

RELATIONSHIPS IN THE NEW WORLD
NINE-PRIMARIED OSCINES

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WILLIAM J. BEECHER has performed a tremendously important service to ornithology through his studies of jaw musculature in passerine birds. His many dissections have given him a factual basis for deductions concerning passerine phylogeny (Beecher, 1950, 1951a, 1951b, 1953). Beecher has not hesitated to depart radically from existing classifications where his interpretations indicate that departures are necessary. This attitude is commendable. It is to be expected, however, that not all systematists will agree with Beecher's conclusions. Beecher recognizes this probability (1953:276) and rightfully suggests that where disagreements arise his published drawings of jaw musculature represent evidence to be reassessed. Perhaps one of Beecher's main contributions will be to call forth discussions from specialists with dissenting opinions. The present paper is an attempt to clarify the relationships of some of the New World nine-primaried Oscines, a group of special interest to me (Tordoff, 1954), utilizing Beecher's data where applicable. This group includes the following families of Hellmayr's "Catalogue of birds of the Americas": Vireonidae, Vireolaniidae, Cyclarhidae, Coerebidae, Compsothlypidae (= Parulidae), Tersinidae, Thraupidae, Icteridae, Catamblyrhynchidae, and Fringillidae.

Beecher (1951a:418-420; 1953:272-276) has made certain basic assumptions which require comment. Having first ascertained that the pattern of the jaw muscles provided useful differences between families and yet was constant within families, he assumed, for convincing reasons, that muscles with parallel fibers were more primitive phylogenetically than muscles with pinnate fibers. His second assumption is that a phylogeny may be reconstructed from a morphological tree of relationships of living forms. Clearly it is impossible to derive any living group from any other living group in a literal sense; instead, Beecher thinks that modern families of passerine birds are of great age. He (1953:273) postulates that certain insectivorous groups with parallel jaw musculature may date back to the Cretaceous Age essentially unchanged. More advanced groups with pinnate musculature he assumes to have diverged soon after the development and radiation of flowering plants in the Upper Cretaceous. Much or perhaps most radiation of birds seems to have taken place earlier than in comparable groups of mammals, but I can not avoid skepticism when I read that Beecher (1953:273) thinks that the Vireonidae (un-

known as fossils) have existed *as vireos* in the New World since some time in the Cretaceous. I grant that, lacking an adequate fossil record, birds must be classified on the basis of morphology and behavior of living forms, but I think that, in general, derivation of modern groups from other modern groups is unwise—especially in taxonomic categories of family rank or lower. The alternative, it seems to me, is to admit our nearly complete ignorance of the actual phylogeny of passerine birds and to label our reconstructed phylogenies based on modern birds as frankly hypothetical.

Beecher (1953:271–272) criticizes those systematists who, hoping “to by-pass the musculature,” have studied avian osteology. He maintains that musculature is more conservative; that “osteological ‘characters’ [are] often the expression of only minor muscle slips.” If this is true, then are we to abandon hope of ever learning much from the avian fossil record? It seems to me that changes in muscles and the underlying bones must usually go hand-in-hand. I think that Beecher’s criticisms are justified only in part; what is needed is not less study of bones but more study of both bones and muscles. Although Beecher discusses the “convergence hazard” (1953:274–275), he has not, in my opinion, completely avoided it (see below). Some problems in relationship seem to yield best to studies of muscles, others to studies of bones. It is encouraging, however, to note the frequent close agreement, discounting different interpretations, between myological, osteological, behavioral, and other kinds of evidence.

ORIGIN OF THE NEW WORLD HIGHER PASSERINES

The New World nine-primaried Oscines (exclusive of the subfamily Carduelinae, family Fringillidae—see below) are, by almost unanimous agreement, an assemblage of families of close relationship and common ancestry. Opinions differ as to the stem stock, however. Wetmore (1951:12) recently reaffirmed his belief that the Fringillidae are the central group of this assemblage—“the modern expression of a main core or stem that through the earlier Tertiary periods has given rise to more specialized assemblages that we now recognize as distinct families.” Glenny (1942:89) reached the same conclusion after a study of the arteries in the region of the heart. On the other hand, Beecher (1953:273) states that the Vireonidae (which he reduces to a subfamily of his Monarchidae) “gave rise to the entire nine-primaried American assemblage.” Beecher’s contention is based primarily on the fact that the vireos have the least pinnate—or most fully parallel—jaw musculature of the groups in question. Additionally, he (1951a) eliminates the Fringillidae as a potential stem stock because the

pinnate character of finch jaw muscles "may be too deep-seated genetically to be readily lost in a food adaptation." Such a loss would be required if the fringillids were the ancestral group (but see below).

I have previously (1954:31) presented in some detail my reasons for agreeing with Wetmore and Glenny in this matter. As is pointed out below, Beecher's data can, by reinterpretation, be construed as lending additional support to consideration of the Fringillidae as the central stock of the New World assemblage.

An explanation of the origin of the higher passerines which seems to explain both the jaw musculature and the bony palate of modern groups is as follows. I have presented (1954:22-26) evidence to the effect that the ancestral stock of the New World assemblage possessed palato-maxillaries as an adaptation to feeding on seeds or fruits. Beecher is convinced that the ancestral stock had largely parallel jaw musculature. In the modern descendents of the hypothetical ancestral stock, powerful biting or squeezing action of the jaws is accomplished in either one of two ways. The emberizines have perfected their adaptation to a hard diet by developing fully pinnate adductors of the lower jaw. The richmondenines seem equally well adapted to hard foods, but they have achieved this through maximum development of palato-maxillaries coupled with less fully pinnate jaw muscles than in emberizines. Perhaps the fully pinnate adductors of the emberizines have permitted the reduction of the palato-maxillaries seen in this group. If this is true, then the shift in diet from seeds to insects and back to seeds again which I postulated earlier (1954:26) to explain the emberizine palate becomes unnecessary.

This interpretation calls for ancestral stock with palato-maxillaries and with at least partly parallel jaw musculature, satisfying the hypothetical attributes required by both Beecher and me. Given this ancestral stock, derivation of the vireos (thin bill, largely parallel jaw muscles, fused palato-maxillaries) at an early date presents no unexplainable problems. The same can be said for derivation of other groups in the assemblage, some of which are discussed in more detail below.

ORIGIN OF THE CARDUELINAE

A major point of disagreement between Beecher and me has to do with the origin of the "northern finches"—the Carduelinae. These are supposed by Beecher to be derived from tanagers. My opinion is that the carduelines are related to the Estrildinae (= Estrildidae of Beecher) of the Ploceidae and are thus Old World in origin.

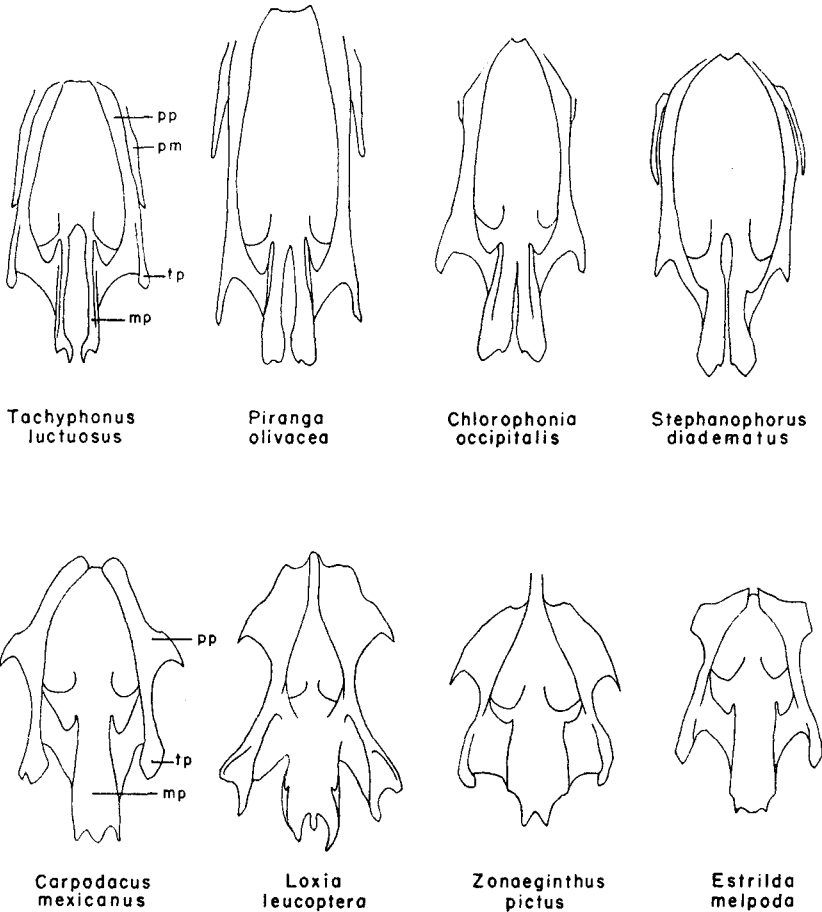


FIGURE 1. Diagrammatic drawings of bony palates in ventral view of tanagers, carduelines, and estrildines. Abbreviations are: pp—prepalatine bar; pm—palato-maxillary; tp—transpalatine process; mp—mediopalatine process.

Beecher's arguments (1951b:278–280; 1953:310–312) can be summed up as follows: the pattern of the jaw muscles of carduelines can be derived, without disjunction, from that of typical tanagers through the following series of genera: *Tachyphonus*—*Piranga*—*Habia*—*Tanagra*—*Chlorophonia*—*Stephanophorus*—*Carpodacus*. He states that the horny palate and plumage support the thesis of close cardueline-thraupid relationship.

In support of an Old World origin of the carduelines I have elsewhere (1954:18–20) presented evidence derived from the structure of the bony palate (see figure 1), distribution, migration habits, social

behavior, and nest sanitation. In all of these, the carduelines show close agreement with the estrildines. Additionally, a sharp break occurs between the tanagers and carduelines in the characters mentioned. I am not convinced that there is any significant resemblance in plumage between carduelines and tanagers. The superficial similarities in color (examples are the widespread occurrence of reds and yellows in both groups) probably are examples of adaptive convergence resulting from the forest-dwelling habit of most kinds in each group. This convergence is not nearly so convincing as the convergence in song, call notes, nesting, flocking behavior, and general proportions between, say, the cardueline genus *Leucosticte* and the emberizine genus *Calcarius*, yet no one postulates a close relationship between the latter kinds. Further, it has been well demonstrated (although not critically analyzed) that red pigmentation in carduelines differs from that in tanagers and in richmondinines. A major characteristic of red cardueline pigmentation is its instability—that is, it seems easily affected by diet and perhaps by climate (see Tordoff, 1952:203).

Beecher (1953:275) admits the possibility of convergence in jaw musculature, and I think the resemblance of carduelines to tanagers in this respect must result from convergence. If we assume for the moment that carduelines and estrildines are of common origin, the matter of jaw musculature remains to be explained.

Comparison of Beecher's illustrations (1953: figures 12 and 15 on pages 302 and 311) of the jaw musculature of estrildines and carduelines reveals, to me, no great differences. M7b (see Beecher's key to jaw musculature, 1953:277) is not pinnate in carduelines but is, seemingly, pinnate in estrildines. The ectethmoid foramen is single and slot-like in carduelines and double in estrildines (but single in other ploceids). Both single and double ectethmoid foramina occur in other passerine families. In other respects the two groups agree closely—even to the possession of posterolateral vaults in the horny palate of at least some forms of each group.

All things considered, there seems to be little evidence of close relationship between the carduelines and tanagers. Evidence for cardueline-estrildine relationship, on the other hand, is good. As stated elsewhere (1954:19), I am highly skeptical of the zoogeographic juggling necessary to derive the carduelines from the tanagers in the New World, and yet explain their present status as primarily an Old World group. In numbers of Recent species, in amount of generic endemism, and in adaptive radiation the carduelines would seem to be of Palearctic origin. The necessary postulation of arrival in the Old World of carduelines *before* the ploceids reached the Pale-

arctic—a postulation with no support in either fact or reason—is avoided by accepting the preponderance of evidence in favor of an Old World origin of the carduelines.

Beecher's (1953:312) allocation of *Fringilla* to the Carduelinae follows that of Mayr and Amadon (1951:28) and is not supported by the structure of the bony palate (Tordoff, 1954:23–24), although Beecher states that this structure in *Fringilla* has been modified as a result of the enlarged palatine salivary gland from the cardueline pattern. *Fringilla* is, in my opinion, a primitive emberizine.

ORIGIN OF THE PARULIDAE

Beecher (1953: 305, 307–308) unites the wood warblers and the emberizine finches into a single family, the Parulidae. The wood warblers are, according to Beecher, “the most slender-billed oscines with fully pinnate adductors” of the lower jaw. He lists some supposed adaptive advantages of this type of musculature for thin-billed birds. Ordinarily, however, development of pinnate adductors is correlated with increase in bill size—in turn correlated with seed-eating. It is difficult to understand the development of pinnate adductors in the thin-billed, mainly insectivorous and nectarivorous, wood warblers if they are, as Beecher states, directly derived from the thin-billed vireos—a group with largely parallel adductors.

Again, reinterpretation of Beecher's data provides an answer. In jaw musculature and in the structure of the bony palate, the wood warblers closely resemble the emberizines. Fairly close relationship between the groups is indicated, and the incongruity of fully pinnate adductors in the thin-billed wood warblers is readily explainable if, rather than considering the wood warblers as having given rise to the emberizines, we reverse the order. The logic of this arrangement strengthens the evidence that the Fringillidae represent the central stock of the New World higher passerines.

ALLOCATION OF CERTAIN FRINGILLID GENERA

Beecher includes *Guiraca*, *Cyanocompsa*, and *Passerina* in the Emberizinae. These genera have typical richmondenine bony palates (see figure 2). In nesting, song, coloration, and external structure they are richmondenine. I see no reason for removing them from their currently accepted position near *Pheucticus* in the Richmondeninae.

I agree with Beecher (1953:308) that the “sporophiline” finches are emberizine. Mayr and Amadon (1951:28) considered most of

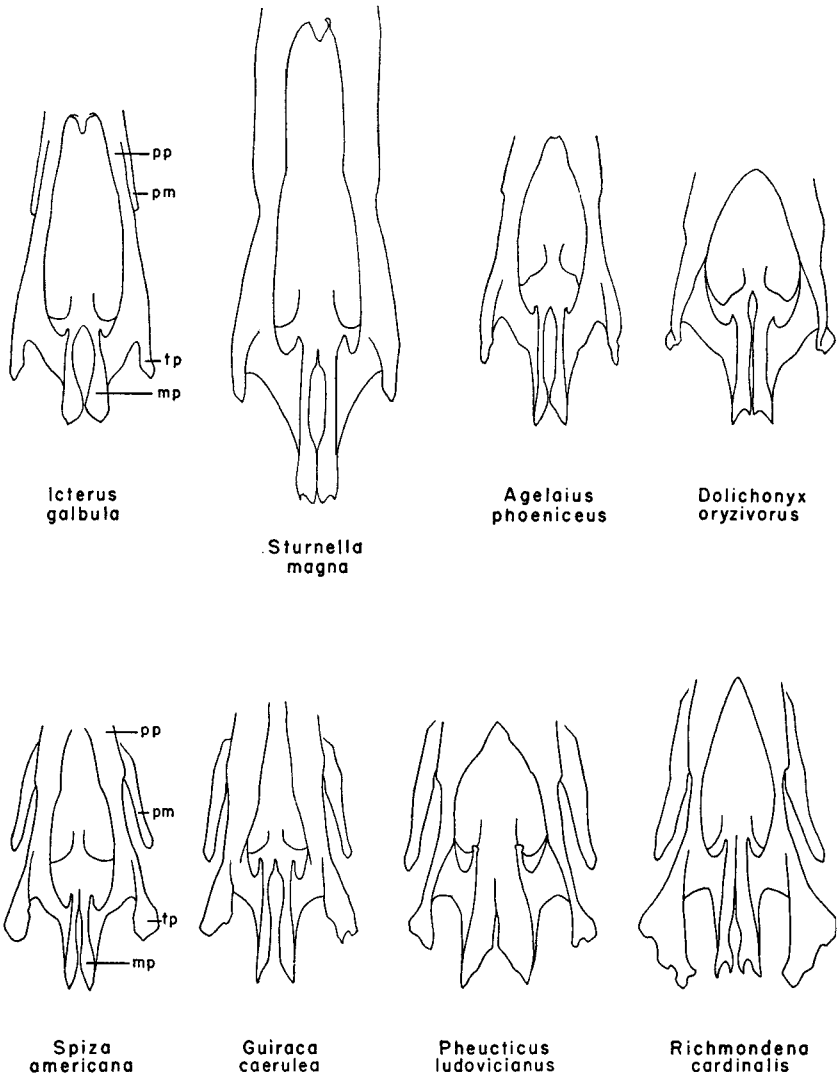


FIGURE 2. Diagrammatic drawings of bony palates in ventral view of icterids and richmondenines. Abbreviations are: pp—prepalatine bar; pm—palato-maxillary; tp—transpalatine process; mp—mediopalatine process.

them richmondenine. *Loxigilla* and *Melopyrrha* are placed by Beecher (1953:310) in the Pyrrhuloxiinae (= Richmondeninae), but he considers them convergent with the sporophiline group (Emberizinae) and recognizes that the two genera may really belong in that group. I think they are, in fact, emberizine, related to *Tiaris* and *Melanospiza*.

TAXONOMIC RANK OF THE GALÁPAGOS FINCHES

Extreme viewpoints regarding Galápagos finches are expressed by Beecher (1953:308), who regards them as worthy of full family rank, and the writer (1954:24), who included these finches with the emberizines and *Fringilla* in one subfamily, the Fringillinae. Beecher thinks that the Galápagos finches were derived from primitive emberizines—perhaps from the same stock as that which gave rise to *Melanospiza* in the West Indies (an idea first expressed by James Bond, 1948:222). I fully agree with this. Beecher, in his “diagnosis” of the Geospizidae, does not give any character or combination of characters which separates the “family” from the emberizines. For those persons who feel that the classification should clearly indicate that the Galápagos finches are monophyletic in origin (a point no one disputes), the best solution might be to retain the separate subfamily Geospizinae. (I agree with Wetmore, 1951:12–13, in being opposed to the use of tribes as a category between the genus and subfamily in birds on the grounds that it seems unnecessary and cumbersome.) In any event, I doubt that many ornithologists familiar with the birds in question will accept the lumping of carduelines, cardinal grosbeaks, and tanagers into one family with simultaneous elevation to full family rank of the Galápagos finches.

ORIGIN OF THE ICTERIDAE

Although Beecher and I agree on the major point that the Icteridae are derived from emberizine stock, I restate here my strong conviction that the Dickcissel (*Spiza americana*) is not an icterid (nor even an emberizine) but is an aberrant richmondene (see figure 2). I discussed this in detail earlier (1954:29) but would like to state here that the supposed similarities in behavior between *Spiza* and the Bobolink (*Dolichonyx*) mentioned by Beecher (1951a:431) simply do not exist. Aside from the fact that both species live in open areas and usually migrate in flocks, there are no convincing similarities. Bobolinks prefer moist grassy fields; Dickcissels favor rank, weedy areas. Bobolinks have an elaborate song; Dickcissels have a simple, unmelodious song. Bobolinks regularly deliver the song in flight; Dickcissels usually sing from perches. Bobolinks, in their nesting, are typical of many ground nesters. The nest is built of grass; it is well concealed and not especially bulky. The eggs are grayish-white with many dark spots and blotches. Dickcissels build a surprisingly bulky nest of grasses and leaves. The nest may be on the ground, above the ground in weeds and bushes, or even in low trees. And most surprising of all, Dickcissel eggs are clear, unmarked blue. Additionally, Bobolinks display extreme sexual dimorphism in color;

in Dickcissels this dimorphism is one of degree only. Bobolinks have an 'eclipse' plumage and consequently two complete molts annually. Dickcissels lack an 'eclipse' plumage and the prenuptial molt is limited to the foreparts.

It must be admitted, however, that the Dickcissel does not fit well into any of the conventional groups of the New World assemblage, despite the typically richmondene palate. Again I should like to state my opinion that *Spiza*, more than any other living genus, satisfies what I consider to be the requirements for the hypothetical fringillid stem stock.

ORIGIN OF THE DREPANIIDAE

I have no first hand knowledge of this group. It seems appropriate, however, to point out that Beecher (1953:312) found the Psittirostrinae strikingly similar in all respects (except plumage) to the cardueline finches. This similarity is equally strong in the structure of the bony palate (as shown by Amadon's figures, 1950:214). Almost all morphologists who have studied the group have postulated cardueline origin whereas Amadon favors origin from some coerebid- or tanager-like stock. Beecher considered the carduelines to be merely a subfamily of the Thraupidae and therefore is not troubled by these divergent opinions. For those who prefer to think of carduelines originally as an Old World group, however, the problem becomes important and I suggest that the question of origin of the family requires further careful study.

ORIGIN OF THE VIREONIDAE

If the vireos represent the central stock which has given rise to all other New World nine-primaried Oscines (which Beecher maintains) then the history of the bony palate of these groups becomes unexplainable. I see no way in which vireos, possessing fused, probably non-functional, palato-maxillaries, considered for the moment to be rudimentary, could have given rise to the rest of the New World assemblage, most families of which possess better developed palato-maxillaries than do vireos. As I pointed out earlier (1954), these bones are an asset primarily to birds with heavy, seed- or fruit-eating bills. I cannot see how wood warblers, as an example, would be under selective pressure to improve on the rudimentary palato-maxillaries of vireos. The fact that all New World nine-primaried Oscines have at least some trace of palato-maxillaries indicates that the ancestral stock possessed these bones—probably in functional condition. Thus, the traces of these bones in the thin-billed forms should be considered vestigial rather than rudimentary. Vireos, with their largely parallel jaw musculature and vestigial palato-maxillaries, seem to have

branched off from the ancestral finch stock earlier than any other living members of the New World group (see also earlier section concerning the origin of the New World higher passerines).

DISCUSSION

Having devoted some space to criticisms of Beecher's interpretations, I here restate my opinion that his studies are of great importance. He has provided a large number of data which are now available for evaluation and interpretation by all ornithologists.

The basic problem, the answer to which is the key to the validity of Beecher's interpretations, is whether parallel jaw muscles in modern birds are actually primitive. It seems likely to me that parallel muscles appeared earlier, phylogenetically, than pinnate muscles. But it does not necessarily follow that modern birds with parallel muscles have never, in their history, had ancestors with pinnate muscles. Stated another way, parallel muscles in Recent birds may at times be secondarily evolved. To use a hypothetical comparison, it might be proved that the earliest birds were black; it would not necessarily follow that all modern black birds are primitive in coloration. Instead, black coloration seems to have evolved repeatedly in independent lines.

As evidence that parallel jaw musculature in modern passerines is phylogenetically primitive rather than secondarily so, Beecher (1953: 329) cites the world-wide distribution of parallel-muscled groups. This pattern, he assumes, dates from Upper Cretaceous time. However, the groups with parallel jaw musculature and world-wide distributions are, in fact, groups of Beecher's own creation! He has united into the family Monarchidae, for example, birds with parallel jaw muscles (judged to be primitive on this basis) which other ornithologists have placed in no less than four families, not previously thought to be closely related. By so doing, Beecher has erected a world-wide family which has "primitive jaw musculature." To say then that the musculature is proved primitive by the world-wide distribution (a distribution which he thinks characteristic of Cretaceous insect-eaters) is clearly circular reasoning. Perhaps all that can be said is that both parallel and pinnate jaw muscles occur, in various groups, throughout the world.

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SUMMARY

This paper is a summary and an attempted re-evaluation of some divergent opinions concerning relationships in the New World nine-primaried Oscines.

Beecher's (1950, 1951a, 1951b, 1953) work in particular is discussed and the following conclusions are drawn: (1) the New World assemblage of nine-primaried Oscines is of common origin and the central stock seems to have been the Fringillidae; (2) the Carduelinae are Old World in origin and probably related to the Estrildinae; (3) Beecher's thesis that carduelines are derived from tanagers is not supported by any available evidence other than that provided by the jaw musculature; the similarities in jaw muscles of carduelines and tanagers must be the result of convergence; (4) reinterpreted, the pinnate adductors of the lower jaw in the Parulidae provide additional evidence of fringillid origin of the family; (5) the question of taxonomic rank for the Galápagos finches is discussed and recognition of the group as a full family seems unwarranted; (6) Beecher and I agree concerning the origin of the Icteridae but disagree regarding the allocation of the genus *Spiza*, considered by Beecher as icterid and by me as richmondene; (7) the anatomical resemblance of at least one subfamily, the Psittirostrinae, of the Drepaniidae to the Carduelinae is noted and further study is suggested; (8) the Vireonidae, considered by Beecher to be the stem of the New World assemblage, are shown to be derivable from primitive finches and the jaw musculature and bony palate agree with what, in my opinion, would be expected in an insect-eating group of finch origin; (9) circular reasoning is demonstrated in Beecher's argument that the world-wide distribution of the families with "primitive" jaw musculature supports the thesis that the groups are, in fact, primitive, since the families in question have been erected by Beecher from groups in various parts of the world which have parallel jaw musculature; (10) it is suggested that parallel jaw musculature in modern birds may often be secondarily evolved and thus not legitimately considered phylogenetically primitive.

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