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ADAPTATIONS FOR FOOD-GETTING IN THE AMERICAN BLACKBIRDS

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A careful study of the American blackbird family (Icteridae) during the past several years reveals that its members have invaded virtually every food niche exploited by passerine birds. The present investigation of the functional modifications of skull, bill, and jaw musculature in the 38 genera suggests that this success stems initially from a general pre-adaptation permitting an entirely new method of feeding. This paper describes first the individual feeding adaptations, then their convergent re-appearance in each of the three major icterid lines. Although the graphic comparison of the genera is presented in the form of a morphological tree of relationships in Figures 7 to 10, the full evidence for these relationships is not offered here. The present paper confines itself rather strictly to the nature of the adaptations themselves.

Methods and Material

Primarily, the method of investigation has been one of attempting to establish valid correlations between skull structure and known feeding functions in the various genera. The diet of North American species was determined from the stomach analyses made by the Biological Survey under such men as Judd, Beal, and McAtee (1900–1910). For Central and South American species the field notes of Wetmore (1916, 1926), Wetmore and Swales (1931), and a few other careful observers were invaluable. Functionally, the method of feeding is of even greater importance than the kind of food taken, and very close observation of birds in field and captivity has been necessary. I am deeply indebted to its designer, Mr. Victor Carbonara, for the use of a Sard 6x 20 binocular, invaluable at ranges down to four feet. Due to its closely approximated objectives, I have been able to interpose a large magnifying lens and use this glass at extremely close ranges with magnifications up to 18. Dissection and drawing of jaw musculature were done under a binocular dissecting microscope not generally exceeding a magnification of 18 times.

For the anatomical specimens and skulls used I am indebted to the United States National Museum, Museum of Vertebrate Zoology, American Museum of Natural History, and particularly to the Chicago Natural History Museum. For the free use of specimens in their care or for advice, I wish to thank Alexander Wetmore, Herbert Friedmann, Frank A. Pitelka, John T. Zimmer, Ernst Mayr, Dean Amadon, Emmet R. Blake, Karl P. Schmidt, and, especially, D. Dwight Davis.

ARCHITECTURE AND MECHANICS OF THE PASSERINE SKULL

The bird skull is as remarkable a structure from the engineering standpoint as exists in nature. Vertebrates, generally, are characterized by *akinetic* skulls in which the pterygoids, palatines, and quadrate are immovably fused with the cranium. The skulls of birds and most reptiles, however, are *kinetic*—a term which expresses the fact that the palato-pterygoid framework is movable with respect to the cranial part of the skull. Resemblance between birds and reptiles ends here for they are functionally very different. As regards birds, the importance of this type of skull is not generally appreciated despite the papers of Moller (1931) and Engels (1940). In fact, no real understanding of the manner in which birds eat is possible without a grasp of the simple mechanism of the kinetic skull.

Movement is readily restored to a dried skull by boiling it a minute or two in water. It will then be seen that the upper mandible may be moved up and down on its articulation with the cranial part of the skull—the naso-frontal hinge (Fig. 1)—and that this movement of the bill is communicated by an articulated series of rod-like elements to a quadrate bone on either side of the skull. These elements are the palatines and pterygoids, which slide along the sphenoidal rostrum medially, and the jugal bars which connect the bill with the quadrate laterally.

Actually, of course, the musculature initiating these movements works the other way around. The quadrate occupies a key position. The muscle that originates on the medial surface of the jaw and inserts on the apex of the long, lever-like orbital process (*f*) of the quadrate pulls the lever down when it contracts (Fig. 1, *Retracted*). This rocks the quadrate backward on its articulation with the cranium, setting up a powerful drag on the rod-like jugal bones laterally and on the pterygoid and palatine bones medially. Since these all connect

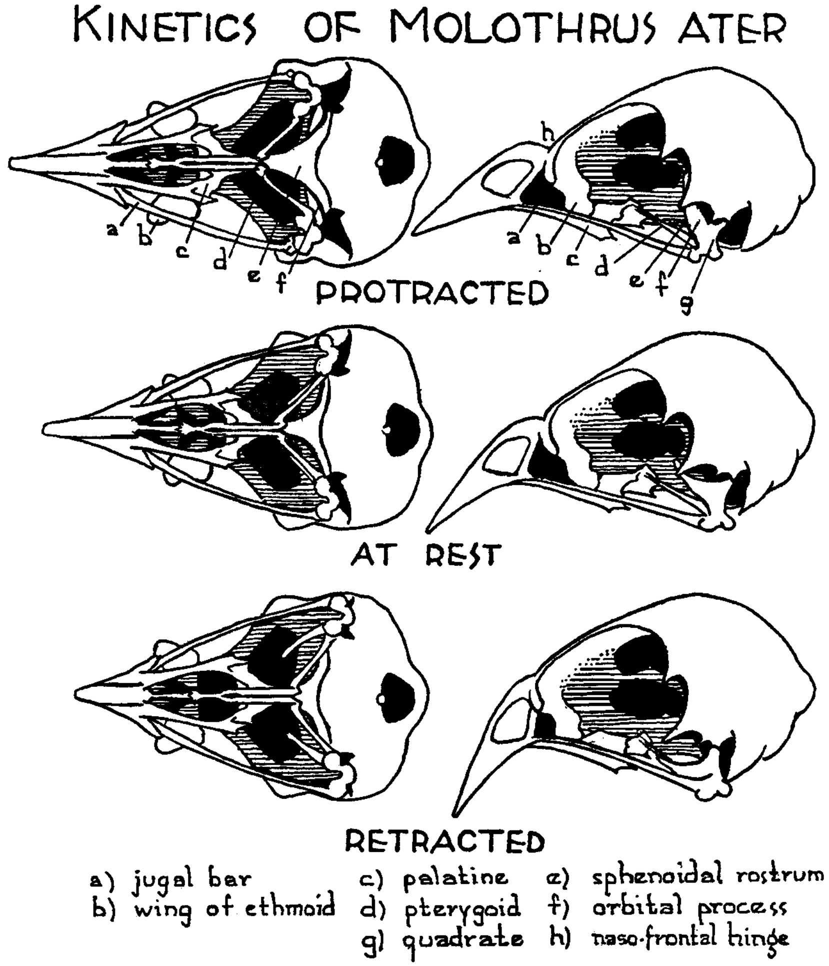


Figure 1. Skull kinetics in the Cowbird, *Molothrus ater*.

with the base of the upper mandible, this drag, acting on the naso-frontal hinge (*h*), is translated into a down-swinging of the tip of the mandible, which terminates in its retracted state. Protraction is accomplished by a reversal of these movements. The muscle whose contraction rocks the quadrate forward does not insert on the orbital process but on the quadrate body and on the pterygoid at its junction with the quadrate. Since its origin is at the postero-internal angle of the orbit, contraction produces an upward pull and a resultant forward rocking of the quadrate. This delivers a powerful thrust upon the rod system which, at the base of the upper mandible, is translated into an upswinging of its tip. It will be seen (Fig. 1) that the rod-like jugals, pterygoids, and expanded palatines thus form a structural framework joining the upper mandible with the quadrate bones on either side. The palatines (Fig. 2 *E*) together form an enclasping element that slides smoothly along the sphenoidal rostrum.

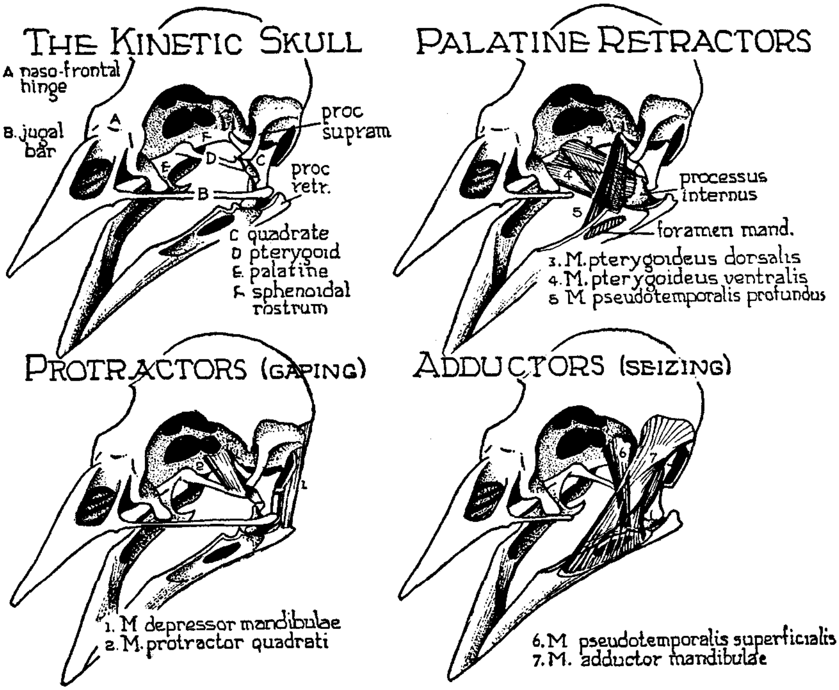


FIGURE 2. Mass functions of muscles in the kinetic skull.

This appears to be a very elaborate arrangement, and the question arises just why a kinetic upper mandible is necessary. When the lower mandible is in place (Fig. 2), its condyle articulating with the head of the quadrate, a remarkable co-ordination of the musculature operating this mechanical system is possible. In general the upper mandible is protracted only when the lower mandible is depressed, and lowered whenever the lower mandible is raised. Of course this is an effective means of increasing the gape, but Moller's (1931: 139) explanation of kinetics as a means of preserving the axis of the bill, especially in long-billed forms, is probably the primary one. The inefficiency of an akinetic bill may be compared to that of a thumb and forefinger in which the latter is immovably fused to the hand. The axis of the bill would change with the degree of gape if the upper mandible were not movable, and this would be hardest on insectivorous species required to snatch their prey very quickly. It is precisely these forms that have the highest degree of skull movement. The jaw musculature appears confusing when fully labelled (Fig. 4) partly due to Lakjer's (1926) admirable job of homologizing avian musculature with that of the Sauropsida. It might be, for instance, more desirable to call the muscle that retracts the quadrate, *M. retractor quadrati,* but this muscle had a different function in avian ancestors and is called *M. pseudotemporalis profundus.* One might prefer to speak of *M. temporalis,* but it is not homologous with that muscle in mammals. The sauropsid term is *M. adductor mandibulae externus superficialis* and it is as indestructible under the concept of homology as any trinomial name. Fortunately this difficulty may be largely avoided in comparing muscle modifications between species; the muscles varying in development are relatively few and may be referred to by number. The simplified musculature given at this point will deal only with muscle groups—not their component parts—and with these according to their function.

These muscle groups so classified (Fig. 2) will be seen to be quite simple. There are only seven and these are broken down into the *protractors* which increase the gape of the mandibles, the *palatine retractors* which draw the upper mandible downward and to some extent raise the lower mandible to meet it, and the *adductors* which powerfully raise the lower mandible.

Under the heading *protractors* it will be seen that there is but a single muscle for depressing the lower mandible on each side. This is *M. depressor mandibulae* (Fig. 2, *1*) which originates on the squamosal area of the cranium and inserts on the *processus internus* and *processus retroarticularis* at the posterior end of the mandible. Similarly, there is but a single muscle for elevating the upper mandible. This is *M. protractor quadrati* (*2*), originating in the postero-internal angle of the orbit and inserting both on the body of the quadrate and on the head of the pterygoid where it articulates with the quadrate.

The *palatine retractors* are three in number. The principal function of this group is to draw the tip of the upper mandible downward but, since the muscles insert on either the inner surface of the lower mandible or on its internal process, they tend at the same time to draw the lower mandible upward. *M. pseudotemporalis profundus* (*5*) initiates these movements, acting on the lever-like orbital process of the quadrate. Its insertion is on the tip of the process and its origin is on the inner surface of the mandibular ramus, actually the lower margin of the mandibular foramen. The *M. pterygoideus dorsalis* (*3*) arises just posterior to the junction of the palatines with the pterygoids on the posterior extension of the palatines and inserts on the internal process of the mandible. The *M. pterygoideus ventralis* (*4*) originates on the surfaces of the palatine and inserts both on the internal process and on the inner surface of the mandible far posteriorly.

Finally, the adductors of the mandible perform the sole function of powerfully elevating the lower mandible and bringing it into contact with the depressed upper mandible for seizing prey, cracking seeds, etc. The *M. pseudotemporalis superficialis* (*6*) is the medial of these two muscle masses. It originates on the posterior wall of the orbit and generally inserts on the medial dorsal surface of the mandible far posteriorly, though in certain finches and "near-finches" the insertion advances anteriorly. By alternate contraction of this muscle on either side, the lower mandible may then be shifted from side to side against the upper in hulling seeds. Additional adducting power is also gained by this forward advance of the insertion. The *M. adductor mandibulae* (*7*) is the very large adductor mass originating in the temporal fossa, on the suprameatic process, and on the quadrate, and inserting on the dorsal and lateral surfaces of the mandible.

This discussion, as well as the diagrams in Figure 2, is much oversimplified. The detail drawing of the muscle pattern of the Cowbird, *Molothrus ater*, in Figure 4 indicates that the discussion must be broken down further for purposes of comparison with other species of the family. There are still seven muscle masses having the functions ascribed above; they are treated individually and referred to as (*7a*), (*7b*), etc. Some of the muscles might be detailed still further, as for example, *M. depressor mandibulae* (*1*). But this would serve no useful purpose and the anatomical picture will be kept as simple as possible.

NATURE OF THE MODIFICATIONS FOR FEEDING

The nature of feeding modifications in both skull and jaw musculature is best studied in a family whose boundaries are rather well agreed upon by ornithologists. Such a family is the Icteridae—and it is especially satisfactory because its species run virtually the entire gamut of food adaptations, with correspondingly great variations in bill and skull. Friedmann (1929) has expressed the opinion, based on extensive work, that the Cowbird, *Molothrus*, is the most primitive member of the Icteridae. There is abundant evidence that the entire family originated from a finch ancestor; the persistence of the angulated commissure in all forms seems significant, to mention a single point. My own anatomical studies (unpublished) of several hundred passerine species point to the emberizine finch *Phrygilus* as being close to the ancestor from which the Cowbirds spring—and *Molothrus* itself is in many structural respects a finch. It might be stated, therefore, that this family has secondarily embraced many other food niches (additional to the seed niche) by an elongation of the bill and the skull and muscle changes that have accompanied it.

Adaptations for Seed-cracking and Insect-eating.—The changes occurring between thick-billed and slender-billed genera were investigated first, emphasis naturally falling on correlations between structure and food habits. The food analyses made by Judd, Beal, and McAtee (1900 to 1910) were broken down to show the relative percentage of vegetable and animal material taken by each species (essentially seeds and insects). Features conspicuously varying with diet were the mass and length of the bill, degree of angulation of the commissure, length of the orbital process of the quadrate, and the degree of kinetics. A special device for measuring the latter included an adjustable plexiglas clamp for holding the cranial part of the skull rigid while the upper mandible was manipulated.

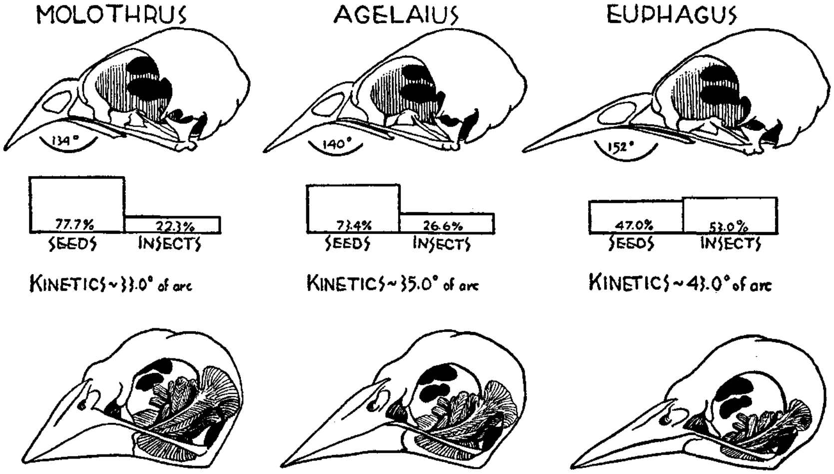


FIGURE 3. Adaptive modifications of the skull with change in diet.

It was found that the finch-like Cowbird has an annual diet averaging 77.7 per cent seeds and 22.3 per cent insects (Fig. 3). Correlated with this is a short, massive bill with a highly angulated commissure (134°), reduced kinetics (33° of arc), a quadrate with the lever-like orbital process much elongate, and a palatine foramen relatively far posterior. The Red-winged Blackbird, *Agelaius phoeniceus*, and the Rusty Blackbird, *Euphagus carolinus*, are progressively more insectivorous in their annual diet (26.6 per cent for the former, and 53.0 per cent for the latter). Correlated with this, movement in the skull is progressively increased (35.0° in *Agelaius*, 43.0° in *Euphagus*), the angulation of the commissure is decreased (140° in *Agelaius*, 152° in *Euphagus*), and the bill is elongated. At the same time the palatine foramen advances forward, and the bill becomes less massive and more forceps-like. Finally, the orbital process of the quadrate becomes shorter. These are, then, skull changes accompanying a more insectivorous diet.

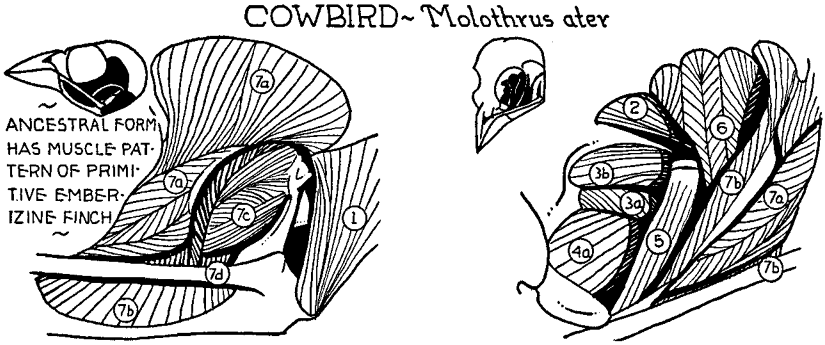
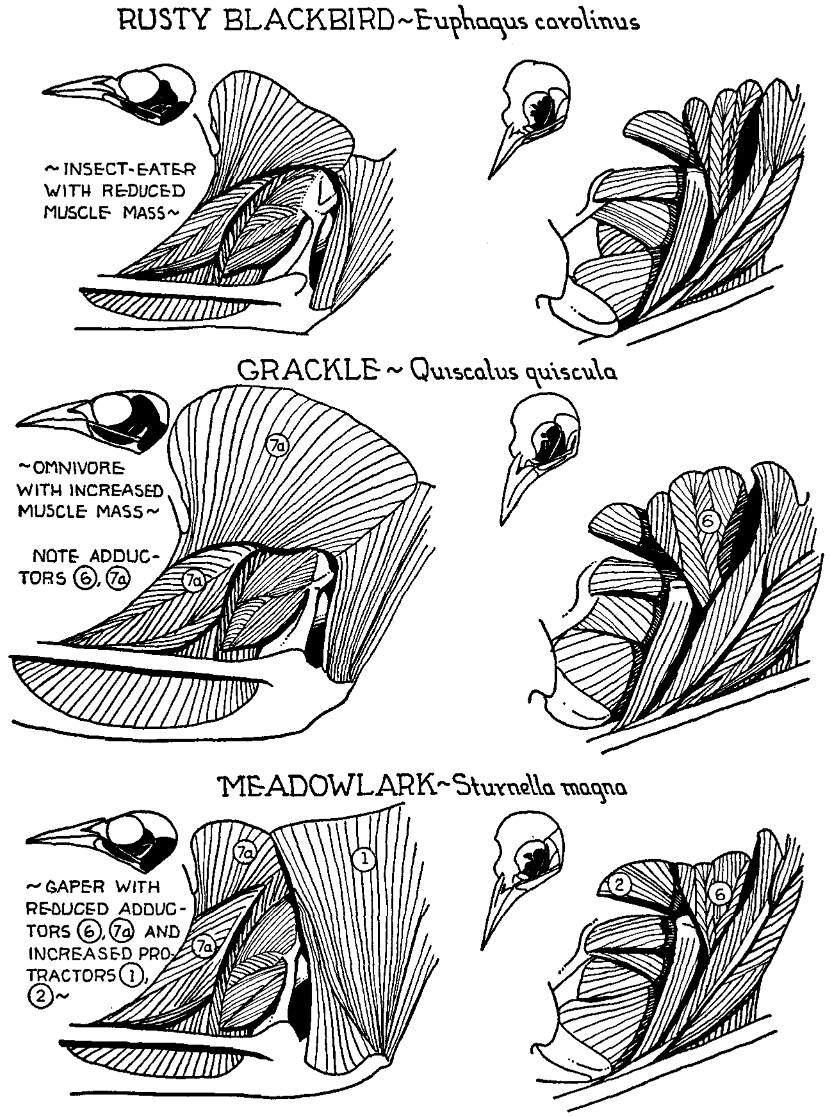


FIGURE 4. Detail drawing of jaw muscle pattern of Cowbird (ancestral finch type).
Protractors. 1 depresses the lower mandible; 2 elevates the upper mandible.
1. *M. depressor mandibulae*
2. *M. protractor quadrati*

Palatine retractors. Combined action draws upper mandible downward.
3. *M. pterygoideus dorsalis:* a) *anterior;* b) *posterior*
4. *M. pterygoideus ventralis:* a) *anterior;* b) *posterior* (underlies a)
5. *M. pseudotemporalis profundus*

Mandibular adductors. Combined action draws lower mandible upward.
6. *M. pseudotemporalis superficialis*
7. *M. adductor mandibulae:* a) *externus superficialis;* b) *externus medialis;* c) *externus profundus;* d) *posterior*

Before carrying the picture of adaptational changes with insectivorous diet into the musculature, it is necessary to call attention to the two basic types of skeletal muscle, pinnate and parallel (Pfuhl, 1936). The parallel type has all the fibers running the full length of the muscle and exerting pull, upon contraction, directly between the points of attachment (Fig. 4, *5*); the entire jaw musculature of primary insect-eaters like the muscicapids is parallel. The pinnate type is one in which the tendon or raphe runs the length of the muscle, and the short fibers originate from it as the barbs originate from the shaft of a feather (Fig. 4, *6*, *7*). Grant (1942: 384) puts the essential difference between the two clearly: ". . . a pinnate muscle has shorter fibers but


RUSTY BLACKBIRD~Euphagus carolinus

GRACKLE ~ Quiscalus quiscula

MEADOWLARK~Sturnella magna

FIGURE 5. Detail drawings of basic icterid muscle pattern showing adaptive modifications in various genera.

a much greater functional cross section for its bulk than a parallel muscle. In other words its pull will be shorter but more powerful." Certain advanced groups of birds have converted the mandibular adductors from parallel to pinnate. The finch groups have done so, and the similar arrangement in the Icteridae further supports the view that this is a finch group secondarily invading other food niches.

In the Cowbird, as in finches generally, the adductor mass is greatly emphasized. But though the mass is reduced as finch character gives way to insectivorous, the pinnate muscle pattern basic to this family is not lost. The decreased kinetics of the finch-like *Molothrus* skull indicates that seed-cracking does not require as wide a spread or gape of the mandibles as does the insect-eating most prevalent in *Euphagus*. *Molothrus*, therefore, appears to require a short but powerful pull in elevating its lower mandible, and this is provided by adductors of the most pinnate type in which the fibers meet the tendon at an obtuse angle (around 45°) and are thus the shortest found in the family. In *Euphagus*, gaping more widely and requiring a longer but less powerful pull in elevating the lower mandible, the fibers meet the tendon at a more acute angle (around 35°, average). The individual fibers are thus longer—the nearest approach to the parallel adductors of primary insect-eaters. The pinnate character due to finch ancestry may be too deep-seated genetically to be readily lost in a food adaptation.

These features are best seen in Figures 4 and 5 in which it is also more apparent that there is a general reduction in muscle mass in *Euphagus*, with reduced areas of origin and insertion on the skull. A final point concerning the musculature is associated with the varying length of the orbital process of the quadrate. As was pointed out initially this is essentially a lever, and the mere fact of its greater length in the finch-like *Molothrus* insures that *M. pseudotemporalis profundus* (Fig. 2, *5*), exerting a downward drag on its apex, will draw the upper mandible downward more powerfully. Since the process is shorter in *Euphagus*, a muscle of exactly the same size would draw the upper mandible downward less powerfully but through a greater angle of arc in correlation with its greater kinetics. This is because the same shortening of the muscle acting on a shorter orbital process will produce a greater excursion of the tip of this lever and rock the quadrate farther back on its squamosal articulation with the cranium. Thus, lever-mechanics alone may solve this problem, and it is unnecessary for the finch to have this muscle pinnate.

The Sawing Adaptation of Grackles.—Since it involves strong emphasis on the adductor mass (Fig. 2) as noted in the Cowbird, the sawing adaptation of the northern grackles, *Quiscalus*, is discussed next. At first glance the powerful development of *M. adductor mandibulae externus superficialis* (Fig. 5, *7a*) seems incongruous in a species whose bill is not nearly as thick and conical as that of a finch. But it can be shown that this adductor mass has the same rôle functionally as in the finch-like Cowbird.

Wetmore (1919) was the first to describe the hard keel projecting downward from the horny palate in the Bronzed and Purple grackles, *Quiscalus*. Sharper and more abrupt anteriorly, this keel extends well below the level of the tomium and is used in a sawing adaptation described by Wetmore and later by Schorger (1941). As Wetmore pointed out, these birds habitually crack acorns by means of this tool—the nuts being scored completely around the shorter diameter, then cracked by powerful adduction. Wetmore also mentioned the cracking of kernels of dried corn, and I have witnessed this in detail with captive birds, using the Sard binoculars at the very close range of four feet. The kernel is oriented longitudinally against the keel by means of the tongue and there follows a persistent chewing or repeated powerful adduction lasting fully a minute. When the kernel is broken in two, one of the halves is oriented crosswise against the keel and champing continues until it has been broken up small enough to swallow. Captive grackles do this even when food trays are well-stocked with small fragments of cracked corn, and it may simply be an additional form of energy release indulged in by caged birds. Although a single muscle has been emphasized above to demonstrate powerful adduction in this genus, the entire adductor and retractor masses (Figs. 2 and 5, muscles *3*, *4*, *6*, and *7*) are very strongly developed, just as in finches.

Wetmore found this keel fully developed in the young bird by the first fall. Also, adults of the northern races, *Quiscalus q. quiscula* and *Q. q. aeneus*, collected in late fall and early spring had the keel much worn, while the southern race, *aglaeus*, had it unworn. Since *Cassidix*, quite likely on the direct line evolving *Quiscalus* (Fig. 9), has the keel undeveloped as a cutting tool, it appears that the development of a keel in *Quiscalus* may be an adaptation adjusting grackles for life in the northern states when this region has been deserted for lack of food by all but "winter-adapted" species.

This is a remarkable adaptation because it seems to be clearly superimposed, as is the similar adaptation in the oriole, *I. gularis* (Wetmore, 1919). In keeping with their omnivorous food habits the northern grackles have a bill structure resembling that of crows. However, the addition of a sharp palatal keel, by specialization of a palatal boss, present in nearly all blackbirds as a primitive feature, and the strengthening of the adductor musculature permit them to exploit a new food niche. This offers some insight into the origin of new adaptations related to feeding. Like other blackbirds, grackles are "resourceful," continually trying new feeding methods. I have seen them picking dead minnows from the surface of a pond (*cf.* Richardson, 1947) and, although performed awkwardly, this is the kind of feat that selection pressure could seize upon and perfect, were it sufficiently advantageous.

The skull of this genus seems to present a clear compromise, re-embracing features of finch ancestors while remaining generalized—and compromises are frequently not successful in nature against the competition of neighbors specialized for a single food type. Finally, I am informed that Mrs. Laskey has discovered that a captive young Bronzed Grackle gapes in the manner to be described for the next genus. This is something I have not yet observed and it places the northern grackles at the head of the list, so far as adaptations for food in this family are concerned.

The Gaping Adaptation of the Meadowlark.—A conspicuous feature in the skull of the Meadowlark, *Sturnella magna*, is the great development of the muscles of protraction (Fig. 2). The muscle for elevating the upper mandible, *M. protractor quadrati* (Fig. 5, *2*) is not ordinarily a powerful muscle in birds. The muscle for lowering the lower mandible, *M. depressor mandibulae* (Fig. 5, *1*), is not powerful in any vertebrates which ordinarily open the mouth only to close it on something. Both of these muscles have become very powerful in the Meadowlark, seemingly at the expense of the adductors which are unusually small; and this is correlated with the method of feeding. These birds drive the closed bill into the ground and open it powerfully against the resistance of the earth. The degree of this adaptation is most evident when one examines the *processus retroarticularis*, the posterior extension of the mandible seen in Figures 2 and 5, upon which *M. depressor mandibulae* acts as a powerful lever. Dr. Wetmore first called my attention to this process and his understanding of its significance is clear from his description (1926: 378) of the earth-probing adaptation in *Amblyramphus*.

Full realization of the bill as a tool in birds, whose forelimbs have become useless as feeding tools through their modification for flight, is achieved in the Meadowlark. Its foraging in short grass, exactly like that of foraging starlings, consists in a repeated, spasmodic opening of the mandibles for the purpose of clearing the area at the roots of the grass for an unobstructed view. This is an extraordinary behavior to watch. A captive European Starling may gape in its food pan with such precision as to roll away a single grain at a time to disclose what lies underneath. A captive Meadowlark raised by Mrs. Nice gapes constantly in exploring its environment, and the significance of this instinct as related to the normal life of the wild bird seems evident; it will insert the closed bill into any small hole in fabric or paper and attempt to enlarge it. It must be added, in view of the widespread impression that the eyes of birds are incapable of much movement in

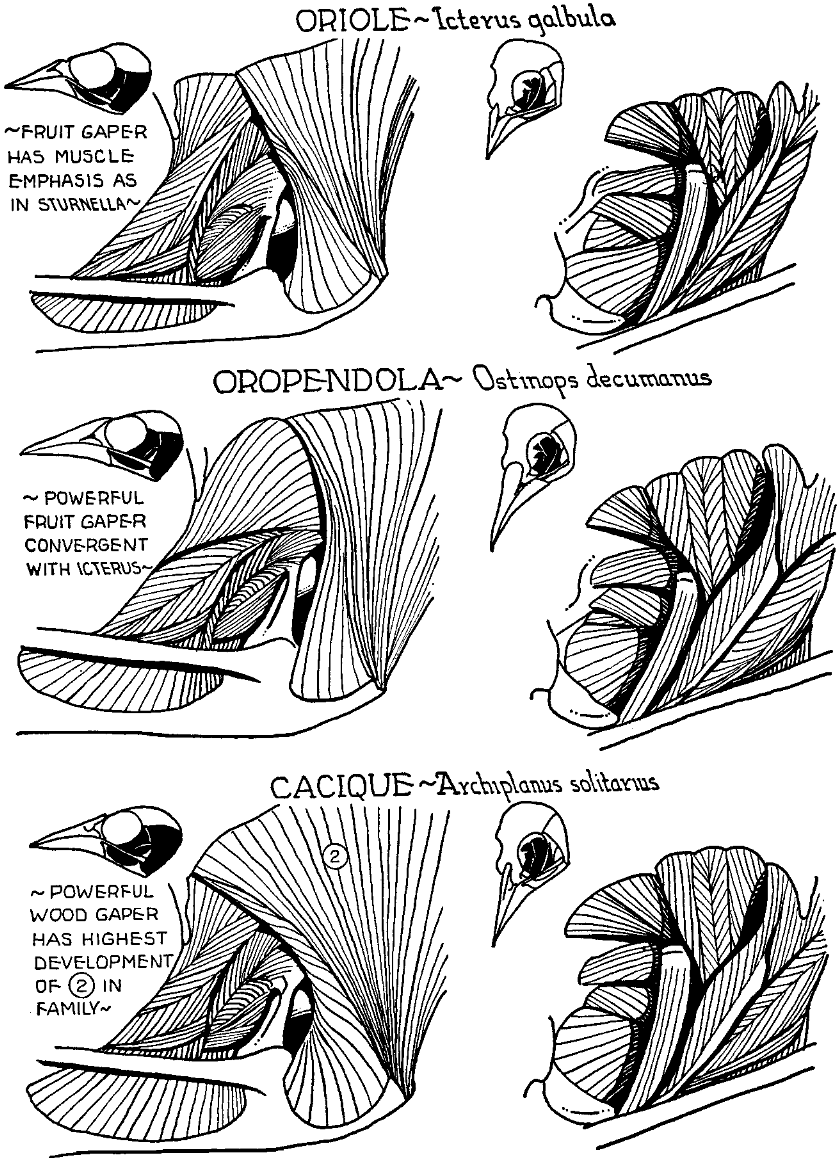


Figure 6. Detail drawings of basic icterid muscle pattern showing adaptive modifications in various genera.

their orbits, that both the Starling and the Meadowlark are apparently able to see forward between the gaping mandibles to examine the substrate cleared. The eyes can be seen to turn far forward and the zygomae, pinched in at the junction of the bill in the Starling, insure even greater forward vision in this highly specialized insect-seeker. The similar constriction in the secondarily-adapted Meadowlark is less apparent, though the free lacrymal bone in this species (noted also in *Pezites*) may be drawn out of the way in gaping. Unlike the Starling, the Meadowlark retains a good deal of adducting power, especially in a large *M. pseudotemporalis superficialis* (Fig. 5, *6*), and includes a considerable proportion of seeds in its annual diet.

Despite its other connotations the term "gaping" is proposed for the feeding behavior described above, other terms proving even more confusing. This same high development of protractors, with lever-like posterior extension of the mandibular ramus for powerfully spreading the mandibles, is the functional basis for the quite different food adaptations in the three groups following.

The Gaping Adaptation of Orioles.—The gaping adaptation as applied by the orioles of the genera *Icterus* and *Bananivorus* to the special problems of fruit-eating and nectar-feeding has already been described (Beecher, 1950). Anatomically, this adaptation is very similar to that noted in the Meadowlark, and Figure 6 shows that here, again, the protractor muscles are emphasized at the expense of the adductors. Apparently no account of the feeding method of American orioles exists, aside from the notes of Wetmore and others indicating that some take nectar. In fact few ornithologists seem to be aware that fruit in season is a major article of diet, and the failure of this food to appear in the stomach analyses of the Biological Survey suggests that it may be taken mainly as juice.

As might be predicted from the great development of the muscles of protraction and the blade-like modification of the mandibular rami in *Icterus*, the feeding method involves the thrusting of the closed bill into the fruit, after which it is opened forcefully against the resistance of the pulp and skin. This gaping increases in extent as the pulp is broken down and the brushy tongue is protruded rapidly, lapping the juice and shredded material. The broadening of the mandibular rami at the point of greatest wear, their turning inward ventrally, and the sheathing in horn uncommonly far posteriorly form a functional wedge of the lower mandible that is matched by the similar contour of the upper.

In the genus of nectar-feeding orioles for which it has been necessary to revive the name *Bananivorus* (Beecher, 1950) these features are largely lacking in the lower mandible, except where certain (mainly island) forms have taken over the fruit-eating niche of the absent *Icterus*. However, the increased development of *M. depressor mandibulae* and of the posterior lever of the mandible persists. These relatively slender-billed species still gape, even though only down the throat of a nectar-filled flower. In short-billed species like *Bananivorus cayanensis*, a hole may be pecked in the side of a long-necked corolla and enlarged by gaping. Both genera of orioles also take insects as food, but there are few passerine birds that do not.

A palatal keel essentially like that of the grackle *Quiscalus* occurs in the orioles, *Icterus gularis* and *I. nigrogularis* (Wetmore, 1919). This is thought (Beecher, 1950) to permit use of seeds as food when fruit and nectar are scarce.

The Gaping Adaptation of Oropendolas.—As may be judged from Figure 6 the entire jaw musculature of *Ostinops decumanus* is powerfully developed, correlated with a relatively massive bill, but again the emphasis is placed on the gaping musculature. Figures 7 to 10 place the oropendolas and caciques in a different phyletic branch of this family from the orioles; hence the gaping trait and pendant nest possessed in common by both branches are considered convergent. The prominent casque found in all members of the oropendola-cacique line, which is evidently functional for gaping in large fruits, at once sets them off and they agree well in other skull features. This casque is so blunt and rounded that it seems the blade-like rami of the lower mandible must do most of the cutting inside the fruit, the upper mandible serving more as an anchor. In this connection it becomes considerably less kinetic in the larger oropendolas (10° of arc in *Ostinops*). But the general narrowing and elongation of the mandibles, the extension of the casque onto the forehead dorsally and of the horny covering of the mandibular rami onto the facial area ventrally are all adaptations for gaping of large fruits. In the most highly evolved oropendolas of the genus *Gymnostinops* the facial area, especially around the eyes and all along the length of the lower jaw, has become denuded of feathers.

I have observed the gaping of the Colonial Cacique, *Cacicus cela*, in the zoo. The closed bill was thrust into an orange with a rapid up and down movement of the head, and almost immediately opened and closed very slightly as though in drinking. As the hole deepened the bill was gaped a few times spasmodically and driven in at different angles and gaped again. In the process the bill is often driven in almost to the eyes and the feathers about the bill became sticky with juice. The tongue may be seen running in and out, although it is difficult to glimpse this.

The Wood-prying Adaptation of Caciques.—In certain caciques we find this same extreme development of protractors, with lever-like posterior extension of the mandibular ramus, put to a functional use that is in part different. Wetmore (1926: 388 ff.) has described the behavior of *Archiplanus* in the field. Unlike orioles which confine their activities to the smaller branches of trees, members of this genus frequent larger branches and dead stumps where they pry in crevices and under bark with the bill partly opened. Dickey and van Rossem (1938: 537) reported *Amblycercus holosericeus,* quite possibly derived from *Archiplanus,* as rapping on branches like a woodpecker. Boucard (1883:445) described it as alighting on and splitting a weed up its length by a single twist. I assume this is done with the bill fixed in the partly open position, and suggest the term "prying" for this behavior of these two genera. They can still gape but appear to have carried the use of the tool a step farther.

A study of the morphological tree as represented in Figures 7 to 10 indicates that these two are possibly modified from the more generalized caciques, differing by reduction of the casque, and general straightening of the bill. Though anatomically similar to each other, differences in the development of *M. depressor mandibulae* and in the posterior process of the mandible, as well as the operculate nostril in *Amblycercus,* leave relationships in doubt. As indicated in Figure 10, *Amblycercus* could perhaps be derived from *Cacicus* stock as easily as from *Archiplanus.* This would mean that they represent independent, essentially parallel origins of the prying adaptation. But certain features run consistently through the entire cacique line. The general narrowing of the skull noted also in orioles and in members of the so-called Coerebidae (e.g. *Coereba*) appear (Beecher, 1950) to be an adaptation for probing in fruits and flowers. The increase in interorbital distance in the skulls of oropendolas, on the other hand, may merely be a structural adjustment necessitated by the extension of the casque onto the forehead. But all gapers are characterized by some constriction of the base of the upper mandible and of the zygomae at its junction for enhanced forward vision. Though no blackbird compares with the Starling, *Sturnus,* in this respect, a turning forward and downward of the orbit is noticeable even in oropendolas and caciques.

MODIFICATIONS IN THE FEEDING MECHANISM OF OTHER GENERA

The remaining genera of the Icteridae fall under one or another of the adaptive categories outlined above. The food niche and the functional modification of the skull and musculature for exploiting it are in each genus variations of one of those illustrated in Figures 4 to 6. Therefore, it has not been considered necessary to make detailed muscle drawings for all the 38 genera, and they have instead been arranged in the form of a tree in Figures 7 to 10 for convenient comparison of skull, musculature, and horny palate. Although this paper does not concern itself much with phylogeny it is here emphasized that any such tree, especially when based entirely on genera existing in the present cross-section of time, is really only an expression of morphological relationships. The moment it is taken to imply descent it becomes hypothetical. Therefore, though it simplifies discussion in the following account to say that genus A appears to give rise to genus B, it must be understood that the real truth may be that both stem from an ancestor unrepresented in the present fauna.

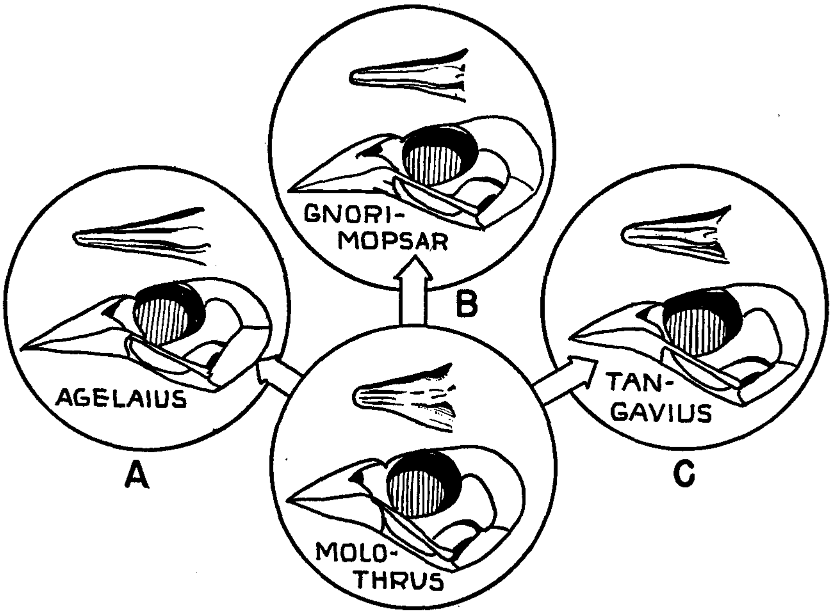


FIGURE 7. Morphological tree showing possible origin of the three major icterid lines from the ancestral cowbird. A. the blackbird-troupial (agelaiine) line; B. the grackle (quiscaline) line; C. the cacique (cassicine) line. The genera figured may closely represent the original divergence and are treated as lying at the base of their individual lines in Figures 8, 9 and 10.

All that the figures show is the relative development of muscle masses, skull form, and palate pattern in the genera. An understanding of the adaptations discussed above permits one to predict with some assurance whether any one of these genera is a gaper, and the field notes of competent observers generally permit us to judge whether the gaping is done in fruit, earth, ground litter, or wood.

Figure 7 indicates three lines which appear to arise from an ancestral stock probably typified by *Molothrus* today. These are: (A) a blackbird-troupial (agelaiine) line; (B) a grackle (quiscaline) line; and (C) a cacique (cassicine) line. The revisions of Sclater (1883–84) and Ridgway (1902) recognized the orioles and meadowlarks as additional lines, but theirs was a static morphological approach and these genera now appear to be unquestionably agelaiine. However, the figures clearly show the same adaptations appearing in each of the lines, and other parallel characters (the pendant nest, for example) appear in all three lines. In a family where convergence even between close genera may be the rule (Beecher, 1950) we can be certain of nothing.

Hence, it is impossible to assign each genus to a particular line with complete confidence. This is not because the lines are not distinct where well characterized by advanced members but, due to the many traits held in common by all icterids, the lines lose their distinctness when traced backward to the initial branching from the ancestral *Molothrus* stock. In the origin of the three lines (Fig. 7) the essential similarity of *Agelaius*, *Gnorimopsar*, and *Tangavius*, both to *Molothrus* and to each other, is apparent; it is only by a careful building up of the series that one can attempt to trace the lines. *Gnorimopsar* appears agelaiine in many respects but has the habits of the grackles and is transitional to genera (Fig. 9) assigned to the grackle line on other grounds. *Tangavius* is clearly a cowbird but seems to be transitional to the giant cowbird *Psomocolax* which appears to be near the direct line leading to the caciques and oropendolas.

The Blackbird-Troupial Line.—In the agelaiine line the old and large genus *Agelaius* (Fig. 8) appears to be the only one with sufficiently wide geographical range to be considered ancestral to all the remaining genera, most of which are little modified from it and appear to come from it or a similar stock independently rather than from each other. The black plumage, which could be so advantageous in *Agelaius* whose vast flocks apparently assemble visually, tends to disappear in solitary descendant forms. The gaping Meadowlarks, *Sturnella*, and the parallel troupials, *Pezites* and *Leistes*—as well as the finch-like Bobolink, *Dolichonyx*, and Dickcissel, *Spiza*—assume protective pattern and color. The most conspicuous forms of the gaping orioles, *Icterus* and *Bananivorus*, which have apparently been selected in large measure for flash-coloration (Beecher, 1950), are protected by the trait of nesting in thorn trees.

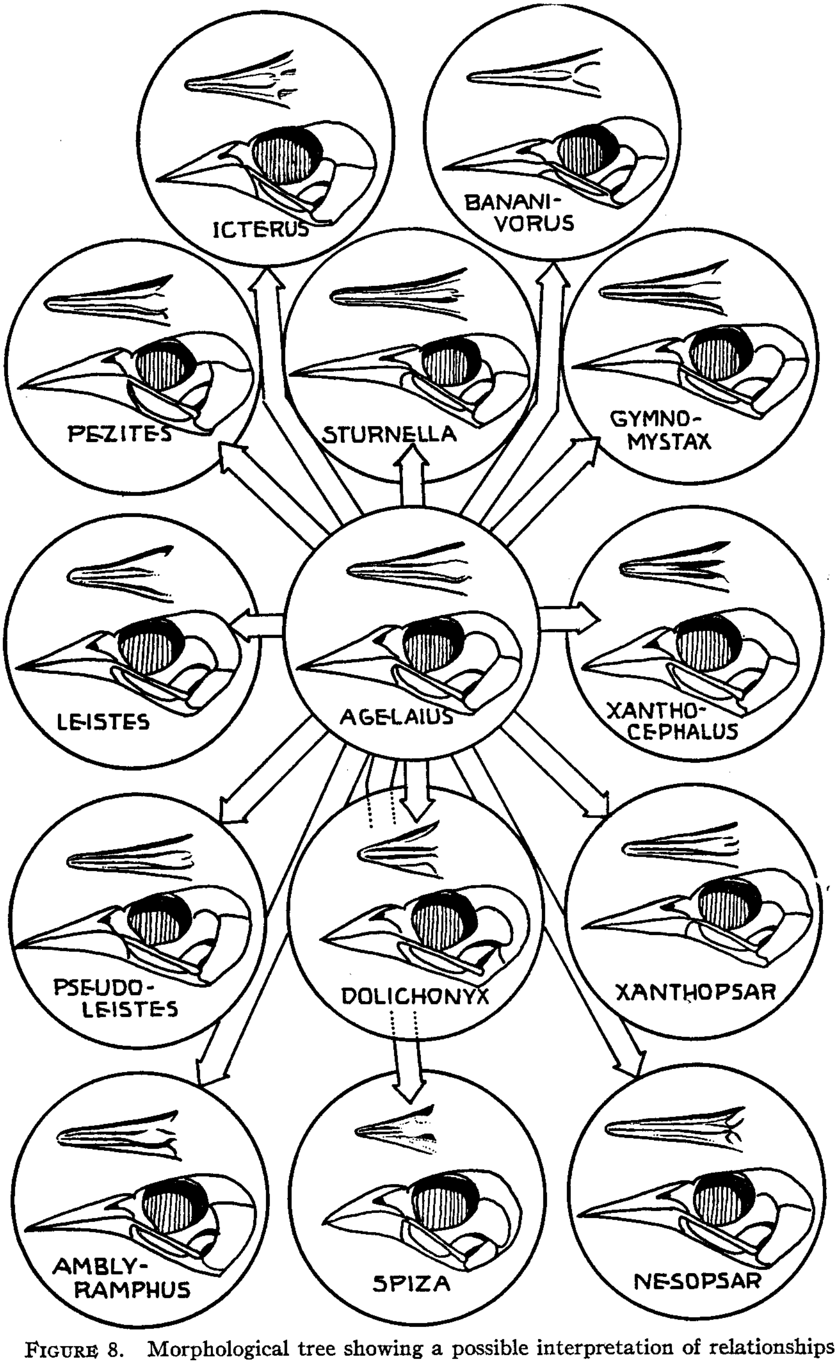


FIGURE 8. Morphological tree showing a possible interpretation of relationships in the blackbird-troupial line.

In the long-billed forms that seem to stem from *Agelaius* stock gaping tends to increase, in short-billed forms, to decrease. I have observed *Agelaius* gaping in captivity and it has *M. depressor mandibulae* well-developed, but *Xanthocephalus, Pseudoleistes,* and *Amblyramphus* (Fig. 8) show progressive increase in the area of this muscle and the trait of gaping in or on the ground. *Xanthopsar* is probably a fruit gaper as is *Gymnomystax,* but the latter is more like a blackbird in habits (Wetmore, 1939: 249) than either the fruit-gaping oriole, *Icterus,* or the nectar-gaping *Bananivorus. Nesopsar* appears to be a bark-prying form confined to the Jamaican rain forest. There is no anatomical evidence that it could be compared with *Archiplanus* in this respect, but Sclater (1861: 74ff.) stated that it habitually perches vertically on tree trunks (which is borne out by the frayed condition of the tail in all specimens examined), and Bond (1936: 360) mentioned one examining a moss-covered limb for food. The gaping *Pezites* and *Sturnella* may have arisen independently in different parts of the range of *Agelaius,* pursuing parallel plumage trends, though the flash color of one is red, of the other, yellow. *Leistes,* with a plumage pattern similar to *Pezites,* is even more finch-like than *Agelaius* and has *M. depressor mandibulae* only intermediate in development. *Dolichonyx* and *Spiza* are obvious seed-eaters in which this muscle is as poorly developed as in *Molothrus* itself.

The pattern of the horny palate conforms to the same type in all members of the Icteridae and, though convergent overlap makes it a poor clue to the boundaries of the three lines, it has some value within a single line. The two rather deep, closely appressed central grooves of the horny palate form three ridges. The central ridge broadens into a rounded boss posteriorly against which the grooves fade out. This pattern seen in the palate sketch for *Agelaius* (Fig. 8) may be a carry-over from the emberizine finches and tends to persist even in the longer-billed blackbirds. The adaptive reduction of the boss in *Leistes* makes it a little unlikely that it could easily reappear in *Pezites;* so it may be that the latter comes directly from *Agelaius* stock. However, it is readily admitted that it could have come from *Leistes* which then modified the palate subsequently. In the same way *Xanthocephalus* and *Dolichonyx* with similarly reduced bosses seem to come from *Agelaius* stock because the palate modification in deriving them from *Molothrus* stock would be much greater. But this type of reasoning may be invalid. Figures 7 to 10 represent a tree of morphological relationships, tempered by considerations of geography, ecology, and behavior so far as they may be gathered at present. They show one possible arrangement; the facts are quite amenable to other interpretation.

Even if convergent overlap makes it difficult to provide a satisfactory arrangement of genera in the Icteridae, there is little doubt concerning the genera that should be included in the family. The Dickcissel, *Spiza americana*, is here included in the Icteridae largely on the basis of jaw muscle pattern and the horny palate which are in complete agreement with these features in this family. Removal of this genus from the Emberizinae to the Icteridae is not so drastic since the latter have arisen from the former, but it is important as signifying that *Spiza* is really a blackbird and not a borderline case as suggested by Sushkin (1925). Ridgway's (1902) diagnosis revealed no reason for keeping it in the Emberizinae, and absence in the Icteridae of emberizine rictal bristles is not a hard and fast rule. These bristles occur in typical icterids like the caciques; hence their presence, much reduced, in *Spiza* is of little diagnostic importance as compared with the evidence of muscle pattern and palate which may be conservative characters.

The plumage pattern of the Dickcissel is only superficially similar to that of the Meadowlark, but the behavior is similar in many respects to that of the Bobolink. Sushkin and Bangs (Sushkin, 1925) believed the apparent extinction of an eastern species, *Spiza townsendi*, and the gradual disappearance of the present species over the eastern half of its range pointed to *Spiza* as an archaic genus. Since Hellmayr gave no reason for placing *Spiza* in the Richmondeninae, his divergence from the opinion of Ridgway and Sushkin is not to be taken seriously.

The Grackle Line.—The genus *Gnorimopsar* (Figs. 7, 9) is selected as one that could give rise to the grackles or is at least close to the stock that did so. Though generalized, without high development of *M. depressor mandibulae*, it may be on the direct line producing forms like *Notiopsar* and *Dives* (Fig. 9) that are powerful gapers. On the other hand, *Oreopsar*, *Hypopyrrhus*, and *Macroagelaius* are apparently not gapers, the latter showing every indication of close relationship with the reputedly tanager-like *Lampropsar*. From its range in the Central Lowlands of South America, *Gnorimopsar* could have originated these genera in the slowly rising Andes in the latter half of the Tertiary, and here *Dives* appears to have evolved on the direct line leading to the more northern grackles. *Ptiloxena* of Cuba is very similar to it, though less powerful in its musculature, while *Holoquiscalus* is modified for more powerful gaping. The Boat-tailed Grackle, *Cassidix*, despite the curved culmen and long tail, could well stem from the latter with emphasis on both gaping and adducting. The palatal boss seems to be transitional to the highly developed ridge in the Bronzed and Purple grackles, *Quiscalus*, as mentioned earlier. The Brewer's and Rusty

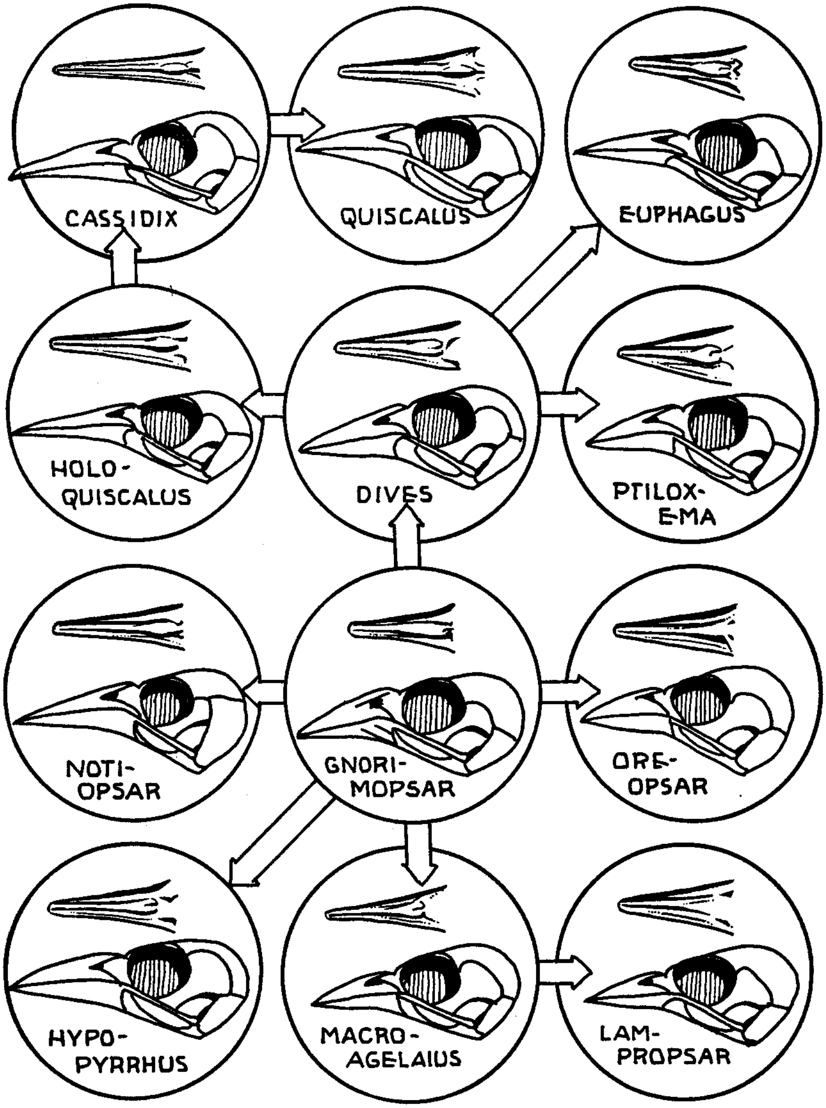


FIGURE 9. Morphological tree showing a possible interpretation of relationships in the grackle line. (For '*Ptiloxema*' read '*Ptiloxena.*')

blackbirds, *Euphagus*, could have evolved from *Dives* stock in Mexico but are hard to place definitely.

The dividing of the palatal boss and its reduction posteriorly appear to reflect a general broadening of the bill posteriorly as an adaptation to insectivorous diet or at least to soft food. *Lampropsar*, reputed to nest like an oriole and to eat fruit (Cherrie, 1916), has virtually lost the boss posteriorly as has *Gymnostinops* among oropendolas. However, if the former is a fruit-eater it certainly does not appear to be a fruit-gaper, judging by anatomical development.

The Cacique Line.—That *Tangavius* is simply an advanced cowbird with a ruff of elaborated feathers on the back for making more effective the courtship display noted by Friedmann (1929) seems fairly certain. The Rice Grackle, *Psomocolax,* with a similar ruff (Fig. 10) seems to be a giant cowbird with grackle traits, though the flattening of the culmen into the beginning of the casque so typical of the caciques and oropendolas strongly suggests that it may be a transition stage in their evolution. Any other such transition forms have disappeared from the living record, possibly reflecting the positive selective advantage of the casque in those species evolving it over others that failed to do so. Relationship of *Psomocolax* to the caciques and oropendolas is also suggested by the fact that *Psomocolax* parasitizes their nests exclusively, despite the presence of numerous hosts of suitable size within its range, including grackles. There appears to be a definite tendency (Friedmann, 1929) for South American cowbirds to parasitize near-relatives.

The presence of the three monotypic genera, *Ocyalus*, *Zarhynchus*, and *Clypicterus*, in restricted ranges in the Andes suggests the origin of oropendolas in the rising northern Andes. All the genera are already highly specialized, but *Ocyalus* may most nearly represent the ancestral stock of the remaining caciques and oropendolas. At any rate a similar ancestral stock appears to have given rise to the much more numerous oropendolas of the genus *Ostinops* which appears to terminate in the very specialized *Gymnostinops*. All of these are gapers with a notable blade-like broadening of the rami of the mandible and a sheathing of the bill with horn far back into the face. This apparently is associated with the method of probing in fruit, and *Gymnostinops* has also adaptively lost most of the feather covering in the facial area.

This same common ancestor, similar to *Ocyalus*, could have evolved the large cacique branch of this phyletic line. *Cacicus* is the large genus of the abundant Colonial Caciques of which *Cassiculus* of western Mexico is apparently a specialized offshoot. *Cacicus* stock could also easily have evolved the specialized wood-pecking cacique, *Archiplanus*, with the same secondary reduction of the casque noted in *Cassiculus*. The adaptations noted in *Archiplanus* seem to culminate in the still more specialized *Amblycercus*, although separate origin of the two from *Cacicus* is just as valid an interpretation. All these genera in the cacique line (possibly even including *Psomocolax*) are

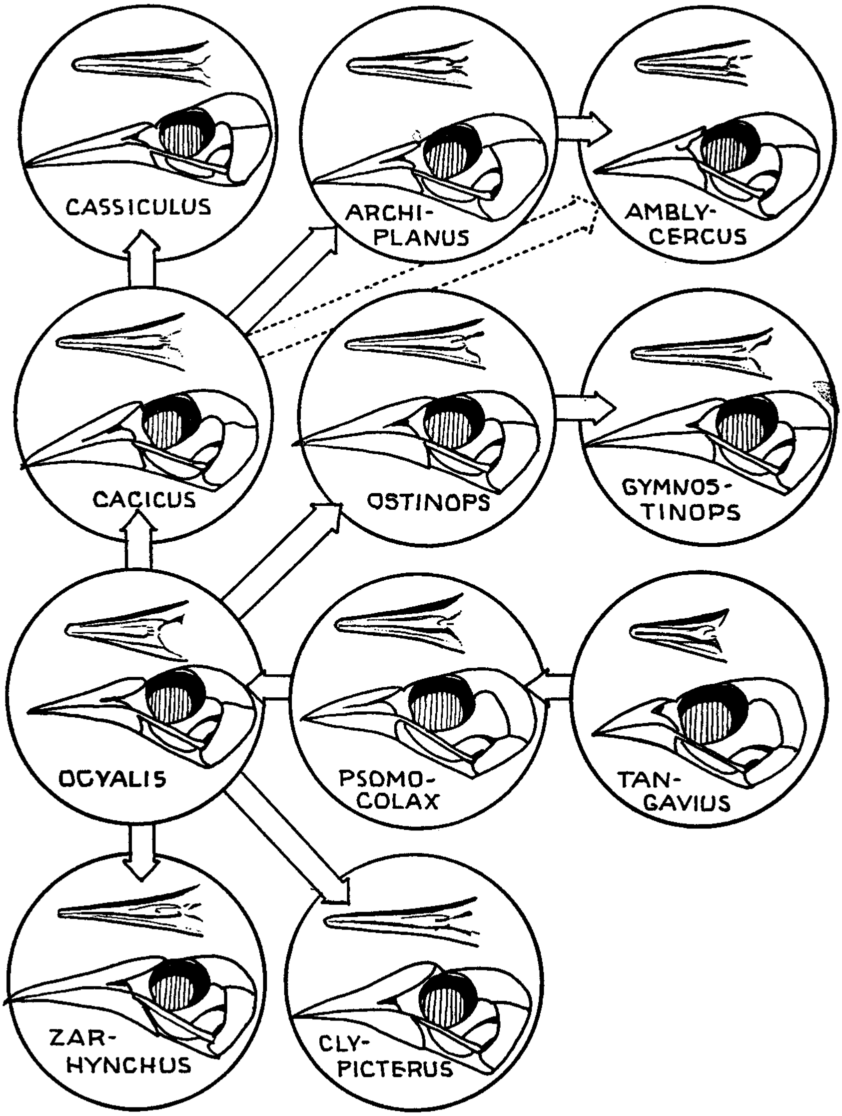


FIGURE 10. Morphological tree showing a possible interpretation of relationships in the cacique line. (For *'Ocyalis'* read *'Ocyalus.'*)

gapers, feeding largely on fruit. Although this is not to be gleaned from the literature, Goodfellow (1901: 476) noted fruit depredation on the part of *Zarhynchus wagleri* and Mr. Ernest Holt has assured me that this is a common complaint against oropendolas.

This line may provide a clue to forces governing body size in related bird forms. *Psomocolax* becomes a large cowbird with a casque, and its larger size may be nothing but a response to the abundance of large fruits on which it feeds. Fruit-eating oropendolas of similar or larger size spring from this stock. So do smaller caciques with reduced casques and these appear to evolve wood-prying forms. This suggests an adaptive increase, then decrease, in body size with diet change in the same phyletic line—a phenomenon also noted in the blackbird line. There the fruit-adapted orioles, *Gymnomystax* and *Icterus icterus*, have evolved from *Agelaius* stock with increased body size and bill-length in probable adaptation to the abundance of large pulpy fruits (Beecher, 1950), whereas the nectar-adapted oriole *Bananivorus* has evolved from the same stock with a smaller bill and body. It appears that the body may follow the adaptive lead of the bill regarding size in such food adaptations.

PHYLOGENETIC IMPLICATIONS OF THESE ADAPTATIONS

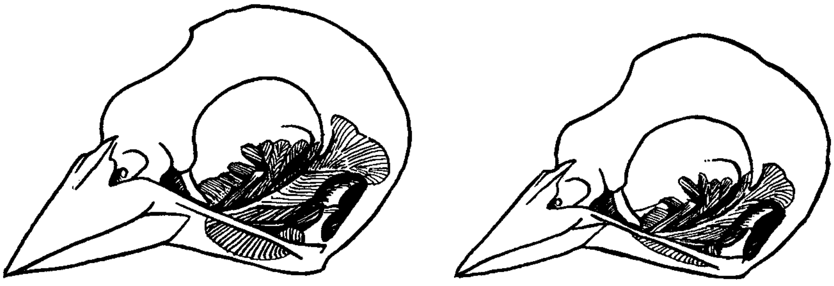
The "explosive" adaptive radiation of the genera of the Icteridae to occupy, in the present cross-section of time, virtually every food niche available to passerine birds is unique. No other case is known to me of birds of a single family (really subfamily) embracing so many diversified adaptive types. The springboard for this rapid radiation was apparently an adaptation (pre-adaptation) of general significance (Wright, 1941), that is, the ease with which the gaping function and elongation of the bill could be acquired. The posterior, lever-like extension of the mandible and the enormous spread of *M. depressor mandibulae* over the posterior area of the skull permitted the bill to be used in an entirely different manner from that prevalent in the ancestral cowbirds or the emberizine finches of the *Phrygilus* type from which they appear to arise.

At any rate the gaping function has clearly permitted a different use of the bill as a tool in the rapidly evolving Icteridae. Whereas the great host of existing passerine species adapted for insect-eating thrashed about in ground litter, picking up debris and tossing it aside, the insect-eating blackbirds moved debris aside by gaping. Whereas a tanager might bite a piece out of a soft fruit, an oriole or oropendola drove the bill into the fruit closed, then opened it repeatedly inside, lapping the juice. The tongue thus became similar to that of nectarfeeders like *Coereba*, and there arose an additional oriole line specialized for nectar-feeding. There was also room among the tree-creepers for a wood-pecking group capable of prying or twisting with half-opened bill and the use of gaping by *Archiplanus* and *Amblycercus* to pry under bark probably has no other counterpart in passerine birds. Thus, by developing new uses for old tools, the Icteridae have originated entirely new ways of exploiting food niches.

In the terminology of Wright (1931 and later) and Simpson (1944) the ancestral cowbird might be regarded as arriving on an adaptive peak from which it has been able to exploit other peaks. Wright (*in* Jepsen, Simpson, and Mayr, 1949: 387) expressed the normal process when he observed that "a single peak is replaced by a higher system of peaks"; but, in the sense I understand the peaks, the Icteridae represent a descent to a lower system of adaptive peaks.

This is because the origins of the major food adaptations (the peaks) in passerine birds appear to have occurred in a definite time sequence. Just as the seed-cracking skull is the most complex and recent, the skull of a primary insect-eater in the Vireonidae is the most simple and primitive. It may be permissible to assume that, before the origin of flowering plants in the Upper Cretaceous, all passerine birds were insectivorous, with the simple, parallel muscle pattern still found today in the Muscicapidae, Vireonidae, and the even more primitive Tyranni (Furnariidae, Dendrocolaptidae, etc.). But with the origin of flowering plants we would expect a powerful selection pressure to be imposed on these birds to make use of new food types. Adaptations for utilizing fruit, nectar, and seeds may have appeared in that order—which is in agreement with the order of skull evolution in passerine families of the American assemblage. The sequence from insect- to seed-eater is one of increasing architectural complexity and muscular complexity, with pinnate adductor muscles replacing parallel ones. Returning to Wright's terminology, therefore, I would regard the seed-cracking adaptive peak as highest both in lateness of origin and anatomical specialization. The fruit-eating and nectar-feeding peaks are lower, and the insect-eating peak is lowest of all, anatomically speaking. The secondary radiation of the finch-like blackbirds into fruit, nectar, and insect niches is, in this sense, a movement from a higher to several lower peaks. Apparently a high rate line (Simpson, 1944) like the Icteridae, starting an adaptive radiation from the highest adaptive peak, can rapidly occupy the lower peaks.

The laboring of this point is not merely academic. The fact is that the remarkable radiation of the Icteridae into all the passerine food niches was accomplished by relatively slight changes in skull architecture and emphasis of certain muscle masses at the expense of the others. There is no change in the basic muscle pattern, such as occurred in each of the less-advanced families that earlier radiated into these niches through perhaps slower evolutionary changes—the vireos, warblers, tanagers, and finches of the American assemblage. The pinnate adductors (of finch origin) persist in the most insectivorous adaptations of blackbirds. The elongation of the pinnate fibers in the Rusty Blackbird, *Euphagus carolinus*, is precisely like that in the largely insectivorous Swamp Sparrow, *Melospiza georgiana*, quite possibly derived (Fig. 11) from the seed-eating Song Sparrow, *M. melodia.*



Melospiza melodia

Melospiza georgiana

FIGURE 11. Reduction of bill, skull, and bulk of jaw muscle in *Melospiza.* The adaptive reduction of these features with increase in insect diet in the Swamp Sparrow, *M. georgiana,* over the condition in the seed-cracking Song Sparrow, *M. melodia,* does not change the basic muscle pattern.

In future publications it will be shown that this basic muscle pattern is different for each of the passerine families. Each appears to be an adaptive branch on the phylogenetic tree, that has budded off under selection pressure induced by food competition; and bill and skull seem to lead the way in the evolution of these higher categories. Contrasted with this high rate of evolution for the jaw musculature, the hind-limb musculature conforms to a single pattern in Passeres, suggesting a lowered or more stabilized evolutionary rate. But, if the jaw muscle patterns are adaptive they are also phylogenetic. Dissection of several hundred species of passerines shows the jaw muscles to be a reliable additional line of evidence for determining relationship at the family level. It is interesting that the manifold food adaptations of icterid genera have been accomplished within a single muscle pattern, possibly imposed by a genetically deep-seated finch ancestry.

SUMMARY AND CONCLUSIONS

An investigation was made of the feeding modifications in the skull in all genera of the family Icteridae, with special attention to the jaw musculature. The kinetics of the upper mandible and its rôle in the feeding function were studied and the location and functional rôle of the major muscle masses of the skull were outlined briefly. For purposes of comparison it was necessary to break these down into individual muscles and to make a sharp distinction between the primitive parallel muscle type of primary insect eaters like the Vireonidae and the advanced pinnate type characteristic of the adductor mass in finches.

All genera of the Icteridae have pinnate adductors—even the largely insectivorous *Euphagus*—and it appears that the family, evolving from the emberizine finches via the cowbird *Molothrus*, is secondarily occupying the insect- and fruit-niches. In its derivation from the ancestral cowbird, the insectivorous *Euphagus* has elongated the bill, forceps-like, straightened the angulated commissure, and increased the kinetics. The lever-like orbital process of the quadrate, long in finches, is shortened. Its adaptively weak jaw musculature is, however, replaced by powerful musculature in the grackles, *Quiscalus*, which saw acorns and dried kernels of corn by means of a sharp keel of the horny palate and powerful adduction. The Meadowlark, *Sturnella*, uses powerful muscles of protraction, especially *M. depressor mandibulae*, to gape the mandibles in the earth or in ground litter with considerable force. The caciques, *Archiplanus* and *Amblycercus*, are able by means of very high development of this muscle to separate the bark from branches and to pry in cracks. All of the 38 genera fall into one or another of the food-niche categories exploited by the genera discussed in detail, and a rough survey of the adaptations in each of the three phyletic lines—the agelaiine, the quiscaline and the cassicine—is made.

It is suggested that the "key" to the ability of the Icteridae to exploit all passerine food niches from finch-like beginnings has been the ease with which the area of attachment for *M. depressor mandibulae* has apparently increased. The fact that this could occur here and also in other muscular attachments, without modification of the basic jaw muscle pattern, suggests the deep-seated genetic nature of these patterns which are specific to each passerine family. Because of this conservatism in the very seat of adaptation, the muscle patterns may be employed as an additional line of evidence in determining the relationships of the passerine families to each other.

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LOUIS BENNETT BISHOP, 1865–1950

BY HILDEGARDE HOWARD

Louis Bennett Bishop, the son of Timothy Huggins and Jane Maria (Bennett) Bishop, was born on June 5, 1865, at the home of his maternal grandparents in Guilford, Connecticut. The Bishops were one of the early families of Connecticut, dating back to John Bishop who settled in Guilford in 1639. The family residence had been in New Haven for two or three generations before Louis was born, and it was there, at 215 Church Street, that Louis grew up.

His earliest schooling was received in a private school maintained by two New Haven ladies. We may picture him, one morning at the tender age of six, trotting through the garden on his way to school, slingshot in pocket, and perhaps a book on a strap. Undoubtedly he is intent on punctuality, for so his parents trained him. But in the garden, close at hand, appears a bird. School is momentarily forgotten, while his trusty slingshot is aimed—oh, so carefully—and the bird falls at his feet. Conflicting emotions bid him—take the bird back to the house, go on to school. Dutifully, he pockets the bird and runs on to school, fearful now of tardiness. We wonder, though, how much he learns this day—the day he collected his first bird. Somehow that bird was preserved and became part of the famous Bishop collection which at the time it was transferred to the Chicago Natural History Museum numbered 53,000 specimens.

Louis was 12 years old, and a pupil in the Hopkins Grammar School in New Haven, before he had any actual training in collecting or preparing bird skins. He and L. C. Sanford were schoolmates and