FURTHER REMARKS ON THE RELATIONSHIPS OF THE GRACKLES OF THE SUBGENUS QUISCALUS.

BY FRANK M. CHAPMAN.

In the 'Bulletin of the American Museum of Natural History' for 1892 (Vol. IV, pp 1–20) I published a "Preliminary Study" of the relationships of the Bronzed, Purple and Florida Grackles. It showed that the Bronzed Grackle breeds from the Rio Grande Valley west to the Rocky Mountains, north to Great Slave Lake and Newfoundland, east to Connecticut and the Alleghanies; that the Florida Grackle ranged from Florida north to South Carolina and west to Louisiana, while the Purple Grackle occupied the area intervening between the ranges of the Bronzed and Florida birds.

It was also shown that throughout its vast range, the Bronzed Grackle varied significantly in color only when it came in contact with the Purple Grackle with which it then completely intergraded. This intergradation was proven, by breeding specimens, to occur from Massachusetts to Pennsylvania but it was believed that it would take place wherever the breeding ranges of the two birds came together. The Florida Grackle, at least in peninsular Florida and north to Charleston, was shown also to be constant in color but the Purple Grackle was found to be so variable that it was described under three phases of color, (1) the bottle-green, (2) the bronze purple, (3) the brassy bluish-green.

In my original paper I expressed a belief that the Bronzed Grackle is a species which intergrades with the Purple Grackle by hybridization, the hybrid being phase No. 3 of the latter; while the Florida Grackle was considered the highest development of phase No. 1 of the Purple Grackle. Further studies confirm my belief in the specific standing of æneus and of its hybridization with the Purple Grackle, which I now find is accomplished in Louisiana, just as it is in the northern states, through phase No. 3 of the Purple Grackle. But instead of considering the Florida Grackle an offshoot of the Purple Grackle, I now take the opposite view and believe that the Florida bird is the ancestral form. This view is the logical outcome of a theory which introduces the climatic influences exerted by the last Glacial Period as fundamental factors in creating the conditions we observe to-day.

It seems clear that, in order to hybridize, the ranges of the forms concerned must come together, and it seems equally clear that, in order to come together, they must previously have been apart. Whether, as my colleague Mr. J. T. Zimmer suggests, the ranges of the Bronzed and Purple Grackles may have been continuous prior to the last Glacial Period, there is certainly ground for the theory that during the height of this Period their ranges were disconnected. To the climatic influences of this time Dr. J. A. Allen was

wont to attribute the presence in Florida, as isolated representatives of western species, the Florida Jay (Aphelocoma cærulescens), the Florida Burrowing Owl (Speotyto cunicularia floridana) and other species of apparent western origin. To this same factor I have attributed the existence in the West Indies, as resident species, of the White-winged Crossbill (Loxia leucoptera megaplaga) and other birds of obvious northern origin. Certainly the presence during this Period of walrus on the South Carolina coast and of musk oxen in Kentucky is in itself sufficient indication of the character of the then prevailing climate.

If we can accept this view as a starting point, we may, in imagination, follow the post-glacial dispersal of Grackles northward until we find the situation of to-day.

For reasons which were doubtless climatic and promoted rapid range extension, the Bronzed Grackle not alone acquired a far wider range than the northern representative of the Florida Grackle, but progressed more rapidly, spreading eastward through New York and reaching central New England in time to prevent the representative of the Florida Grackle from advancing beyond Massachusetts. Eventually it reached Newfoundland at the northeast and Great Slave Lake at the northwest, while still retaining its residence in southern Texas. This vast territory, I repeat, has been occupied as a breeding range without appreciable exhibition of geographic or climatic variation.

The Florida Grackle, on the other hand, as it extended its range northward in the Atlantic States and westward in the Gulf States, very gradually underwent what appears to be geographic variation, though it may be the cumulative result of prolonged hybridism. Westward, in the vicinity of New Orleans, it is still present but intergrades completely with phase No. 2 of the Purple Grackle, its apparent geographic representative. Farther westward, on Avery Island and vicinity, true Florida Grackles have almost entirely disappeared (one male in 32 breeding birds) and the Purple Grackle, phase No. 2, with intergrades between it and the Florida Grackle, is the prevailing form.

Northward the Florida Grackle ranges unchanged, at least to Charleston, S. C., but specimens from Newport News, Virginia, as remarked beyond, show an approach to phase No. 2 of the Purple Grackle.

In my early paper the further development of phase No. 2, and its mergence with phase No. 3, is traced while the development of the latter as an apparent hybrid between phase No. 2 and the Bronzed Grackle in southern New England, Long Island, the Hudson valley and eastern Pennsylvania is shown.

Subsequently received material now demonstrates the intergradation of these two birds in the same way in southern Louisiana, as described beyond. A report of this and other 'new' material is given here as a report of progress and to arouse interest in a problem which calls for much additional material and particularly field work. Specimens and observations from any breeding colony of Grackles between the ranges of the Florida and Bronzed Grackles are desirable. Existing conditions are evidently the cumulative result of the countless generations of Grackles that have appeared since these two birds first came together. In the north the area of intergradation is comparatively wide; in Louisiana, as we shall see, it is comparatively narrow. In Tennessee, the Purple Grackle, phase No. 2, breeds west of the Alleghanies; in Pennsylvania, the influence of *xneus* extends east of the Alleghanies.

The student lacking representative series of specimens may, perhaps, be better prepared to observe if he is briefly informed of the features characterizing the Bronzed and Florida Grackles and the intergrade between them which we call the "Purple Grackle."

FLORIDA GRACKLE.

BRONZED GRACKLE.

Head, neck Shining dark violet, more or less Shining greenish to purplish blue, and chest. bluish anteriorly and bronzy posteriorly.

rarely bluish violet.

Back.

at the base of the bottle-green end. markings.

Bottle-green, the feathers with a Uniform brassy bronze to oliveusually concealed iridescent bar bronze, no iridescent or other

Rump.

Purplish or violet, more or less washed with bronzy and with rounded iridescent spots near or at the ends of some feathers.

Like back.

Tail.

Greenish or bluish black.

Purplish black.

Wings.

Primaries blackish green; inner quills largely purplish violet, more pronounced on coverts; the lesser (rarely median) usually with iridescent tips.

Primaries black, inner violet, bronze-tinged, more pronounced on coverts; no iridescent markings.

Center of abdomen. Bluish, purplish or violet.

Slightly duller than sides.

Bill.

Comparatively slender; depth at Comparatively stout; depth at nostril, .42 inches.

nostril. .46 inches.

The connecting links between these two species, as I believe them to be, form the (1) bottle-green, (2) the purple-bronze, and (3) the brassy-green phases of the Purple Grackle.

The characters of these three color phases have been described in my original paper, to which students should refer. Here I repeat briefly that phase No. 1 resembles the Florida Grackle but has the head, neck and chest greenish or purplish blue instead of dark violet. It occurs rarely as far north as Chester County, Pennsylvania (2 specimens out of 61) and as far west as southern Louisiana. It is associated with phase No. 2 and is either a geographic intergrade between it and the Florida Grackle or represents, atavistically, the former's relationship to the Florida Grackle.

It should be noted that in my 1892 paper I ranked the Florida Grackle as phase No. 1 of the Purple Grackle, whereas now it stands alone, and under phase No. 1 I include only those representatives of the Florida bird possessing a greenish or bluish head or which otherwise approach phase No. 2.

In phase No. 2 the head varies from greenish to purplish blue and rarely violet, the back and sides are bronzy purple with more or less concealed iridescent bars, the rump is purplish bronze, sometimes with bluish spots. The breeding range of this phase lies between the breeding ranges of the Florida Grackle and phase No. 3 of the Purple Grackle, from Louisiana to New York City and occasionally farther east and north.

Phase No. 3 has the head variable, as in No. 2, the back and sides brassy-green, and the rump bronze, as in the Bronzed Grackle. It is evidently a hybrid between the Bronzed Grackle and phase No. 2 of the Purple Grackle and breeds in the area between the breeding ranges of these two birds wherever they come in contact, from Massachusetts to Louisiana.

This is a very brief statement of conditions which began to develop when, with the retreat of the ice, the Bronzed and Florida Grackles first came together. But, in connection with my earlier paper, it may serve to state our problem and help prepare us to consider more recently acquired evidence.

Nomenclature.

Seldom has a biological problem been more confused by nomenclatural issues than in the case of these grackles. With a hope that this phase of the subject might continue to be overlooked, I closed my eyes to it in preparing my original paper. But 'murder will out' and in 1918 (Auk, XXXV, p. 440) Mr. Arthur T. Wayne showed that as quiscula of Linnæus is based on Catesby's description of the bird from the South Carolina coastal region, which is referable to the Florida Grackle, aglæus of Baird, the latter name is a synomym of quiscula, and the Florida bird becomes Quiscalus quiscula quiscula (Linn.), the name previously applied to the Purple Grackle.

A year later Dr. H. C. Oberholser (Auk, XXXVI, p. 549), in confirming Mr. Wayne's views, called attention to the fact that their adoption left the Purple Grackle without a name and he proposed to call it *Quiscalus quiscula*

ridgwayi. His type, from Washington, D. C., is, however, not a true Purple Grackle, of phase No. 2, which appears to be the characteristic breeding bird at Washington, but a typical specimen of phase No. 3 which, as I have tried to show, is a hybrid between phase No. 2 and æneus. It was taken March 30 about two weeks before Grackles are recorded as breeding in the District of Columbia (Cooke, Proc. Biol. Soc. Wash., 1929, p. 45), and may be a migrant on its way toward a locality where the Bronzed and Purple Grackles intergrade.

The case raises two questions: (1) can a name be properly based on a hybrid; (2) in any event is the name *ridgwayi* applicable to phase No. 2 of the Purple Grackle?

There is, however, a difference between sporadic hybridism, resulting in an occasional individual here and there, and that type of intergradation by hybridization which produces intergrades wherever the ranges of two forms adjoin. Certainly, for purposes of identification and the expression of relationships, it would make our use of names more exact and intelligible if we should retain the name ridgwayi for phase No. 3 of the Purple Grackle with a range from southern New England to Louisiana in the area between the ranges of the Bronzed Grackle and phase No. 2 of the Purple Grackle, while the latter, as apparently a geographic representative of the Florida Grackle, should receive a new name. In this event, I propose for this phase No. 2, as described above, the name Quiscalus quiscula stonei¹ with the type from Lakehurst, N. J. (No. 99687, Amer. Mus. Nat. Hist., June 8, 1907, W. DeW. Miller and J. P. Chapin) and a breeding range from southern Louisiana to southern New York in the area between the breeding ranges of the Florida Grackle (Quiscalus quiscula quiscula) and Quiscalus quiscula ridgwayi.

This procedure would still leave unsettled the proper scientific name of the Bronzed Grackle. The facts presented by its distribution and stability of characters throughout an exceptionally wide range argue for its specific distinctness, when custom would accord it the binomial Quiscalus aneus, just as we retain Colaptes auratus for the Yellow-shafted Flicker and Colaptes cafer for the Red-shafted Flicker, though the two are known to intergrade by hybridization.

With the Grackles, however, the intergradation is more regular and complete and is accomplished by a finely graded series of intermediates. Many of these intermediates are obviously far nearer to æneus than they are to ridgwayi and it would more nearly express their relationships to call them Quiscalus quiscula æneus than Quiscalus quiscula ridgwayi. In this event, to be consistent, we should defy custom and use the trinomial for the species, true æneus.

¹ For Dr. Witmer Stone.

As for common names, we may of course continue to use Florida Grackle and Bronzed Grackle as heretofore. Purple Grackle may also be still employed for the birds that connect them, but the component forms may be known respectively as Stone's Grackle and Ridgway's Grackle.

NEW MATERIAL.

It remains to examine certain specimens received since the publication of my paper which, in my opinion, throw important light on the relationships of these birds. They were collected chiefly in southern Louisiana and include a large series of breeding birds from Avery Island and vicinity presented by Mr. E. A. McIlhenny, and a smaller series from Baton Rouge Parish from Mr. Andrew Allison. In connection with these birds a series from Mandeville, on Lake Ponchartrain, previously reported on, calls for re-examination. These specimens, unfortunately, are without date. They were secured by C. S. Galbraith, a millinery collector, who for several years (about 1886-89) was resident at Mandeville in the spring and there rediscovered Bachman's Warbler (Auk, V. 1888, p. 323). The American Museum has specimens of this bird taken by Galbraith at Mandeville in March and April and it is wholly probable that the Grackles in question were procured by him during these months. This belief is confirmed by the identity of four males collected by George E. Beyer at New Orleans from March 23 to May 17. One of these birds is a typical Florida Grackle (Quiscalus quiscula quiscula), two are referable to phase No. 2 of the Purple Grackle (Quiscalus quiscula stonei) and one is intermediate.

Much the same conditions exist in the Mandeville series. Four are Florida Grackles with dark violet heads and bottle-green backs and sides. Six are referable to *stonei*, with purple-bronze backs and heads varying from bluish or greenish to bronze-purple. Six are variously intermediate and demonstrate the complete intergradation of *quiscula quiscula* with *stonei*.

The remaining two birds are typical Bronzed Grackles! The absence of specimens of phase No. 3 (Quiscalus quiscula ridgwayi), the brassy green bird resulting from a union of æneus with stonei, suggests that these two specimens were not local breeders while their rather dull plumage indicates that they were not winter visitants. Rather does it indicate that the breeding range of æneus is not far distant from Mandeville, and this belief is confirmed by six males from west Baton Rouge Parish on the east bank of the Mississippi River, approximately 65 miles west of Mandeville, taken from April 20 to May 20 and labelled by the collector, Andrew Allison, as "breeding." Three of these birds are referable to ridgwayi, one is æneus and two are intermediates, one of which, except for a narrow brassy green postnuchal band, is typical æneus. In other words, these six birds demonstrate the intergradation of the Bronzed and Purple Grackles through

the same color phase (No. 3) by which they merge wherever their ranges adjoin.

From west Baton Rouge Parish, Mr. Allison has also sent us two males taken March 5. They are labelled as "probably about to breed." One is typical of *stonei*, the other of *ridgwayi*, giving us, therefore, from one locality, birds typical of both parent forms (*stonei* and *æneus*) and of the results of their union.

Let us now continue westward along the Louisiana coastal region to Avery Island. It may at once be said that although the birds from this locality have uniformly been referred to the Florida Grackle, only one specimen in my series of 32 is typical of that species. The remaining 31 may be identified as follows: Avery Island, stonei, 9; intermediates between stonei and quiscula quiscula, 8; ridgwayi, 1; St. Landry Parish, stonei, 5; intermediates between stonei and quiscula quiscula, 3; Vermilion Parish, intermediates between stonei and quiscula quiscula, 3; St. Mary's Parish, intermediate, 1; Terre Bonne Parish, stonei, 1.

It will thus be seen that, so far as this series goes, the typical Florida Grackle has almost been replaced in the Avery Island region. The occurrence of a specimen of *ridgwayi* calls for comment. This bird was taken April 2 and probably indicates the proximity of breeding *æneus* either toward the north or west or very likely in both directions.

The average measurements of 16 specimens from the Avery Island region are, wing, 5.45; tail, 5.00; exposed culmen, 1.27; depth of bill at nostril, .48 in. The bill, therefore, is notably heavier than in the Florida bird which is characterized by a comparatively slender bill (24 east coast males, exposed culmen, 1.25; depth at nostril, .42 in; see also measurements in my 1892 paper, p. 6).

Before we leave the Gulf States, it will be well to examine again 9 breeding males sent me by the late Dr. W. C. Avery from Greensboro, Alabama, and vicinity. In their purplish bronze backs and sides, four of these birds agree with *stonei* but all have the violet head of the Florida bird. This, however, sometimes appears in northern specimens of *stonei* to which form I should refer these birds. The remaining 5 birds are intermediate between *stonei* and *quiscula quiscula* and demonstrate their intergradation. As a whole, therefore, the series agrees with that from Avery Island.

On the Atlantic coast it has been shown that the range of the Florida Grackle extends at least to Charleston, South Carolina. Five specimens collected by W. and H. H. Bailey in mid-May, 1895, at Newport News, Virginia, are very near the Florida Grackle. Three have the violet head of that bird but, in the color of the back and sides, approach stonei. Two have a violet head slightly tinged with bluish but the back and sides are greenish. In other words, these birds are intergrades between quiscula

quiscula and stonei, nearer the former. They can be matched in color by specimens from Avery Island, Louisiana. In measurements, they are close to the Florida bird, thus: wing, 5.41; tail, 4.89; exposed culmen, 1.24; depth of bill at nostril, .44 in.

The character of the variations shown by the specimens we have just considered from Virginia, Alabama and Louisiana is such as we are accustomed to find in geographic variants. On the other hand, it may be questioned whether we should expect to find a species of presumed Florida origin exhibiting essentially the same kind and degree of variation on the coasts of Louisiana and Virginia; and this causes us to ask whether the variations exhibited by these birds may be in whole or part the cumulative result of prolonged hybridism, which, in the course of innumerable generations has extended its influences from the boundaries of the range of aneus to well within the territory now occupied by the Purple Grackle. Personally, I favor the theory that stonei and its intergrades with quiscula quiscula are geographic variants, but the case is not proven.

While I present this paper merely as a report of progress, I hope that in connection with my publication of 1892, it will serve to state the problem and arouse interest in it. There is not a breeding colony of Grackles in the area between the breeding ranges of the Bronzed and Florida Grackles that cannot supply data of interest concerning the relations of these birds and the history of their intergradation. The laboratory worker using specimens with labels that do not state whether or not the birds were breeding may be misled by assuming that certain specimens were breeders when in truth they were migrants or stragglers. For example, in my 1892 paper I recorded as breeding males from Chester County, Pennsylvania (that is, specimens taken after April 15) the following: phase No. 1, 2; phase No. 2 (stonei), 15; intermediates between them, 11; phase No. 3 (ridgwayi), 19; intermediates between stonei and ridgwayi, 13; intermediates between ridgwayi and æneus, 1.

If these were all breeding birds, they indicate an amazing complexity of intergradation and suggest that physiographically the region is open to invasion from south, east and west. If they are not breeding birds, what are the factors that brought them together during the breeding season? Where is the nearest point at which æneus is the prevailing form? What are the intervening topographic conditions? Answers can be supplied only by the field-worker.

Specimens from eastern Tennessee (Washington Co., presented by B. P. Tyler and R. B. Lyle) are *stonei*, but specimens collected by A. F. Ganier in central and western Tennessee are æneus and in Tennessee the two species are unknown to intergrade. This circumstance is explained by Mr. Ganier of Nashville who writes that in eastern Tennessee the valley of the Tennessee

River and its tributaries is connected with Virginia, while central and western Tennessee belong in the Mississippi Valley. The two are separated by the Cumberland Plateau where Grackles are unknown to breed.

Thus again, a study of distribution, and hence relationships, calls for that intimate knowledge of local conditions which can be supplied only by the field-worker.

Here is the opportunity for the outdoor ornithologist. Some specimens are of course essential; but the characters of the forms concerned are so obvious that after one has become familiar with them identifications of nesting birds may be made in the field. Let us hope that some day we may be able to plot the breeding localities of all the Grackles connecting the Bronzed and Florida species. The resulting map would make an invaluable contribution to our knowledge of the factors governing distribution and to the history of species-making.

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