at an elevation of 793 meters. *Pauxi pauxi* has been collected from 366 to 2000 meters, but the preferred elevation seems to be between 1000 and 1500 meters, at least in the coastal range of Venezuela, according to Schäfer (1953).

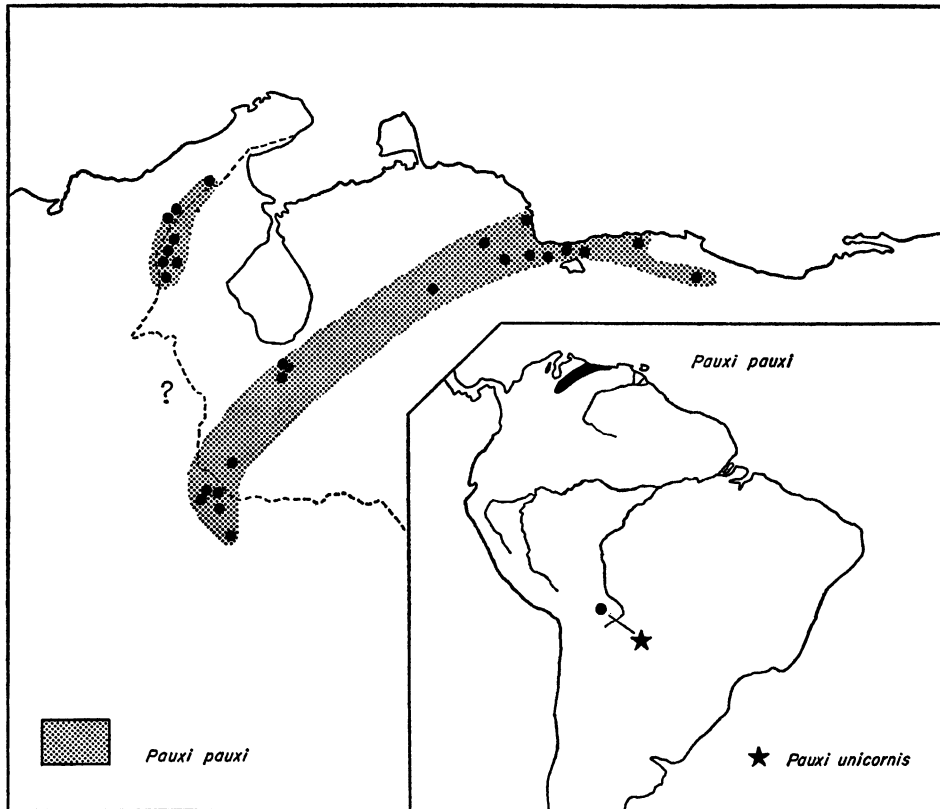
VARIATIONS IN COLORATION AND STRUCTURE

The males of the two species are pure velvety black on the head and neck, not glossy, the rest of the plumage being glossy and very dark green above, chiefly dull black below the upper breast, and the abdomen, under tail coverts, long tufts of feathers that grow from the base of the thighs, and the tip of the tail white. The gloss is highly developed in *Pauxi pauxi* and has a distinct Prussian-blue cast, but *P. unicornis* is very dark, dull olive-green and rather poorly glossed. The dull black edges of the feathers are broad in *P. pauxi*, averaging about 4 or 5 mm. in width, and create a sharp scalloped or squamated pattern similar to that of *Mitu*, but these dull edges are much narrower and faint in *P. unicornis*, with the result that the plumage is virtually uniform, not distinctly patterned as in *P. pauxi*.

The feathers of the whole head and neck are velvety black, with a slight sheen under shifting light, in *Pauxi pauxi*, but not in *P. unicornis*, which differs very conspicuously from *P. pauxi* (pl. 16, figs. 1, 2) by being very glossy on the top of the head, nape, and upper hind neck. These glossy feathers are erect and rather stiff, and their metallic tips are very tightly curled forward to form a very strange crest. *Pauxi pauxi* has no crest. Although the feathers of its crown are also erect, they are soft and not curly.

The face, except for the lower eyelid, is fully and densely feathered.

The two species have a large, elevated, bony helmet (fig. 4), which surmounts the base of the bill and the forehead and is covered by partly keratinized skin which shrinks after death, but not by the rhampho-

FIG. 31. Distribution of the genus *Pauxi*.

theca of the bill which ends at the base of the helmet. This helmet is swollen at the top in *P. pauxi*, shaped like a fig (fig. 4), but is cylindrical in *P. unicornis* and shaped like a horn, being broader at the base than at the tip.

The females average smaller than the males (table 1) and are either "black and white" and identical with the males in coloration, or are brown, with an interrupted plumage. These two plumages are present in *Pauxi pauxi*, but perhaps not in *P. unicornis*; the only female of the latter known so far is black and white, but a brown plumage may also exist.

The females in the brown plumage are black on the head, neck, and outer tail feathers, which are broadly tipped with buffy white, but the rest of the plumage is reddish brown above, including the central tail feathers, dark ochraceous on the breast, pale rufous on the upper abdomen, and is vermiculated, mottled, or barred with black-

ish brown or dark brown, these dark markings forming rather regular concentric and interrupted bars on the breast and mantle. The middle rows of the upper wing coverts, the greater coverts, and some of the scapulars are also broadly tipped with whitish buff, the pale tips forming more or less regular "wing bars."

The two plumages of females of *Pauxi pauxi* were discussed by me in another paper (1967d). I believe the brown plumage is the original coloration of the female which has been lost by secondary modification and replaced by the malelike black-and-white plumage which appears to be a mutation. These mutants are far more abundant than the brown females, which are now no longer found in northern Venezuela, although the two phases seem to have been equally numerous there about 100 years ago. Brown females are still found in the other parts of the range but are fewer than the black-and-white ones.

- ¹ The differences between the males of *Crax globulosa* and those of *C. blumenbachii* are quite distinct but appear to be relative when expressed in a key. Misidentification is, however, very improbable, as *C. blumenbachii*, which is on the verge of extinction, is extremely rare and known from only six males or fewer. Moreover, the ranges are quite different; *C. blumenbachii* is or was restricted to the coastal districts of Brazil, from southern Bahia to Rio de Janeiro, whereas *C. globulosa* inhabits the upper Amazon Basin.

- *C. blumenbachii* (female)
 7. Wing feathers uniformly black, not mottled with chestnut; white markings in crest very small and indistinct *C. globulosa* (female)
 Middle and greater upper wing coverts, alula, primaries, and secondaries heavily mottled with reddish chestnut; crest regularly and very conspicuously barred with white *C. blumenbachii* (female)
 8. Face and nape sharply and regularly barred with black and white *C. rubra* (female, in part)
 Face and nape not barred with black and white 9
 9. With highly developed wattles and smaller knob, or with highly developed knob and smaller wattles 10
 Without either wattles or knob 11
 10. Wattles and knob bright blue in life; knob less highly developed than wattles *C. alberti* (male)
 Wattles and knob bright yellow in life, or yellow tinged with reddish orange; wattles less highly developed than knob *C. daubentoni* (male)
 11. Breast and abdomen uniformly black; membranes at base of bill yellow in life *C. fasciolata* (male)
 Breast and abdomen not uniformly black . 12
 12. Primaries chestnut or cinnamon and chestnut and vermiculated with brown *C. alberti* (female, in part)
 Primaries barred with black and white of varying width; white markings extremely broad and about as broad as black markings, or reduced to narrow lines or only a few small marginal spots or edges of white on outer web 13
 13. Breast and abdomen dark ochraceous cinnamon, barred with black, black markings usually restricted to upper or middle breast; tail conspicuously and regularly barred *C. fasciolata* (female, in part)
 Breast and abdomen barred, either black on breast and abdomen, or black on breast but creamy or buffy yellow on abdomen; tail not barred, or with slight irregular vestigial streaks restricted almost entirely to outer web 14
 14. Throat regularly and conspicuously barred with white *C. alberti* (female, in part)
 Throat uniformly black, or with only a few concealed small white markings at base of feathers 15
 15. Breast and abdomen black, barred with pure white bars averaging about 3 mm. in width; primaries virtually all black, marked

with only a few small marginal spots or edges of white on outer web; tail not barred; crest very highly developed

. *C. daubentoni* (female)
 Breast black but abdomen creamy or buffy yellow, breast barred with narrow wavy lines of buffy white, abdomen heavily barred with black at sides but not on center where bars irregular and broadly interrupted; primaries narrowly barred on both webs; tail feathers very slightly streaked on outer web; crest poorly developed *C. fasciolata pinima* (female)

DISTRIBUTION

The genus *Crax* is widely distributed (fig. 32) in heavily forested regions from the twenty-fourth parallel in northeastern Mexico south along the escarpment of eastern Mexico to the Isthmus of Tehuantepec, and through southern Mexico, Central, and South America to Misiones, eastern Formosa, and northeastern Chaco in extreme northeastern Argentina, but only to northwestern Ecuador west of the Andes.

The seven species are perfectly allopatric. There is no proof of overlap anywhere, but *Crax alberti* and *C. rubra* very probably meet in the valley of the upper Rio Sinu in Colombia where they have been collected only a few miles apart. It is quite possible also that *C. alector* and *C. globulosa* meet near the mouth of the Rio Negro. The distribution, which is not clear in this region, has been discussed by me in another paper (1967c). The records available so far suggest that the ranges of the two species approach very closely in the region east of Manaos.

The Orinoco or the Amazon forms the boundary between the ranges of *Crax daubentoni*, of *C. alector*, and of *C. fasciolata*, the species replacing one another on the opposite banks of the river. This distributional pattern is similar to that of *Ortalis* in South America, with the conspicuous difference that *Ortalis* is absent from central Brazil where it is probably replaced by the small and relatively unspecialized *Penelope superciliaris*, with which it may not be able to compete.

The distribution shows some gaps on the map, which may or may not exist. *Crax rubra* is cut off from *C. alector* and *C. globulosa* by the Andes, of course, and the narrow

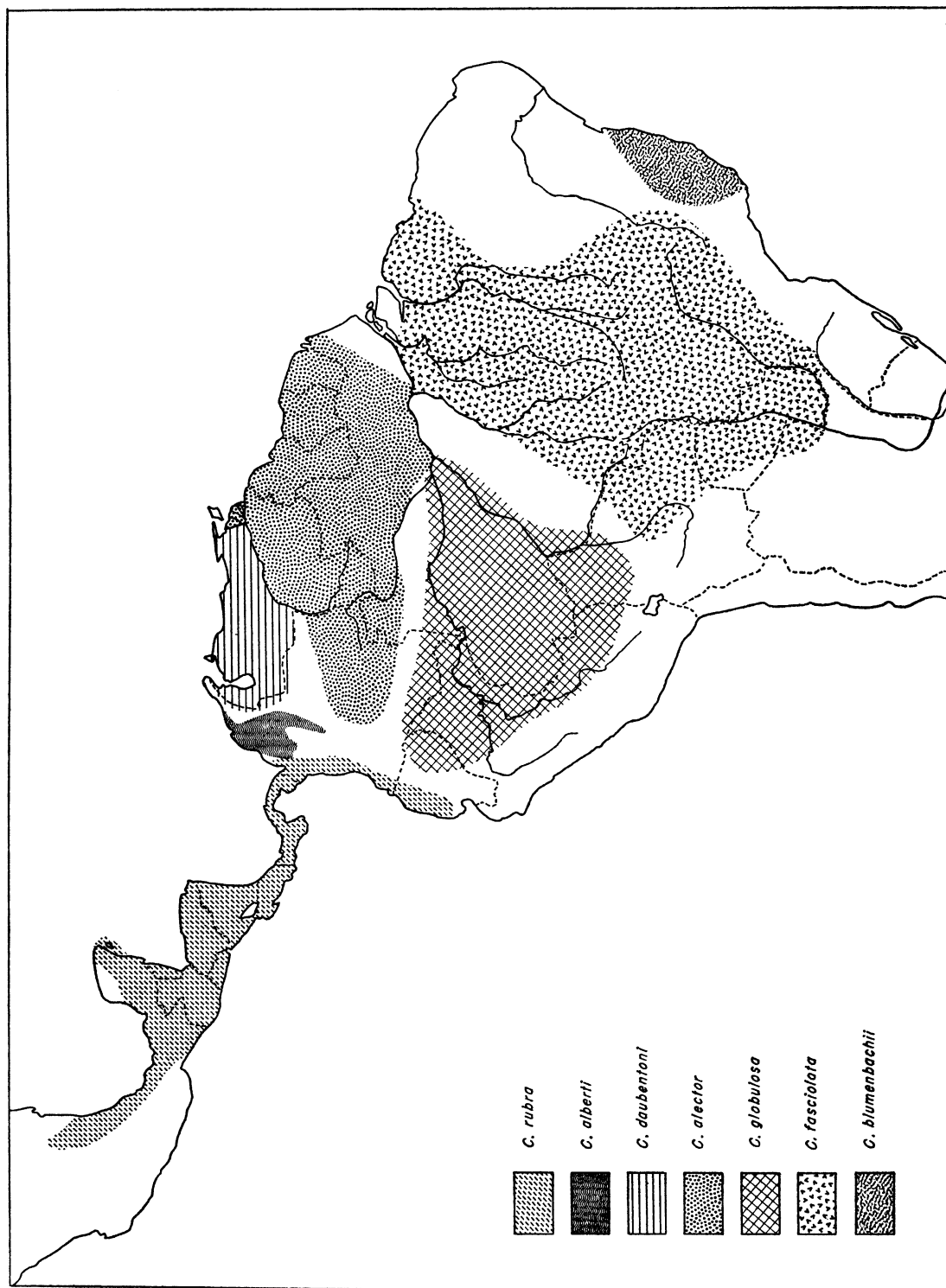


FIG. 32. Distribution of the genus *Crax*.

gap between the range of *C. alberti* and that of *C. daubentoni* seems also to be a well-established fact. It is difficult to account for the gaps between the range of *C. daubentoni* and that of *C. alector* in northeastern Colombia, between that of *C. alector* and that of *C. globulosa* north of the Amazon, and between that of *C. globulosa* and that of *C. fasciolata* east of the Madeira. The possibility that the necessary ecological conditions do not exist seems doubtful, and the lack of records may reflect only insufficient exploration of the regions concerned. The latter probably accounts for the large blank in Amapa, as I believe the range of *C. alector* is probably more extensive in northeastern Brazil north of the Amazon.

Some of the records on which my map is based are very far from recent. It is certain, for instance, that *Crax blumenbachii* had vanished from most of its range by the beginning of the twentieth century, and highly probable that *C. fasciolata* is extinct in Para east of the lower Tocantins. The latter has not been collected in this region since 1842, and it has probably disappeared also from Maranhão where the last specimen was taken in 1907. The form concerned is the extremely rare and very distinct *C. fasciolata pinima* which is known from a total of only seven specimens. *Crax blumenbachii* was found on the Rio Doce, in Espírito Santo, in 1939, but is nearly as rare as *C. f. pinima*, as the total number of existing specimens seems to be a dozen or fewer.

Crax is restricted chiefly to the lowlands, down to sea level, but some species ascend to moderate elevations. The highest altitude on record seems to be 1900 meters for *C. rubra*, on the volcanoes of Chiriqui, Panama, which was mentioned by Wetmore (1965, p. 295). The highest records furnished by the large amount of material that I have seen were: 1533 meters for *C. rubra* on the Cerro de Espírito Santo in Honduras; for *C. alector*, above Villavicencio in Colombia; about 1363 meters for *C. alberti* near Cincinnati in Santa Marta; and 852 meters for *C. daubentoni* in the Sierra Negra in Colombia. Most of the specimens of these and of the other species that I have examined had been collected at considerably lower elevations.

VARIATIONS IN COLORATION AND STRUCTURE

The males are black and glossy, except for the lower abdomen, under tail coverts, and the long tufts of feathers that grow from the base of the thighs and lower flanks—all of which are snow-white. The outer rectrices, but not the central tail feathers, are broadly tipped with white in three species (*Crax daubentoni*, *C. fasciolata*, and *C. alberti*), but are all black in the other four species. The gloss is stronger on the upper parts, but is, as a rule, only moderately well developed, and varies from dark purplish blue in *C. alector* to dull greenish blue or dull greenish black in the other species. The plumage is normally uniform, not well patterned as in *Mitu* and *Pauxi pauxi*, but the feathers are edged with dull black when very fresh, as in *Mitu* and *Pauxi pauxi*, but these edges are very much narrower and fainter in *Crax* and wear off very rapidly.

The crest is well developed, but to different degrees (pl. 15); it is most highly developed in *Crax rubra* and is least full in *C. alector*. The feathers are rather stiff, except at the tip which is very gracefully curled, and are uniformly but moderately glossy. The rest of the head and neck is pure velvety black, not glossy, but with a slight sheen under shifting light. The crest is black in the adult male, not spotted or barred with white as in the female, but a few small white spots are present occasionally in the crest of the immature male of *C. alector*, *C. globulosa*, *C. fasciolata*, and *C. alberti*, and perhaps in the immature males of the other species as well.¹

The face is not fully feathered, and the lores are bare in some species (pl. 15). The eye is surrounded by a ring of bare skin, which connects with the skin of the lores (when bare), and expands behind the eye to form a small triangular patch. This bare area is usually quite restricted, except in *Crax fasciolata* in which the extent of the naked area varies individually.

The basal half of the bill is covered by

¹ It is possible that this juvenal character is retained in a very occasional adult male of *Crax alector*, but, as some specimens that I have seen were certainly not sexed correctly, this question can be settled only after an examination of birds of known age and sex.

naked fleshy membranes (pl. 15) which form appendages in six of the seven species. These consist of a knob at the base of the culmen and of a pair of wattles at the base of the mandible, which are developed to a different degree in all the species. *Crax alector* entirely lacks these appendages, and the wattles are not developed in *C. fasciolata* and *C. rubra*. The color of the membranes and appendages varies from species to species, as shown in plate 15. The membranes are present in the female, but do not form appendages.

Crax is sexually dimorphic. The females average smaller than the males, lack their fleshy appendages on the bill, and are also sexually dimorphic in coloration, the degree of this dimorphism varying enormously. *Crax alector* represents one extreme; *C. rubra*, the other. The plumage of the latter is completely different from that of the male and is very complex, exhibiting three color phases, but the female of *C. alector* is black and white and identical with the male, with the sole exception that its crest is barred or spotted with white.

The only characters that seem not to vary sexually are the development of the crest, the degree of feathering on the lores and face, and, as far as I can determine, the color of the iris. All the other characters (size, fleshy appendages, color and pattern of the plumage, and color of the bill and tarsus in life) vary sexually.

The white markings of the crest vary enormously. In *Crax daubentoni*, which represents the dark extreme, the white markings are small, very irregular, and usually consist of a single row which is not distinct as it is buried down to almost the very base of the feathers, but in some individuals slight traces of a second row exist. These white markings are also very small and narrow in *C. globulosa*, but they are more regular than in *C. daubentoni*. They are narrow also in *C. alector*, but usually average somewhat broader than in *C. globulosa* and in some cases form an additional row. The white bars are broader in all the other species, and the rows often merge in *C. fasciolata*, *C. rubra*, and in one of the two color phases of *C. alberti* to form a single very

broad but irregular white patch. This patch is expanded in some individuals to invade most of the crest; only the very base and the curly tips remain black.

The variations in the coloration and pattern of the rest of the plumage are too extensive to be described briefly, but are summarized below. The female of *C. alector* is black and white and identical with the male (other than in the crest), as stated above. *Crax globulosa* resembles *C. alector* but is rufous where *C. alector* is white. *Crax blumenbachii* is also rufous, but, in addition, is heavily mottled with reddish chestnut on the wing. *Crax daubentoni* has a plain plumage, which is black and white and resembles that of the male, but differs very conspicuously by being heavily barred with white below the throat.

The plumage of *Crax fasciolata*, *C. alberti*, and *C. rubra* is more complex and can be characterized as barred, in at least one color phase. Two very distinct color phases exist in *C. alberti*, and three in *C. rubra*, but a true color phase does not exist in *C. fasciolata*, although its variation is striking, although purely geographical. The variation in *C. fasciolata* involves the degree of barring, the bars varying, geographically, from about 1 to 13 mm. in width, and the color of the under parts, of the rump and upper tail coverts, and of the edge of the wing.

The plumage of *Crax alberti* varies from black above, more or less distinctly and broadly barred with white, to dark reddish cinnamon below, not barred, or black barred with white, the primaries varying also and to the same degree. Two color phases can be recognized (a rufous and a barred) which are more or less connected by intermediates.

The plumage of *Crax rubra* is the most complex, and three color phases can be recognized (a dark phase, a red phase, and a barred-backed phase), the first two being more or less connected by intermediates. The upper parts vary from black, or blackish, to chestnut brown, bright reddish chestnut, or dark reddish cinnamon, and are uniform, or mottled, or very boldly barred. The under parts vary from chestnut to dark ochraceous or buff, and as a rule are uniform. In this species the face and the whole of the neck are

cross-barred with black and white in all three phases, a pattern that is unique in the genus and the family.

The variation in the color of the soft parts in life is certainly very important, because it undoubtedly plays the dominant role in species recognition. The most important of these differences is the color of the bill and that of its fleshy appendages in the male, which are illustrated in plate 15. The variation is summarized below, but some of the information is deficient. For example, the color of the skin of the lores and face and the color of the bill of some females have not been recorded. The information on the color of the tarsus and iris is also contradictory. Some of the contradictions in the literature, or on the labels of specimens, concerning the color of the tarsus, iris, or other soft parts, or concerning the size of the fleshy appendages, certainly reflect changes in vascularization correlated with the breeding cycle. I repeat, the females have no fleshy appendages at the base of the bill.

The color and the appendages of the bill in the species are as follows:

Crax alector: Male, no appendages, skin yellow near base, grading into orange or reddish orange anteriorly, horny bill gray or bluish; female similar to male.

Crax globulosa: Male, knob and wattles very highly developed, skin bright rose-red, horny bill pure black; female, skin and bill similar to those of male; skin yellow rather than red in some males and females, but, I believe, invariably bright red during sexual activity.

Crax blumenbachii: Male, wattles well developed but knob less well developed than wattles, skin carmine-red, horny bill grayish blue; female, skin black, tip of horny bill pale in specimens, probably yellowish in life.

Crax daubentoni: Male, knob very highly developed but wattles less developed than knob, skin chrome-yellow, horny bill pure black; female, skin blackish or dark brown, horny bill blackish.

Crax fasciolata: Male, no wattles, fleshy base of culmen swollen to a degree but not developed into knob, skin sulphur-yellow, horny bill bluish gray; female, no direct information, skin said to be "blackish" or "similar to [that of] male," horny bill said to be "blackish."

Crax alberti: Male, wattles very highly developed, but knob less developed than wattles, skin bright cerulean blue, horny bill pale and yellow

low at tip; female, no direct information, skin probably blackish, horny bill probably similar to that of male.

Crax rubra: Male, knob very highly developed but no wattles, skin pale cadmium-yellow, in some cases slightly tinged with orange, horny bill neutral gray or grayish blue shading to black anteriorly; female, skin blackish or dark brownish gray, horny bill, no direct information, said to be "yellowish," "blue," or "gray."

The color of the tarsus is as follows:

Crax alector: Blackish, plumbeous gray, or blue-gray in male and female.

Crax globulosa: Olivaceous, grayish blue, or red in male, gray-blue or pink in female.

Crax blumenbachii: Blackish and perhaps red in male, dull red in female.

Crax daubentoni: Greenish, ashy blue, or blackish in male and female.

Crax fasciolata: Fleshy pink or red in male and female.

Crax alberti: Fleshy pink, red, or pale purplish red ("dark orchid"). in male, pale fleshy pink in female.

Crax rubra: Grayish or bluish in male, purplish white or pale gray in female.

The color of the iris in both sexes is as follows:

Crax globulosa, *C. blumenbachii*, *C. daubentoni*, and *C. fasciolata*: Reddish brown.

Crax alberti: "Brown"; black has also been mentioned.

Crax alector and *C. rubra*: Hazel brown, brown, or lake; black has also been mentioned for *C. rubra*.

The feathering of the lores, the color of the skin (when bare) of the lores, and the color of the skin of the orbital region in both sexes are:

Crax alector: Lores bare or with a few small, pinpoint feathers, bare patch around eye very moderate in size, no information on color of skin, but black in specimens and probably dark blue in life.

Crax globulosa: Lores and patch as in *C. alector*, skin dark blue in life.

Crax blumenbachii: Lores narrowly bare or with pinpoint feathers, bare patch moderate in size, skin purplish in life.

Crax daubentoni: Lores feathered or with pinpoint feathers, bare patch narrow, no information on color of skin in life but black in specimens.

Crax fasciolata: Lores broadly bare, size of bare patch varying individually but invariably extensive and greater part of face bare in some individuals; skin black in life.

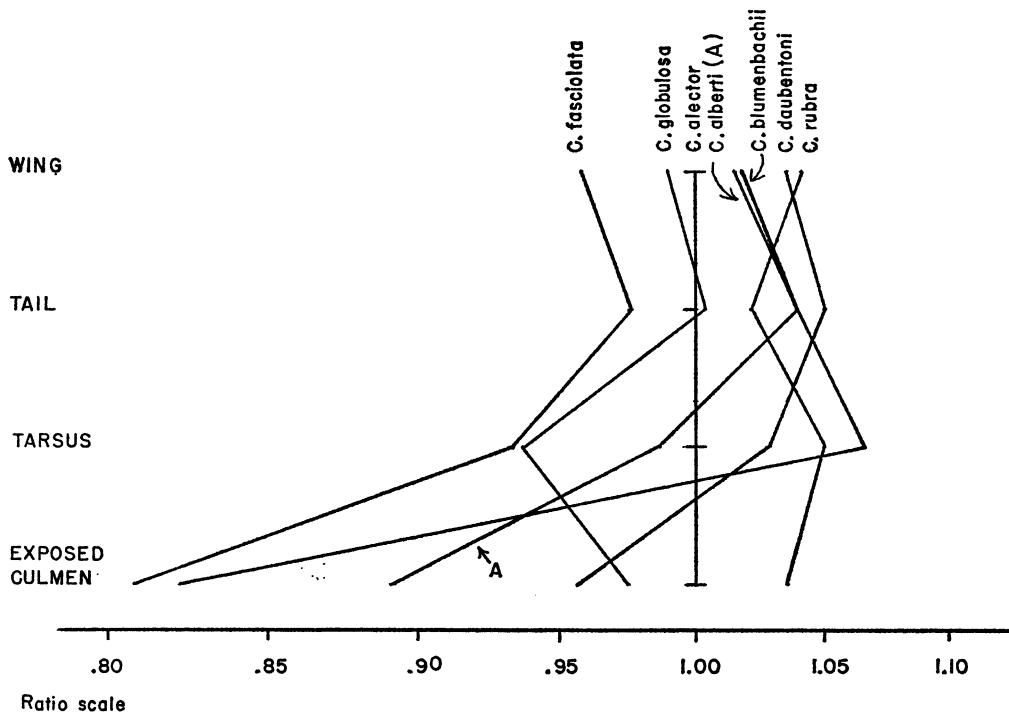


FIG. 33. Comparison by ratio diagram of the proportions of the adult males of the genus *Crax*. A identifies *C. alberti*.

Crax alberti: Lores feathered or with pinpoint feathers, bare patch narrow, no information on color of skin in life, but blackish in specimens.

Crax rubra: Lores well feathered or broadly grown with pinpoint feathers, bare patch very narrow, skin dull black in life.

VARIATIONS IN SIZE AND PROPORTIONS

The measurements of *Crax* are given in table 1. The females average somewhat smaller than the males. The relative proportions of the males are shown in a ratio diagram (fig. 33), in which *Crax alector* is the standard of comparison. The relative proportions of the males of *Mitu* are shown in another ratio diagram (fig. 34), in which the same standard of comparison and the same scale as in the ratio diagram of *Crax* are used. The proportions of the males of these two genera and of the males of *Nothocrax* and *Pauxi* are compared in figure 27.

The proportions of *Crax* do not vary significantly, but the bill is proportionally longer in *C. alector* and *C. rubra* than in the other species. The difference is curious, because *C. alector* has no appendages at the

base of the bill, whereas the knob on the culmen is very highly developed in *C. rubra* (pl. 15). The presence or absence of a fleshy knob on the culmen apparently does not affect the length of the bill; the proportions are identical in these two species.

In *Mitu*, however, the modification of the base of the culmen results in a proportionate increase in the length of the bill, as is apparent in figure 34, where the ratio is about .80 in the case of *M. tomentosa* in which the base of the culmen is not swollen, as against about 1.18 in *M. mitu* in which it is greatly swollen.

The other proportions do not vary significantly in *Crax* and *Mitu*, although the tarsus varies a little more in *Crax*.

PHYLOGENY

The phylogeny of the seven species of *Crax* cannot be expressed satisfactorily in a linear sequence because they all seem to have evolved by radiation from an ancestral form. These species can be arranged, however, in a morphological sequence from *C. alector* to *C.*

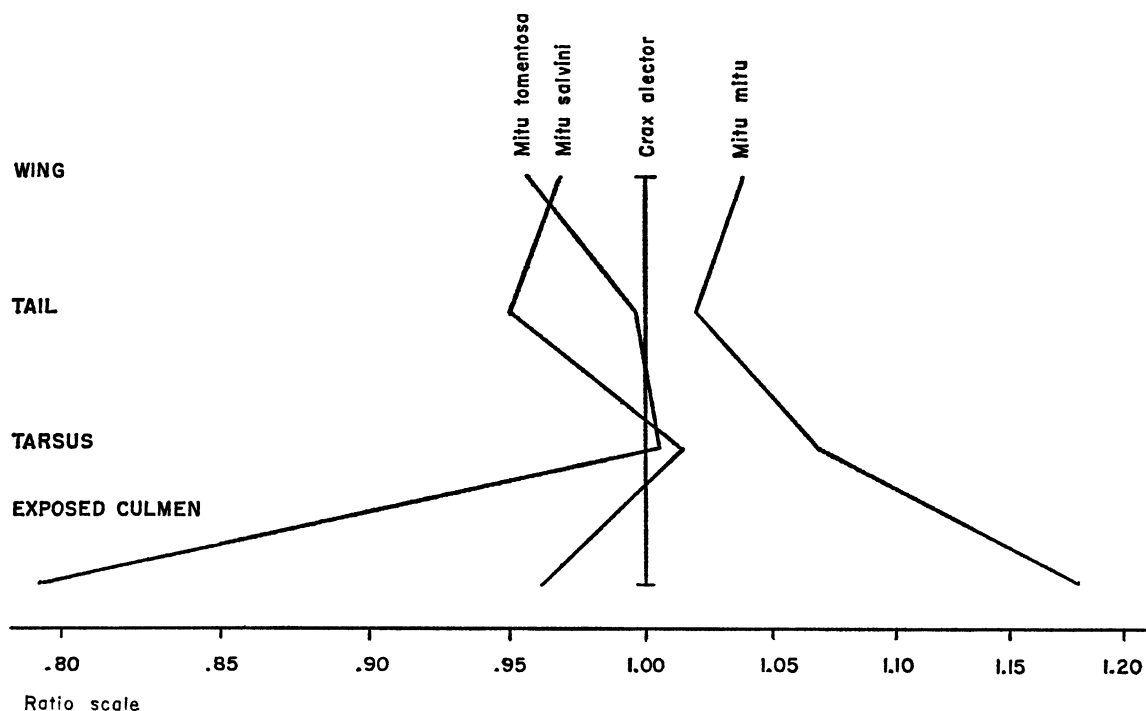


FIG. 34. Comparison by ratio diagram of the proportions of the adult males of the genus *Mitu*.

rubra based on the characters of the females.

The characters of the males are too uniform for one to determine the sequence, or they consist of variations in structure and coloration that were very probably developed to insure species recognition and are subject to much displacement. For instance, in the case of *Crax rubra* and *C. alberti*, which very probably come into contact in Colombia, the bill of *C. rubra* has a large and very conspicuous fleshy knob at the base of the culmen which is bright yellow in life, but with no wattles on the mandibles, whereas in *C. alberti* the wattles are very highly developed, but not the knob, and are very bright blue in life. This character displacement occurs in all the species and appears to have no phylogenetic significance. The plumage is black and white and identical in all the males except only that the tail is broadly tipped with white in three species.

In a sequence based on the characters of the females (but which also takes into consideration the characters of the males when relevant), *Crax alector* must be placed first

because the female does not have a distinctive plumage. The two sexes are black and white, and are identical except that the feathers of the crest of the female are narrowly barred with white. This difference may represent a secondary modification, a loss of the "female plumage," similar to the loss of the white tips of the tail in *C. rubra* which persist as only slight traces in an occasional specimen. The fact that all the characters of *C. alector* are, however, simplified argues against this possibility. The crest is more poorly developed in *C. alector* than in any other species, is not well marked with white in the female, and the male has no fleshy appendages at the base of the bill of any kind. These appendages are developed to a varying degree in the other species.

The plumage becomes sexually dimorphic in *Crax globulosa*, but the color pattern remains extremely plain. Females of *C. globulosa* differ from those of *C. alector* only to the extent that the former are rufous whereas the latter are white. The crest averages slightly longer in *C. globulosa* but

remains very poorly developed, and its white markings in the female are usually even less developed than in *C. alector*.

The characters of *Crax blumenbachii* are clearly more advanced. The female is rufous, as in *C. globulosa*, but it is also heavily mottled with reddish chestnut on the wings, whereas the wings are black and uniform in *C. globulosa* and *C. alector*. The crest of *C. blumenbachii* is also much better developed and much better barred with white in the female.

A barred plumage first appears in *Crax daubentoni*, as the female is conspicuously barred with black and white on the under parts, but the coloration remains plain when compared with that of *C. fasciolata*, *C. alberti*, and *C. rubra*, and *C. daubentoni* lacks the rufous pigments of the other three species. The crest is very full but not well marked with white in the female. The tail is broadly tipped with white in the male and female, whereas it is black, not tipped with white, in both sexes of *C. alector*, *C. globulosa*, and *C. blumenbachii*. These white tips are present also in *C. fasciolata* and *C. alberti*, and seem to have been present in *C. rubra*, from which they have disappeared through secondary modification in the great majority of specimens.

The plumage of females of *Crax fasciolata*, *C. alberti*, and *C. rubra* becomes progressively more complex; two color phases appear in *C. alberti* and three in *C. rubra*. The crest becomes also very white in these species and is most highly developed in *C. rubra*. The very large crest of *C. rubra*, its three color phases, the unique cross-barred pattern of the head, the well-feathered lores, and the fact that it is also the largest of all the species argue that *C. rubra* is incontestably the most evolved species.

The species of *Crax* can then be arranged in the following sequence: *C. alector*, *C. globulosa*, *C. blumenbachii*, *C. daubentoni*, *C. fasciolata*, *C. alberti*, and *C. rubra*. This sequence is based on morphology, from the least to the most specialized, and is not necessarily phylogenetic. My opinion is that all the species are closely related to one another to the same degree, and the pattern of their distribution also suggests dispersal.

LIST OF THE SPECIES

Crax alector

DIAGNOSIS¹: Plumage black, except lower abdomen, under tail coverts, and long tufts of feathers growing from thighs snow-white. Female identical with male except feathers of crest narrowly barred with white. Gloss moderate, but better developed than in other species of genus, dark purplish blue, dull greenish blue or dull greenish black in other species.

RANGE: The range of *Crax alector* extends from the delta of the Orinoco and the Guianas westward through Venezuela, south of the Orinoco, to the foothills of the Eastern Andes of Colombia north to the region of Villavicencio, and south to northern Brazil to the Rio Negro, and the north bank of the Amazon, east of the Rio Urubu, to at least Lago Cupeua (longitude 54° 55' W. It extends also to northern Amapa, and probably farther east and south, north of the Amazon, than the limit drawn in figure 32. The range of *C. alector* on the lower Rio Negro and east of its mouth is not clear and has been discussed by me in another paper (1967c). It is quite possible that the range of *globulosa*, which is known from Manaus, comes into contact with the range of *C. alector* in the region between Manaus and the lower Rio Urubu.

Crax globulosa

DIAGNOSIS: Coloration of male identical with that of *Crax alector*, but gloss dull greenish blue. Female differing from female of *C. alector* by having lower abdomen, under tail coverts, and long tufts of feathers growing from thighs dark rufous. Crest not highly developed but a little larger than that of *C. alector*, very narrowly barred with white in female, white markings less developed, as a rule, than in female of *C. alector*.

RANGE: Upper Amazon Basin, from the region of Manaus at the mouth of the Rio

¹ The variations in the coloration of the soft parts in life, the fleshy appendages of the males, and the feathering of the face are important diagnostic characters. To avoid repetition, and because the variation is made clearer by a comparison of these characters together (see p. 234), they are not mentioned in the diagnoses, with one or two exceptions.

Negro and from the Rio Madeira and Rio Guaporé westward to the foothills of the Andes, north to the Rio Caqueta in Colombia, and south through Ecuador and Peru to about latitude 14° 30' S. on the Rio Beni in northwestern Bolivia.

Crax blumenbachii

DIAGNOSIS: Characters more advanced than those of *Crax alector* and *C. globulosa*; crest much better developed and plumage of female more elaborate. In female lower abdomen, under tail coverts, and long tufts of feathers growing from thighs rufous, as in *C. globulosa* but darker, especially chestnut tufts of feathers; differing conspicuously from female of *C. globulosa* and female of *C. alector* by very heavy mottling of reddish chestnut on middle and greater upper wing coverts, alula, primaries, and secondaries. Crest very well developed, more so than that of *C. alector* and *C. globulosa*, more barred with white in female, but a little less full than that of *C. rubra*. Gloss of plumage more greenish, less bluish, than that of *C. globulosa* and less purplish than that of *C. alector*.

RANGE: Coastal districts of Brazil from southern Bahia south through eastern Minas Gerais and Espírito Santo to Rio de Janeiro. *Crax blumenbachii* is, however, on the verge of extinction, so its range and status have become uncertain.

Crax daubentoni

DIAGNOSIS: Outer tail feathers broadly tipped with white. Female differing from male and from females of other three species by being very conspicuously barred with white on breast, upper and middle abdomen, and thighs. Crest highly developed but indistinctly marked with white in female, white markings more reduced than in any other species.

RANGE: Venezuela, north of the Orinoco, from the tip of the Peninsula de Paria west to Merida and Zulia, and neighboring Colombia in the mountains that form the border between Venezuela and Colombia, south through eastern Norte de Santander to northwestern Arauca.

Crax fasciolata

DIAGNOSIS: Differing from all other species by being much less feathered on lores and face. Tail tipped with white. Crest only

moderately well developed, but whiter in many females than in other species. Female barred above and below, barring varying very strongly geographically, as described below.

RANGE: The range of *Crax fasciolata* is greater than that of any other species (fig. 32); it extends from the coast of Maranhão and Para west to the Tapajoz River, and south through central Brazil to central and southeastern Bolivia, Paraguay, and extreme northeastern Argentina to eastern Formosa, northeastern Chaco, and Misiones. *Crax fasciolata* replaces *C. globulosa* in Bolivia south of about latitude 15° S. on the Rio Mamoré, but the ranges of the two species apparently do not come into contact. In Brazil, the eastern limits of the range seem to extend more or less to the Tocantins River, the Rio São Francisco in Minas Gerais, and the western parts of São Paulo and Paraná.

GEOGRAPHICAL VARIATION: The geographical variation seems to affect only the coloration of the female and is very strongly marked. Three subspecies can be recognized: *pinima* at the northeastern end of the range, *grayi* in Bolivia, and nominate *fasciolata* in the rest of the range. *Crax f. pinima* is very dark, *grayi* very pale, and nominate *fasciolata* is more or less intermediate but shows a very strong tendency toward *grayi* in the southern part of its range. This variation seems to be clinal, but the distribution at the northern end of the range is poorly known, and it is not certain that *pinima*, which seems to be extinct, was connected to nominate *fasciolata* by an intermediate population.

The three subspecies and their distribution were discussed by me in detail in another paper (1967c). *Crax f. pinima* can be characterized as being dull greenish black above, barred with very narrow wavy lines of buffy white that are scarcely more than 1 mm. in width, very heavily barred with black on the breast and flanks, with the white bars in the crest poorly developed. The buffy lines on the upper parts, remiges, and tail are broader and much more regular in nominate *fasciolata*; they form bars which vary from about 2 to 3 mm. in width in birds from the northern part of the range, but these bars become considerably broader in those from the south, attaining about 7 mm. in width in some individuals. In *grayi*, these pale bars are extremely broad and attain 13 mm. in

width. The rump and upper tail coverts are black in *pinima*, brown in nominate *fasciolata*, and ochraceous, with irregular blackish markings, in *grayi*. The under parts also vary. The breast and the border of the upper abdomen are heavily barred with black in *pinima*, the spaces between the bars and the area that is not barred being creamy or pale buffy yellow. The black bars are usually restricted to the breast in nominate *fasciolata*, and end at the border of the upper breast in *grayi*. The breast and abdomen are darker in these two subspecies than in *pinima*; they are dark ochraceous, rather than creamy or pale buff. The white bars in the crest are highly developed in nominate *fasciolata*. They vary individually in width, but are invariably very broad, and the two rows merge in some individuals, the white area expanding so that only the base and tip of the crest remain black. The white bars are more variable in *grayi*, the crest being as white as or blacker than that of nominate *fasciolata*.

The birds of Bolivia (*grayi*) are also very much paler on the outer lesser and middle upper wing coverts than the other populations of the species. The pale area is ochraceous and is not streaked in some individuals, this forming a very large patch at the edge of the wing, whereas these feathers are black, barred with buffy white, in the other populations. This character varies individually in *grayi* but is not found in specimens of nominate *fasciolata* from the Mato Grosso which show a very strong tendency toward *grayi* in other respects.

The records from the northern end of the range of the species are so deficient that these, and the status of *pinima*, require comment. The only records that I have found (other than those of *pinima* from northeastern Para and northern Maranhão) are one record of nominate *fasciolata* from the region of Santarem near the mouth of the Tapajoz, and one other of this subspecies from Conceição do Araguaia. The latter is situated at latitude 8° 35' S., or about 900 kilometers southeast of the mouth of the Tapajoz, and the nearest record of *pinima* seems to be removed by about 600 kilometers.

The gaps between these records are thus very great. It is presumed that the range of nominate *fasciolata* still extends north to the

Amazon, east to perhaps the left bank of the lower Tocantins, where it may have met *pinima*, which has been collected in the region of Cameta, though perhaps on the right bank of the Tocantins opposite Cameta rather than in the town itself which is on the left bank. It is most probable, at any rate, that the range of the species no longer extends to northeastern Para and northern Maranhão, because *pinima* seems to be extinct. The latter is one of the rarest of all the Cracidae as it is known from a total of only seven specimens. Four of these were collected between 1830 and 1842 in Para west to the region of Cameta; three, in northern Maranhão in January and February, 1907.

Crax fasciolata and *C. rubra* are the only two species that vary geographically.

Crax alberti

DIAGNOSIS: Male differing from that of *Crax daubentoni* only in color of soft parts in life and slight difference in development of fleshy appendages at base of bill (pl. 15). Plumage of females complex, showing two color phases: one rufous, one barred (see below).

The two color phases were discussed by me in detail in another paper (1967c). In the rufous phase, the throat is uniformly black, not barred, the upper breast is uniformly black or slightly barred to a varying degree, and the rest of the under parts is dark reddish cinnamon and uniform, not barred, including the thigh or the greater part of it. The primaries are pale reddish chestnut and uniform, with the exception of the extreme tip and the inner web of the inner primaries, which are more or less slightly mottled with brown. The bend of the wing, outer primary coverts, and alula are also reddish chestnut, with or without a few brownish bars. The upper parts are black, narrowly, but regularly barred with white, and the white bars in the crest are not highly developed.

In the barred phase, the under parts, including the throat and thighs, and also the bend of the wing, outer primary coverts, and alula are barred with black and white or buffy white. The primaries are black, barred with white on the outer web, mottled slightly with chestnut on the inner web. The upper parts are black, narrowly barred with white on the wing and scapulars as in the

rufous phase, but the white bars have disappeared from the tail or are reduced to faint traces, and to a few narrow edges or spots on the mantle and upper tail coverts. The crest, on the other hand, is much whiter than in the rufous phase, the white bars being very broad or merging to form a single and expanded white area.

I have not examined enough specimens to determine the distribution of the two color phases, but it is possible that the barred phase may be restricted to the northern foothills of the Santa Marta Massif, where it occurs with typical specimens of the rufous phase and others that are intermediate between the two phases. The specimens that I have seen from the rest of the range were all of the rufous phase, although two or three were somewhat intermediate but much more similar to the rufous phase.

The barred phase was described as a new species by Todd (1915a), who named it *annulata*, but this phase had been discussed and illustrated with a very good color plate much earlier by Sclater (1879, p. 544, pl. 93) under the mistaken impression that the specimen he was discussing was "a second example" of *C. incommoda*, a form that he had described in 1872 as a "new species." The type of the latter is, however, only a slight individual variant of *C. daubentoni* G. R. Gray, 1867.

RANGE: The range of *Crax alberti* is much smaller than that of the other species (fig. 32) and is restricted to northern Colombia, from the northern and western foothills and lower slopes of the Santa Marta Massif south to Bolivar, northern Antioquia, and the northern Magdalena Valley to the region of Honda in extreme northern Tolima.

Crax rubra

DIAGNOSIS: Male differing from males of *Crax daubentoni*, *C. fasciolata*, and *C. alberti* by having no white tips on tail, and by differences (pl. 15) in color of bill, soft parts, and appendages of bill. Female differing from females of other species by being cross-barred with black and white on head and neck. Crest very full, more highly developed than in any other species, lores better feathered, and ring of bare skin around eye very narrow.

The coloration of the females is extremely

variable, more so than in any other species, and presents three types of coloration, as against two in females of *Crax alberti*, but the color pattern of the head remains the same in the three phases. This pattern, which is peculiar to *C. rubra*, consists in the fact that the feathers of the whole face, neck, upper nape, and upper two-thirds of the throat are cross-barred with black and white, which results in a somewhat scalloped appearance, the white bars varying in width but being much smaller, of course, on the face.

The variation is very complex and has been described in detail by Ridgway and Friedman (1946, pp. 13-20) who called the three types, or color phases, the dark phase, the red phase, and the barred-backed phase. These are briefly characterized below.

Dark phase: The mantle is black or blackish, grading posteriorly into dark chestnut brown; the upper wing coverts are bright reddish chestnut, uniform in coloration, or mottled very irregularly with buffy white or blackish brown. The primaries and secondaries are darker than the coverts and are much more heavily mottled with blackish brown, or are more or less vermiculated with buffy white. The color of the tail varies from being uniformly black or blackish, or virtually uniform, to dark chestnut, mottled with black or vermiculated with buffy white, but the tail is not barred. The under parts vary from chestnut to russet, tawny, and dark ochraceous below the blackish lower throat, and are normally uniform, although a few vague spots or irregular bars of blackish brown are present occasionally on the lower flanks. The individual variation is extreme in this phase, and scarcely any two specimens are identical.

Red phase: The whole of the upper parts, below the blackish lower nape and upper border of the mantle, and the upper surface of the wing, vary from pale bright reddish chestnut to dark reddish cinnamon, or pale orange-chestnut, and are uniform or obscurely spotted with blackish. The tail is very boldly barred with black, chestnut, and dark or pale buff, the dark bands as a rule being very much broader than the pale bands. The primaries are chestnut and are usually uniform. The color of the under parts is similar to that of the dark phase, or paler, except that the lower throat is rufous also,

not blackish as in the dark phase. The individual variation is less pronounced in the red phase than in the dark phase, but the two phases are more or less connected by intermediate specimens.

Barred-backed phase: In this phase, the whole of the upper parts, lower throat, upper breast, and tail are very boldly barred with white or buffy white, and with black or dark brown, the pale and dark bars being about equal in width, or the dark bars may be broader. The white bars on the face, neck, upper nape, and throat are broader in this phase than in the other two, and the crest is much whiter, being chiefly white barred with black, rather than black barred with white.

I state above that the tail of the male is black, not tipped with white, and this is indicated also by the key to the species. This condition is normal, but "in some cases the rectrices are slightly margined with white," as Ridgway and Friedmann wrote (1946, p. 13). These margins, which are very slight, were present in only three or four of the 46 males that I have examined, but they are interesting because they suggest to me that the tail was probably originally tipped with white in the male, a character I believe was lost by secondary modification.

RANGE: The range of *Crax rubra* is very wide, extending from northeastern Mexico, from about the twenty-fourth parallel in the region northwest of Ciudad Victoria in Tamaulipas, south along the forests of the escarpment of eastern Mexico to the Isthmus of Tehuantepec and through southern Mexico and Central America to the Chongon Hills of western Ecuador. The range is restricted to the region of the Pacific in South America and penetrates eastward only to longitude 76° 17' W. in the valley of the upper Rio Sinu in Colombia where it meets the range of *C. alberti*.

GEOGRAPHICAL VARIATION: The variation affects the size and the distribution of the three color phases of the females. The birds from the southern part of the range are smaller than those from the north, but a regular cline of decreasing size is apparent only in the measurements of the males. The mean wing length (in round numbers) of the two sexes varies as follows: Mexico, males 410, females 386; Central America (Guate-

mala to Costa Rica), males 402, females 386; Panama, males 394, females 371; Colombia and Ecuador, males 390, females 371.

The population of Cozumel Island, off Yucatan, is considerably smaller than any from the continent. The four females that I have seen from the island have a wing length of only 344, as against 386 in Mexico and Central America. I have not measured any males from Cozumel, but their measurements are reported to be quite small also, and a separate subspecies (*griscomi*) is recognized for Cozumel.

The distribution of the three color phases of the females was studied by me in another paper (1967c). I reported on 110 females and found that all those from eastern Mexico north of the Isthmus of Tehuantepec were of the dark phase, whereas all those from Panama, Colombia, and Ecuador were of the red phase, except one which was intermediate between the two phases. This segregation does not represent subspecific variation, however, because typical specimens of the red phase are found as far north as the mountains that form the border of Guatemala and Honduras; typical specimens of the dark phase, as far south as southern Costa Rica; and intermediates between the two phases, as far as northern Quintana Roo in the Yucatan Peninsula. The dark and the barred-backed phases both occur in the Yucatan Peninsula, Chiapas, and on the Isthmus of Tehuantepec, and have been collected at the same localities in Quintana Roo (Puerto Morelos), Campeche (Champoton), and Oaxaca (Tutla). The barred-backed phase seems to be restricted only to the Yucatan Peninsula, Chiapas, and the Isthmus of Tehuantepec and is rare in collections; only seven of the 110 specimens reported were of this phase. The others consisted of 58 of the dark phase, 30 of the red phase, and 15 intermediates between the dark and red phases. Intermediate between the barred-backed phase and the other two phases seem to be unknown so far, but may exist.

The barred-backed phase and the red phase were described as distinct species. The barred-backed phase was named *hecki* by Reichenow in 1894; *chapmani*, by Nelson in 1901. The red phase was named *panamensis* by Ogilvie-Grant in 1893.

CHECK LIST

THE DISTRIBUTION OF THE FORMS recognized in this check list is stated in the text. The synonymy is believed to be complete for the scientific names that have been introduced, including their emendations, but does not account for the many forms that have been misidentified. A list of the latter, and a list of references to the literature, compiled to December 31, 1939, were given by Hellmayr and Conover (1942, pp. 114-197). All the citations or references in the present work have been verified personally, with the single exception of a book by Schlegel which I could not obtain.

An English name and a Spanish name are given for all the genera, and also a Portuguese name when it applies. An English name is given for each species, which is a well-established one, as a rule, but I had to introduce a new name, or modify one, in a few instances, to reflect the taxonomic conclusions that I have reached. I prefer to retain some well-established patronymics, such as Orton's Guan (for *Penelope ortonii*) or Blumenbach's Curassow (for *Crax blumenbachii*), rather than to replace them by the new English names that have been proposed very recently. I am indebted to Dr. Helmut Sick of Brazil for his advice concerning the Portuguese names, and to Mr. Eugene Eisenmann for the English names of the species, but the decision about the latter was taken by me.

TRIBE PENELOPINI

GENUS ORTALIS MERREM

CHACHALACAS, GUACHARACAS, ARACUÁS

Ortalis MERREM, 1786, p. 40. Type, by monotypy, *Phasianus motmot* Linnaeus.

Ortalida "Merrem" CUVIER, 1816, p. 442. Type, by monotypy, *Phasianus motmot* Linnaeus.

Ortaldia FLEMING, 1822, p. 230. Type, by monotypy, *Phasianus motmot* Linnaeus.

Penelops REICHENBACH, 1853, p. xxvi. Type, by monotypy, *Penelope albiventris* Gould, which equals *Penelope albiventer* Lesson [i.e., *Penelope leucogastra* Gould], preoccupied.

Penelopsis REICHENBACH, 1862, p. 147. Type, by subsequent designation of Hellmayr and Con-

over, 1942, p. 159, *Penelope adspersa* Tschudi, a synonym of *Ortalis guttata guttata* Spix.

Peneloides VAN ROSSEM, 1942, p. 77. Type, by original designation, *Ortalida Wagleri* G. R. Gray.

Ortalis vetula

PLAIN CHACHALACA

Ortalis vetula mcalli

Ortalida McCalli BAIRD, 1858, p. 611; Boquilla, Nuevo Leon, Mexico.

Ortalis vetula vetula

Penelope vetula WAGLER, 1830, col. 1112, Mexico; type collected in vicinity of city of Veracruz.

Ortalida plumbeiceps G. R. GRAY, 1867, p. 11; Honduras, type collected at Omoa.

Ortalis vetula plumbeiceps [sic] DEARBORN, 1907, p. 78; Los Amates, Guatemala.

Ortalis vetula intermedia PETERS, 1913, p. 371; Camp Mengel [now Alvaro Obregon], Hondo River, Quintana Roo, Mexico.

Ortalis vetula jalapensis MILLER AND GRISCOM, 1921a, p. 46; Jalapa, Veracruz, Mexico.

Ortalis vetula fulvicauda MILLER AND GRISCOM, 1921a, p. 47; Tolosa, Oaxaca, Mexico.

Ortalis vetula vallicola BRODKORB, 1942, p. 182; Malpaso, Chiapas, Mexico.

Ortalis vetula pallidiventris

Ortalis vetula pallidiventris RIDGWAY, 1887, p. 209; Yucatan, type from Merida.

Ortalis vetula deschauenseei

Ortalis vetula deschauenseei BOND, 1936, p. 356; Utila Island, Honduras.

Ortalis garrula

CHESTNUT-WINGED CHACHALACA

Ortalis garrula frantzii

Ortalida Frantzii CABANIS, 1869, p. 211; Costa Rica.

Ortalis cinereiceps saturatus MILLER AND GRISCOM, 1921b, p. 1; near Matagalpa, Nicaragua.

Ortalis garrula cinereiceps

Ortalida cinereiceps G. R. GRAY, 1867, p. 12; "Northwest coast of America"; San Miguel, Pearl Islands, Panama Bay, designated as the type locality by Aldrich, 1937, p. 55.

Ortalis struthopus BANGS, 1901, p. 61; San Miguel, Pearl Islands, Panama Bay.

Ortalis garrula olivacea ALDRICH, 1937, p. 53; Paracote, eastern shore of Montijo Bay, 1 mile

south of the mouth of the Angulo River, Veraguas [Azüero Peninsula], Panama.

Ortalis garrula mira

Ortalis garrula mira GRISCOM, 1932a, p. 318; Ranchon [near Puerto Obaldia], Caribbean slope of extreme eastern Panama.

Ortalis garrula chocoensis

Ortalis garrula chocoensis DE SCHAUENSEE, 1950, p. 2; Rio Jurado, Choco, Colombia.

Ortalis garrula garrula

Phasianus garrulus HUMBOLDT, 1805, p. 4, pl. 1, no. iii, figs. 1-6; Magdalena River, Colombia.

Ortalis ruficauda

RUFIOUS-VENTED CHACHALACA

Ortalis ruficauda ruficrissa

Ortalida ruficrissa SCLATER AND SALVIN, 1870, p. 538; Valledupar, southeastern foothills of Sierra Nevada de Santa Marta, Magdalena, Colombia.

Ortalis ruficrissa baliolus OSGOOD AND CONOVER, 1922, p. 31; Orope, Zulia, Venezuela.

Ortalis ruficrissa lamprophonia WETMORE, 1953, p. 1; Serrania de Macuire, above Nazaret, Guajira, Colombia.

Ortalis ruficauda ruficauda

Ortalida ruficauda JARDINE, 1847, p. 374; Tobago Island.

Ortalida bronzina G. R. GRAY, 1867, p. 11; Venezuela.

Ortalis erythroptera

ECUADORIAN CHACHALACA

Ortalida erythroptera SCLATER AND SALVIN, 1870, p. 540, ex Natterer MS; Babahoyo and Guayaquil, Ecuador; type, examined, from Babahoyo.

Ortalis guttata

SPOTTED CHACHALACA

Ortalis guttata araucuan

Penelope Araucuan SPIX, 1825, p. 56 (in part, description of male): São Domingos near Minas Novas, northeastern Minas Gerais, Brazil.

Penelope albiventris WAGLER, 1830, col. 1111, "Brasília versus flumen Amazonum," error, as it is based on the same specimen on which Spix based the description of the male of his *Penelope araucuan*, fide Hellmayr, 1942, p. 162.

Penelope Aracuan MAXIMILIAN, 1833, p. 549; [from the] Rio Doce [north to] Mucuri, Alcobaca, Bahia, and [eastern] Minas Gerais.

Ortalis guttata squamata

Ortalida squamata LESSON, 1829, p. 195; "l'Amérique meridionale," the type is from Santa Catarina, Brazil.

Ortalis guttata remota PINTO, 1960, p. 11; "Porto do Sapé (Rio Pardo, Estado de Mato Grosso)," but probably Rio Parana; see Vaurie, 1965b, p. 8.

Ortalis guttata subaffinis

Ortalis guttata subaffinis TODD, 1932, p. 211; Buenavista [in Santa Cruz], Bolivia.

Ortalis guttata guttata

Penelope guttata SPIX, 1825, p. 55, pl. 73; Rio Solimões, Brazil; restricted to Coari by Gyldenstolpe, 1951, p. 48.

Penelope adspersa TSCHUDI, 1843, p. 386; Peru. *Ortalis guttata caquetae* CHAPMAN, 1923, p. 2; La Morelia, Caqueta, Colombia.

Ortalis guttata columbiana

Ortalis columbiana HELLMAYR, 1906, p. 694; Colombia; Bogota has been suggested as restricted type locality.

Ortalis columbiana cauae CHAPMAN, 1914, p. 168; Guengüe, 20 miles south [east] of Cali, Cauca Valley, Colombia.

Ortalis superciliaris

SUPERCILIATED CHACHALACA

Ortalida superciliaris G. R. GRAY, 1867, p. 10; "South America," based on aviary bird; Belem, Para, suggested as type locality by Pinto, 1964, p. 108.

Ortalis spixi HELLMAYR, 1906, p. 695; Rio Itapicuru, Maranhão.

Ortalis motmot

GUIANA CHACHALACA

***Ortalis motmot motmot*¹**

Phasianus Motmot LINNAEUS, 1766, p. 271; "Brasilia, Guiana," based chiefly on *Phasianus guianensis* of Brisson, Cayenne, French Guiana.

Phasianus Katraca BODDAERT, 1783, p. 9; based on Daubenton's "Planches enluminées," pl. 146 "Le Katraca (faisan)," which is from French Guiana.

Phasianus Parraka GMELIN, 1789, p. 740; Cayenne.

Phasianus Parraqua LATHAM, 1790, p. 632; Cayenne.

¹ *Penelope Paraca* Schomburgk, 1848, p. 31, Takutu River, Guyana (former British Guiana), quoted as a synonym by Hellmayr and Conover, 1942, p. 160, is a *nomen nudum*.

Penelope parrakoua TEMMINCK, 1815 [1813, 1815, vol. 3], pp. 85, 695; Cayenne.

Penelope Parrakua "Temm." BURMEISTER, 1856, p. 341; Guiana and "Colombia," error.

Ortalis motmot ruficeps

Penelope ruficeps WAGLER, 1830, col. 1111; Brazil; Santarem, Para, suggested as type locality by Pinto, 1964, p. 108.

Ortalis leucogastra

WHITE-BELLIED CHACHALACA

Penelope albiventer LESSON, 1842, p. 174; Realejo, Nicaragua; preoccupied by *Penelope albiventris* Wagler, 1830, a synonym of *Ortalis guttata araucuan*.

Penelope leucogastra GOULD, 1843, p. 105; locality unknown and type lost; Mazatenango, Suchitepequez, Guatemala, suggested here as type locality.

Ortalis poliocephala

WEST MEXICAN CHACHALACA

Ortalis poliocephala wagleri

Ortalida Wagleri G. R. GRAY, 1867, p. 12; California and Mexico; type, examined, from "western Mexico," restricted to San Blas, Nayarit, by van Rossem, 1934a, p. 431.

Ortalis wagleri griseiceps VAN ROSSEM, 1934a, p. 431; Alamos, Sonora.

Ortalis poliocephala poliocephala

Penelope poliocephala WAGLER, 1830, col. 1112; Mexico; type collected at Real de Arriba, near Temascaltepec, southwest of Toluca, Mexico.

Ortalis poliocephala longicauda LAMPE, 1906, p. 232; Mexico.

Ortalis poliocephala lajuelae MOORE AND MEDINA, 1957, p. 230; Lajuela, Colima, Mexico.

Ortalis canicollis

CHACO CHACHALACA

Ortalis canicollis pantanalensis

Ortalis canicollis pantanalensis CHERRIE AND REICHENBERGER, 1921, p. 2; near mouth of Rio São Lourenço, southwestern Mato Grosso, Brazil.

Ortalis canicollis canicollis

Penelope canicollis WAGLER, 1830, col. 1112; Paraguay; based on Azara's number 336, the "Yacú-Caraguatá." Wetmore, 1926, p. 118, stated that the "type locality must be located in southern Paraguay or the adjacent provinces of Argentina," and it was restricted to the region of Asuncion, Paraguay, by Vaurie, 1964, p. 5.

Ortalis canicollis grisea CHERRIE AND REICHEN-

BERGER, 1921, p. 2; Suncho Corral, Santiago del Estero, Argentina.

Ortalis canicollis ungeri STEINBACHER, 1962, p. 25; Orloff, Gran Chaco, Paraguay.

GENUS PENELOPE MERREM

GUANS, PAVA DE MONTE, JACUS

Penelope MERREM, 1786, p. 39. Type, by subsequent designation of Lesson, 1828, p. 214, *Penelope Marail* "Linn." Gmelin, which equals *Phasianus Marail* P. L. S. Müller.

Salpiza WAGLER, 1832, col. 1226. Type, by subsequent designation of Sclater and Salvin, 1870, p. 521, *Penelope pileata* Wagler.

Stegnolaema SCLATER AND SALVIN, 1870, p. 521. Type, by monotypy, *Ortalida montagnii* Bonaparte.

Salpizusa HEINE AND REICHENOW, 1890, p. 301. Emendation for *Salpiza* Wagler.

Penelope argyrotis

BAND-TAILED GUAN

Pipile argyrotis BONAPARTE, 1856, p. 875; Caracas, Venezuela.

Penelope lichtensteinii G. R. GRAY, 1860; p. 269, Venezuela.

Penelope montana REICHENBACH, 1862, p. 151; Venezuela; ex Lichtenstein MS.

Penelope argyrotis olivaceiceps TODD, 1932, p. 210; San Rafael, near Cumanacoa, Sucre, Venezuela.

Penelope argyrotis albicauda PHELPS AND GILLIARD, 1940, p. 3; La Sabana, Rio Negro, Perija District, Zulia, Venezuela.

Penelope argyrotis mesaeus CONOVER, 1945, p. 125; Pamplona, Santander del Norte, Colombia.

Penelope argyrotis colombiana

Penelope colombiana TODD, 1912, p. 213; Las Taguas, Santa Marta, Colombia.

Penelope argyrotis barbata

Penelope barbata CHAPMAN, 1921, p. 3; Taraguacocha, Zaruma-Zaraguro trail, Cordillera de Chilla, El Oro, southwestern Ecuador.

Penelope inexpectata CARRIKER, 1934, p. 317; Porculla Pass, Lambayeque, northwestern Peru.

Penelope ortonii

ORTON'S GUAN

Penelope ortonii SALVIN, 1874, p. 325; near Mindo "on the western slope of the volcano of Pichincha, in [western] Ecuador, at an elevation of about 6000 or 7000 feet," but altitude probably incorrect as Mindo is situated at 4086 feet.

Penelope montagnii

ANDEAN GUAN

Penelope montagnii montagnii

Ortalida montagnii BONAPARTE, 1856, p. 875; "Nouvelle Grenade"; type a trade skin from Bogota; Chapman, 1917, p. 194, suggested El Piñon, above Fusagasuga, Cundinamarca, Colombia, as type locality.

Penelope montagnii atrogularis

Penelope montagnii atrogularis HELLMAYR AND CONOVER, 1932, p. 328; Alaspungo, western Ecuador.

Penelope montagnii brooki

Penelope brooki CHUBB, 1917, p. 5; Baeza, eastern Ecuador; not above Baeza, as emended by Chapman, 1926, p. 153.

Penelope montagnii plumosa

Penelope sclateri plumosa BERLEPSCH AND STOLZMANN, 1902, p. 45; Maraynioc, Junin, central Peru.

Penelope montagnii marcapatensis BLAKE, 1962, p. 121; Chilichili, Marcapata, Cuzco, Peru.

Penelope montagnii sclateri

Penelope sclateri G. R. GRAY, 1860, p. 270; Bolivia; restricted to Yungas de la Paz, by Vaurie, 1966b, p. 18.

Penelope superciliaris

RUSTY-MARGINED GUAN

Penelope superciliaris superciliaris

Penelope superciliaris "Illiger" TEMMINCK, 1815 [1813, 1815, vol. 3], pp. 72, 693; "*Brésil, et plus particulièrement dans le district de Para.*"

Penelope superciliaris pseudonyma NEUMANN, 1933, p. 93; Rio de Cumana [sic], equals Rio de Canuma.

Penelope superciliaris jacupemba

Penelope jacupemba SPIX, 1825, p. 55, pl. 77; Presidio de São João, near Rio de Janeiro, Brazil.

Penelope superciliaris argyromitra NEUMANN, 1933, p. 94; Veadeiros, northwest of Forte, central Goyaz, Brazil.

Penelope superciliaris ochromitra NEUMANN, 1933, p. 94; Lagoa da Missão, near Parnagua, southern Piauí, Brazil.

Penelope superciliaris major

Penelope purpurescens [sic] *major* BERTONI, 1901, p. 19; Alto Parana at latitude 25° 43' S., Paraguay.

Penelope marail

CAYENNE GUAN

Penelope marail marail

Phasianus Marail P. L. S. MÜLLER, 1776, p. 125, based on "*Le Marail*" of Buffon, 1771, p. 390; Cayenne, French Guiana.

Penelope Iacupema MERREM, 1786, p. 39, pl. 11; "Guyana."

Penelope greeyii G. R. GRAY, 1866, p. 206, pl. 22; based on aviary bird said to have been received from "Santa Martha, New Granada," but locality erroneous.

Penelope marial CHUBB, 1916, p. 25; British Guiana (now Guyana), error for *marail*.

Penelope marail jacupeba

Penelope jacupeba SPIX, 1825, p. 54, pl. 71; "*in sylvis Parae*"; restricted to region of Obidos, Para, by Vaurie, 1964, p. 7.

Penelope dabbenei

DABBENE'S GUAN

Penelope dabbenei HELLMAYR AND CONOVER, 1942, p. 154; new name for *Penelope nigrifrons* Dabbene, 1918, p. 102; Cerro de Calilegua at 2300 meters, Ledesma, Jujuy, Argentina; preoccupied by *Penelope nigrifrons* "Temm." Lesson, 1831, p. 482, a synonym of *Pipile jacutinga* Spix.

Penelope obscura

DUSKY-LEGGED GUAN

Penelope obscura bronzina

Penelope obscura bronzina HELLMAYR, 1914, p. 178; Colonia Hansa, Santa Catarina, Brazil.

Penelope obscura obscura

Penelope obscura "Illiger" TEMMINCK, 1815 [1813, 1815, vol. 3], pp. 68, 693; based on the "*Yacuhu*," no. 335 of Azara, "*Paraguay . . . y aun se acerca al rio de la Plata.*"

Penelope nigricapilla G. R. GRAY, 1860, p. 269; Brazil.

Penelope olivacea BERTONI, 1901, p. 20; Alto Parana at latitude 26° 53' S., Paraguay.

Penelope obscura bridgesi

Penelope bridgesi G. R. GRAY, 1860, p. 270; Bolivia, restricted to Villa Montes, Tarija, by Vaurie, 1966a, p. 18.

Penelope jacquaçu

SPIX'S GUAN

Penelope jacquaçu perspicax

Penelope perspicax BANGS, 1911, p. 187; San Luis, Bitaco Valley, Western Andes, Colombia.

Penelope jacquaçu jacquaçu

Penelope Jacquaçu SPIX, 1825, p. 52, pl. 68 (labeled *jacuaçu*); Rio Solimões, Brazil, restricted to Coari by Hellmayr and Conover, 1942, p. 142.

Penelope boliviana REICHENBACH, 1862, p. 151, pl. 271, figs. 2493, 2494; "Bolivia," but probably error for northern Peru, *vide* Hellmayr and Conover, 1942, p. 142.

Penelope rufescens "Natterer" PELZELN, 1869, p. 339; listed as synonym of *Penelope boliviana* Reichenbach, 1862, not available under Article 11 (d) of International Code of Zoological Nomenclature.

Penelope jacquaçu: SALVADORI AND FESTA, 1900, p. 38, Valley of Zamora, Ecuador.

Penelope jacquassu IHERING, 1905, p. 451; emendation for *jacquaçu* Spix.

Penelope jacquaçu orienticola

Penelope jacquacu orienticola TODD, 1932, p. 211; Manacapuru, north bank of Rio Solimões, Brazil.

Penelope jacquaçu granti

Penelope granti BERLEPSCH, 1908, p. 297; new name for *Penelope marail* Ogilvie-Grant, 1893, p. 495, Takuta River, British Guiana (now Guyana), not *Phasianus Marail* P. L. S. Müller.

Penelope jacquaçu speciosa

Penelope speciosa TODD, 1915a, p. 82; Rio Surutu, Provincia del Sara, Santa Cruz, Bolivia.

Penelope purpurascens**CRESTED GUAN****Penelope purpurascens purpurascens**

Penelope purpurascens WAGLER, 1830, col. 1110; Mexico, probably state of Veracruz.

Penelope purpurascens aequatorialis

Penelope aequatorialis SALVADORI AND FESTA, 1900, p. 38; Rio Peripa, western Ecuador.

Penelope purpurascens brunnescens

Penelope purpurascens brunnescens HELLMAYR AND CONOVER, 1932, p. 333; Rio Cogollo, Perija, Zulia, Venezuela.

Penelope albipennis**WHITE-WINGED GUAN**

Penelope albipennis TACZANOWSKI, 1877, p. 746; Santa Lucia, near Tumbes, northwestern Peru.

Penelope jacucaca**WHITE-BROWED GUAN**

Penelope Jacu-Caca SPIX, 1825, p. 53, pl. 69; near Poçoens Encima, Bahia, Brazil.

Penelope iacucaca SNETHLAGE, 1914, p. 56; emendation for *jacu-caca* Spix.

Penelope ochrogaster**CHESTNUT-BELLIED GUAN**

Penelope ochrogaster "Natterer" PELZELN, 1869, p. 337; Rio das Flechas, and [Engenho do] Pari, Mato Grosso, Brazil; type from Rio das Flechas.

Penelope pileata**WHITE-CRESTED GUAN**

Penelope pileata WAGLER, 1830, col. 1109; state of Para, Brazil.

Penelope comata "Lichtenstein" PELZELN, 1869, p. 340; Para.

Penelope leucothrix "Natterer" PELZELN, 1869, p. 340; listed as a synonym of *Penelope pileata* "Lichtenstein" Wagler, 1830, not available under provision of Article 11 (d) of International Code of Zoological Nomenclature.

GENUS PIPILE BONAPARTE**PIPING GUANS, PAVAS RAJADORAS, JACUTINGAS**

Pipile BONAPARTE, 1856, p. 877. Type, by tautonymy, *Crax pipile* Jacquin.

Cumana COUES, 1900, p. 65. New name for *Pipile* Bonaparte, the author believing that *Pipile* Bonaparte was preoccupied by *Pipilo* Vieillot.

Pipile pipile**BLUE-THROATED PIPING GUAN****Pipile pipile pipile**

Crax (Pipile) JACQUIN, 1784, p. 26, pl. 11; "am Orinokoflusse bei Kumana," Venezuela, error, based on live bird in Imperial Menagerie of Vienna, which had been acquired via Martinique; Trinidad suggested as correct type locality by Vaurie, 1967a, p. 4.

Pipile Jacquini REICHENBACH, 1862, p. 154; new name for *Crax pipile* Jacquin.

Pipile pipile cumanensis

Crax (cumanensis) JACQUIN, 1784, p. 25, pl. 10; "am Orinokoflusse bei Kumana," Venezuela; probably error, based on live bird in Imperial Menagerie of Vienna, which had been acquired via Martinique; delta of Orinoco suggested as correct type locality by Phelps and Phelps, 1958, p. 83.

Penelope Leucolophos MERREM, 1786, p. 43, pl. 12, French Guiana.¹

¹ Hellmayr, (1942, p. 191) stated that *Penelope leucolophos* was based by Merrem on a live bird in a private aviary in Bremen, but that Merrem identified it with *Crax cumanensis* Jacquin, and with "l'Yacou" of Bajon (1777, p. 398, pl. 5), which Bajon secured on the upper Oyapock River, French Guiana.

Pipile Jacou REICHENBACH, 1862, p. 154, pl. 271c, fig. 5056; based on "*l'Yacou*" of Bajon, 1777, and the "*Yacou*" of Latham, 1783, p. 681, which was based on "*l'Yacou*" of Bajon, 1777.

Pipile pipile grayi

Penelope Grayi PELZELN, 1869, p. 284; new name for *Penelope Jacquinii* G. R. Gray, 1867, p. 8, "Peru. From Mr. Gould's Collection"; pre-occupied by *Pipile Jacquinii* Reichenbach, 1862, a synonym of *Pipile pipile* Jacquin. "Peru" emended to Paraguay by Laubmann, 1939, p. 126, but, as origin of Gould's specimen is not known, Sangrador, Mato Grosso, Brazil, suggested as correct emended type locality by Vaurie, 1967a, p. 4, because Pelzel's specimen had been taken at Sangrador, not in Paraguay.

Pipile cujubi

RED-THROATED PIPING GUAN

Pipile cujubi cujubi

Penelope Cujubi "Natterer" PELZELN, 1858, p. 328; Para, Brazil, restricted to Belem, by Pinto, 1964, p. 112.

Pipile cujubi nattereri

Pipile Nattereri REICHENBACH, 1862, p. 154, pl. 271c, fig. 5060; "Rio das Frechas" [*sic*], which equals Rio das Flechas, Mato Grosso, Brazil.

Pipile cumanensis naumburgae TODD, 1932, p. 213; Arimã, Rio Purus, Brazil.

Pipile jacutinga

BLACK-FRONTED PIPING GUAN

Penelope Jacutinga SPIX, 1825, p. 53, pl. 70; "*sylvis inter Bahiam et Rio de Janeiro*."

Penelope nigrifrons "Temm." LESSON, 1831, p. 482; "*Du Para, du Brésil*"; type from Rio de Janeiro.

Penelope leucoptera MAXIMILIAN, 1833, p. 544; [southeastern] Brazil.

GENUS ABURRIA REICHENBACH

Aburria REICHENBACH, 1853, p. xxvi. Type, by original designation and monotypy, *Aburria carunculata* "Temminck" Reichenbach, a synonym of *Penelope aburri* Goudot.

Opetioptila SUNDEVALL, 1873, p. 118; new name for *Aburria* Reichenbach.

Aburria aburri

WATTLED GUAN, PAVA ABURRIDA

Penelope aburri GOUDOT, 1828, p. 215; "*montagnes de la Nouvelle-Grenade . . . Muzo, . . . Bogota, . . . vallée du Cauca, montagnes du Quindiu*,

entre Ilague et Carthago," restricted here to Muzo, Boyaca, Colombia.

Aburria carunculata "Temminck" REICHENBACH, 1853, p. xxvi; mountains of New Granada.¹

GENUS CHAMAEPETES WAGLER

SICKLE-WINGED GUANS, PAVAS DE ALA TAJADA

Chamaepetes WAGLER, 1832, col. 1227. Type, by monotypy, *Ortalida Goudotii* Lesson.

Chamaepetes unicolor

BLACK SICKLE-WINGED GUAN

Chamaepetes unicolor SALVIN, 1867, p. 159; Veraguas, Panama, type from Calevevora.

Chamaepetes goudotii

RUFous SICKLE-WINGED GUAN

Chamaepetes goudotii sanctae-marthae

Chamaepetes sanctae-marthae CHAPMAN, 1912, p. 141; El Libano, Sierra Nevada de Santa Marta, Colombia.

Chamaepetes goudotii goudotii

Ortalida Goudotii LESSON, 1828, p. 217; "*montagnes du Quindiu*" which equal Quindio Range, Central Andes, Colombia.

Chamaepetes goudotii antioquiiana CHUBB, 1919, p. 22; Valdivia, Antioquia, Colombia.

Chamaepetes goudotii fagani

Chamaepetes fagani CHUBB, 1917, p. 4; Mindo, western Ecuador.

Chamaepetes goudotii tschudii

Chamaepetes Tschudii TACZANOWSKI, 1886, p. 275; Moyobamba and Tamiapampa, Peru; type from Tamiapampa.

Chamaepetes goudotii rufiventris

Penelope rufiventris TSCHUDI, 1843, p. 386; Chilpes, Junin, Peru.

GENUS PENELOPINA REICHENBACH

Penelopina REICHENBACH, 1862, p. 152, Type, by monotypy, *Penelope niger* Fraser.

Penelopina nigra

BLACK PAJUIL, PAJUIL

Penelope niger FRASER, 1852, p. 246, pl. 29; no locality, based on aviary specimens; van Rossem, 1934b, p. 364, suggested Guatemala as type locality.

¹ The description consists merely of a reference to [Reichenbach] "Ic. Av. t. 269 ic. 1500," said to have been published in 1848, the locality being "*Gebirgen von Neu-Granada*," i.e., Colombia.

Penelopina nigra dickeyi VAN ROSSEM, 1934b, p. 364; Los Esesmites, Chalatenango, El Salvador.
Penelopina nigra rufescens VAN ROSSEM, 1934b, p. 365; Ocotal, Nicaragua.

TRIBE OREOPHASINI

GENUS **OREOPHASIS** G. R. GRAY

Oreophasis G. R. GRAY, 1844, p. 485, pl. 121, fig. 3. Type, by monotypy, *Oreophasis Derbianus* G. R. Gray.

Oreophasianus SCHLEGEL, 1857, p. 387, emendation for *Oreophasis* G. R. Gray.

*Oreophasis derbianus*¹

HORNED GUAN, GUAN CORNUDO

Oreophasis Derbianus G. R. GRAY, 1844, p. 485, pls. 121, fig. 3; Guatemala.

Oreophasis Derbyana REICHENBACH, 1862, p. 155, pl. 270, fig. 1508; Volcan de Fuego, Guatemala.

TRIBE CRACINI

GENUS **NOTHOCRAX** BURMEISTER

Nothocrax BURMEISTER, 1856, p. 347. Type, by monotypy, *Crax Urumutum* Spix.

Nothocrax urumutum

NOCTURNAL CURASSOW, PAUJI NOCTURNO, URUMUTUM

Crax Urumutum SPIX, 1825, p. 49, pl. 62; Rio Negro, Brazil.

GENUS **MITU** LESSON

RAZOR-BILLED CURASSOWS,
PAUJIS, MUTUM CAVALOS

Mitu LESSON, 1831, p. 485. Type, by tautonymy, *Ourax mitu* Temminck, which equals *Crax Mitu* Linnaeus.

Mitua STRICKLAND, 1841, p. 36; emendation for *Mitu*.

Mitu tomentosa

CRESTLESS CURASSOW

Crax tomentosa SPIX, 1825, p. 49, pl. 63; Barceños, Rio Negro, Brazil.

Mitu salvini

SALVIN'S CURASSOW

Mitua salvini REINHARDT, 1879, p. 5; no locality, but is eastern Ecuador.

¹ *Penelope fronticornis* van der Hoeven (1855, p. 664), quoted by Hellmayr and Conover (1942, p. 196) as a synonym, is a *nomen nudum*. Hellmayr and Conover stated that they were not able to verify the reference to van der Hoeven that they cited.

Mitu mitu

RAZOR-BILLED CURASSOW

Crax Mitu LINNAEUS, 1766, p. 270, based mainly on "*Mitu vel Mutu*" of Marcgrave, 1648, northeastern Brazil; restricted to Alagoas, by Pinto, 1954, p. 24, but emended later to Pernambuco by Pinto, 1964, p. 100.

Crax nudifrons LICHTENSTEIN, 1793, p. 37; Brazil.

Crax tuberosa SPIX, 1825, p. 51, pl. 67a; Rio Solimões, Brazil.

Ourax erythrorynchus SWAINSON, 1837, p. 352; new name for *Ourax Mitu* Linnaeus, 1766.

Mitu brasiliensis REICHENBACH, 1862, p. 137, pl. 272, figs. 1512-1513; Brazil and Peru, but based mainly on Marcgrave, 1648.

GENUS **PAUXI** TEMMINCK

HELMETED CURASSOWS,
PAUJIS COPETE DE PIEDRA

Pauxi TEMMINCK, 1813 [1813, 1815, vol. 2], pp. 456, 465. Type, by tautonymy, *Crax pauxi* "Latham et Gmelin," = Linnaeus.

Ourax CUVIER, 1816, p. 440. Type, by subsequent designation of Sclater and Salvin, 1870, p. 519, *Pauxi galeata*, which equals *Crax galeata* Latham, a synonym of *Crax Pauxi* Linnaeus.

Lophoceros SWAINSON, 1837, p. 353. Type, by monotypy, *Crax galeata* Latham, a synonym of *Crax Pauxi* Linnaeus.

Urac "Cuvier" REICHENBACH, 1853, p. xxvi. Type, by subsequent designation of Sclater and Salvin, 1870, p. 519, *Pauxi galeata*, which equals *Crax galeata* Latham, a synonym of *Crax Pauxi* Linnaeus.

Pauxis SCLATER, 1875, p. 285, emendation for *Pauxi* Temminck.

Pauxi pauxi

HELMETED CURASSOW

Pauxi pauxi pauxi

Crax Pauxi LINNAEUS, 1766, p. 270; "habitat in Mexico," error for Venezuela, restricted to Cumbre de Valencia by Phelps and Phelps, 1958, p. 77.

Crax galeata LATHAM, 1790, p. 624; Curaçao.

Pauxi pauxi gilliardi

Pauxi pauxi gilliardi WETMORE AND PHELPS, 1943, p. 144; Tierra Nueva, Serrania de Valledupar, Sierra Negra, Magdalena, Colombia.

Pauxi unicornis

BOLIVIAN HELMETED CURASSOW

Pauxi unicornis BOND AND DE SCHAUENSEE, 1939, p. 1; above Bolivar, near Palmar, Yungas de Cochabamba, Bolivia.

GENUS **CRAX** LINNAEUS

CURASSOWS, HOCOFAISANES, MUTUMS

Crax LINNAEUS, 1758, p. 157. Type, by subsequent designation of Ridgeway, 1896, p. 207. *Crax rubra* Linnaeus.¹

Alector MERREM, 1786, p. 40. Type, by tautonymy, *Crax Alector* Linnaeus.

Mituporanga REICHENBACH, 1862, p. 136. Type, by subsequent designation of Ogilvie-Grant, 1893, p. 474, *Crax globicera* Linnaeus, 1766, a synonym of *Crax rubra* Linnaeus, 1758.

Crossolaryngus REICHENBACH, 1862, p. 136. Type, by subsequent designation of Ogilvie-Grant, 1893, p. 474, *Crax globulosa* Spix.

Sphaerolaryngus REICHENBACH, 1862, p. 136. Type, by monotypy, *Crax Alberti* Fraser.

Crax alector

BLACK CURASSOW

Crax Alector LINNAEUS, 1766, p. 269; "*America calidiore*," restricted to Cayenne, French Guiana, as *alector* Linnaeus is based chiefly on "*Le Hocco de la Guiane*" of Brisson.

Crax erythrogna SCLATER AND SALVIN, 1877, p. 22; "*Columbia int[er]iore*."

Crax globulosa

WATTLED CURASSOW

Crax globulosa SPIX, 1825, p. 50, pls. 65, 66; Rio Solimões.

Crax yarrellii BENNETT, 1831, p. 227; Rio Marañon, Peru.

Crax globosa BURMEISTER, 1856, p. 346; error for *globulosa*.

Crax blumenbachii

BLUMENBACH'S CURASSOW

Crax Blumenbachii SPIX, 1825, p. 50, pl. 64; "*provinciae Rio de Janeiro*."

Crax rubrirostris SPIX, 1825, p. 51, pl. 67; "*inter Rio de Janeiro ac Bahiam*"; *blumenbachii* represents the female and *rubrirostris* the male.

Crax daubentoni

DAUBENTON'S CURASSOW

Crax Daubentoni G. R. GRAY, 1867, p. 15; "Central America," error, as type examined is from "South America"; Puerto Cabello, Venezuela, designated as correct type locality by Phelps and Phelps, 1958, p. 79.

Crax Mikani PELZELN, 1869, p. 343; Brazil.

¹ *Crax Alector* Linnaeus, 1766, is often cited as the type of the genus, but it was not one of the two species, *nigra* and *rubra*, originally included by Linnaeus.

Crax incommoda SCLATER, 1872, p. 690; no locality; based on aviary bird, which I have examined, said to have been received from South America.

Crax fasciolata

FASCIATED CURASSOW

Crax fasciolata pinima

Crax Pinima "Natterer" PELZELN, 1869, pp. 341, 342; [Praia de] Cajutuba, northeastern Para, Brazil.

Crax fasciolata fasciolata

Crax fasciolata SPIX, 1825, p. 48, pl. 62a; "*in sylvis Parae*."

Crax Sclateri G. R. GRAY, 1867, p. 14; "Mexico," error, type, examined, is from Brazil.

Crax sulcirostris IHERING, 1899, p. 409; São Paulo.

Crax fasciolata grayi

Crax grayi OGILVIE-GRANT, 1893, p. 480; South America; Bolivia suggested here as type locality.

Crax alberti

BLUE-KNOBBED CURASSOW

Crax Alberti FRASER, 1852, p. 246, pl. 27; based on aviary bird of unknown origin; "New Granada" [= Colombia] suggested as type locality by Sclater and Salvin, 1870, p. 517, here restricted to northern Colombia.

Crax viridirostris SCLATER, 1875, p. 282; no locality; based on living bird in gardens of Zoological Society of Amsterdam; type, examined, labeled "South America."

Crax annulata TODD, 1915a, p. 170, Don Diego, Santa Marta, Colombia.

Crax rubra

GREAT CURASSOW

Crax rubra rubra

Crax rubra LINNAEUS, 1758, p. 157; "America," based on *Gallina peruviana rubra* of Albin from "Peru," which equals western Ecuador.

Crax globicera LINNAEUS, 1766, p. 270; "Brasilia, Curaçao," error.

Crax Albini LESSON, 1831, p. 484; no locality; based on Albin.

Crax Temminckii TSCHUDI, 1844, p. 308; no locality; based on same source as *Crax rubra*.

Crax panamensis OGILVIE-GRANT, 1893, p. 479; "southern Nicaragua and Costa Rica to the United States of Colombia"; type, examined, is from Lion Hill, Panama.

Crax hecki REICHENOW, 1894, p. 231, pl. 2; no locality; based on bird in zoological garden, Berlin.

Crax chapmani NELSON, 1901, p. 170; Puerto Morelos, eastern Yucatan [= Quintana Roo], Mexico.

Crax rubra griscomi

Crax globicera griscomi NELSON, 1926, p. 106; Cozumel Island, Quintana Roo, Mexico.

INCERTAE SEDIS

Crax nigra LINNAEUS, 1758, p. 157; "*America australi*."

Meleagris cristata LINNAEUS, 1766, p. 269; "*America australi*."

Penelope vociferans GMELIN, 1789, p. 735, "*novae Hispaniae*."

Crax carunculata TEMMINCK, 1815 [1813, 1815, vol. 3], pp. 44, 690, pl. 4, fig. 3; "*Brésil*."

Ortalida Caracco WAGLER, 1832, col. 1227; Peru.

Crax Sloanei REICHENBACH, 1862, p. 131; Curaçao.

Crax Pseudalektor REICHENBACH, 1862, p. 131, pl. 273, figs. 1515, 1516; Yucatan.

Crax Edwardsii REICHENBACH, 1862, p. 134, pl. 272b, fig. 5036; based on aviary bird of unknown origin.

Crax Aldrovandi REICHENBACH, 1862, p. 134, pl. 272b, fig. 5038; Guiana?

Penelope Guan REICHENBACH, 1862, p. 149; based partly on same composite and ambiguous sources as *Meleagris cristata* Linnaeus.

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