

AMERICAN MUSEUM NOVITATES

Number 43

September 6, 1922

59.88,18

THE SPECIES AND GEOGRAPHIC RACES OF *STEGANURA*¹

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Despite the modern tendency toward subdivision, ornithologists have come to think of the paradise whydah as a single species. In some recent papers, it is true, a northeast African subspecies has been recognized, under the name *verreauxii*, and some authors, too, have followed Professor Oscar Neumann² in calling the Senegal bird *Steganura paradisea aucupum*. Aside from the browner nape of *aucupum*, the characters of these subspecies have been regarded with some hesitation. A shorter wing was believed to distinguish *verreauxii* from the south African *paradisæa*.³

Examination of the series of *Steganura* in the museums of Washington, Philadelphia, Cambridge (Mass.), London, Tring, Tervueren, and Vienna, in addition to material in the American Museum, has confirmed my view as to the existence of two distinct species; and in Vienna I was surprised to find a very broad-tailed specimen of *S. aucupum*, collected by Mr. Rudolf Grauer at Uvira, on the north end of Lake Tanganyika. So *aucupum* is not confined to northwest Africa, but extends, I find, to Eritrea, Angola, and even Gazaland. Furthermore, its range is intercepted on the west by the great Cameroon-Congo forest, where no paradise whydah occurs; and in northeast, east, and southern Africa its representatives are subspecifically distinct from the typical Senegal bird. *S. paradisæa* is exclusively east and south African, and cannot be subdivided.

The five forms of the genus which I find recognizable are shown in Figure 1. While the ranges of the two species overlap extensively, every form has a definite geographic distribution, as follows:

Steganura aucupum aucupum—Senegal to Shari River region.

S. a. longicauda—Upper Uelle District.

S. a. nilotica—Kordofan and Blue Nile to Eritrea.

S. a. obtusa—Kenya Colony and Lake Kivu, south to Gazaland and west to Angola.

Steganura paradisæa—Eritrea and Abyssinia south through East Africa to Cape Colony, also to Damaraland and Angola on the west.

¹Scientific Results of the American Museum Congo Expedition. Ornithology, No. 7.

²1908, Bull. Brit. Orn. Cl., XXI, p. 43.

³Sclater and Præd., 1918, Ibis, pp. 459-460.



Fig. 1. The forms of *Steganura*. One-third natural size.

- A.—*S. aucupum*, Diourbel, Senegal, October 8, 1907 (type).
 B.—*S. a. longicauda*, Farafje, Uelle district, November 9, 1911 (type).
 C.—*S. a. viticola*, near Abu Zor, Blue Nile, January 6, 1913 (type).
 D.—*S. a. obtusa*, Fungo Andongo, Angola, July 1, 1903 (Ansorge coll.).
 E.—*S. paradisiaca*, Tertale, S. Abyssinia, June 8, 1912 (Mearns coll.).

The adult males differ most markedly in the form and dimensions of the long tail feathers, which are relatively constant in each subspecies when once they have reached their full growth. But *S. a. nilotica* and *S. paradisæa* are also distinguished by their yellower hind-necks; and *S. a. obtusa* has a decidedly longer wing than any other form.

My interest was first aroused in this question by the specimens of paradise whydah which Mr. Herbert Lang and I collected in the north-eastern corner of the Belgian Congo. They are clearly nearest the Senegal form, though coming from so nearly the center of Africa. They agree in the brownish color of the nape; but a far better character is the shape of the longest pair of rectrices, which do not taper towards the tip in *aucupum*, as in so many of the birds from eastern and southern Africa. Strangely enough this distinction was not even mentioned by Neumann.

I am by no means the first to make this fact known. One would think that Linnæus might have noticed it, for his description of *Emberiza paradisæa*, in 'Systema Naturæ.' 10th edition, 1758, p. 178, was based on figures of earlier authors which showed tails of both shapes. His description, in this edition, cannot be restricted to any one of the forms since recognized, and the habitat was stated simply as Africa. In the 12th edition, however, of 1766, p. 312, besides adding one more reference (from Brisson), Linnæus improved the description by stating that the longest tail feathers were acuminate and falcate, and that the bird lived in Angola. Thus it is clear that he meant particularly the species figured in color by Edwards in 'Nat. Hist. Birds,' part 2, 1747, p. 86, Pl. LXXXVI.

Taxonomic importance was first attributed to the form of the tail by Cassin, when he described *Vidua verreauxii* from Abyssinia¹ with a tapering tip to the tail, and attempted to fix the name *paradisæa* on west African birds with broad-tipped tails. His attention, no doubt, had been called to this by the observant collector, J. Verreaux; and the name *Vidua sphænura*, which Bonaparte proposed for the same Abyssinian form a few months later,² was stated to be a manuscript name of Verreaux's.

So Verreaux long preceded me in the opinion that the difference in the tails is of more than subspecific value, and his view was adopted by authors of some well-known works on African birds. Reichenbach accepted *paradisæa* and *sphænura*,³ referring to the first-named as coming

¹1850, Proc. Acad. Nat. Sci., Philadelphia, V, p. 56.

²1850, 'Consp. Gen. Avium,' I, p. 449.

³1862, 'Die Fortsetzung der Singvögel,' p. 63.

with certainty only from Angola. Finsch and Hartlaub¹ called them tentatively *paradisæa* and *verreauxi*. Of recent years it has become customary to treat these at most only as subspecies. Then in 1908 Neumann showed that the Senegal bird was still without a name, although it was the best-known variety in captivity. He named the northwestern bird *S. paradisæa aucupum* and retained the name *verreauxi* for northeastern birds; but the latter is really not separable, I find, from the form Edwards described from Angola, and on which *paradisæa* of Linnæus is based.

What I have to propose, therefore, is (1) the specific distinctness of *aucupum* and *paradisæa*; and (2) the recognition of three new subspecies of *aucupum*, from regions in which the species has hitherto been unrecorded, but where two of them sometimes live side by side with *paradisæa*.

More complete descriptions follow.

***Steganura aucupum aucupum* O. Neumann**

Steganura paradisæa aucupum O. NEUMANN, 1908, Bull. Brit. Orn. Cl., XXI, p. 43 (type locality Diourbel, 150 km. E. of Dakar, Senegal).

Vidua paradisæa SWAINSON, 1837, 'Birds of West Africa,' I, p. 172 (Senegal).

ADULT MALE IN BREEDING DRESS.—The longest (=2d) pair of rectrices is band or ribbon-shaped to within a very short distance of the tip. Hind-neck of a light golden-brown color, very like that of the chest. Eighteen adult males give the following measurements: wing, 73–80; longest rectrices, 203–260. Care must always be taken in measuring the tail to ascertain, by examining the bases of the feathers, that it is fully grown.

SPECIMENS EXAMINED (adult males in breeding plumage).—Senegal: Diourbel, 3; Tieli, 3; Thiès, 1; Kirtaona, 1; "Senegal," 8. "Senegambia," 2. Gambia River, 2. "Sierra Leone," 1. French Sudan: Beledugu region, 2. Gold Coast Colony: Gambaga, 2. Northern Nigeria: near Sokoto, 2. Lake Chad territory: Zinder, 2. Shari River region: Abarin, 1; Gulfei, 1; Bahr Keta, 1. Ubangi region: Fort Sibut, 1.

DISTRIBUTION.—From Senegal and the French Sudan eastward to Lake Chad and the Shari River. On the south the limits appear to be fixed by the forests of the Guinea coast and the Cameroon. The specimens from "Sierra Leone" may not be accurately labeled. The easternmost representatives, collected by the second expedition of the Duke of Mecklenburg in the neighborhood of the Shari and Ubangi, are typical *aucupum*, for their longest tail feathers range from 203 mm. (Abarin)

¹1870, 'Vögel Ost-Afrikas,' p. 424.

to 260 mm. (Ft. Sibut). Throughout all this area *Steganura paradisæa* is unknown.

***Steganura aucupum longicauda*, new subspecies**

TYPE.—♂ ad. in breeding plumage, No. 161983, Amer. Mus. Nat. Hist.; Faradje, Uelle District, November 9, 1911 (Amer. Mus. Congo Exp.).

MEASUREMENTS OF THE TYPE.—Wing, 78 mm.; longest rectrices, 298; exposed culmen, 10.5; metatarsus, 17.

DESCRIPTION OF TYPE.—Coloration exactly as in the preceding form, the brown of the breast rather light, and of small extent, the feathers of the hind-neck of the same golden brown. The long rectrices are however much better developed than in *S. aucupum aucupum*, and in the two other males from Faradje they measure 284 and 295 mm., the wings being 78 and 79 mm.

SPECIMENS EXAMINED.—Upper Uelle district: Faradje, 2 immature males, and 3 adult males in breeding plumage.

DISTRIBUTION.—None of the male specimens seen in any other museum can be referred to this form, so that for the present it is known only from the region of Faradje on the Dungu River. I saw living birds in breeding plumage, however, at Niangara, on the Uelle River, and Aba, on the border of the Lado Enclave. That the range of the subspecies is even more extensive may be assumed from the fact that it is somewhat migratory, and found in the Upper Uelle only from early November to January. Probably the rest of the year is spent to the northward in the southern Bahr-el-Ghazal.

Here again the range is not known to be shared with *S. paradisæa*, although one specimen of the latter was collected by Emin at Lado.

***Steganura aucupum nilotica*, new subspecies**

TYPE.—♂ ad. in breeding plumage, No. 63579, Museum of Comparative Zoölogy; 10 miles above Abu Zor, Blue Nile, January 6, 1913. (Phillips Sudan Exp.)

MEASUREMENTS OF THE TYPE.—Wing, 78 mm.; longest rectrices, 217; exposed culmen, 10; metatarsus, 17.5.

DESCRIPTION OF TYPE.—Brown of the chest somewhat darker and more extensive than in *S. a. aucupum* and *longicauda*, whereas the whole hind-neck, in distinct contrast to the chest, is of a pale straw-yellow.¹ The tail feathers average much shorter than in either of the preceding races. The 12 adult males of *nilotica* measured by me give the following results: wing, 75–80 mm.; long rectrices, 191–224.

SPECIMENS EXAMINED (adult males in breeding plumage).—Eritrea: Mai Uassen, 1; Scetel, 1. "Abyssinia," 1. Sennar: Abu Usher, 1; Roseires, 5; 10 miles above Abu Zor, 1; Abu Haraz, 1; "Sennar," 1.

¹Wear and bleaching through exposure, in the other races of *aucupum*, sometimes cause the nape to become unusually yellow.

White Nile: Jebelein, 4; "White Nile," 1. Kordofan: Barra, near El Obeid, 1; "Kordofan," 3. "Sudan" (probably Kordofan), 1. "Bahr-el-Ghazal," 1. "Northeast Africa," 1.

DISTRIBUTION.—From Eritrea to the Blue and White Niles, Kordofan, and perhaps the northern Bahr-el-Ghazal. The eastern edge of its range is shared with *S. paradisæa*, but *nilotica* is either very rare or altogether wanting in Abyssinia.

***Steganura aucupum obtusa*, new subspecies**

TYPE.—♂ ad. in breeding plumage, No. 25812, collection of Mr. J. H. Fleming, Toronto; from Luchenza, Nyasaland (collected by Nisbet).

MEASUREMENTS OF THE TYPE.—Wing, 82 mm.; longest rectrices, 200; exposed culmen, 10; metatarsus, 14.

DESCRIPTION OF TYPE.—The brown of breast is as dark as in *paradisæa*, and consequently much more marked than in any other race of *aucupum*. There is, moreover, much the same contrast between the nape and chest as in *paradisæa*, for the hind-neck is yellow with very little trace of brown. On the other hand the long rectrices differ more than ever from those of *paradisæa*, for they are shorter and broader than in the other races of *aucupum*. In the type these feathers measure 35 mm. in width, and of course do not dwindle in size till close to the tip.

Measuring the width of the longest rectrices in a number of examples of each race of *aucupum*, I obtained the following figures: *aucupum*, 25–27; *longicauda*, 29–32; *nilotica*, 24–30; *obtusa*, 35–37. There is much the same difference in the width of the median pair of rectrices, for in the type of *aucupum*, I found them 23 mm. broad, and in a specimen of *obtusa* from Angola 35 mm. This median pair of tail feathers is usually entirely hidden by the second, greatly lengthened pair. Figures of the birds often show them too plainly, and this is equally true of the figure accompanying the present paper. It seemed desirable to indicate their length, otherwise only the upper borders and the hair-like tips, at most, should have been visible.

There is a good deal of variation in the color of the hind-neck of *obtusa*. In some skins, like the type, it is as yellow as in many *paradisæa*, but in others a distinct brownish wash is perceptible, probably when the feathers are freshest. The dark brown of the chest, often a deep chestnut, in combination with the broad, stubby tail feathers, makes it easy to recognize.

The 30 adult males I have measured have longer wings than any other group in the genus, 80–89 mm. Their tails were from 176 to 216 mm. in length.

The difference in length of wing which Sclater and Præd¹ pointed

¹1918, *Ibis*, p. 460.

out between paradise whydahs from southern and from northeastern Africa is to be explained as follows: in the British Museum there are many specimens of *S. a. obtusa* from the south, especially from Nyasaland, and these would bring up the average very considerably, even were the southern *paradisæa* included with them.

SPECIMENS EXAMINED (adult males in breeding plumage).—Kenya Colony: Escarpment, 1. Kivu district: Kibati, 1; Uvira, 1. "Tanganyika," 1. Manyema district: Munie Mboka, 1; Lubilu, 1; Dogodo, 1; Niembo, 1. Katanga district: Funda Biabo, 3; Lualaba River, 1; Kaluli River, 1. Northern Rhodesia: Petauke, 1. Nyasaland: Luchenza, 1; Mlanji, 3; Chiradzulu, 1; Mpimbi, 1; Namaramba Lake, 1; Ntondwe, 1; Fort Lister, 1; Zomba, 2; Lake Shirwa, 1; "Nyasaland," 1. Northern Gazaland, 1. Loanda: Pungo Andongo, 1. Mossamedes: Gambos, 1; Tuandiva, 1; Kasinga River, 1.

DISTRIBUTION.—The most northerly record known to me is that of a male collected by Doherty at Escarpment, Kikuyu Mts., Kenya Colony, but the bird must be uncommon in that part of East Africa. It has also been taken at Kibati, just north of Lake Kivu, by Pilette, and by Grauer at Uvira, on Lake Tanganyika. Southeast of the Congo forest it becomes more common; Pilette secured four more males in the Manyema district between Tanganyika and Kasongo, and they have been taken in the Katanga by Neave and by de Baillet-Latour. In Nyasaland this is the common paradise whydah, and numbers have been collected by Sharpe and Whyte. Angola has both *obtusa* and *verreauxii*, as shown by the collections made by Anson for Lord Rothschild. He obtained *obtusa* at Tuandiva, Gambos, and Pungo Andongo. A specimen of van der Kellen's is from the Kasinga River. In southeast Africa the species extends even farther than Lake Shirwa, for Swynnerton has taken a specimen in northern Gazaland.

***Steganura paradisæa* (Linnæus)**

Emberiza paradisæa LINNÆUS, 1758, 'Systema Naturæ,' 10th Ed., p. 178 (type locality Africa, restricted in 12th Ed. to Angola).

Vidua verreauxii CASSIN, 1850, Proc. Acad. Nat. Sci. Philadelphia, V, No. 3, p. 56 (Abyssinia).

Vidua sphænura BONAPARTE, 1850, 'Consp. Gen. Avium,' I, p. 449 (Abyssinia).

Steganura paradisæa australis HEUGLIN, 1861, 'Forschungen über die Fauna des Rothen Meeres und der Somali-Küste,' Petermann's Mittheilungen, VII, p. 24 (Abyssinia, Danakil, and Somali coasts).

Vidua paradisæa orientalis HEUGLIN, 1871, 'Orn. Nordost-Afrikas,' I, p. 583 (Northeast Africa).

ADULT MALE IN BREEDING DRESS.—The elongated second pair of rectrices has a characteristic outline, broad at the base but beginning to taper at less than one-half the length, and extending out as thin, pointed streamers. Their length is more variable than is usual in *S. aucupum*, but there the variation is not geographic. The brown of the breast is dark, and contrasts strongly with the straw-yellow of the hind-neck.

To make sure that northern and southern birds of this species were not separable, I have carefully compared their measurements. In 24 adult males from north of the equator (Eritrea to Kenya Colony) I find: wing, 76–81; long rectrices, 245–344. For 21 from south of the equator (Transvaal and Angola to Tanganyika Territory): wing, 76–83; long rectrices, 270–336.

SPECIMENS EXAMINED (adult males in breeding plumage).—Eritrea: Salamona, 1. Somaliland: Raia Wachali, 1; Smith River, 1. Abyssinia: Tadejemulka, 1; Koomeglee, 2; Dire Daoua, 3; Ourso, 12; Tertale, 3; Goura, 1; Furza, 1; Dire Ela, 3; Karaba, 1; Galla countries, 4; Darro Mts., 1; "Abyssinia," 3. Anglo-Egyptian Sudan: Sennar, 1; Mongalla, 9; Lado, 1. Kenya Colony: Baringo, 1; Muressi (Turkwell R.), 1; Mutias Mumomi, 1; Kerio River, 1; Manda Island, 1; Lamu, 1; Athi River, 1; S. E. Mt. Kenia, near Tana R., 1; Kitui, 1; Kibwesi, 1. "British E. Africa," 1. Tanganyika Territory: Morogoro, 1; Ukami, 1; Ugogo, 2; Dar-es-Salaam, 1; "Tanganyika," 1. Mozambique: Tette, 4. Angola: Loanda, 1. Mossamedes: Tuandiva, 1; Cavallana, 1; Catequero, 1; Chahivi, 2. Damaraland: Omaloko, 1. Southern Rhodesia: Bulawayo, 4; Nonyonko (?), 1; Tati, 1. Transvaal: Rustenberg, 5. Zululand: Etchowe, 2. Natal: Port Natal, 1. "South Africa," 1. (One specimen of *paradisæa* in the British Museum is labelled "R. Gambia, Whitely," but surely in error. The only specimen taken with certainty west of the White Nile is one collected at Lado by Emin Pasha.)

DISTRIBUTION.—From Eritrea across Abyssinia to Mongalla and Lado on the Upper White Nile, and to the coast of Kenya Colony. Thence southward to Tanganyika Territory, Southern Rhodesia, Angola, the Transvaal, and eastern Cape Colony. Thus in the northeast its range overlaps that of *S. aucupum nilotica*, and on the east and south to some extent with that of *S. aucupum obtusa*. It is possible that the two species have slightly different preferences as to haunts or food; but it is worth mentioning that at Tuandiva, in Mossamedes, Anson collected a male of each, both in breeding plumage, on the same day, March 16, 1906.

It will be noted that I have abandoned Cassin's name *verreauxii*,

which is a synonym of *paradisæa*. It is perfectly clear that it cannot be confused with *S. a. nilotica*, for I have examined Cassin's type of *verreauxii*, in the Philadelphia Academy. In case there may be any doubt as to the importance of the shape of the tail feathers, I may call attention to the fact that I have yet to see them of a shape intermediate between *aucupum* and *paradisæa*. Dr. A. G. Butler,¹ to be sure, does say that "The tail-plumes decrease in breadth, but increase in length with age." Fortunately he tells us just how much the increase was, 48 mm. in four annual molts; this is not as great as the variation I show for the subspecies of *aucupum*. If the shape of the feather-tip depended merely upon growth, then the *paradisæa* form should be found in northwest Africa. In other parts of the continent, where two forms do inhabit the same territory, one varies geographically, the other does not.

Nor it is probable that the two forms are Mendelian in character, interbreeding, yet preserving their distinctness. Far more probably the females will be found to show points of difference as well. In any event, the males in the eclipse plumage assumed each year do appear to be distinguishable. By comparing several specimens of *aucupum* in this plumage from Senegal and Zinder with others from parts of the continent where *paradisæa* alone has been found (southern Abyssinia especially), I found that *paradisæa* males in eclipse differ from those of *aucupum* in being generally darker above, the blackish markings predominating more over the rufous and buff. The light median crown-stripe is narrower in *paradisæa*, 4 mm. (as against 6-7.5 in *aucupum*), the black streaking on the back is much coarser, the upper tail coverts more blackish, and the middle pairs of rectrices apparently blacker and broader. The breast of *paradisæa* is even deeper cinnamon than that of *aucupum*, and it appears to be always more streaked. There are short triangular or arrow-shaped spots of blackish extending all across the chest.

This opinion as to the eclipse plumage of *paradisæa* is strengthened by Edwards' plate, which shows the same captive specimen of *paradisæa* in breeding and eclipse plumage. The spotted chest is very noticeable in the latter, whereas in undoubted males of *aucupum* there are only the faintest traces of spots. About the differences between females I cannot be so confident, but am inclined to think that here, too, *paradisæa* is more spotted on the chest. Most of the brown birds in collections are either females or young males, rarely adults in eclipse.

¹1894, 'Foreign Finches, in Captivity,' pp. 282, 283.

Now let us see whether any explanation can be offered for the origin and present distribution of these five forms of paradise whydah. I shall not attempt to offer final proof, but simply a plausible hypothesis. From what I know of these birds in the wild state, they abhor rain-forest. Living on grass seeds, burdened with enormous tail feathers during a large

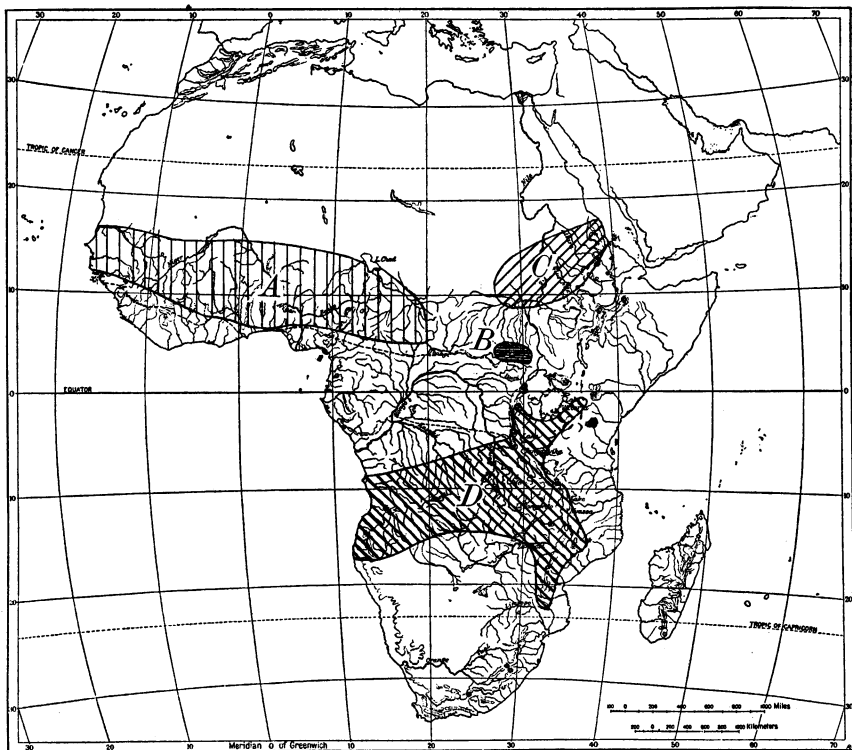


Fig. 2. Approximate areas occupied by the subspecies of *Steganura aucupum*.
A.—*S. a. aucupum*; B.—*S. a. longicauda*; C.—*S. a. nilotica*; D.—*S. a. obtusa*. The ranges of the first three, however, will probably be found to meet in the region north of the Ubangi River.

part of the year, they are most at home in a short-grass plain, with a few trees as lookouts for the wary males. This is sufficient not only to show why they are found only in savannas and steppes, but even to give us a hint as to the probable inception of the two species. One cannot avoid being impressed by the importance of isolation in the past evolution of birds. This, more than any other influence, seems to have facilitated the origin of new forms, whether subspecies; species, or genera. I do not say "caused," for the cause may be something quite different.

The probable reason for the isolation of the paradise whydahs was the greater extension of the equatorial forest at some time in the past, in eastern Africa. Many botanists hold this to be extremely likely. It is my belief that *Steganura aucupum* was then restricted to the grasslands north of the forest, where it still monopolizes more than half the width of



Fig. 3. Approximate distribution of *Steganura paradisæa*.

the continent, and that *S. paradisæa* occupied those of the south. Then came the reduction of the forest to the east, but the two species were already so differentiated that when *aucupum* extended southward, and *paradisæa* northward into Abyssinia, they did not interbreed. There is no longer complete segregation, and yet we still see the same influences at work in the case of *S. aucupum*, with its widely scattered populations. They stretch over a vast area, and are still partially isolated by the Congo forests, with the result that slight differences in coloration, and in the dimensions of the wing and tail, have already begun to appear.

Steganura paradisæa is still homogeneous; even wing-length will not distinguish northeastern specimens from southern. A glance at the map will show how much less the Congo forest intercepts its distribution. If my assumption is correct, that *aucupum* and *paradisæa* no longer interbreed, it will be a good example of the slight external characters that suffice to hold allied species apart. Such differences in the shape of the tail may well have arisen by mutation, but their extension to a species as a whole must, I feel sure, be favored by this sort of isolation.

In some similar manner, in the more remote past, the related genera *Tetrænura*, *Linura*, and *Vidua* may have had their beginning, first as allied species—even now they are scarcely valid genera—under the influence of some condition affecting intercommunication. Once differences had been established that would forestall interbreeding, the birds might again spread into one another's areas. Why the stocks, once isolated, should tend to diverge is a question far beyond the scope of this paper; but I believe it to be the case.