CONVERGENT EVOLUTION IN THE AMERICAN ORIOLES

WILLIAM J. BEECHER

Chicago Natural History Museum, Chicago, Illinois

THE problems of adaptive convergence in bird taxonomy present many fascinating and often neglected aspects. The present paper describes the evidence for convergence of 2 genera of American orioles that are scarcely distinct but apparently arise from opposite ends of the variable blackbird genus *Agelaius*, and show hitherto unsuspected evolutionary trends toward nearly exact resemblance.

Sclater (1883), Ridgway (1902), and Hellmayr (1937) placed the orioles under a single genus (*Icterus*), and Hellmayr's nomenclature is followed here with indicated exceptions. However, evidence from functional anatomy and field study indicates that 2 phyletic lines are involved. It is proposed to retain the genus *Icterus* Brisson for the line to which the Baltimore Oriole belongs but a new name is needed for the line embracing the Orchard and Cayenne Orioles. The latter apparently arises virtually without plumage change from the black *Agelaius thilius* in the pampas region of South America. For this genus with its slender, nectar-adapted bill, the rather appropriate name *Bananivorus* Bonaparte seems to be the earliest available.

Icterus, on the other hand, appears to arise in the same region with little plumage change from *Xanthopsar*—a yellow blackbird formerly included in *Agelaius*. It is primarily a fruit-eating genus with a straight, conical bill, though the occurrence in this line of forms secondarily adapted for nectar has caused much confusion in the above reviews. Convergence comes about when northern forms of *Icterus* reduce the amount of yellow while those of *Bananivorus* reduce the black. It is the principle aim of this paper to interpret this convergence in terms of selection pressure and environmental change.

Osteological and anatomical specimens used in this investigation have been obtained from the collections of the United States National Museum, the American Museum of Natural History, the Museum of Vertebrate Zoology and, primarily, from the Chicago Natural History Museum. The bird skins used are entirely from the collection of the last museum. For use of the collections in their care, for suggestions or services, I am deeply indebted to Alexander Wetmore, Herbert Friedmann, John T. Zimmer, Ernst Mayr, Dean Amadon, Frank A. Pitelka, A. J. van Rossem, Josselyn Van Tyne, Alfred E. Emerson, Karl P. Schmidt, D. Dwight Davis, Austin L. Rand, Emmet R. Blake, Melvin A. Traylor, Jr., Robert F. Inger, Bryan Patterson, Rainer Zangerl, and Philip S. Humphrey.

The Role of Anatomy and Selection Pressure in Convergence

Natural selection may produce structural changes in birds in many different directions but most adaptive modifications producing new passerine lines have been primarily dietary. Selection pressure of this sort is ever present and is strongest upon a species which is pre-adapted for the use of a food type which is being insufficiently utilized.

Let us pursue this. Anatomically the blackbird subfamily (Icterinae) can be shown to stem from the buntings (Emberizinae), primitive South American members of which have the squamosal area of the posterior skull similarly flattened (it is inflated in advanced buntings). This pre-adaptation permitted the exploitation of many food niches besides seed-cracking simply by permitting the spread of *M. depressor mandibulae* (muscle nomenclature follows Lakjer, 1936) over the posterior region of the skull (Fig. 1).

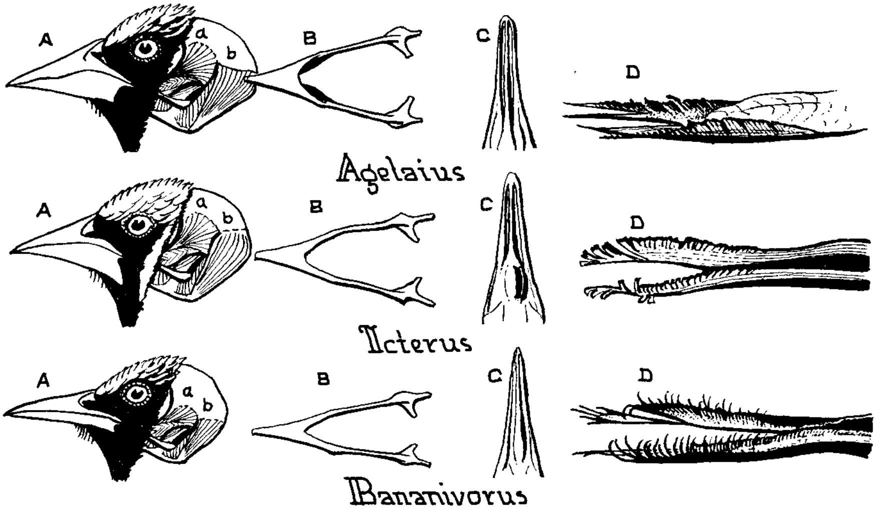


FIG. 1. Functional changes accompanying evolution of the oriole from *Agelaius*. Relationships are shown between *Agelaius phoeniceus*, *Icterus gularis*, and *Bananivorus cayanensis* The partially skinned heads in A. show the structure of the bill with horn in place as wel as two large muscle masses: *M. adductor mandibulae* (a) and *M. depressor mandibulae* (b) B. shows the mandible in ventral aspect; C, hard palate; D, tongue.

The cowbird (*Molothrus*) is very close to this original, primitive form, having the flattened squamosal area but low development of the muscle. This ancestral form appears to have evolved three main branches—the cassiques, grackles, and marsh-blackbirds—each embracing many genera and species. *Agelaius* as the principle genus of the last branch has reached a special peak of its own with full development of this muscle, from which it has given rise to many diverging stocks including the orioles. Briefly, it is more generalized than

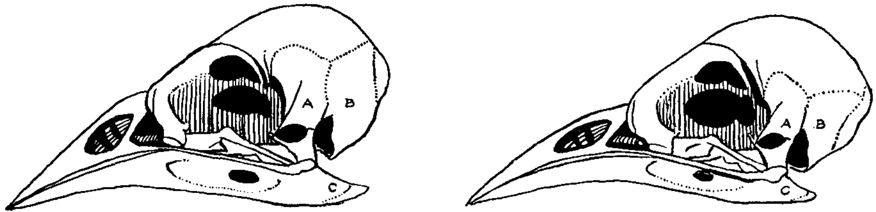
Molothrus with a less powerful bill capable of exploiting insect food in higher degree as well as seed food. Its outstanding features are seen in Figure 1. Under A, the partially skinned head of *Agelaius* reveals 2 large muscle masses: the anterior one is *M. adductor mandibulae* (a); the posterior one, originating on the flattened squamosal and inserting on the lever-like posterior process of the mandible, is *M. depressor mandibulae* (b). The anterior muscle serves with others not shown to adduct the mandible. The posterior one is the *only* muscle for *depressing* the mandible and the fulcrum effect of so large a muscle upon a lever-like posterior extension depresses it powerfully. This development, very unusual in birds, is linked with a habit of sometimes spreading the mandibles in foraging. In B, a ventral view of the mandible shows it to be relatively broad and expanded at the symphysis so that it is narrower dorsally than ventrally. The horny palate in C bears a rounded boss posteriorly against which seeds may be cracked but is still generalized. Finally the tongue is seen in D to be bifid and almost brushy—less finch-like than in *Molothrus*.

Each of these features of *Agelaius* is seen as a pre-adaptation for the fruit-eating modification in the oriole *Icterus*. In A, it is seen that this genus has broadened the ramus of the mandible dorso-ventrally and carried the horny sheath sharply backward in correlation with extreme development of *M. depressor mandibulae* (b). In B, the elongation of the posterior process of the mandible upon which this muscle powerfully acts is obvious, as is also the narrowing at the symphysis. In fact, the blade-like rami turn inward ventrally making the forcibly lowered mandible a functional wedge, stressed and sheathed in growing horn at the points of greatest wear just back of the symphysis. The tongue is more deeply bifid and much more brushy.

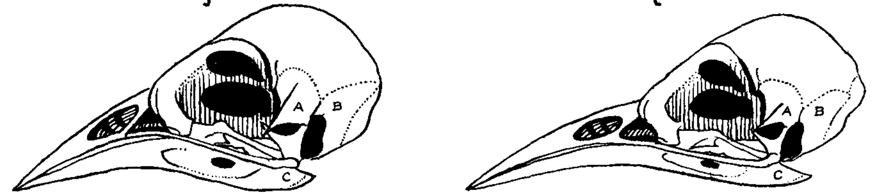
From the above it was actually possible to predict how *Icterus* must feed and see the prediction fulfilled by observation in zoos. The bill is thrust into the fruit *closed*. It is then pried opened against the resistance of the pulp, giving the brushy tongue access to the laked juice. Regardless of how many insects may be eaten when they are abundant, the primary adaptation is for powerful "gaping" inside fruit, which also permits nectar feeding when many trees are blooming in spring. Though I have figured *Icterus gularis*, the palatal knob for cracking seeds is superimposed in this species; it does not affect the fruit-eating adaptation.

Passing on to *Bananivorus* in Figure 1, we note in A that the bill is decurved and greatly reduced in mass; the ramus is weak and its horn not projected posteriorly. The reduction of *M. depressor mandibulae* and in B the shortening of the posterior process of the mandible indicate reduced gaping power. But the elongate, gently rounded form of the central palatal ridge in C and the full development of the nectarine tongue in D (see Moller, 1931) reveal high perfection of the nectar-feeding adaptation. The mandibles, figured for all 3 genera under B, clearly show the narrowing of the angle of divergence of the rami in the sequence: *Agelaius—Icterus—Bananivorus.* This lessens the resistance of fruit to gaping but also reflects the important fact that the skulls in dorsal aspect are narrower in this sequence. The nectarine warbler *Coereba* (Beecher, unpublished) has the skull narrower than normal warblers and the skulls of cassiques are similarly designed—an obvious adaptation for delving into flowers or gaping in fruit. Finally, all the foregoing forms except *Agelaius* have unusual development of the palatine salivary gland, thought to secrete the enzyme, invertase. The sucrose in nectar must be inverted to laevulose or glucose before assimilation (Pryce-Jones, 1944: 132; Wood and Osol, 1943: 1048).

We may think of *Agelaius* as being pre-adapted for gaping in soft fruit, so that *Icterus* and *Bananivorus* were evolved with relatively slight modifications.



Icterus chrysater Icterus pectoralis



Icterus mesomelas Bananivorus cucullatus

FIG. 2. Functional changes in skulls of orioles for fruit- and nectar-feeding. A shows the scar for the origin of *M. adductor mandibulae*; B, the scar for the origin of *M. depressor mandibulae*; C, its insertion on the lever-like posterior process of the mandible.

Molothrus, being hardly at all pre-adapted for this type of diet, probably responded more readily to a pressure to perfect the seed-cracking adaptation. This permits us to understand how certain members of the fruit-adapted genus *Icterus* may become secondarily nectar-adapted. A change in the direction of selection pressure occurs when the fruit-eating bill has become widely perfected —for it then becomes advantageous to take up nectar feeding to avoid competition.

The skulls in Figure 2 provide examples of this adaptive shift. *Icterus chrysater* is a highly-adapted, fruit-eating species in which A shows the fossa or scar for *M. adductor mandibulae* while B indicates the scar for the origin of *M. depressor mandibulae* and C, the scar on the mandible for its insertion. *Icterus mesomelas,* the nectar-feeding form derived from *chrysater,* has these scars much less extensive and the posterior process of the mandible much shorter. The loss of power for gaping is in direct relation to the loss of mass resulting in a more slender bill for flower probing. The same is seen in *Icterus pectoralis*, a nectar-feeding form derived from *I. pustulatus*, which achieves the greatest bill reduction in the genus. Finally, we see in the banana oriole, *Bananivorus cucullatus*, the more highly-adapted skull of a primarily modified nectar feeder.

Ecological demands due to seasonal change in the arid tropical zone imposed a still further adaptive change on the orioles invading it. Since flowering and fruiting here is seasonal, orioles nesting in this zone are obliged to migrate in the dry season, and it is easy to see how selection pressure would bear on these species to utilize seeds as food. *Icterus gularis* (and to lesser degree, *I. nigrogularis*) has evolved the palatal knob which, while not interfering with fruit eating and even some nectar feeding, permits it to remain resident the year round in this unfavorable zone.

THE ROLE OF GEOLOGICAL EVENTS IN SPECIATION

Mountains, Rain Forests, and Rain-shadow Deserts. Despite the constant presence of the selection pressures noted above, the oriole species could hardly have become distinct genetic entities without the isolating influences of Late Tertiary geological events. We are primarily concerned with the topographic and climatic effects of the Late Miocene-Pliocene uplift of the Northern Andes and Central American Highlands (Schuchert, 1935: 46). All of northern Colombia was block-faulted, the stepped graben of the Magdalena valley being 400 miles long and 15 wide with a downthrow on the eastern side of 6500 feet. Equally startling crustal movements resulted in the east-west trend of the mountains of Central America in Late Pliocene, eastern Chiapas rising over 7000 feet with many horsts and grabens passing into fold mountains northward. A major break is indicated in this highly volcanic region which, with the fault block of the Acapulco Deep off the coast of Guatemala (21,288 feet below sea level), has experienced a total crustal displacement of 32,000 feet.

These topographic changes have many indirect effects on species isolation aside from the obvious chance that populations may be split by a mountain range or lava flow. The most important source of isolation in the orioles was the climatic change accompanying uplift. When the rising Andes intercepted the deflected Southeast Trades which are the onshore winds of the Colombian west coast (Murphy, 1939: 24), the climate of the entire corridor into Central America changed. Today these onshore winds, cooled by passing over the Humboldt Current, strike the warmer coast of Peru and southern Ecuador without producing rain—hence, this area is desert. But farther north they pass over a warmer ocean surface to a cooler coast and the precipitation on the western slopes of the Andes has produced the impassable Chocó forest of northwestern Ecuador, Colombia, and eastern Panama. Berry's paleobotanical studies (1938, 1945) appear to date this Andean uplift at Lower or Middle Pliocene.

The interception of the Pacific onshore winds deprived the lowlands extending from eastern Colombia into Venezuela of all precipitation from this source. Winter drought does not permit establishment of a forest here, and nearer the coast a semi-desert occurs. In fact, only the summer rain from the Northeast Trades saves the whole region from becoming a vast rain shadow desert. This moisture supports the grasslands known as the llanos north of the Guaviare River (Pennell in Shelford, 1926: 625) and east to the Orinoco delta. These trades, intercepted by the Central American Highland farther north, provide the year-round rain responsible for the Caribbean rain forest, almost continuous along its eastern slopes.

Therefore, the period of oriole dispersal northward into Central America has seen a forest change to steppe and desert in Caribbean Colombia and Venezuela —a desert change to forest farther north on the Caribbean coast of Central America. Hence, a selective bridge has existed in Central America which has at times, allowed the passage of forest forms, at times, semi-desert forms. Range disjunctions and speciation have been the rule for orioles in this corridor, especially for arid zone forms. It is open to forest forms at present but this has apparently been so only in Recent times.

Biotic Effects of the Pleistocene Glaciation. The climatic alterations due to the Pleistocene glaciation had dramatic effects on biotic distribution in the tropics. The Pleistocene extension of Arapaho Glacier in the Colorado Front Range was nearly 4000 feet lower than its present front (personal observation). Since a similar differential existed in northern Colombia (Schuchert, 1935: 627), it may be assumed that all life zones must have been displaced downward about 4000 feet. The tropical zone was probably driven out of the Cauca valley and even south of the Amazon (cf. Tate, 1939: 154), surviving in the Caribbean areas of South and Central America only as a narrow coastal fringe.

The Pleistocene was a period that favored advanced forms. Subtropical species expanded at the expense of tropical species; the latter were thrust together in restricted areas where only the better-adapted survived to flow back into the present-day tropical zone with the climatic return to normal. A very important effect is the probable elimination of the tropical zone in the Colombia-Panama corridor. Here a lowering of the subtropical zone even 2000 feet from its present position on Serrania del Darien would have blanketed all of Panama, accounting for the present disjunctions of tropical forms. This also explains Chapman's (1917: 157) "Panama fault." He believed subsidence in Panama isolated subtropical forms in northern Central America but the post-Pleistocene return of the tropical zone to the lowlands seems more likely. Schuchert (1935: 558) shows this subsidence to be less than 400 feet.

Since virtually all water gaps were closed by Late Miocene they do not enter; only *I. graduacauda* appears to have been isolated by the Tehuantepec gap.

Dispersal and the Island Isolation of Primitive Forms. Primitive forms may be expected at the periphery of a uniform ecological habitat as a theoretical consequence of Wright's (1943; 1946) view that a favorable mutation will pass readily through the "neighborhood" populations. Since such peripheral forms are slightly less specialized for this habitat they may be better able to adapt to even small habitat changes encountered outward. Such changes may explain the fact that we normally find the most advanced forms at the periphery. Applying this, the pampas region of southwestern Brazil, Bolivia, Paraguay, Uruguay, and northern Argentina appears to be the ancestral home of the Icterinae—3 out of 4 species of cowbirds and 4 out of 8 species of marsh blackbirds overlap sympatricly here. Friedmann (1929: 343), on the basis of song, courtship, and plumage believes that the most primitive cowbird is *Molothrus badius*. It is confined to this range while the most advanced form (*M. ater*) is our North American species. I find a similar relationship among the blackbirds (*Agelaius*)—the single North American species is the most advanced. Because of parallel plumage trends in this immediate ancestor of the orioles, the probable history of *Agelaius* is briefly outlined below.

The origin of the blackbirds from the buntings was arbitrarily put at Middle Miocene because there is good reason to doubt that the finches could have evolved as a type before the grasslands came into existence in the Lower Miocene (Elias, 1942). Since Weeks (1948) has recently shown that the La Plata marine embayment of the Middle Miocene probably separated the pampas from the Brazilian shield by 300 miles of sea, the possibility of isolating the several sympatric species of *Agelaius* in the pampas today becomes apparent. In the following account these are divided into 2 groups—one black with brighter humeral patches, the other black with brighter head and breast. Both are thought to stem from *Agelaius cyanopus* (Fig. 3, *5*) of the Brazilian Highlands, whose black plumage may relate it to the ancestral cowbird. However, the suffused chestnut of its back and wing would have a strong tendency in the Icterinae not only to concentrate in the humeral area but to give way to yellow. The isolation in the pampas of *A. thilius* (number 1 in figure 3) by the maximum extension of the La Plata embayment is thought to have fixed this tendency, *thilius* being black with yellow humeral patches.

In the group lacking the humeral patch, *A. cyanopus* (*5*) appears to have evolved from *A. ruficapillus* (*6*), a form with chestnut crown and breast which may have become isolated in the pampas either by waifing across the embayment or by going around its head during a temporary recession. Imperfect isolation later permitted it to differentiate a northern race in the Brazilian Highlands from which the advanced *A. icterocephalus* (*7*) arose in the Guiana Highlands, largely by replacing the chestnut of head and breast with yellow. The specialized yellow *Xanthopsar flavus* (*8*) is believed to have arisen from *A. ruficapillus* in the pampas south of the embayment as a final phase when the Argentine fault scarps west of Sierra de Cordoba dammed off and dried up

FIG. 3. Evolution in the marsh blackbirds. 1. *Agelaius thilius*; 2. *A. phoeniceus*; 3. *A. humeralis*; 4. *A. xanthomus*; 5. *A. cyanopus*; 6. *A. ruficapillus*; 7. *A. icterocephalus*; 8. *Xanthopsar flavus*.

the head of the bay. Rich (1942) considers these scarps (Sierra de Ulapes, Sierra de Guayaguas) a "fading expression" of the Central Andes (thus probably Late Miocene or Pliocene in time). Whether or not the above hypothesis as to the mode of isolating several sympatric species in an area devoid of geographic barriers today is correct in detail, it is obvious that the means for isolation existed at the right time in the La Plata embayment and in the north-south fault scarps that beheaded it.

Now taking up the group of *Agelaius* having humeral patches, we see that *A. thilius* (*1*), cut off by the embayment, could only disperse southward and northward in the marshes of the slowly rising Andes. There is no direct evidence that the species ever ranged north of eastern Bolivia where a race occurs today but *Macroagelaius* of Colombia's Eastern Andes, with its chestnut humeral patches, almost certainly stems from it. Moreover, the occurrence of forms with the humeral patch in both Central America and the Greater Antilles requires an explanation.

A curious relationship exists here. All three races of *A. thilius* (Fig. 3, *1*) have the humeral yellow patch. *A. humeralis* of Cuba (*3*) has a chestnut patch but *A. xanthomus* of Puerto Rico (*4*), certainly derived from *humeralis*, again has a yellow patch. The replacement of chestnut by yellow in more advanced forms was implied in the derivation of *thilius* from *cyanopus*. It has occurred in *Macroagelaius* where the form of the Guiana Highlands has substituted yellow for the chestnut of the Andean form—also in *Gymnostinops* and *Xanthornis* among the cassiques. But the above picture for *Agelaius* is exactly duplicated in species of *Bananivorus* where the yellow humeral patch replaces the chestnut one of earlier forms. Since *Bananivorus* is believed to stem from *Agelaius thilius*, it is noteworthy that in the latter genus of exclusive march-dwellers the Antillean forms alone are arboreal. However, the work of Taber (1934) and Palmer (1945) indicates that the vast present-day marshes of Cuba are Recent, nearly all of the island being submerged by the return of Pleistocene melt water to the sea. *A. humeralis* may have reached Cuba from the ancestral *thilius* stock of Central America as a typical marsh-dweller when it was emergent in the Early Pliocene. The Recent inundation accounts for its arboreal adaptations.

A relict marsh may have survived on the Zapata Peninsula (Barbour and Peters, 1927) but the marsh adaptations of *humeralis* did not. In it we see the first stages of such a transition as in the pampas resulted in the origin of the new genus of Cayenne Orioles, *Bananivorus*. The bill is not greatly modified but the claws are shorter and strongly decurved like those of *Bananivorus cayanensis*. *A. xanthomus* is apparently the result of a colonization of Puerto Rico by the Cuban form across the sea after the stock had become arboreal. The recent discovery of *humeralis* on Haiti (Wetmore and Swales, 1931) suggests hurricane winds as the agency. The yellow-bordered red humeral patch of *A. phoeniceus* (*2*) in Central and North America is suspected of being a further elaboration of yellow in the transition from the primitive chestnut—the deep orange of mainland orioles in contrast to the yellow of Antillean relatives suggests how red might be intensified under selection.

Cuba thus appears to be a haven for relicts in the Icterinae and the retention there of primitive plumage patterns will be seen in *Bananivorus* presently. I believe that in *Agelaius* the chestnut humeral patch of the Cuban species reflects the (elsewhere displaced) primitive condition. *Humeralis* and *xanthomus* alone in the entire genus lack plumage dimorphism. I am drawn to the possibility that the ancestral form of *A. thilius* which evolved *Bananivorus cayanensis* at the northern border of the pampas may have had chestnut humeral patches like the latter, and that in both genera these have gradually given way to yellow. Genetically, reverse evolution with yellow-shouldered *A. thilius* evolving into chestnut-shouldered *humeralis* or *B. cayanensis* is just as possible, but the color trends do not seem to support this alternative.

The evolution of the orioles from the marsh-blackbirds is therefore regarded as having occurred fairly early in the history of the latter so that the evolution of the two has been comtemporary. Once the nectar- and fruit-adaptations were made, the break with *Agelaius* was complete, and the orioles radiated rapidly into the new forest habitat with ever-increasing specialization. From this point *Agelaius* became channelized as a seed and insect feeder. The difficulty of making further adaptations of the same kind in the face of oriole competition eliminated it from the contest. True, its pre-adaptation placed it under pressure to evolve a mud-probing form with the same gaping mechanism seen in the orioles, and *Amblyramphus* (Wetmore, 1926: 389) was evolved to fill this niche. But its value to this paper has run out.

A Phylogenetic Arrangement of the Orioles

Although Mayr (1942) expresses the accepted view in stating that convenience is a major consideration in classification, he adds that it should also express evolutionary relationships so far as possible. Once again as we enter the detailed discussion of the orioles we must emphasize the failure of the old systematics in its attempt to solve this problem. Its static morphological approach did not permit us to consider such a genus as will be proposed below; the genetic basis of the new systematics does not permit us to ignore it.

I. The genus *Bananivorus* Bonaparte

Bananivorus Bonaparte, Compt. Rend. Acad. Sci. Paris, **35:** p. 834, 1853. Type by original designation, *Oriolus bonana* Linnaeus.

Diagnosis. Due to the complete convergence of this genus with *Icterus* and consequent overlap of external characters normally used in taxonomy, all attempts to characterize it have failed. No diagnostic anatomical differences have been found but none were expected in such close genera—nor did X-rays of skins with undamaged skulls covering all species reveal clear-cut distinctions. In general, members of this genus are very markedly smaller with more slender, nectar-adapted bills; but island forms such as *B. laudabilis*, *oberi* and *northropi* show the typical "island effect" by increasing the mass of the bill. Hence it is often less slender than that of *I. pectoralis* (the most slender-billed of the nectar-adapted species of *Icterus*). Some of these island outlyers even exceed temperate *Icterus* species in total size (e.g. *I. galbula*).

It is obviously unreasonable, since these are convergent genera, to expect a clear-cut diagnosis of *Bananivorus* that will exclude all forms of *Icterus*. Both reduce body bulk northward but comparisons to be valid must be made in the same area and life zone, thus eliminating specialized outlyers. This method reveals that in the deciduous forest of North America, *B. spurius* is much smaller than *I. galbula*; in California *B. cucullatus* is smaller than *I. bullockii*; in arid Central America *B. cucullatus* is smaller than *I. pustulatus*, *pectoralis*, *chrysater* or *gularis*; in arid Colombia *B. auricapillus* is smaller than *I. nigrogularis* or *icterus*. Finally, in the temperate oak-pine of El Salvador *B. maculi-alatus* is smaller than *I. chrysater*; in the Caribbean rain forest *B. prosthemelas* is smaller than *I. mesomelas*; and in the Amazonian rain forest *B. cayanensis* and *chrysocephalus* are smaller than *I. icterus*. Comparisons between island forms are invalid because the two genera never occur on the same islands and the island forms of *Bananivorus* have obviously increased in size of body and bill to take over fruit-eating functions normally belonging to *Icterus*. The reverse tendency in *Icterus* (taking over nectar feeding in the absence of *Bananivorus*) is seen in island races of *I. nigrogularis* and in *I. leucopteryx* with their longer, more slender bills. Regional comparison for convergent genera occupying the same range seems to be the only valid method and it completely separates *Bananivorus* and *Icterus* without overlap.

The bill is too responsive to adaptation to be a good character in these convergent genera. Though *Bananivorus* has its slender bill longer with respect to skull-length, *B. spurius* in temperate North America obviously does not require a long bill for the small flowers and fruits of northern trees—nor, strangely, does *B. cayanensis* in the rain forest. Its bill and gaping musculature like that of *Coereba* suggest that, like that species, it pierces through the side of a flower corolla. All remaining species of *Bananivorus* are clearly flower probers with bills longer proportionately than any species of *Icterus* except *I. icterus*, whose long bill is also an obvious specialization for probing large flowers and fruits.

The method used in separating this genus from *Icterus* has been one of tracing opposite trends or clines in each northward from the centers of origin at the northern border of the pampas where each originates independently from agelaiine stock. To designate the two phyletic lines as subgenera (cf. Simpson, 1945: 18) would be to de-emphasize their separate origin as well as the fact of convergence.

A final character, perhaps sufficient in itself, is a non-morphological one which, nevertheless, clearly expresses the underlying gene complex: a unique method of building the nest in *Bananivorus*. Small and compact, it is invariably woven of palm fibre if available and joined to the underside of a palm or banana frond by *sewing through* the living leaf and pulling its sides down about the nest. Though temperate forms depart from this habit for want of large leaves, *B. parisorum* still sews to the underside of yucca leaves. The nests of *wagleri* and *spurius* are small, compact, unlike the long, pendant nests of *Icterus*.

The Origin of Bananivorus from Agelaius thilius. Bananivorus cayanensis is believed to have evolved from an ancestral form of *Agelaius thilius* in the ecotone where the northern part of the grassland gives way to Amazonian rain forest. Since *Agelaius* today is well adapted to take both nectar and fruit occasionally, it is plausible that individuals and then populations under selection pressure invaded the low plantains or palms adjacent to their marsh habitat for this abundant food. This is thought to have occurred as discussed above through adaptive modification of the bill without much immediate pressure to alter the chestnut humeral patch of the black plumage.

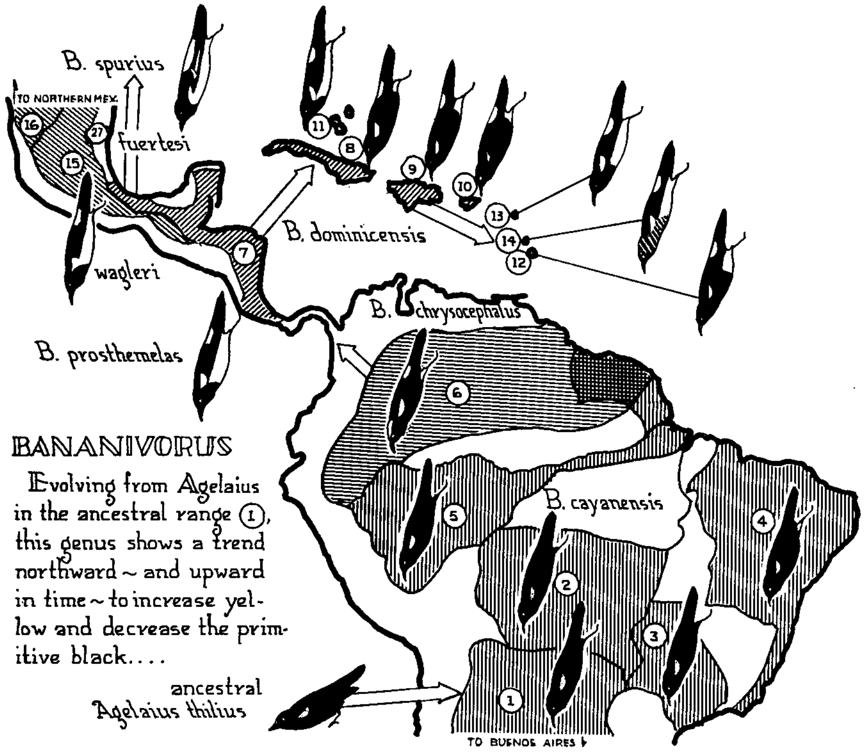


FIG. 4. Evolution in the genus *Bananivorus*.

1. *Bananivorus cayanensis pyrrhopterus*
2. *Bananivorus cayanensis periporphyrus*
3. *Bananivorus cayanensis valencio-buenoi*
4. *Bananivorus cayanensis tibialis*
5. *Bananivorus cayanensis cayanensis*
6. *Bananivorus chrysocephalus*
7. *Bananivorus prosthemelas*
8. *Bananivorus dominicensis melanopsis*
9. *Bananivorus dominicensis dominicensis*
10. *Bananivorus dominicensis portoricensis*
11. *Bananivorus dominicensis northropi*
12. *Bananivorus laudabilis*
13. *Bananivorus oberi*
14. *Bananivorus bonana*
15. *Bananivorus wagleri wagleri*
16. *Bananivorus wagleri castaneopectus*
27. *Bananivorus fuertesi*

Note. The temperate zone *B. spurius* is not mapped.

Trend Toward Addition of Yellow in Humid South America. If *B. cayanensis pyrrhopterus* (Fig. 4, *1*) was under little pressure in its new habitat to alter plumage the same is true of *B. c. periporphyrus* (*2*), the next form northward. But *B. c. valencio-buenoi* (*3*) entering the Brazilian Highlands has the humeral patch distinctly more yellow-chestnut and *B. c. tibialis* (*4*) still farther north has not only the humeral patches but the tibial area yellow. In fact, just within this race a cline increasing yellow occurs northward. Meanwhile, *B. c. cayanensis* (*5*), probably forced into its present range south of the Amazon by the southward advance of the subtropical zone in the Pleistocene, has also changed its humeral patch to yellow. *B. chrysocephalus* (*6*), which has added yellow to the head and rump in addition to humeral and tibial areas, has apparently reinvaded the entire area north of the Amazon in Recent times from a Pleistocene refuge in the Caribbean coast tropical zone fringe. Its ability to do so against the competition of less-advanced *cayanensis* to the south suggests a selective advantage for increased yellow in the plumage.

Trend Toward Addition of Yellow in the Antilles. The more arid-adapted members of *Icterus* take over the winter drought range in Colombia and Venezuela along the Caribbean but we find *Bananivorus* again in the Caribbean rain forest of Central America as *B. prosthemelas.* This species is the logical culmination of the steady northward increase of yellow in the humid tropical zone, having added this color to its entire abdomen and upper breast. The abrupt increase in yellow is probably only apparent, however, due to wiping out of the intervening population by the dry-season rain shadow of northern Colombia following the uplift of the northern Andes. What this intervening population looked like and what an earlier *prosthemelas* population looked like may probably be inferred from the forms which reached the Greater Antilles from it across a partial Pliocene land bridge from Honduras. These forms most resemble *B. chrysocephalus* but lack the yellow of the head which that species probably developed subsequently.

Once again, therefore, Cuba appears to preserve a relict plumage pattern but, since this genus is younger than *Agelaius*, disjunction with mainland forms is less strong. *B. dominicensis melanopsis* of Cuba (*8*) has the tibiae and crissum barely yellow whereas *B. d. dominicensis* of Hispaniola (*9*) increases yellow on the lower abdomen and *B. d. portoricensis* of Puerto Rico (*10*) is intermediate. As often happens in island colonization, these forms may have met with relatively little competition and thus experienced little pressure to increase yellow at the mainland rate.

There are, however, peripheral forms in the Bahamas and Lesser Antilles that have added yellow almost to the extent of *prosthemelas*, though I agree with Chapman (1891: 539) and Bond (1945: 144) that *northropi* (*11*) of Andros and Abaco is an offshoot of *B. dominicensis*, not of *prosthemelas.* It was undoubtedly carried there from either Cuba or Hispaniola by hurricane winds as were the Lesser Antillean forms carried from Hispaniola by hurricane winds athwart which they lie (cf. Darlington, 1938: 283). I agree with Bond that the latter are distinct species related to *B. dominicensis* for it appears that each must have colonized the islands separately from the Greater Antilles. The southernmost form on Santa Lucia, *B. laudabilis* (*12*), shows little more yellow than the Hispaniolan bird and may not have been isolated as long as the northernmost form, *B. oberi* (*13*) of Montserrat which is almost as yellow as *northropi.* The suffusion of chestnut in the yellow of these forms culminates in the erythristic *B. bonana* (*14*) of Martinique in which the black of head and breast is replaced by chestnut grading into dusky orange ventrally. Such a color anomaly, involving possibly a simple gene change at one locus, should not obscure the fact that, toward the parent *B. dominicensis*, all three species show the same increase of yellow noted in *northropi.*

Since the Montserrat form is separated from the Martinique form by two large islands (Guadeloupe and Dominica) on which no oriole occurs, it is difficult to link them as races of a Lesser Antillean species, nor does the inclusion of all Caribbean island forms under a single polytypic species seem warranted. Nevertheless, there is little doubt of their Greater Antillean origin from *B. dominicensis* and the tendency for all Bahaman and Lesser Antillean peripheral forms to add yellow recalls the trend away from the primary center of origin in South America. Since one moves upward in time as one moves outward through all of these populations, the increase in yellow is seen to be a time trend.

Selection for Yellow as a Time Trend. The black plumage of the ancestral *Agelaius*, so advantageous for flocking marsh dwellers, seems singularly unadapted for forest-dwelling orioles. The increase in the more conspicuous yellow, during time as well as in space is therefore being selected. It may be asked why, then, the chestnut humeral patch of *B. c. pyrrhopterus* (*1*)—the oldest form at the center of origin—has not been replaced by yellow. This may be happening, just as it is thought to have happened in *Agelaius thilius,* but the process could be greatly decelerated by the following principle of diffusion:

The sparse, ever-expanding peripheral populations are probably under strong pressure to increase yellow. It would be useful in keeping contact among pioneering groups, vital to island colonizations. Each slightly different habitat encountered outward results in a more yellow population and this added yellow, being selected for, will tend to spread in all directions, even backward toward the center of origin. But on that side is met an established, less yellow population through which the change must diffuse slowly, whereas on the peripheral side no resisting population exists and yellow increase can be rapid. In a concentric distribution of populations, therefore, it appears that each more peripheral race will buffer any race lying closer to the center of origin from backward diffusion of further increments of yellow fixed in the pioneering populations. Thus, in Figure 4, *B. c. pyrrhopterus* (*1*) is buffered by *periporphyrus* (*2*) and *valenciobuenoi* (*3*) from advances in yellow made by *cayanensis* (*5*) and *tibialis* (*4*). Nevertheless, these southern populations seem to be gradually succumbing to the backward diffusion of advances in yellow made by the more northern populations. Their present plumage is non-adaptive in the sense of Robson and Richards (1936).

This may be why *B. c. pyrrhopterus* at the center of origin still has the original plumage pattern of ancestral *Agelaius thilius*. One might predict from the above that the older *Agelaius* would have had time to complete the replacement of chestnut by yellow so that only the Cuban relict, *humeralis*, reflects the former aspect. On the other hand, loss of chestnut in the Cuban *Bananivorus* indicates the probable pressure on this younger genus to increase yellow in the forest. Chestnut was probably suppressed before its expanding populations reached Central America.

Convergence in the Arid Tropical Zone of Central America. Occupying virtually the entire Caribbean rain forest, *B. prosthemelas* (*7*) appears to be the evolutionary culmination of movement toward yellow in the humid tropical zone. It has also gone as far as it can go, for it is hemmed in on all sides by the arid tropical and temperate zones. Under the resulting competition, selection pressure to adapt to new life zones would be extremely severe on peripheral populations and probably produced those arid tropical species so strangely convergent with forms of *Icterus* in the same zone. This required only the further addition of yellow to head and neck.

To the north on the arid Caribbean coasts of Mexico *prosthemelas* evolved the Hooded Oriole, *B. cucullatus* (Fig. 5, *19* to *25*) and to the south in arid northern Colombia and Venezuela, *B. auricapillus* (*26*). The essential difference between the two is that the latter lacks white in the wing as does *prosthemelas* while the former adds white in the wing but lacks the yellow humeral patch. Otherwise they are very similar as noted by Todd and Carriker (1922: 473)—and, coming from opposite ends of the *prosthemelas* population, are correctly designated separate species. At the outset in this study the relationships of all oriole species were determined on the basis of horny palate as a control upon plumage convergence. This additional line of evidence shows that the bill of *auricapillus* has diverged little from that of the parent *prosthemelas*; that of *cucullatus* has become more slender and decurved.

Concerning time relations, the isolation of *auricapillus* from *prosthemelas* could hardly have occurred before the Andean uplift produced the winter-drought area of northern Colombia and Venezuela, probably in Early Pliocene. The origin of *cucullatus* from *prosthemelas* on the north is ascribed to Late Pliocene volcanic activity which is roughly checked by the time of disjunction between *B. c. cucullatus* (*20*) on the arid Caribbean coast of Mexico and *igneus* (*22*) and *masoni* (*25*) on arid Yucatan. Since this occurrence probably dates from the origin of the Caribbean rain forest when the Late Pliocene uplift of the Central American Highlands intercepted the Northeast Trades, it follows that *B. cucullatus* antedates this geological event. This should also dispel any notions of relating this species to the convergent *Icterus pectoralis* which arose inland much later—too late to reach the arid parts of the Caribbean coast at all because the forest was already there.

It is in the arid tropical zone that convergence between the 2 genera of orioles reaches that point where plumage patterns are virtually identical (Fig. 12). The pattern is apparently being selected for and, since it represents the maximum addition of yellow (now supplemented by white), this varied pattern may be the most conspicuous one possible. Construction of nests in protected situations (e.g. thorn trees) may explain how such a thing can have survival value.

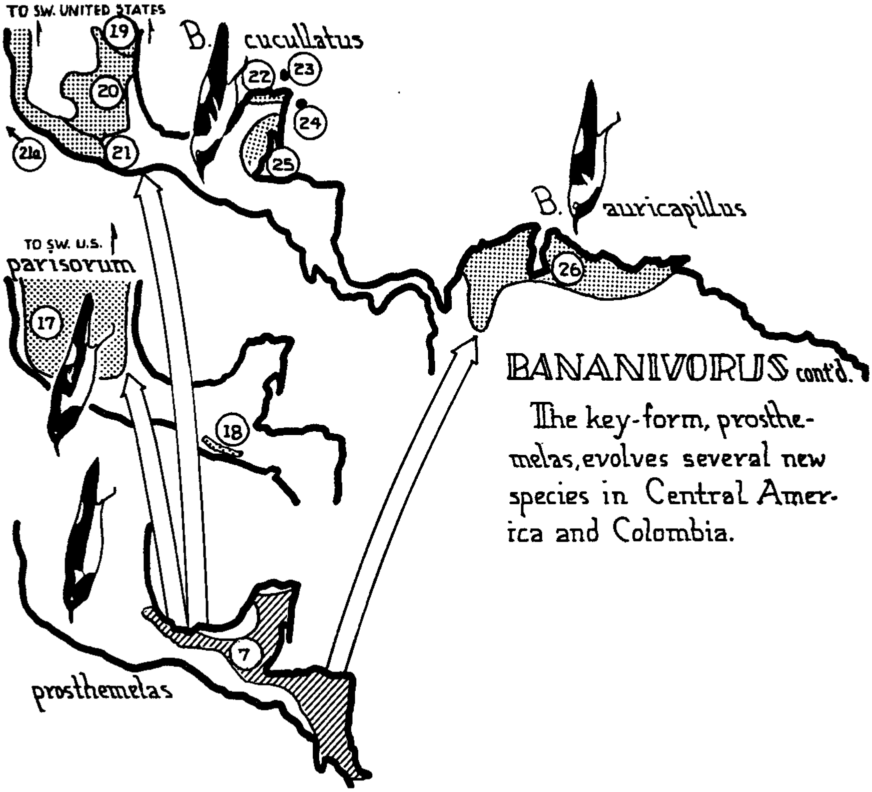


FIG. 5. Evolution in the genus *Bananivorus.*

7. *Bananivorus prosthemelas*
17. *Bananivorus parisorum*
18. *Bananivorus maculi-alatus*
19. *Bananivorus cucullatus sennetti*
20. *Bananivorus cucullatus cucullatus*
21. *Bananivorus cucullatus californicus*
21a. *Bananivorus cucullatus trochiloides*
22. *Bananivorus cucullatus igneus*
23. *Bananivorus cucullatus duplexus*
24. *Bananivorus cucullatus cozumeli*
25. *Bananivorus cucullatus masoni*
26. *Bananivorus auricapillus*

Convergence in the Temperate Zone of Mexico and Northward. The same environmental pressure which produced the arid tropical species just treated caused *B. prosthemelas* to adapt to other life zones. Above its Caribbean lowlands between 3000 and 6000 feet it evolved *B. wagleri wagleri* (Fig. 4, *15*) as a highland subtropical species which, with its race *castaneopectus* (*16*), ranges south to Nicaragua. Northward, it evolved temperate Scott's oriole, *B. parisorum* (Fig. 5, *17*)—possibly conspecific with the relict *maculi-alatus* (*18*)—which ranges into southwestern United States. But the selection trend has changed in these more temperate forms. True, *parisorum* in temperature semi-desert has added white wing-bars in partial approach to arid *cucullatus* but *wagleri* has actually added black to the crissum in probable response to a temperate zone trend toward reduced conspicuousness.

A volcanic area extends across all of Mexico from Jalapa, Vera Cruz to Cape Corrientes on the Pacific coast which will be seen to disrupt the range of every oriole species in this area. It apparently cut off the important species *B. fuertesi* from *prosthemelas*. This rare form of the Caribbean coastal forest to the north of the Volcanic Province has slightly decreased the black area of the upper breast and is simply an ochraceous version of the Orchard Oriole, *B. spurius*, which replaces it in eastern North America. The atavistic replacement of yellow by chestnut in this familiar species, already evident in *fuertesi*, marks a reversal of selection pressure. A similar though less advanced reduction of yellow in the Baltimore Oriole, *Icterus galbula*, suggests a general selection against conspicuousness in the temperate zone. This with the simultaneous occurrence of sexual dimorphism giving protective coloration to females may be correlated with the dying out northward of thorn trees and protecting wasp colonies utilized by orioles in their tropical range. *B. fuertesi* may be only a race of *spurius* (Wetmore, 1943: 323).

Nectar-feeding in Bananivorus. Although the primary modification of the bill for nectar-feeding in this genus was first suspected on anatomical grounds, the literature provided ample basis from field observations. Dickey and van Rossem (1938: 534) report hundreds of *B. spurius* in migration feeding on nectar in a flowering ceiba. Bailey (1928: 651) found *B. parisorum* feeding on nectar and insects at flowers of agave and yucca and notes that Grinnell found *B. cucullatus californicus* feeding with hummingbirds at "a profusely blooming ironwood;" the fruit eaten was negligible. Wetmore (1926: 383) found that *B. cayanensis pyrrhopterus* fed on "blossoms of such trees as the lepacho (*Tecoma obtusata*) and at all seasons were partial to vines and creepers," often swinging head-down in their efforts. Wetmore and Swales (1931: 409) also report seeing *B. d. dominicensis* congregated in flocks about flowers especially of agave and orange with honey-creepers, hummingbirds, and woodpeckers. The race *portoricensis* Wetmore found (1916: 115) "fond of the sweet flower juices of plants . . . the bucare (*Erythrina sp.*) being visited frequently in blossom" as well as the banana. Although I have seen *Icterus galbula* feeding on flowers in spring (e.g.

horse chestnut), this is incidental. Except for the forms of this genus secondarily modified for nectar-feeding, *Icterus* is fruit-adapted. That both genera eat many insects at times should not be surprising. Few birds are complete specialists as to food type.

Nesting in Bananivorus. The need of this genus for broad-leaved plants—banana or palm—to which to sew the compact nest of palm fibres doubtless stems from its humid tropical origin. Naumburg (1930: 397) reports the habit for *B. cayanensis pyrrhopterus* in Matto Grosso, and Beebe (1917: 243), for *B. chrysocephalus* in Venezuela. It is typical also for *B. d. dominicensis* in Hispaniola (Wetmore and Swales, 1931: 409) for *laudabilis* on Santa Lucia (Semper, 1872: 649) and *bonana* on Martinque (Taylor, 1864; Lawrence, 1879). *B. oberi* was first reported by Grisdale (1882: 487) in mountain palms on Montserrat in which Bond (1939: 194) has since found it nesting—while *northropi* (Allen, 1890) was found only in the coastal palms of Andros in the Bahamas. In Central America, Richmond (1893), Salvin and Godman (1904: 467), and Griscom (1932: 392) report *B. prosthemelas* nesting the same way.

But even species of the arid tropics cling to the trait. Todd and Carriker (1922: 473) report it for *B. auricapillus,* and Bailey (1910: 35) reports that 40 out of 52 nests of *cucullatus* were in fan palms. Ewan (1944), Huey (1944), and Grinnell (1944), carry on an interesting discussion of it in California. In more arid areas *cucullatus* and *parisorum* nest under the overhanging leaf of the yucca, using the fibres of the same plant and sewing through the leaf (Bailey, 1928). The transition away from broad leaves, which had to be made if the genus was ever to enter the humid temperate zone, is suggested by *cucullatus* nests I have seen from a sycamore (*Platanus*) taken in Arizona, and a thorn tree (*Randia*), in Yucatan. In both, the nest fibres pass through holes in the leaves. Pettingill (1942: 89) even reports the species threading fibres through pierced holes in his tent blind.

But eventually the transition must be made. *B. wagleri* in the oak-pine has a nest compactly woven of grass (Salvin, 1859: 468) as is that of *spurius* in the eastern deciduous forest. But the fondness of the Orchard Oriole for the bushes and reeds of the Louisiana marshes (Oberholser, 1938: 591) links it by way of *fuertesi* to the primitive members of the genus in the Amazonian forest borders.

II. The genus *Icterus* Brisson

Icterus Brisson, Orn., 1760, I, 30; II, 85. Type, by tautonymy, *Icterus* Brisson—*Oriolus icterus* Linnaeus.

Diagnosis. Convergence with *Bananivorus* renders clear-cut characterization impossible. *Icterus* is always larger under regional comparison, however, and the nest is typically long and pendant; not even the shorter nests of temperate forms equal the tight, round nests of *Bananivorus* (see Diagnosis).

The Origin of Icterus from Xanthopsar flavus. In the phylogeny of the blackbirds (Fig. 3), *Agelaius* was seen to produce a *thilius* group and a *cyanopus* group. Whereas *thilius* clearly evolves the black banana orioles, *Bananivorus*, the *cyanopus* group produces a largely yellow form, *Xanthopsar flavus*, considered the most likely ancestor of the genus *Icterus*. *Gymnomystax* with its agelaiine horny palate could be considered for this position but in all other respects it is already an oriole. *Xanthopsar*, therefore, probably evolved both *Gymnomystax* and *Icterus*. Their larger size and longer bills are humid tropical adaptations to large fruits, seen also in the evolution of large oropendolas from small cowbirds. The peculiar nectar-feeding habits of *Bananivorus* called for no such size increase.

The derivation of *Icterus* is necessarily speculative, however, and all we know is that it stems from an agelaiine blackbird that was probably largely yellow. *Gymnomystax*, ranging from Amazon to Caribbean, could have evolved the oldest *Icterus* species (*jamacaii* and *icterus*) but the bare mandibular and ocular areas (probably a selective result of sticky fruit juices fouling plumage) are more specialized in *Gymnomystax* than in these supposed derived forms. The lanceolate breast feathers of the latter and the long first primary of *Xanthopsar* indicate that specializations have occurred since the splitting off that will always cloud exact ancestry.

Trend Toward Addition of Black in Humid South America. The most significant generalization about *Icterus* is that, from a mainly yellow ancestral condition at the center of origin in the southern part of the Amazonian forest, the plumage tends to add black peripherally. This is seen to be a northward trend precisely opposite that observed in *Bananivorus* and may reflect the gradual shift from humid to arid tropical zones. At any rate it is clearly a movement in the direction of that exact pattern apparently being selected for by both genera in the arid tropical zone.

The troupials—*Icterus jamacaii* (Fig. 6, *1*, *2*, *3*) and *I. icterus* (*4*, *5*)—seem to be conspecific as suggested by Hellmayr (1937), the forms replacing each other geographically. They illustrate the above plumage trend. *I. icterus strictifrons* (*1*) and *croconotus* (*2*) in the ancestral Paraguayan and Amazonian lowlands respectively, are the forms with most yellow and least black. Radiating outward from these, the form of the Brazialian Highlands, *jamacaii* (*3*) and the forms of semi-arid Colombia and Venezuela, *ridgwayi* (*4*) and *icterus* (*5*), add black on head and back, and increase a white wing patch which mainly involves the secondaries and elongates the lanceolate breast feathers. The latter two northern forms also increase the bare postocular area and bill length in possible adaptation to the fruit and nectar of the giant cactus (see Todd and Carriker, 1922: 475). A habitat shift seems to occur northward also; the bamboo nesting site on the Amazon gives way on the semi-arid Caribbean coast to sites in scrubby second growth. In this group Brodkorb's (1937) race *paraguayae* is regarded as a variation of *strictifrons*.

I. graduacauda graduacauda (*6*) and *auduboni* (*7*) are thought to represent a relict population of the early, forest-dwelling *I. icterus*, cut off by the

Tehuantepec water gap since late Miocene and now found largely in temperate forest from the Mexican Highlands to the Rio Grande valley. The relatively short bill and yellow back suggest the probable aspect of the ancestral *I. icterus* before specialization (Fig. 6). Dull color and solitary habits permit survival in the north, though competition and climatic change have prevented its southward spread since the Lower Pliocene closing of the gap. Two new forms of this species have been described by van Rossem (1938: 137)—*dickeyae* in the Sierra Madre of Guerrero and *nayaritensis* from Tepic. Sclater (1939: 141) described another, *richardsoni*, from Tehuantepec, Oaxaca.

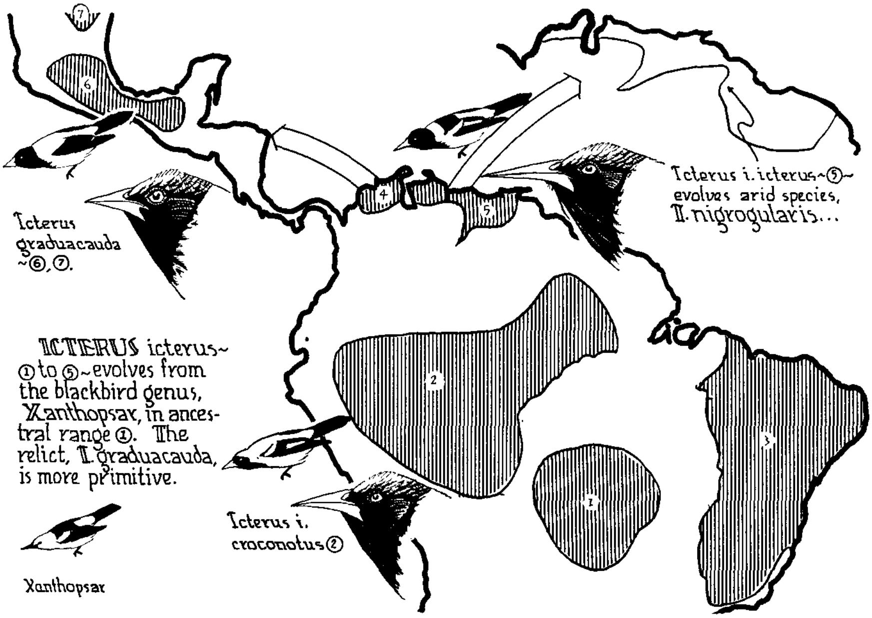


FIG. 6. Evolution in the genus *Icterus*.

1. *Icterus icterus strictifrons*
2. *Icterus icterus croconotus*
3. *Icterus icterus jamacaii*
4. *Icterus icterus ridgwayi*
5. *Icterus icterus icterus*
6. *Icterus graduacauda graduacauda*
7. *Icterus graduacauda auduboni*

The creation of semi-desert in Caribbean Colombia and Venezuela by the uplift of the Northern Andes probably resulted in the evolution of arid zone *Icterus nigrogularis* from an ancestral, unspecialized *I. icterus* (Fig. 6). This is suggested by the yellow back of *nigrogularis* (Fig. 7, *8*), like that of *graduacauda*. The island forms of *nigrogularis*—*trinitatis* (*9*) on Trinidad and Monos, *helioeides* (*10*) on Margarita and *curasoensis* (*11*) on Curacao, Bonaire and Aruba—increase bill-size and wing-length.

Trend Toward Addition of Black and Diet Specialization in the Arid Tropical Zone. The key form *nigrogularis* appears to have reached a position similar to that of *B. prosthemelas* with unusual opportunities for invading new niches. Wetmore (1919: 195) noted that this species of arid Colombia and Venezuela has a palatal knob such as he described for Central American *I. gularis*. Examination of many examples of *nigrogularis* shows, however, that some individuals lack the knob entirely. It seems to exist as an allele that adaptively segregates under isolation in *gularis*.

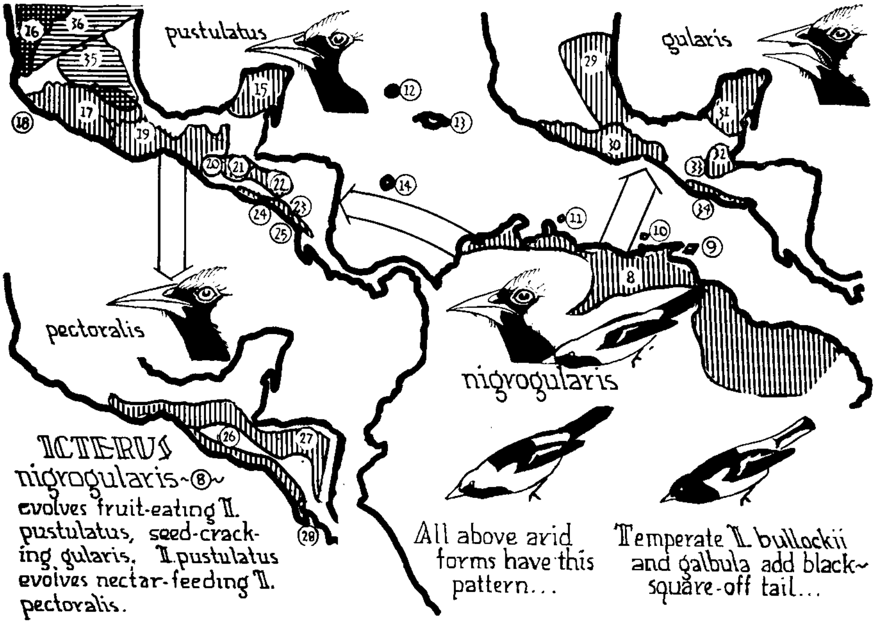


FIG. 7. Evolution in the genus *Icterus*.

8. *Icterus nigrogularis nigrogularis*
9. *Icterus nigrogularis trinitatis*
10. *Icterus nigrogularis helioeides*
11. *Icterus nigrogularis curasoensis*
12. *Icterus leucopteryx bairdi*
13. *Icterus leucopteryx leucopteryx*
14. *Icterus leucopteryx lawrencii*
15. *Icterus pustulatus auratus*
16. *Icterus pustulatus microstictus*
17. *Icterus pustulatus pustulatus*
18. *Icterus pustulatus graysonii*
19. *Icterus pustulatus formosus*
20. *Icterus pustulatus maximus*
21. *Icterus pustulatus alticola*
22. *Icterus pustulatus flammulatus*
23. *Icterus pustulatus pustuloides*
24. *Icterus pustulatus connectens*
25. *Icterus pustulatus sclateri*
26. *Icterus pectoralis pectoralis*
27. *Icterus pectoralis anthonyi*
28. *Icterus pectoralis espinachi*
29. *Icterus gularis tamaulipensis*
30. *Icterus gularis gularis*
31. *Icterus gularis yucatanensis*
32. *Icterus gularis xerophilus*
33. *Icterus gularis gigas*
34. *Icterus gularis troglodytes*
35. *Icterus bullockii abeillei*
36. *Icterus bullockii bullockii*

Note. The temperate zone *I. galbula* is not mapped.

A more extensive range must be assumed for *nigrogularis* in the early Pliocene for two distinct groups spring from it to follow largely parallel evolutionary trends. The first stems from *I. chrysater* (Fig. 8), a yellow-backed subtropical offshoot of *nigrogularis* in northern Colombia and Venezuela. This black-tailed, black-winged species which has the variable wing white of *nigrogularis* completely suppressed, gives rise to a nectar-feeding derivative, *I. mesomelas.* Peripheral forms of each in Ecuador and Central America add black and white as an evolutionary advance.

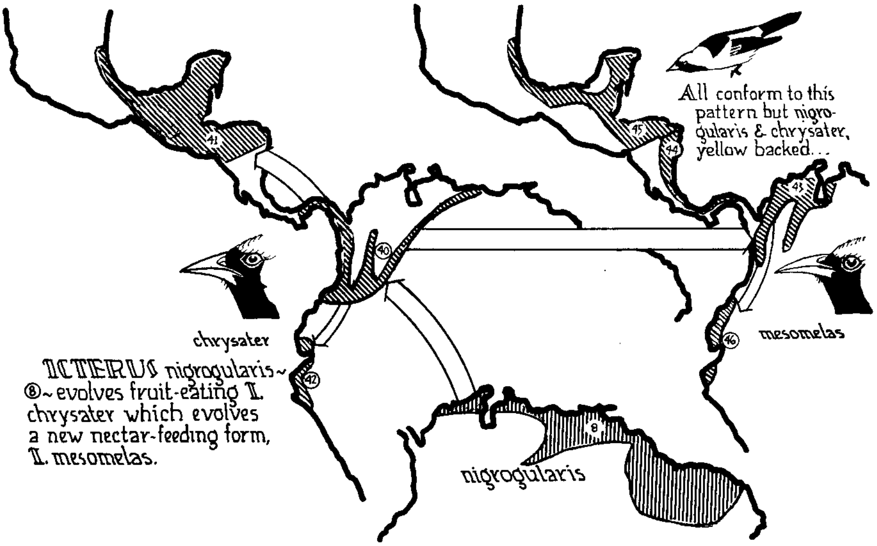


FIG. 8. Evolution in the genus *Icterus.*

8. *Icterus nigrogularis nigrogularis*
40. *Icterus chrysater giraudii*
41. *Icterus chrysater chrysater*
42. *Icterus grace-annae*
43. *Icterus mesomelas carrikeri*
44. *Icterus mesomelas salvinii*
45. *Icterus mesomelas mesomelas*
46. *Icterus mesomelas taczanowskii*

The second group (Fig. 7) has the wing white of *nigrogularis* in all forms and likewise progressively adds black to the back. More important, it shows the segregation of the palatal knob in *I. gularis* as a seed-cracking adaptation. A fruit-adapted counterpart, *I. pustulatus,* lacks it entirely, even evolving the nectar-adapted species *pectoralis*—and all three occupy the same Central American range, from which they have evidently displaced the parent *nigrogularis.* All have roughly the same plumage pattern—one which is virtually identical with that of convergent *Bananivorus cucullatus.*

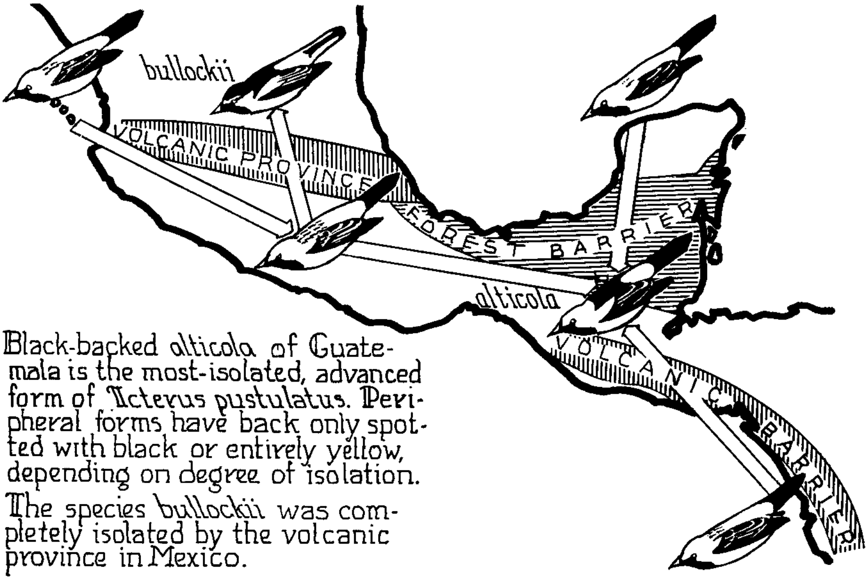
The chrysater-mesomelas Group. Taking up the first group in detail, *Icterus chrysater* (Fig. 8, *40* to *42*) is believed to be a subtropical offshoot of *nigrogularis* (*8*) in northern Colombia and Venezuela. It is yellow-backed like *nigrogularis* but completely lacks wing white in the ancestral range occupied by *I. c. giraudi* (*40*)—under which Miller (1947) has synonymized *I. hondae* Chapman. The fruit-adapted *grace-annae* (*42*), cut off from *giraudi* in the subtropical zone of West Ecuador by the early Pliocene origin of the Chocó forest, has added black to the back and introduced some white in wing and tail. The Ecuadorean form of the associated nectar-feeder—*I. mesomelas taczanowskii* (*46*)—also adds white to these parts. Examining the representatives isolated in Central America, however, we find that *I. chrysater chrysater* (*41*) is little different from the Colombian parent form, *giraudi*. In fact the range disjunction is probably post-Pleistocene. But the same Pleistocene lowering of life zones resulting in the subtropical bridge linking them from Colombia to northern Nicaragua is believed to have eliminated the tropical zone from Panama. Hence, the range disjunction between *I. mesomelas carrikeri* (*43*) in Colombia and *salvini* (*44*) in western Panama is of Pleistocene origin. Whereas these forms are correspondingly similar, *I. mesomelas mesomelas* (*45*) in the northern part of the Caribbean rain forest shows longer isolation from *carrikeri*, and introduces white in the wing as did *taczanówskii* (*46*) in Ecuador. All forms of *mesomelas* differ from *chrysater* in having yellow outer tail feathers, a character which may be specially selected for in the humid forest.

That the advance in these peripheral forms to black back and wing white represents a trend upward in time as well as outward in space from the center of origin can be supported readily. *I. mesomelas*, as a nectar-adapted form derived from *I. chrysater*, is later in time, and wherever forms of the two occur in the same region *mesomelas* is more advanced in these characters.

The pustulatus-pectoralis-gularis Group. There seems to be little doubt that a population of *nigrogularis* (Fig. 7, *8*) became isolated in Central America when the northern part of the Chocó forest cut this arid region off from arid northern Colombia. This population probably evolved the island species *I. leucopteryx* in the Caribbean: *I. leucopteryx bairdi* (*12*) may have ventured out on the partial Cuban bridge after *Bananivorus* and, finding the ridge from Cuba's Sierra Maestra faulted out, remained on Grand Cayman; *leucopteryx* (*13*) may have used another incomplete birdge to Jamica; *lawrencei* (*14*) could have reached St. Andrews by a short hop from the same bridge. But it was probably in volcanic Guatemala that *nigrogularis* broke down into the three modern species which have adaptively segrated its bill characters.

The *nigrogularis* population evidently occupied all of arid Central America and one might easily take *auratus* of Yucatan (*15*) to be a form of the ancestral species. It is, however, more likely a form of the modern Central American descendant of *nigrogularis*, i.e. *Icterus pustulatus* (*15* to *25*), from which it has become separated by the late Pliocene origin of the Caribbean rain forest. *I. pustulatus auratus* (*15*) may thus be seen to grade into the races formerly known under *I. sclateri* (*19* to *25*) but which Dickey and van Rossem (1938: 522) have shown to be conspecific with *I. pustulatus* (*15* to *18*). Hence, *Icterus pustulatus* as here recognized includes forms *15* to *25* in figure 7.

There is a significant plumage gradient in this species outward from arid Guatemala where the black-backed *alticola* (*21*) is considered the most advanced form. Those races formerly under *sclateri* which occur on both sides of this form—*formosus* (*19*), *maximus* (*20*), and *flammulatus* (*22*)—have the black of the back broken up into streaks or spots with alternate yellow. The south-ranging races of the former *sclateri*—viz. *pustuloides* (*23*), *connectens* (*24*), and *sclateri* (*25*)—seem to be retarded peripheral forms in which black is even less developed. Similarly, the north-ranging races—*pustulatus* (*17*), *microstictus* (*16*), and *graysonii* on Tres Marias islands (*18*)—show less black in that order. The last form often has the back completely yellow. This is also the case with Yucatan-isolated *auratus* (*15*) and marks all these peripheral forms as static representatives of *pustulatus* in relatively stable environment—thus little advanced beyond ancestral *nigrogularis*. Conversely, the increase in black on the backs of forms isolated in the strike-faulted, volcanic Guatemalan area (Fig. 9) is evidently the result of repeated population disjunctions. Indeed, the position of any form on the gradient toward the plumage pattern under selection in the arid tropical zone seems to be a function of the number of distinct population isolations in its phylogenetic history.



Black-backed alticola of Guatemala is the most-isolated, advanced form of Icterus pustulatus. Peripheral forms have back only spotted with black or entirely yellow, depending on degree of isolation. The species bullockii was completely isolated by the volcanic province in Mexico.

FIG. 9. Plumage gradient in the forms of *Icterus pustulatus* and origin of *Icterus bullockii*.

It is significant that *nigrogularis* appears to have evolved the 3 modern forms which segregate its bill characters in Guatemala. The variable palatal knob, an allele that may be present or absent in *nigrogularis*, has become fixed in *gularis* but completely lost in *pustulatus* which otherwise closely resembles that species. Variable bill length in *nigrogularis* has been further segregated in *pustulatus* to evolve the slender, decurved bill of nectar-feeding *pectoralis*. A single species has become 3, largely as a result of diet adaptations.

Griscom (1930: 16) has pointed out that *Icterus pustulatus*, *pectoralis* and *gularis* vary in a parallel manner. He observes (1932: 399) that "The variations of all three species are exactly alike, wherever they occur together, provided they do vary." All uniformly decrease in size peripherally throughout the arid tropical zone; show overlapping habitat preference; and, as Dickey and van Rossem observe (1938: 520), all three may nest in the same mimosa tree. Gause (1934: 20) and Lack (1944: 274) have shown that such an occurrence would be possible only when the diet is different in each species. Although field observations are lacking to show that this is so, the anatomical picture is unmistakable. *Icterus pustulatus* with its strong mandibular ramus and posterior extension of the mandible—a lever to be acted upon by the over-developed *M. depressor mandibulae*—clearly eats fruit by gaping. The palatal knob and heavier bill and adductor musculature of *I. gularis* permits it to crack seeds as well as eat fruit. The slender, decurved bill of *I. pectoralis*, with its weakened ramus and *M. depressor mandibulae*, does not prevent it from eating fruit but is obviously better adapted for probing flowers. Curiously, its only potential oriole competitor, the convergent *B. cucullatus*, does not occur in its range (Figures 5, 7) though it overlaps completely with *gularis* and *pustulatus*. Biotic pressure between these two nectar-adapted forms has apparently resulted in mutally exclusive ranges.

The conclusion seems warranted that, while all 3 species may be able to feed on fruit, nectar, and insects, each gets out of competition with the others in a hard pinch by going off into its special feeding niche. Only *I. gularis* is permanently resident where it breeds (Dickey and van Rossem, 1938: 526); *pustulatus* and *pectoralis* migrate during the dry season. This species probably eats seeds at such times, but what is needed here is a thorough ecological study of the 3 species.

We may append some information about time relations. *Icterus gularis* (Fig. 7, *29* to *34*) apparently arose before *pectoralis* since the forms of the arid *gularis*—viz., *tamaulipensis* (*29*) and *yucatanensis* (*31*)—have been separated by the Caribbean rain forest. As in the case of *Bananivorus cucullatus*, this dates *gularis* as earlier than the late Pliocene uplift which set up the conditions for this forest. On the other hand, since *pectoralis* (*26* to *28*) does not occur on the Yucatan Peninsula at all and is prevented from getting there today by the forest, the latter was already there when this species arose. Finally, if *pustulatus* arose by segregation of the palatal knob, it is the same age as *gularis* by inference.

Trend Toward Further Addition of Black in Temperate North America.

Further addition of black to the arid zone pattern could only reduce conspicuousness, and the black head and neck of the Baltimore Oriole in eastern North America seems to have precisely this purpose. This species, *I. galbula*, evolving from *pustulatus* through the intermediate Bullock's Oriole, *bullockii*, has followed a parallel trend to become convergent with the Orchard Oriole, *Bananivorus spurius* (frontispiece). Convergence, then, explains the many dissimilarities between these familiar species of the humid temperate zone.

Icterus bullockii bulockii (*35*) and its race *abeillei* (*36*) are clearly more northerly derivatives of *I. pustulatus.* Juvenal specimens of *bullockii* occur which are strikingly like the most advanced, black-backed forms of *pustulatus* in interior Guatemala. Some of these have the head nearly yellow and the black of the head in adults is always underlain by yellow. It is believed, however, that *bullockii* arose from the form *I. p. pustulatus* (*17*) farther north in the *volcanic province* of the Mexican Plateau (Fig. 7, 9). Although this form does not have a completely black back like *bullockii*, we have seen abundant indication that this feature is being selected for with each new isolation.

The present area of overlap between *pustulatus* and *bullockii* is the most likely scene of the original isolation producing the latter; it is in fact a great physiographic province. Hill (1908) describes the Mexican Plateau as a peneplain elevated in the Pliocene and dipping northward beneath the scarp of the Colorado Plateau. Near its southern face, on an axis between Cape Corrientes on the west and Jalapa on the east, the folding becomes abruptly east-west instead of the northwest-southeast prevailing northward. A major fracture is indicated in this area which Thayer (1916) has called the *volcanic province* (see Fig. 9). Volcanic peaks rise 5000 to 10,000 feet above the plateau and lava and other volcanics in filling the extensive lakes have caused them to overflow into adjacent drainage patterns. The barrier (see Pleistocene deposits on Map 13 in Sanchez, 1942) was virtually complete.

Since this barrier is late Pliocene-Pleistocene in age and completely separated populations to north and south except on the extreme Pacific side, virtually all the orioles in this area show range disjunctions. In fig. 6 the range of *I. graduacauda graduacauda* (*6*) is disjunct from the ranges of *auduboni* (*7*) and the new forms farther north, though *graduacauda* has partially re-occupied the devastated area. In Figure 7 the ranges of *I. p. pustulatus* (*17*) and *I. bullockii abeillei* (*35*) are disjunct with an expected degree of recent confluence; so are the ranges of the *gularis* races, *tamaulipensis* (*29*) and *gularis* (*30*). In Figure 5 *B. parisorum* (*17*) may owe its original disjunction from *maculi-alatus* (*18*) to this barrier. The latter then gradually succumbs to competition with *wagleri* (see Griscom, 1932: 391). *B. cucullatus cucullatus* (*20*) is disjunct from *californicus* (*21*) here, though the latter apparently did not have its range completely severed along the Pacific coast. *B. wagleri* appears not to conform, the break between *wagleri* (*15*) and *castaneopectus* (*16*) coming too far north. This seems to be a taxonomic error, however; Griscom (1932: 393) shows that specimens from Tepic, Jalisco, and Colima on the Pacific side (where the range would be less broken by volcanism) are as large as any *castaneopectus* examples. Finally, Dickey and van Rossem (1938: 530) remark a gradual blending of the two forms inland (to be expected after volcanism subsided there), and further note that the southern boundary of *castaneopectus* cannot yet be fixed.

Returning now to *Icterus bullockii*, we see in this species the first sign of increasing black in the head which will bring the derived Baltimore Oriole into convergence with the Orchard Oriole in eastern North America. Following its isolation north of the *volcanic province*, *bullockii* could range through all the arid country west of the Rocky Mountains in North America—even entering the westernmost tongue of the oak-hickory forest in southern Texas by early Pleistocene. Since variants increasing black in the head and decreasing wing white were probably under selection here, a physiographic-climatic barrier isolating this population in the more humid oak-hickory could have resulted in *I. galbula.*

Such a barrier in southern Texas can hardly be visualized before the Pleistocene. Recent studies of Pleistocene pollen profiles in peat bogs indicate that the northern spruce-fir forest reached as far as Florida on the east (Davis, 1946) and Austin, Texas, on the west (Potzger and Tharp, 1947)—at least as outlying bogs. Stenzel (personal communication to Potzger and Tharp) believes the Austin forest came from the Rocky Mountains via the Edwards Plateau. It would thus have interposed a wedge between the pinyon-juniper to the west and the oak-hickory to the east—contiguous today—blocking the eastward spread of *bullockii.* The latter could only enter the oak-hickory where it meets the desert scrub on the Texas coastal plain below the Balcones Escarpment—the south face of the plateau. If this corridor were blocked by a wedge of marsh cutting north to the escarpment from the Rio Grande embayment or delta (Schuchert, 1935; Barton, 1930), the population evolving into *I. galbula* could have been isolated in the oak-hickory—its black head and neck becoming fixed under selection.

The isolation resulting in the Baltimore Oriole was probably of short duration. Sutton's discovery of a narrow hybrid zone in Oklahoma (1938) suggests that subsequent withdrawal of the spruce-fir from the Edwards Plateau permitted *bullockii* to re-enter the oak-hickory to the north. A complete series of intergrades with *galbula* occurred here. The occurrence in the same part of Oklahoma of the hybrid zone for the xeric Lazuli Bunting (*Passerina amoena*) and the Indigo Bunting (*P. cyanea*) of the oak-hickory suggests the isolation of other species in the deciduous forest with *galbula.* Kinsey's gall wasps (1930), especially *Cynips mellea* and *villosa*, suggest a spruce-fir barrier on Edwards Plateau. Disjunctions between grackles and jays in Florida and Texas (Chapman, 1939; Amadon, 1944a and b) suggest that the deciduous forest may have been largely forced back to these points in the Pleistocene (cf. Braun, 1947).

Hybrid zones imply a temporary barrier recently removed—a condition most readily met by glaciation and volcanism. Hybridization in the Pacific Northwest is probably due to Quaternary volcanism (see Lobeck, 1941); the Mexican hybrid towhees reported by Blake and Hanson (1942) and worked out by Sibley (in press) may be due to Pleistocene volcanism. Since hybrids are less well-adapted than either parent form (Dobzhansky, 1941: 288), they probably tend to be resorbed rather promptly.

A slightly different situation resulted in the isolation of the Orchard Oriole (*B. spurius*) from *fuertesi*. In the Pleistocene the latter could probably range into Texas in shrubby borders of the coastal marsh (Thayer, 1916: 83) and could have isolated *spurius* in the oak-hickory when the plain pinched out against the scarp. The present range of *fuertesi* in southern Tamaulipas is the result of subsequent obliteration of the coastal plain in the intervening area. At any rate the Louisiana marsh habitat of *spurius* described by Oberholser (1938: 591) is strangely like that noted for *fuertesi* along the Tamesi river by Chapman (1911).

Principles and Trends Noted in the Orioles

It has not been possible to make valid comparison between the present phylogenetic scheme of the orioles (frontispiece) and the listings of previous reviewers because their works did not emphasize relationships, except as they might be inferred by position in a linear series. It is evident that their methods were in strictest adherence to the taxonomic procedure of inferring degree of relationship from degree of morphological (really external) resemblance. Adaptive modification of bills obscuring the relationship of close forms on the one hand and plumage convergence falsely indicating relationship in more distant forms on the other, could not be dealt with under a static approach.

Evolution is a process of movement and change. The 2 genera, 26 species and 76 forms of orioles here recognized are the result of intense selection in a constantly changing environment. In fact, so large a number of forms can only be accounted for by the wide latitudinal range of the group, broken up by physiographic and climatic barriers throughout its developmental history.

Geographical Isolation. The salient fact is that the area of greatest geological activity (northern South America and Central America) has produced the most forms. Moreover, the repeated close agreement of relative date of geological event with that required by the observed speciation in both genera (and of duration of isolation with degree of difference) is far too consistent to be of chance occurrence. Although we may see in the Amazonian races of *Bananivorus cayanensis* examples of Wright's (1943, 1946) "isolation by distance," the isolation of all other species and even races has been traced to some geological event. This is strong support for the view that all vertebrate species, including sympatric species, result from geographical isolation (Mayr, 1942, 1947).

My most striking case of sympatric species is that of the closely related

Icterus pustulatus, *pectoralis*, and *gularis* (Fig. 7) which not only occupy the same range in Central America but frequently nest in the same mimosa tree. There is every reason to believe that their initial isolation occurred in Guatemala as a result of the late Pliocene crustal movement and volcanism that has produced the present physiography there (Powers, 1918). With the uplift of the Sierra de las Minas, *I. pustulatus* of the Motagua valley (Fig. 10 A) could have pinched off the population which to northward in the Negro-Chixoy valley evolved as *gularis* (B). To the southward *pustulatus* is believed to have evolved *I. pectoralis* (C) in the Pacific Lowlands as a result of the extreme volcanic activity in the more recent Pacific Cordillera. Since the latter shows considerable black spotting on the breast not found in the other two, we should expect southern races of *pustulatus* to have individuals with this character. Dickey and van Rossem (1938: 524) report this in specimens of *I. pustulatus alticola* and *pustuloides*. Since *pectoralis* also has a curved, nectar-adapted bill, it is interesting to note that southern races of *pustulatus*—e.g. *sclateri* and *microstictus*—show greater indication of curvature in the culmen than northern races.

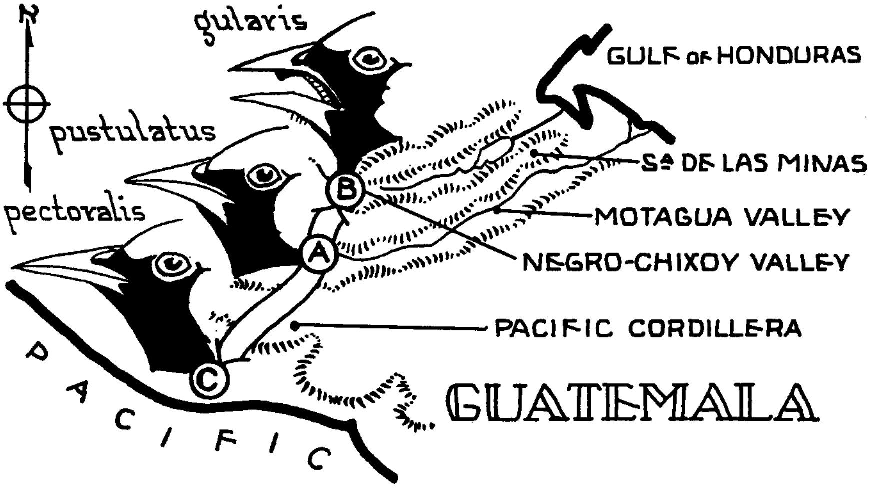


FIG. 10. Sympatric speciation in *Icterus pustulatus*, *pectoralis*, and *gularis*. *Icterus pustulatus* in the Motagua valley of Guatemala (A) isolates gularis in the Negro-Chixoy valley (B) by the uplift of Sierra de las Minas. *I. pectoralis* becomes isolated from *pustulatus* in the Pacific lowlands (C) by the volcanism in the Pacific Cordillera. Subsidence of volcanism and revegetation permits all three species to range throughout arid tropical zone of Central America.

Thus, a combination of block-faulting and volcanism in the east-west mountains of Central America, trending athwart northward dispersal from South America, has provided opportunities for isolation unexampled elsewhere. No oriole range has crossed the Mexican Volcanic Province (Fig. 9) without breaking up and Guatemala has presented a similar barrier. The strike-faulted transverse valleys—arid inland but blocked by forest on the east coast and by volcanism headward—could have initially isolated these sympatric species, subsequent revegetation upon volcanic subsidence permitting their ranges to flow together. Increased post-Pleistocene aridity doubtless helped.

It may be argued that these two genera illustrate divergence southward instead of convergence northward. The objections to northern origin of the orioles are many and I will give only a few. The sympatric overlap of most of the species of *Molothrus* and *Agelaius* in the pampas region of South America, whereas only one form of each occurs in North America, strongly argues southern origin for the orioles evolving from the latter genus. An abrupt origin from *Agelaius phoeniceus* in the north of brightly colored orioles which then southward subdue their color until it is almost black in the Amazonian forest would lack an explanation in terms of selection pressure—to say nothing of the unlikelihood of so disjunct an origin from *A. phoeniceus* at the outset. Moreover, the geological events causing speciation in the orioles from northern Colombia to southwestern United States succeed each other in the time scale northward so that the northernmost forms are the most recent; it does not "work" backward. Finally, the replacement in northern South America of the three sympatric Central American species by a single variable species, *nigrogularis*, which would perpetuate their adaptive bill characters as variants, can have no known evolutionary mechanism.

Adaptive Plumage Trends. One could predict that oriole speciation, northward in latitude, upward in altitude and often in new life zones, would lend itself to the following of trends. This is obviously true, since the convergent movement of the two genera out of the humid tropics into the arid tropics and finally into the temperate zone is as clearly a progression upward in time as outward in space from center of origin. As such it furnishes a picture of response to selection pressures infinitely more valuable—since these birds are all living—than a mediocre fossil record. The convergence of *B. cucullatus* and *auricapillus* toward the identical plumage pattern found in the three sympatric species of *Icterus* suggests a perfection of this pattern for the arid tropical zone. Since the female is as bright as the male protection is apparently not a factor, being assured by the trait of nesting in thorn trees or trees with wasp nests—noted also in the colonial cassique (*Cacicus cela*) by Cherrie (1916: 204). Nests of *I. gularis* on telephone wires (Sutton and Pettingill, 1943: 130) may be associated with thorn-protected ones by predators and left alone.

There is, however, a gradual tendency northward for orioles entering the temperate zone of North America to evolve sexual dimorphism with duller females and to select hidden nest sites. Dickey and van Rossem (1938: 138) cite this in the northern races of *I. pustulatus* and suspect it in *graduacauda* while I have found it in northern races of *B. cucullatus*. All orioles reaching the United States are dimorphic besides generally reducing yellow in favor of black in the plumage, though the woodland forms of *Icterus* introduce yellow flash-markings in the tail, as does *B. parisorum*. This general trend toward inconspicuousness extends to habit also and may be due to the dropping out of thorn trees and wasp nests in the north. The "abrupt" reappearance of chestnut in *B. spurius* in this trend is only apparent, the color having only been suppressed in earlier forms. It is still evident in specimens of *B. cayanensis* and *chrysocephalus*, and is only partly displaced by yellow in *prosthemelas*. The latter will be recalled as evolving *fuertesi* which is transitional to *spurius* in the revival of chestnut. The color also persists in Caribbean forms of *Bananivorus*.

The question may arise as to the amount of compliance in these trends to Gloger's (or Allen's) rule. As stated in Hesse, Allee and Schmidt (1937: 395), mammals and birds inhabiting humid regions are supposed to have more melanin pigmentation and those of arid regions, more phaeomelanin (yellow and reddish-brown) pigmentation. The opposite trends of *Bananivorus* and *Icterus* within the humid tropical zone indicate little agreement with the principle and it is thought that it may not be applicable to species obviously developing ruptive patterns. On the other hand, the tendency to add black as both genera enter the humid temperate zone suggests compliance.

Within a given life zone we have seen that the plumage pattern tends to remain static while new species arise with bill adaptations to different diet; with changing life zones the plumage pattern tends to change while the bill adaptation for a particular diet remains static. Whatever the combination in a given species it appears to be highly adapted for the niche it occupies. Aside from the possible exception of *B. cayanensis* which still bears the blackbird plumage pattern at the center of origin, I cannot point to a single non-adaptive feature in orioles. It seems likely that in a highly competitive group they are eliminated. From the Pleistocene and Recent fossils described by Wetmore, Miller and others, it is clear that the number of poorly-adapted forms extinguished even in so young a group as the Icterinae may be startling.

Evolution and Systematic Categories. Evolution in the orioles, despite extinctions, is smooth. Species and even the genera arise without strong disjunction and it is generally unnecessary to invent hypothetical ancestors because the parent forms still exist. The derivation of orioles from blackbirds may suggest that the borders of the higher categories are unreal but the disjunctions in bill, diet, and habitat can, under selection pressure, only diverge still more. Against this, it may be seen from races and hybrids that the species is not as real at the borders as many workers at this level like to believe; it is real but its chief merit lies in its position as a definable, fundamental unit. However, even as the species tends to stabilize itself with time, so does the higher category based on diet and habitat adaptations, draw away from other higher categories.

I am unable, therefore, to follow Kinsey (1936) in his contention that there are no higher categories and no centers of origin. Every vertebrate species must have a center of origin by virtue of its initially complete isolation from a parent species. Nor are the higher categories unreal; they are branches on a phylogenetic tree, each in adaptive response to selection pressure in a particular direction. The same is evident at the species level in the orioles and genetic drift (Dobzhansky, 1941: 332; Wright, 1940) seems to have been ineffective against selection here. The opposite plumage clines, occurring as convergent time trends in two distinct phyletic lines, strongly suggest the elimination of variants from the pattern under selection.

SUMMARY

An attempt is made to explain in evolutionary terms the apparent convergence of two phyletic lines (genera) in the orioles. It is shown that selection of new lines of birds usually hinges on dietary modification of the bill and jaw musculature and that the two lines have arisen from opposite ends of the blackbird genus *Agelaius* by specializing its pre-adaptations. The fruit-adapted *Icterus*, including the Baltimore Oriole, increases the gaping power of the mandibles; the nectar-adapted *Bananivorus*, including the Orchard Oriole, reduces the mass of bill and skull. The segregation of the genera and species results from the isolating influence of geological events which have often operated indirectly through associated climatic change.

The replacement of chestnut by yellow in the plumage of *Agelaius* is regarded as a time trend; the chestnut humeral patches of the relict *A. humeralis* on Cuba reflect the ancestral condition of *A. thilius* at the time it evolved the oriole *Bananivorus* in the pampas region of South America. No clear-cut characters separate the latter from *Icterus* because of the convergence but comparison of the two in the same region and life zone shows *Bananivorus* to be always smaller. It evolves from *A. thilius* north of the pampas without plumage change, simply by adapting to nectar and soft fruit, but adds yellow northward under obvious selection pressure to increase conspicuousness in its new forest habitat. The same trend is noted in the Caribbean where peripheral Bahaman and Lesser Antillean forms derived from *B. dominicensis* of the Greater Antilles increase yellow, and this is seen as a trend upward in time as well as outward in space from center of origin. *B. prosthemelas* of the Caribbean rain forest evolves arid zone forms which increase yellow still more to achieve the pattern convergent with that of *Icterus* forms in the same zone. Northward in the temperate zone, under apparent shift in selection, it evolves less conspicuous forms also convergent with *Icterus* forms there.

The fruit-adapted *Icterus* arises in the pampas region from the yellow agelaiine *Xanthopsar*, its forms showing an opposite trend northward to reduce yellow which results in the arid zone convergence with forms of *Bananivorus*. Two lines branch from the key species *nigrogularis*—a humid-adapted *chrysater* group with a derived nectar-feeding form and the arid zone *pustulatus* group of

Central America. The latter segregates among three species bill adaptations for fruit, seeds, and nectar existing as variants in the parent *nigrogularis*. Evolving from this group northward, *bullockii* splits off the Baltimore Oriole in the oak-hickory forest where it is convergent with the Orchard Oriole, evolved by *B. prosthemelas* via intermediate *fuertesi*.

Certain trends and principles are illustrated by both genera. The importance of geographical isolation is emphasized, the splitting off of virtually each form being assigned a geological or climatic event. The convergence toward identical plumage in Central America suggests selection for conspicuous pattern; that northward suggests selection shift favoring inconspicuous pattern as the protection of thorn trees and wasp nests dies out. Although evolution of species from species is smooth the evidence of geographical isolation in the orioles does not support Kinsey's view that there are no centers of origin and no higher categories. The suggestion is made that numerous other cases of inter-generic convergence and especially parallelism may occur in passerine birds.

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Several occurrences of the Evening Grosbeak (*Hesperiphona vespertina*) in eastern Ohio were recorded in the winter of 1949–50:

(1) Along Mill Creek, near Youngstown—8 on December 26;

(2) Five miles northwest of Salem—11 on January 1;

(3) Near Londonville—66 on January 2.

Stimulated by these records, I am making a survey of this invasion into Ohio and adjacent areas. Will persons please send me records of Evening Grosbeaks for this survey?

Raymond O. Marshall
RFD #2, Columbiana, Ohio

Ornithologists are urged to collect data on the timing of bird songs because this aspect has been neglected. To record the data merely write position of second hand at first notes of successive phrases during continuous song. Example: Towhee, June 24, '49, 10 A.M., 77°F, Palmyra, N. J.; 14-20-28-34-39-45-52-5-11-16. For fast singers such as the Red-eyed Vireo, record the number of phrases in 60 seconds. I shall be glad to correspond with anyone desiring to collect records.—George B. Reynard, 728 Parry Ave., Palmyra, New Jersey.