COMMENTS ON SOME RECENT STUDIES OF SONG BIRD PHYLOGENY

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THE classification of the families and orders of birds, particularly that of the song birds, was until recently one of the most neglected branches of ornithology. For fifty or seventy years little progress had been made in this field except for the occasional reassignment of a doubtful genus or for a reshuffling of the sequence of families. In recent years a newly awakened interest in bird anatomy has led to studies which have resulted in a number of stimulating publications. Two of these have been selected for discussion here. A critical evaluation of the methods and principles underlying such studies is urgently needed in order to point out potential pitfalls to other investigators engaged in similar work.

TORDOFF'S STUDIES OF THE BONY PALATE

The objective of Tordoff's (1954*a*) study is specific and his method straightforward. It starts from the well-known work of Sushkin, who divided the finches into a number of subfamilies (Cardinalinae, Emberizinae, Carduelinae, etc.), each diagnosed by characters of the horny and bony palates. Tordoff attempts to ascertain whether these subdivisions are well founded, whether some of them are more closely related to each other than to others (in fact, whether "the finches" are a natural group), which other families are closely related to the finch group, and where some of the genera that have not previously been assigned to any of the subfamilies belong. To answer these questions he studied the bony palate in representatives of about 175 genera of finches and related families. The number of differences in the palate which are not largely determined by functional needs is small. The principal object of such a study, in fact, is to find out which of the similarities are functional adaptations and which are due to common descent. As far as the palates of finches are concerned, Tordoff decides that the presence or absence of palato-maxillaries is the most crucial character, in conjunction with the conformation of the pre-palatine bars. On the basis of these characters, Tordoff concludes that the finches consist of two unrelated assemblages, the carduelines (goldfinches, purple finches, etc.) on the one hand, and all the remaining ones (true finches, buntings, cardinals, etc.) on the other. (The term "bunting" throughout this discussion refers to any emberizine finch, including the American "sparrows," towhees, and juncos. The members of the genus *Passerina,* called buntings in America, belong to the subfamily of cardinals.)

Tordoff presents good evidence to indicate that the Carduelinae are related to the weaver finches (Estrildinae). By a happy coincidence, Prof. H. Steiner of Zürich was working concurrently on a similar problem. He reached the same conclusion independently on the basis of a study of the Estrildinae (work presented at the International Ornithological Congress at Basel in June, 1954). Steiner showed that the "Ploceidae" of textbooks are, like the finches and as suspected previously by Chapin, an artificial group, consisting of true weavers and the unrelated weaver finches. Tordoff and Steiner find that the association of Carduelinae and Estrildinae is supported not only by anatomical, but also by life-history data.

Tordoff finds characters of the bony palate of the chaffinch genus *Fringilla* which seem to him to justify its exclusion from the cardueline complex and its association with the Emberizinae. This taxonomic disposition of *Fringilla* is not entirely satisfactory. There is in the chaffinch a cardueline resemblance in plumage coloration and bill structure, in the gape color of nestlings (similar to that in *Coccothraustes*), and in nest structure (finely woven). *Fringilla* also differs from the usual emberizine pattern in the color of the eggs. Sushkin (1925:256) believed that the characters of horny and bony palates indicated relationship of the chaffinch with the Carduelinae. It would seem far better not to combine *Fringilla* with the buntings but to retain for this genus a separate subfamily. Tordoff is right in keeping it separate from the carduelines, from which it differs not only in the stated osteological characters but also in the apparent absence of a crop.

Tordoff's findings concerning the cardinals, buntings (as defined above), and tanagers are as follows: No sharp line can be drawn between emberizids and tanagers, as far as skull structure is concerned. This parallels the findings of the bird skin taxonomist, who had long been in doubt as to where to place certain genera. By drawing an arbitrary line between genera with free and those with fused palato-maxillaries, a sharp separation can be made between cardinals and buntings. Yet this forces one to assign quite a few genera to a different subfamily from that in which they had been placed on the basis of plumage characteristics. Regardless of possible shifts of genera on the basis of other characters, the essential fact of the very close relationship of the New World finches and the tanagers is well established. (Tordoff found no characters which would justify separating Darwin's finches from the subfamily of buntings.) It is likewise clear that the Icteridae, Parulidae, and Vireonidae belong to the same general assemblage of families.

What is still in doubt is the direction of evolution. At first sight it would seem simplest to accept as ancestral a type with an unspecialized bill (such as that found in certain tanagers and vireos) and to derive from it the two specialized finch types (cardinals and buntings), as well as the various more extremely specialized insectivorous and nectar-feeding types. This solution is rejected by Tordoff because it would require the repeated independent origin of fully-developed, functional palato-maxillaries, as well as an explanation for the occurrence of fused palato-maxillaries in groups where they seem to have, at present, no functional significance. As a consequence, Tordoff postulates that some cardinal-like finches were the ancestors of all New World nine-primaried song birds (including icterids, vireos, wood warblers and honey-creepers), which subsequently lost free palato-maxillaries. This is a tenable hypothesis, and yet it raises so many awkward phylogenetic problems that one should keep an open mind concerning an alternative hypothesis. The fact that many thick-billed seed-eaters (Ploceidae, Carduelinae) lack the palato-maxillaries indicates that such a structure is not a functional necessity and develops only where there is a predisposition for it. Perhaps this potentiality has an embryological cause (a separate ossification center?). The textbooks of comparative anatomy and paleontology list literally hundreds of instances where a potentiality in a group is realized independently a number of times. This does not constitute polyphyletic origin because the character is in each case produced by essentially the same gene complex. Perhaps the fused palato-maxillaries condition is a rudimentary trait and not an indication of obsolescence. It is difficult, in the absence of fossils, to decide which way to read such a morphological series. The rich development of insects during the Cretaceous makes it hard to believe that the principal insect-eating birds of North America would have evolved so late, and as descendants of finches, at that!

Tordoff's study is an important contribution to our knowledge of the structure and relationships of passerine birds. The evidence is clearly presented throughout, and where it causes difficulties, this is not glossed over, but discussed in detail. The 77 drawings of bony palates permit a rapid check of the characteristics discussed, even if one does not have access to specimens. It is improbable that the author's modest warning will prove justified: "Further studies of structures other than the bony palate may show that many conclusions expressed here must be modified." Rather, it seems that Tordoff's essential conclusions are sound and will be substantiated further.

Beecher's Studies of Jaw Musculature

Far more ambitious than Tordoff's investigation of the bony palate of finches is Beecher's work of the past several years, devoted primarily to the arrangement of the jaw muscles of birds. It has resulted in the publication of a series of papers culminating in a new phylogeny of the song birds (Beecher, 1953). Beecher's concepts of the phylogeny and classification of the song birds differ so drastically from previous theories and arrangements that a critical analysis of his findings and interpretations seems to be in order. This has already been done in part by Tordoff (1954*b*), with particular reference to Beecher's conclusions regarding the New World nine-primaried oscines. Yet, in view of the growing interest in bird anatomy, I feel that there is need for a broader evaluation and, in particular, an *analysis of the principles* by which Beecher has interpreted his findings.

The broad basis and the importance of Beecher's work is indicated by the fact that he dissected the jaw muscles of nearly one thousand specimens belonging to more than six hundred species. On the strength of his anatomical findings he suggests a new placement for many genera, subfamilies, and families, leading in many instances to a considerable improvement of avian classification. His argument (1951*b*) that the Coerebidae are a polyphyletic group consisting of superficially similar flower-visiting wood warblers and tanagers seems convincing and is consistent with the plumage characters and palatal structure of the respective genera. Worthy of special attention are his suggestions (1953:281) of placing *Oxylabes, Prunella, Thamnornis,* and *Zeledonia* with the Saxicolinae, the Mimidae near the thrushes (p. 282) rather than the wrens, *Tylas* and *Hypositta* with the Vangidae (p. 298) and the Vangidae near the Prionopidae (p. 298), while separating the monarch flycatchers (Monarchinae) from the true flycatchers (Muscicapinae).

Especially valuable features of Beecher's studies are the utilization of a new set of characters (the jaw muscles) and his presentation of numerous semidiagrammatic drawings which permit other workers to make their own interpretations of his data. (It is difficult to evaluate how diagrammatic these drawings are. Some of the jaw muscles are interlaced in a rather intricate manner, and in some of my own dissections I have been unable to establish the clear patterns shown in Beecher's diagrams. This may be due to lack of aptitude on my part.)

It is possible, if not probable, that interpretations very different from those of Beecher might be made. Indeed, the past history of phylogenetic researches reveals how often different authors have come to diametrically opposite conclusions on the basis of the same evidence. Evidently, this field is full of intellectual pitfalls. Before accepting Beecher's drastic proposals, let us first see on what assumptions they are founded. Although most of these are only tacit in Beecher's publications, they so clearly underlie his reasoning and interpretations that it does not seem unfair to clarify the discussion by stating them succinctly.

ASSUMPTION 1.—*An established morphological series equals a phylogenetic* *series; simple structures are primitive, and more complex structures are derived from them secondarily; morphological trends are irreversible.*

This tripartite assumption applied to the jaw muscles of song birds leads Beecher to the following conclusions: Since the parallel-fiber type of muscle (with a terminal attachment of tendons) is morphologically simpler than the pinnate type in which fibers are attached laterally to a longitudinal central tendon, the higher the proportion of parallel-type jaw muscles, the more primitive the species. Therefore, the families of song birds can be arranged in a series or several series according to the increasing proportion of pinnate jaw muscles. This morphological series equals a phylogenetic series. Beecher's entire new arrangement of the song birds rests essentially on this basis.

I believe that this basic assumption, as well as the taxonomic conclusions drawn from it, are wrong. In groups like the mammals and the reptiles, in which there is good fossil material available, it has been shown again and again that a morphological series is not necessarily a phylogenetic series. In fact it is of almost regular occurrence that a structure begins in a simple condition, becomes complex later in its evolution, but is eventually again simplified. The more important a structure is functionally, the more plastic it will be in evolution.

Specifically, there is no evidence whatsoever that a high proportion of parallel jaw muscles is an indication that a given genus of song birds is primitive.

Unfortunately not much is known about the relative frequency of parallel (longitudinal) and pinnate jaw muscles among the lower vertebrates or in the older orders of birds, but this much is certain, that pinnate muscles are an ancient invention. They occur where heavy traction is needed between two bones that are in close proximity. Thus they have a clear functional significance. Since functional characters, especially those connected with feeding habits, are known in many instances to have reversed the direction of their evolution, it is highly presumptive that the development of jaw muscles in birds has also done so at times. It is highly probable that many of the ancestral song birds fed on a mixed diet and had a generalized equipment of parallel and pinnate jaw muscles, and that from this primitive condition there have been various specializations either in the direction of more parallel muscles or toward more pinnate muscles and probably back again in many cases. If this is true, then a modern pattern of jaw musculature consisting almost exclusively of parallel muscles is as specialized as the reverse. It might be added, incidentally, that it is quite impossible to draw a sharp line between parallel and pinnate muscles—intermediate stages occur frequently.

Beecher seems to have been influenced in his reasoning by "Dollo's Law" of the irreversibility of evolution. Although this law is valid as far as the broad history of the earth is concerned, it is by no means always true when single organs or evolutionary trends are concerned. Indeed, evolution often is reversible, particularly when strong selection pressures exist and genetic systems are essentially the same, as in close relatives. (For a discussion and further references, see Huxley, 1942:501–503 and Simpson, 1953:310–312.) The application of "Dollo's Law" to such a plastic structure as the jaw muscles within such a closely knit assemblage as the song birds is certainly misleading.

ASSUMPTION 2.—*The pattern of jaw muscles is constant within a given family; function does not vitally affect muscle pattern; similarity of muscle pattern therefore proves close relationship.*

Beecher is aware of potential objections to this assumption and cites therefore the family Icteridae, with its varied feeding habits. He dissected all of the more divergent genera without finding any major deviation from the basic pattern of the jaw muscles (Beecher 1951*a*). Yet, this point is not convincing. To begin with, the bills of the Icteridae are not sufficiently different in form and function to prove that adaptive radiation could not induce shifts in muscle pattern within a family. Indeed, if Tordoff (1954*a*) is right in stating that the Dickcissel (*Spiza*) is a cardinal, rather than an icterid as demanded by the muscle pattern, the basic premise is weakened considerably.

Furthermore, every student of the higher categories knows that a given character may be highly constant in one group and highly variable in another. Perhaps the muscle pattern is relatively constant among members of the Icteridae, but quite variable within the other families? Beecher himself cites abundant evidence to prove that this is indeed the case. He proposes (1953:278): "A major phylogenetic division of oscinine families . . . largely on the basis of the parallel or pinnate character of adductor slip *M7b* [*M. adductor mandibulae externus medialis*]." Yet, scattered through his account are numerous examples of variation in this muscle, as well as in "*M7a*" (*externus superficialis*), within a single family. For instance, in 25 per cent (two out of eight) of the vireos, *M7b* is not parallel, in spite of the fact that the functional difference is very slight; *M7b* is parallel in *Motacilla citreola* but pinnate in the remaining motacillids; it is usually pinnate in the wood warblers (Parulidae) but is parallel in the broad-billed genera *Setophaga, Myioborus,* and *Basileuterus.* These do not appear to be the most primitive genera of wood warblers, Beecher's assertion to the contrary notwithstanding! In the family group diagnosed (p. 278) as having a pinnate *M7b* are several families, such an tanagers, cardinals, and Carduelinae in which it is stated in the text: "*M7* (not *M7b*) pinnate." The muscle pattern is highly diverse in the Honey-eaters (Meliphagidae, p. 301) and the Hawaiian Honeycreepers (Drepaniidae, p. 312), so that these families surely would have to be broken up if muscle patterns were decisive. Tanagers and carduelline finches intergrade imperceptibly in their muscle patterns, but are not closely related on the basis of other criteria. Here, obviously, parallelism is involved, as also in the case of the finch-like Drepaniidae with their extraordinary resemblance to carduelines. The embarrassing frequency of a parallel *M7b* in groups that "should" have it pinnate induces Beecher to say with respect to the wren-creeper-titmouse assemblage (p. 315) : "*M7b* might be considered parallel but not in the same sense as in Sylvioidea." In what sense then, one might ask (since Beecher's attempt at an answer in subsequent sentences is no solution) ?

A close study of the variation in these muscles shows how closely they are correlated with function. One can establish quite a consistent functional series from the weak-billed insect-eaters through the stronger-billed shrike-flycatchers and shrikes to nectar-, fruit-, and seed-adapted or omnivorous groups. These latter "are in every way more complex, with increased pinnate musculature, stronger bills, more intricate palate relief, a tendency toward double ectethmoid foramina . . ." (Beecher, 1953:278). Only there is, contrary to Beecher's contention, no evidence that this functional-morphological series is a phylogenetic series. Beecher admits the artificiality of groups like "finches," "shrikes," and "flycatchers," based on the form of the external bill, but precisely the same criticism can be raised against the use of internal functional characters. Pinnate muscles are clearly correlated with powerful biting action and heavy jaws or other functional adaptations (nectar-feeders), in contrast to the largely parallel jaw muscles of the thin-billed groups. Even Beecher seems occasionally unable to escape the force of the evidence which shows that the jaw muscles, like all other functional characters associated with food intake, may be subject to rapid evolutionary changes and convergences, hence to polyphyletic groupings. He admits for certain slender-billed babblers (Timaliidae) that (p. 313) "in them the pinnate character of *M7b* has virtually disappeared as it has in many honey-eaters and in the true wrens."

ASSUMPTION 3.—*A valid phylogeny and classification of the oscines can be erected on the basis of a single character, the pattern of variation of the jaw muscles.*

In spite of his protestations to the contrary, Beecher (1953:276) cannot escape the fact that he has built the imposing structure of a new phylogeny of higher passerine birds essentially on a single character, namely on a few variations in a set of seven jaw muscles. There is so little potential variation among the functionally possible patterns of these muscles that much similarity is quite inevitable. Other characters cited by Beecher, such as the sculpture of the horny palate, and the shape of the tongue and that of the bill, are functionally so closely correlated with each other, and with the jaw muscles, that they certainly cannot be regarded as four independent characters. From the point of view of selection pressure they are a single-character complex, even though some basic potentialities may not be affected (for example, bifid vs. trifid tongue).

Additional characters used by Beecher, such as the formation of the ectethmoid foramen and the shape of the lacrimals, do not seem to contribute much to our understanding of oscinine relationships beyond showing that some families differ from each other in these characters. The character of plumage coloration must be singled out for a more detailed discussion. In recent decades plumage characters have been found to be conservative in many birds, and it is quite in order for Beecher to utilize plumage patterns. In so doing, however, he makes questionable suggestions, for example (p. 284), that close relationship between swallows and starlings is corroborated by the fact that in both groups streaked plumage occurs in both immatures and adults, as well as iridescent black plumage in adults. The widespread occurrence of such patterns of plumage in other orders and in other passerine families clearly renders the character useless taxonomically. Equally questionable are the suggestions (p. 288) that the bare nape of bulbuls may be "associated with" the naked nape of certain birds of paradise and that the long nape "hairs" of bulbuls may be the forerunners of the specialized plumes of the paradiseids and hence endorse their relationship! Likewise Beecher's statement (p. 289) that the variable black and white plumage of the bulbul *Microscelis madagascariensis* suggests that of the Corvidae is not convincing.

It would seem advisable to use color pattern as a clue to relationship only when it can be evaluated carefully. A color character which is maintained without or against selection pressure, is highly valuable phylogenetically. For instance, the white spots in the tail feathers of the crag martins ("*Ptyonoprogne*") of Eurasia and Africa indicate their close relationship with *Hirundo*, an association which is also supported by voice and by nest structure. The sandy coloration of the desert-living *Ptyonoprogne*, however, is a character that has developed under high selection pressure and is of low phylogenetic value. A cryptic general coloration of sandy brown with a disruptive pattern of dark shaft streaks occurs in so many non-passerine and passerine families of grassland birds that it is obviously of no use as an indicator of relationship. Nevertheless this color pattern is used by Beecher to support his association of larks, pipits, and cisticolas (1953:314). White bellies, or black breast bands likewise are so widespread among birds that they are virtually useless as phylogenetic clues.

It has become almost axiomatic in modern taxonomy to accept that classification as the best which is based on the greatest number of characters. But quantity alone is not decisive. Such characters must also be weighed. It is often stated that taxonomy is an art. This is to some extent true. The art consists in the proper weighing of characters. The validity of many recent classifications has been greatly strengthened by the generous reference to habits and other biological characteristics. Unfortunately, even biological characters are not immune from convergence. This is evident from the occurrence of domed or pendant nests in many unrelated groups of birds or the "teetering" of spotted sandpipers and wagtails. Such characters are of value nevertheless when used in combination with others, particularly in order to place an ambiguous species or genus. They are of very dubious value when used to support the association of otherwise dissimilar families, such as the true wrens (Troglodytidae) and the Australian warblers (Malurinae) because both have the habit of "carrying the tail over the back" (Beecher, 1953:317).

ASSUMPTION 4.—*A phylogenetic tree can be devised on the basis of a morphological progression of contemporary families.*

This basic flaw in Beecher's philosophy of phylogeny has by implication already been exposed in part above (see Assumption 1). Tordoff (1954*b*) points out that it induces Beecher to push the origin of living families of birds, such as the vireos, back to the Cretaceous. At that, Beecher derives the vireos through the monarch flycatchers from the grass warblers, which therefore ought to be much older still!! Although specialized families often seem to have a higher evolutionary rate than more primitive ones, there is no evidence available that would favor Beecher's extreme interpretation. Indeed it seems improper to use the term phylogenetic tree for a morphological series as presented on his fig. 18 (p. 324). Phylogenies can be established only by unequivocal evidence from comparative anatomy or by fossil finds. It is much safer to use a neutral term, such as "dendrogram" (Mayr, Linsley, and Usinger, 1953:58), for a diagram of hypothetical descent based exclusively on the comparison of living forms. In view of the mounting evidence for frequent evolutionary reversal and convergences in adaptive characters, it is quite inadmissible to apply the term "phylogenetic tree" to a diagram that portrays merely morphological sequences.

This plea for caution should not be misunderstood by evolutionists. If one believes in evolution (and which biologist does not?), one is justified in proposing hypotheses concerning the probable relationships of families and genera, and concerning the probable characteristics of their common ancestors. However, one should at no point confuse fact with hypothesis. This is for two reasons particularly important with respect to birds, the almost complete lack of crucial connecting links in the fossil material that is so far available, and the anatomical uniformity of birds, particularly the song birds. The case is not quite hopeless, since morphological assignments have often been confirmed by ethological findings (such as the relationship of sandgrouse to pigeons, and penguins to tubinares). Yet it is advisable to exercise great caution and to weigh carefully the phylogenetic versus functional significance of each character.

My final criticism is raised on grounds of logic. As pointed out previously by Tordoff (1954*b*), Beecher frequently indulges in circular reasoning. One example relating to the age and distribution of the "stem" groups has already been discussed. An additional example follows: Beecher states that seed-eating song birds and shrikes (super-family Timalioidea) have a pinnate *M7b*. Seemingly this functional adaptation is associated with the food habits of shrikes and finches. Beecher then concludes (1953:278) that his sylvioid assemblage with parallel *M7b* was unable to develop shrikes or finches and that the ability of the timalioid groups to do so constitutes a major point of distinction between the two superfamilies. The logic of this is vulnerable, to say the least, since the arrangement of the fibers of *M7b* is Beecher's fundamental criterion of distinction between the two groups. He has made certain that no members of the Sylvioidea has a pinnate *M7b* by placing all groups in which this muscle is pinnate in the Timalioidea! He cannot justifiably argue then that the Sylvioidea lack the ability to evolve a pinnate *M7b* since the distinction is an artifact.

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As a consequence of having made the various assumptions listed above, Beecher proposes a phylogeny of song birds which is unsatisfactory in many respects. There are numerous indications that Beecher has placed unrelated forms together merely because they have become specialized or de-specialized in a similar manner. Some of the instances, such as bringing together the tanagers and the cardueline finches or placing the Indigo Bunting and its relatives in the Emberizinae, have been criticized previously by Tordoff (1954*b*). I would like to cite some other proposals of Beecher's which to me seem highly dubious: The derivation of the larks from the Cisticolinae; placing *Hemipus* with the monarch flycatchers and *Tephrodornis* with the Prionopinae; associating the parrot-bills with the larks, while making the unsupported claim (p. 314) that "The parrot-bills are basically similar to larks and pipits in . . . bill"; wide separation of *Remiz* (p. 319) from the flowerpeckers; inclusion of *Rhipidura* with the monarch flycatchers, and deriving *Pachycephala* and the vireos from the monarchs; the separation of *Aegithalos* (p. 315) and *Aegithaliscus* (p. 319); the placing of Carduelinae and Estrildinae at opposite ends of the system (fig. 18); and the establishment of certain phylogenetic series, such as that of Monarchinae — Cisticolinae — Troglodytidae — Certhiidae — Sittidae — Paridae.

Conclusions

It is evident from the above discussion that Beecher's attempt to establish a new phylogeny of the oscinine birds, based primarily on the morphology of the jaw muscles, is not an unqualified success. He has shown numerous variations in the jaw muscles, many of them previously unknown, thus making a distinct contribution to descriptive avian anatomy. Yet, it seems to me that his basic contention, namely that the stated anatomical differences support the postulated phylogenetic sequence, remains unproven. Indeed, the close correlation established by Beecher between pattern of jaw muscles and habits suggests strongly that the specific development of these muscles is functionally conditioned. This does not deprive these muscles of all phylogenetic significance, because closely related genera will have a larger number of similar potentialities than will distantly related genera. Yet this evidence must be used with much caution.

The papers of Tordoff and of Beecher have shown that the song birds are not nearly so uniform anatomically as was formerly believed and that the study of previously neglected structures may shed new light on function and relationship. It is to be hoped that the newly awakened interest in bird anatomy and bird phylogeny will result in many other stimulating contributions. Let the students in this field, however, be aware of the great logical difficulties of the subject and of the many intellectual booby traps into which the unwary may stumble.

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