A PHYLOGENY OF THE OSCINES

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INTRODUCTION

IN recent years ornithologists working with passerine birds have grown increasingly aware that they are dealing with a top-heavy classification. Current taxonomic methodology, while permitting vast refinement at the species level, has added nothing to our understanding of the higher categories. Some families are still but vaguely defined, and we know little about the inter-relations of over 60 families in the suborder Oscines (song birds), an assemblage comprising nearly half of all bird species. The situation, alluded to by Mayr and Vaurie (1948: 238), is most serious as it affects the ornithological contribution to the history of world faunas. This contribution can only be a misleading one so long as the arrangement of these families into a phylogenetic tree remains unaccomplished. With few exceptions, the relationships of groups occupying widely-separated faunal regions may only be guessed at now.

The present investigation was undertaken to clarify the relationships of these higher categories of Oscines and to construct a phylogeny by applying the methods of comparative anatomy. Nearly a thousand specimens (over 600 species) from virtually all currently recognized oscinine families were dissected, and the taxonomic arrangement is based mainly on several independent lines of anatomical evidence in the head region, with particular attention to jaw musculature. Thousands of additional skulls and skins were studied, and the classification is not only supported by the external characters normally used in taxonomy but by such non-morphological characters as behavior.

This survey has made nearly exhaustive coverage of the oscinine species in the spirit collections of the United States National Museum, American Museum of Natural History, and Chicago Natural History Museum. A few specimens were borrowed from the Museum of Vertebrate Zoology, from the British Museum (Natural History), and the Dominion Museum (Wellington, N. Z.). For use of, or help in obtaining, specimens, I am indebted to Alexander Wetmore, Herbert Friedmann, Ernst Mayr, Dean Amadon, Charles O'Brien, Frank A. Pitelka, Keith L. Dixon, Richard Meinertzhagen, David Lack, Francis C. Fraser, Robert A. Falla, Karl Plath, Albert J. Franzen, Thurston Wright, Karl P. Schmidt, and D. Dwight Davis. Mayr, Amadon, and Davis also read the manuscript and offered suggestions, as did James L. Peters, John T. Zimmer, James P. Chapin, Jean Delacour,

Josselyn Van Tyne, Alfred E. Emerson, Sewall Wright, and Austin L. Rand. Harvey I. Fisher and Emmet R. Blake gave valuable suggestions and advice. The writer alone is responsible for the classification. This paper is offered in partial fulfillment of the requirements for the Ph.D. degree in the Department of Zoology, University of Chicago.

HISTORICAL

What any discipline is, or even what it may become, is largely influenced by its past history. The refinement of the classification of passerine birds at the species level is a direct outcome of the acceptance of the museum study skin as the ultimate working unit of taxonomy, and this has virtually limited diagnosis to external characters. True, Müller (1845) early differentiated between the oscinine (song) birds and suboscinine birds on the basis of syringial musculature, and anatomy had its brief vogue under Garrod, Gadow, Fürbringer, and others, but none of them attempted the anatomical diagnosis of passerine families. Nor was this vogue in any way widespread; before it and during it, the taxonomy based on skins flourished and in the end may have brought about the early decline of comparative anatomy. Scientists employed by museums were increasingly occupied with describing new species, and it was more productive to mine ornithological knowledge where the vein was rich. Some museums ceased eventually to collect anatomical material.

The universal acceptance of the bird skin is readily understandable. Such a bird specimen with complete data is adequate to diagnose a new species. It shows perfectly the distinctive features of the plumage, feet, and bill, and it permits counting and measuring flight feathers. Species systematics based on skins was invaluable (Mayr, 1942) in demonstrating evolutionary mechanisms. There is, thus, no justification for the extreme view that ornithologists "save the skin and throw away the characters." An anatomical specimen in alcohol is sodden, patternless, tedious to study, difficult to store. It is only regretted that anatomical work at a higher level did not keep pace with the phenomenal growth at the species level. But species could be arranged on the basis of common external characters into genera and these genera into families, so anatomy seemed superfluous. However, it was less easy to arrange families, thus contrived, into larger groups within the order, because the end product of this method is a jumble of *miscellaneous* families that cannot easily be related in a phyletic scheme.

It was deeply ingrained in ornithological opinion that anatomy could yield results only after years of tedious dissection, and too often osteology was taken up by systematists who hoped to by-pass the musculature. These static morphological comparisons of bony skull processes and muscle scars by workers who apparently made no attempt to understand their adaptive rôle led to much erroneous conjecture. The musculature, largely responsible for these features, is more basic. It is also more conservative than the misleading osteological "characters" (often the expression of only minor muscle slips), and it falls into an easily recognizable hierarchy of pattern.

METHODS AND ASSUMPTIONS

A Working Hypothesis.—The body of this paper necessarily details the characters of the oscinine groups and would be hard to follow without an understanding of my working hypothesis and assumptions which are presented below.

This project was launched five years ago in the spirit of functional anatomy, and it was recognized at once that food-niche specialization has played a dominant rôle in passerine evolution. First, the degree of individual variation in jaw musculature was studied for a number of common species, using from 6 to 10 specimens, without finding the slightest deviation from the typical muscle pattern. Once the negligible degree of anatomical variation within the species was established, it was considered basic to phylogenetic work to determine the extent of variation occurring with diet differences among the species of an entire family. The blackbird family (Icteridae), selected for this initial study (Beecher, 1951a), embraces members which exploit virtually all food-niches occupied by passerine birds. Yet, through extremes of skull modification including thick-billed finch types and thin-billed insect- and nectar-adapted types, a single pattern of jaw musculature persists in the family. This pattern, characterized by the highly pinnate adductors found in finches, helps relate the blackbirds to buntings, while similar features in the latter relate them to the wood warblers. Each of these higher groups in turn exhibits a similar constancy of pattern within itself.

An exploratory survey of the Oscines early in 1947, using a few characters additional to jaw musculature, suggested the feasibility of similarly diagnosing all oscinine families. Moreover, with the added assumption that muscles with parallel fibers are phylogenetically primitive, and pinnate muscles advanced (Beecher, 1951a), it was possible to arrive at a basic morphological type from which all other oscinine types could be derived—so the means existed for linking the families in a phyletic scheme. This basic type, simple in structure and function, is ideally realized in the living Old World warblers, the

Sylviinae (figure 2)—a group with a pattern of parallel-fibered muscles, and which, on distributional evidence, may date back to the Cretaceous. Then we face the final assumption, viz., that a phylogeny may be derived from a morphological tree of relationships, and we can only point out that passerine fossils to date fit well in living families.

The essential uniformity of the parrots, the trogons, and other pantropical non-passerine families today implies early origin before the tropical biota severed tenuous northern connections and retreated to the equatorial regions of Old and New Worlds. In contrast, except for certain eurythermal world-wide families like swallows, passerines are represented by entirely different groups in Old and New World—groups that evidently evolved in isolation from each other *after* the northern exchange corridor was closed. It appears that this order, comprising perhaps the only generalized insectivorous birds at the time flowering plants evolved in the Upper Cretaceous, was in a position to evolve forms to fill the many new niches provided by this plant group. The impact of this abundant new food source, which also conditioned the origin of many insect groups, resulted in a radiation completely out of proportion to that in other orders, so that the numerous passerine families do not show the great morphological disjunctions characteristic of non-passerine ones.

Judging from anatomical and other characters, the insectivorous American vireos (Vireonidae) are apparently descendants of the Old World insect-eaters that were cut off when the northern exchange corridor submerged or became too cold. Subsequently, the vireos gave rise to the entire nine-primaried American assemblage. They appear directly ancestral to the fruit-eating tanagers and the mainly insectivorous warblers, each of which evidently evolved a nectar-adapted line and several finch lines convergently (Beecher, 1951b). In a parallel manner the Sylviidae evolved a similar assemblage adapted to the plant-niches of the Old World, and more recent interchange between these assemblages has been in direct relation to the ability of species to cross the northern cold barrier. This is taken as evidence that the Oscines existed only as insect-eaters when the Vireonidae became isolated in the New World, and we may be justified in assuming that this happened *before* the origin of flowering plants or about the same time. Fossil evidence from passerine birds is notoriously poor, but Milne-Edwards (1867) lists a titmouse and a starling from the Upper Eocene of France (hardly primitive types) and there is evidence of early origin from Suboscines to be given later.

Evolutionary Rates and Taxonomic Categories.—The tenet that only characters not under the influence of adaptation may be used in taxonomy has been badly misinterpreted. Wright's "genetic drift" and gene linkage provide a theoretical basis for the appearance of but a small proportion of non-adaptive characters at the population level, and Davis (1949: 86) doubts the occurrence of Simpson's inadaptive stages. So do I. In fact, a taxonomist separating species of wood warblers, for example, is engaged in classifying adaptations. What makes taxonomy possible is the existence of different *levels* of adaptation, reflecting that the parts of an organism are evolving at different rates (Simpson, 1944). Each of these warbler species has essentially the same pattern of hind limb musculature, a character holding so far as investigated for the entire order Passeriformes. Each has the same pattern of syringial musculature, a character embracing the entire suborder Oscines—as well as the jaw muscle pattern which is the hallmark of the Parulinae. Each of these characters is adaptive. They differ in being progressively less deep-seated, the jaw muscle pattern reflecting the diet specialization that resulted in a new group. The fact that a jaw muscle pattern *holds for a particular oscinine group* (family) gives it taxonomic value at the family level. The more conservative syringial musculature provides subordinal characters which are safeguards against errors due to external convergence. It prevents classifying, for instance, a tyrannid flycatcher as a muscicapid.

The Convergence Hazard.—That jaw muscle patterns are a clue to phylogenetic relationships at family level had to be determined by testing them against characters of known value. The reality of most oscinine families is unanimously recognized by ornithologists, and the muscle patterns not only hold for these large groups but permit the assignment of those rather rare species whose family affinities were uncertain. Such species often show external convergence with groups to which they do not belong and, where convergent species occupy the same range, the most expert taxonomists may have difficulty in resolving a complex on the basis of external characters alone. The species of the "family" Coerebidae appear to be nectar-adapted warblers and nectar-adapted tanagers (Beecher, 1951b), and the subfamilies of finches, arising from warblers and tanagers, will be shown to be convergent. A more complicated case of convergence at generic level was indicated in the American orioles (Beecher, 1950).

In classifying the oscinine families, one must face the practical task of assigning species whose affinities cannot be decided on external characters alone (Mayr and Amadon, 1951). The anatomical placing of such convergent species as exist in spirit collections was not hard and is not highly subjective. This is because the reality of the groups, as diagnosed by internal as well as external characters, is a matter of fact, however much one may question their arrangement into a phyletic scheme.

At the same time precautions were taken against being misled by convergence in the jaw muscle patterns which, rarely, approach each other without indicating near relationship. As a safeguard, several additional characters, forming completely independent lines of evidence, were studied in all specimens and are figured. The relief pattern of the horny palate was greatly valued by Sushkin (1927: 3) for diagnosing large groups of birds. It shows great conservatism and is often useful in linking related groups (Beecher, 1951b). Like the musculature it is more complex in advanced groups and affords further opportunities for group distinctions between convergent groups forming terminal twigs like the finch groups. We now know that the bill itself may often show convergent resemblance in unrelated groups, but a palate facies persists in a family—even through the varied bills of icterid genera (Beecher, 1951a)—so the character is useful when supported by collateral evidence. Operculation of the nostril and rictal bristles vary adaptively in a group as does the tongue, and therefore these must be weighted accordingly. The free lacrymal (figure 1), constant for whole assemblages of families, may occur in scattered individual species of other groups, possibly as an adaptation to forward vision. The ectethmoid foramen (figure 1), conducting the olfactory nerves through the bony plate separating the orbital and nasal cavities, is always single in primitive stem groups. In more advanced groups, particularly in the superfamily Sylvioidea, a general tendency toward pinched or double foramina is noted, and this is also constant in a group. The ectethmoid itself may be unusually winged or truncate.

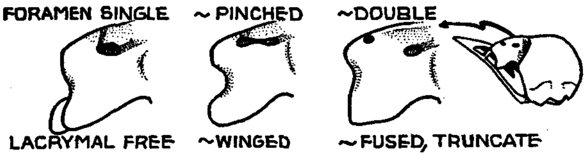


FIGURE 1. Characters of the ectethmoidal plate.

The Real Problem in the Oscines.—The striking anatomical uniformity of all oscinine families, except with regard to the feeding mechanism, presented a peculiar problem. We had constant characters tying the families together (the hind limb and syringial musculature) and characters for distinguishing the families fairly well. But we lacked characters for showing the relation of the families to each other. The jaw muscle patterns with a few additional characters of head and bill do this—and only *because* they reflect adaptive differences in food preference between families. If we may judge from the present diet of most families, their entire evolution is the result of selection pressure acting on primitive insectivorous stocks arising from the stem Sylviidae—pressure to fill the new food-niches provided by the flowering plants. The jaw muscle patterns simply confirm the reality of the families as true groups already recognized on other lines of evidence, so this is hardly a one-factor diagnosis of families. But in addition these patterns perform the needed function of ranging the families in a hierarchy from simple (presumably primitive) to complex (presumably advanced) families. No other traits are likely to do this.

In this hierarchy, the muscle patterns suggest that some of the groups are of lower level and should be subfamilies. For instance, the differences in muscle pattern between primitive groups at or close to the stem stock may be slight. Between the warblers (Sylviinae), flycatchers (Muscicapinae), and chats (Saxicolinae) there is little difference in muscle pattern, so added characters are needed to tell them apart. The Sylviinae always have the ectethmoid foramen single, the other two double. Of the other two, the Saxicolinae often have the outer of the two foramina outside or nearly outside the orbit and have a much narrower bill. Here muscle pattern combines related groups into larger families, other characters being necessary to differentiate the subfamilies. This suffices to show that more than jaw musculature is used in my phyletic arrangement; there are not sixty different muscle patterns in the Oscines! But as the more advanced groups diverge from the stem Sylviidae, greater complexity of the jaw musculature permits designation of small but constant facies differences for nearly all families.

My arrangement is not a single-factor diagnosis of families. The families were already diagnosed by other lines of evidence. The jaw muscle patterns provide what is so far found nowhere else in the morphology of the Oscines—a key to relationships of all families. They are apparently directly due to phylogenetic differentiation as the families became adapted to new food types.

The Illustrations.—In anatomical work nothing can take the place of accurate drawings. For those who cannot accept my interpretations, they represent facts to be reassessed. Several families are presented in each figure. For each, the small skull vignettes give a general idea of structure and at the same time outline in black the muscle area enlarged. Thus the jaw muscle pattern is shown in side view and in oblique view, looking into the orbit from which the eye has been removed. The ectethmoid plate is drawn at the top left. The tongue is drawn at the top right and below it the relief pattern of the horny palate—below that the bill. Nomenclature follows the sauropsid terminology of Lakjer (1926), but for easy comparison, muscle masses are numbered from 1 to 7 with subdivisions a, b, and c. Figure 2 serves as the key and may be referred to when necessary to determine the name of a particular muscle; but it is easy to memorize the position of each muscle by number since there are always just seven in the Oscines, and the discussion will be restricted to numbers.

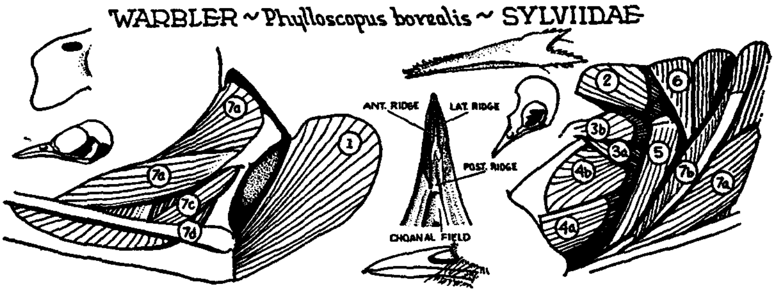


FIGURE 2. Detail drawing of jaw muscle pattern of an Old World warbler, showing primitive (parallel) musculature, with characters of ectethmoid plate, tongue, horny palate, and bill.

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*
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*

The origins and insertions of muscles and their specific functions in the kinetic bird skull are well-described in Moller (1931) and Fiedler (1951). The brief discussion in Beecher (1951a) may be enough for general needs, and figure 2 in that paper, showing mass functions of muscles, should help in visualizing functional emphasis in various groups.

The family diagnoses of Sharpe (1874–1898), Ridgway (1901–1907), and others were really detailed accounts of the range of variation in the group and often failed to eliminate species which they did not intend to include. To save space some features of the familiar key are adopted here. Superfamily and assemblage characters are not repeated under group *diagnoses*, which are very brief, so that the figures themselves must take the place of lengthy description. To show relationships, similarities are often emphasized, but each group has a combination of characters that sets it apart from other groups.

DIAGNOSES AND PHYLOGENY OF THE OSCININE HIGHER GROUPS

If we erect a phylogeny on the basis of jaw muscle patterns and other internal and external characters, the logical procedure is to work outward from the simple and primitive to the complex and advanced. We thus arrive at a typical tree with the weak-billed insect-eaters at the base giving rise to stronger-billed shrike-flycatchers and shrikes, or to nectar-, fruit-, and seed-adapted or omnivorous groups as the terminal twigs (figure 18). We find that these terminal groups are in every way more complex, with increased pinnate musculature, stronger bills, more intricate palate relief, a tendency toward double ectethmoid foramina, and generally more complex plumage, habits, and behavior. But it follows that these differences decrease as we come lower down in the tree and, where a number of groups leave the stem Sylviidae, their relationships are often not so clear. Whether they come from each other, from the Sylviidae or from a common ancestor may never be known. Where such cases arise I have tried to present the problem and give reasons for my own decision.

A major phylogenetic division of oscinine families into the superfamilies Sylvioidea and Timalioidea appears possible, largely on the basis of the parallel or pinnate character of adductor slip *M7b* (figure 2). Though small, this difference holds remarkably well for these two large groups, and one is tempted to conjecture that inability to evolve a pinnate *M7b* prevented Sylvioidea from producing shrike or finch adaptations so typical of the more numerous Timalioidea in which it is pinnate. Theoretically, the simpler Sylvioidea, embracing the stem Sylviidae (figure 18), evolved the Timalioidea with its complex *M7b* via such a group as the Cisticolinae, then may have been unable to go further in this direction against the competition of that group. However, it did apparently evolve several family assemblages with a parallel *M7b:* the crows, cuckoo-shrikes, and bulbuls; the flycatchers, thrushes, swallows, and starlings; the Old World nectar-feeders, exclusive of the Meliphagidae.

This major division is most open to question at the very stem where the grass and bush warblers (Cisticolinae) are split off from the sylviine warblers (Sylviinae) as the basic stock of the Timalioidea. Here further study may reveal a gradient between the two warbler groups rather than a sharp break. But in drawing a phylogenetic tree it would still be necessary to recognize the extremes of the gradient as having different evolutionary potentials due to parallel or pinnate *M7b*. The timalioid flycatchers (Monarchidae), however, seem to be separated from the sylvioid flycatchers (Muscicapinae) by an absolute dichotomy of four characters. The former has *M7b* pinnate, ectethmoid winged, foramen single, young unspotted; the latter has *M7b* parallel, ectethmoid truncate, foramen double, young spotted. They may prove homogeneous, but present evidence suggests partial parallelism in ecological niche (and hence in plumage) following slight initial divergence. With this preamble we now take up the higher groups and, since it would be impossible to express their relationships in any linear sequence (figure 18), each line is pursued to its evolutionary termination from supposed beginnings in the stem Sylviidae.

THE SUPERFAMILY SYLVIOIDEA

This is the smaller of the two superfamilies making up the suborder Oscines and may have been restricted in its adaptive radiation through competition with the more efficient Timalioidea.

OLD WORLD INSECT-EATERS (SYLVIIDAE).—The several subfamilies listed are regarded as having evolved to fit different food-niches: warblers (Sylviinae), bulbuls (Pycnonotinae), flycatchers (Muscicapinae), and grass warblers (Cisticolinae). All have the ectethmoid truncate, its foramen single (except Muscicapinae), and the lacrymal fused (figure 1).

WARBLERS (SYLVIINAE).—*Diagnosis:* Muscle pattern (figure 2) simple, parallel; *M6* bifid. Bill notched, weak, narrow, with operculate nostril and rictal (and often nasal) bristles. Palate relief simple with lateral and central ridges disappearing posteriorly, the latter separated by a slight vault from a posterior ridge encircling the choanal field. Tongue slender with extensive reedy tip. (By "reedy" I mean blade-like. The passerine tongue usually ends in an extension of the ventral keratinized sheath, resembling the reed of a clarinet.) Ten-primaried, world-wide insect-eaters with mainly plain plumage, unspotted young. *Species dissected: Abroscopus schistaceps, Acrocephalus arundinaceus, Calamocichla newtoni, Calamonastes cinereus, Camaroptera griseiventris, Camaroptera sp., Chlorotesia sp., Cryptolopha sp., Conopoderas familiaris, Dromaecercus seebohmi, Ephthianura tricolor, Erythrocercus mccalli, Macrosphenus concolor, Oligura superciliaris, Orthotomus sutorius, Phylloscopus borealis, Polioptila dumicola, P. plumbea, Ramphocaenus rufiventris, Seicercus poliogenys, Seicercus sp. Discussion:* The diagnostic characters, including the single foramen, are considered primitive, and this world-wide group fulfills the requirements of an ancestral oscinine stock. The similarity of the long-billed *Orthotomus, Macrosphenus,* and *Ramphocaenus* poses a problem (Rand and Traylor, 1953), but I regard them as independent, endemic derivatives of generalized sylviid stock in the Oriental, Ethiopian, and Neotropical regions respectively—not closely related species. *Function:* These three genera differ from generalized warblers in greater expansion of the protractors *M1* and *M2* for prying in the manner of starlings and American icterids

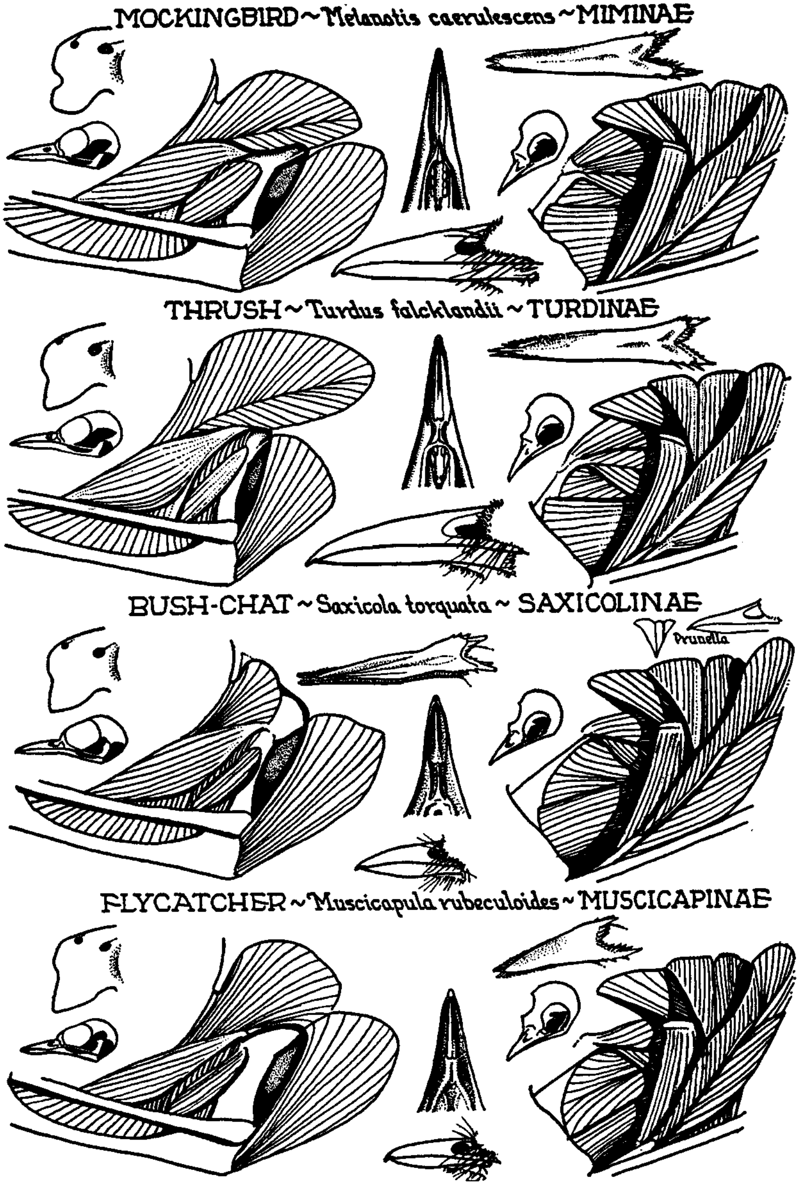


FIGURE 3. Characters in the flycatchers and thrushes.

(Beecher, 1950; 1951a). This is further evident in the dorso-ventral strengthening of the laterally compressed bill, especially in *Macrosphenus* which pries in dead branches for insects (Bannerman, 1936: 127).

Flycatcher, Thrush, Starling, Swallow Assemblage.—Arising from Muscicapinae (figure 18), these groups show strong affinities in plumage and internal structures, but diverge in feeding adaptations. All have the ectethmoid truncate (except Sturnidae), foramen double, and lacrymal fused.

Flycatchers (Muscicapinae).—*Diagnosis:* Muscle pattern (figure 3) similar to that of the Sylviinae but aponeurosis of *M7b* very narrow. Bill notched, broad, flat, with non-operculate nostril and abundant rictal and nasal bristles. Palate as in Sylviinae but no vault, the posterior ridge crowding the central one anteriorly. Ectethmoid truncate. Broad tongue tapering to short, bifid, reedy tip. Ten-primaried Old World flycatchers with plain or streaked plumage and spotted young. *Species dissected: Anthipes moniliger, Arizelomyia latirostris, Artomyias sp., Culicicapa ceylonensis, Melaenornis sp., M. pammelaina, Muscicapa latirostris, M. murinus, M. parva, M. rubeculoides, M. sundara, M. thalassina, M. tickelliae, Stizorhina frazeri.* Following Delacour (1947) I have synonymized 7 genera under *Muscicapa*. *Discussion:* Double ectethmoid foramen, spotted young, and flycatching may be advances over Sylviinae. *Artomyias*, with flycatcher behavior and musculature but wing, skull, and bill approaching the swallows, suggests how this group could have evolved the Hirundinidae.

Thrushes (Turdidae).—The included subfamilies, linked by several lines of evidence, appear to be diverging under selection by slightly different food-niches: chats (Saxicolinae), thrushes (Turdinae), mimic thrushes (Miminae), and dippers (Cinclinae).

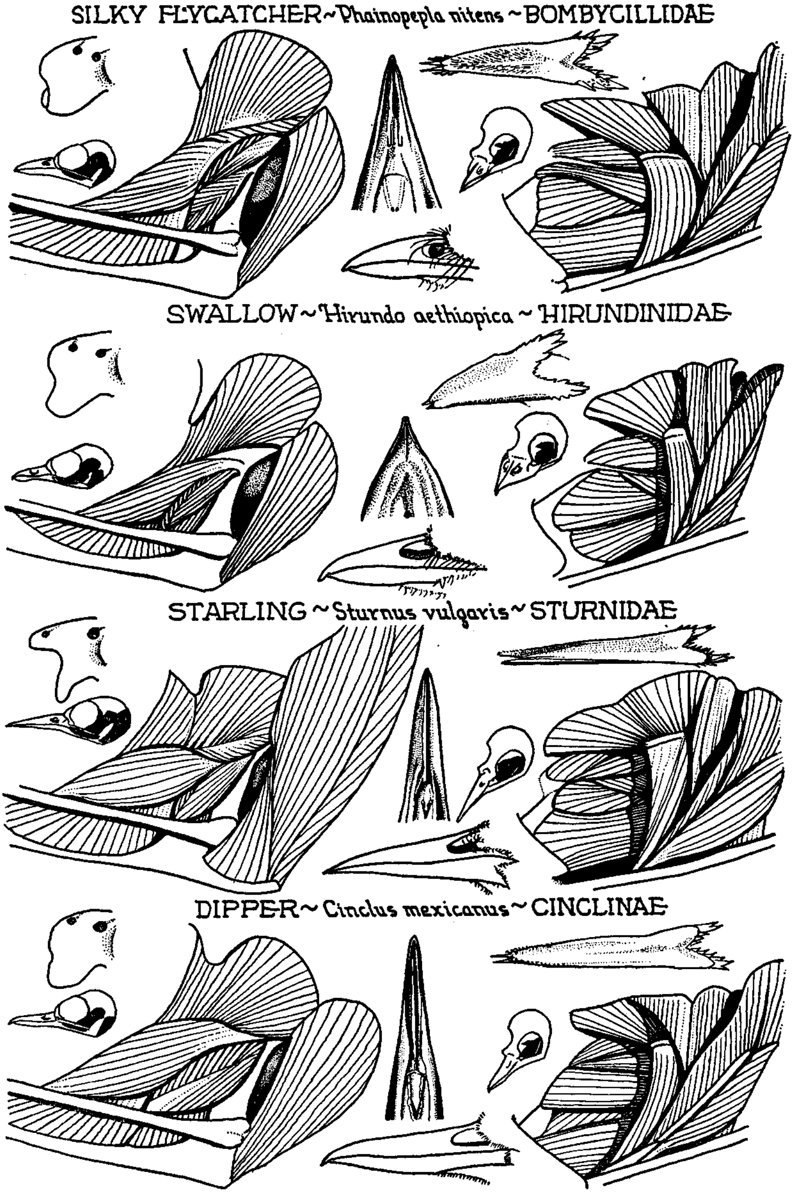
Chats (Saxicolinae).—*Diagnosis:* Muscle pattern (figure 3) similar to that of the Muscicapinae but generally weaker adductors *M7a* and stronger palatal retractors *M4a*. Protractors *M1* and *M2* reduced. Unlike Muscicapinae, the outer ectethmoid foramen (figure 1) is often outside or nearly outside the orbit. Bill notched, narrower than in Muscicapinae, non-operculate (except *Prunella*), rictal bristles virtually lacking. Palate similar to that of the Sylviinae but posterior ridge less prominent. Tongue also similar to that of the Sylviinae. Ten-primaried flycatchers, mostly terrestrial, and Old World, with usually plain (some streaked) patterns and spotted young. *Species dissected: Brachypteryx leucophrys, Cercomela familiaris, Cichladusa sp., Copsychus saularis, Enicurus maculatus, Erithacus rubecula, Erythropygia barbata, Ixoreus naevius, Kittacincla malabarica, K. tricolor, Luscinia calliope, L. cyanea, L. sibilans, L. svecica, Myiadestes genibarbis, Myiomela leucura, Myrmecocichla arnauti, Oenanthe oenanthe, Oxylabes madagascariensis, Phoenicurus ochruros, P. phoenicurus, Pratincola sp., Prunella modularis, Saxicoloides fulicata, Sialia sialis, Thamnornis chloropetoides, Zeledonia coronata.* *Discussion: Oxylabes* and *Thamnornis* have often been put in the Timaliidae or Sylviidae, but the double ectethmoid foramen and complex *M3b* (never found in those groups) place them here. *Prunella* has very strong palatal ridges; its trifid *M6* and the trifid pinnate *M6* of *Zeledonia* are unique in this family. Both should be given at least the status of tribes, the Prunellini apparently being nearest *Phoenicurus*. *Function:* The chats seem to stem directly from the Muscicapinae on the basis of plumage (especially spotted young) and internal characters. In *Muscicapa* (Muscicapinae) fibers split off *M3b*, to form a distinct *M. retractor palatini*, inserting on the basitemporal; this "complex" *M3b*, retracting the palate and drawing the upper mandible down powerfully, is elaborated in the chats *Oxylabes, Thamnornis, Saxicoloides, Oenanthe, Erithacus, Phoenicurus, Myiadestes*, and *Sialia*. In *Cichladusa* and *Enicurus* (the aquatic forktail), *M3a* is advanced anteriorly along the palatine clasp as in the dipper, *Cinclus*, and this added retracting power may be related to holding slippery prey. Revision by Ripley (1952).

THRUSHES (TURDINAE).—*Diagnosis:* Muscle pattern (figure 3) similar to that of the *Saxicolinae* but more massive, with complex *M3b* and pinnate temporal slip of *M7a*. Bill notched, stronger, non-operculate, with rictal bristles. Palate similar but with papillae anterior to choanae. Tongue as in Saxicolinae. World-wide, ten-primaried ground-feeders. *Species dissected: Hylocichla guttata, H. ustulata, Mimocichla sp., M. rubripes, Myiophonus temminckii, Oreocincla lunulata, Turdus falcklandii, T. migratorius, Zoothera sp. Discussion:* The thrushes seem to be more terrestrial than chats. *Function:* The dorso-ventral strengthening of the laterally compressed bill, especially in *Myiophonus* and *Zoothera*, with the massive retractor *M3b*, may be an adaptation for grasping slippery prey, and the evolution of some forms may be associated with a diet of earthworms. Revision by Ripley (*op. cit.*).

MIMIC THRUSHES (MIMINAE).—*Diagnosis:* Muscle pattern (figure 3) similar to that of the Turdinae but *M7a* smaller, *M6* and *M1* larger. Bill, palate, and tongue similar, but bill usually decurved (bill of *Toxostoma* is un-notched, palate flat). Ten-primaried New World ground-feeders with plain, streaked, or spotted plumage. *Species dissected: Cinclocerthia ruficauda, Donacobius atricapillus, Dumetella carolinensis, Margarops fuscatus, Melanoptila glabrirostris, Melanotis caerulescens, Mimodes graysoni, Mimus gundlachii, M. polyglottos, Nesomimus trifasciatus, Oreoscoptes montanus, Toxostoma curvirostre, T. longirostre, T. rufum. Discussion:* The double ectethmoid foramen and the muscle differences suggest that the supposed affinity of the Miminae to the babblers or wrens is the result of convergence. The Miminae may stem from the Turdinae, via *Margarops* for instance, thrashers being a specialized end product. *Function:* The palate-retracting musculature of ancestral thrushes might preadapt thrashers for pick-ax digging (Engels, 1940) by bracing the more solid, bony mandibles against resistant earth.

DIPPERS (CINCLINAE).—*Diagnosis:* Muscle pattern (figure 4) similar to that of the Turdinae but *M3a* advanced anteriorly on the palatine clasp. Protractors *M1* and *M2* expanded. Bill narrow, notched, dorso-ventrally strengthened, upturned, operculate, without rictal bristles. Palate and tongue similar to those of the Turdinae but narrower. Ten-primaried world-wide, montane, stream-bottom feeders. *Species dissected: Cinclus mexicanus. Discussion:* This group may have arisen from the Saxicolinae. The forktails (see *Microcichla*) show most of the adaptations of dippers, even the advanced *M3a* and aquatic feeding; but they retain rictal bristles and lack the dense plumage. *Function:* The expansion of protractors *M1* and *M2* and dorso-ventral strengthening of the upturned bill suggests some prying under the rocks of stream beds in both groups.

SWALLOWS (HIRUNDINIDAE).—*Diagnosis:* Muscle pattern (figure 4) similar to that of the Muscicapinae but adductors *M6* and *M7* weaker, protractors *M1* and *M2* expanded. Bill notched, very broad and flat with operculate nostril and vestigial rictal bristles. Palate broad, with weak relief; tongue broad, tapering to a short, bifid, reedy



SILKY FLYCATCHER ~ Phainopepla nitens ~ BOMBYCILLIDAE

SWALLOW ~ Hirundo aethiopica ~ HIRUNDINIDAE

STARLING ~ Sturnus vulgaris ~ STURNIDAE

DIPPER ~ Cinclus mexicanus ~ CINCLINAE

FIGURE 4. Characters in dippers, starlings, swallows, and silky flycatchers.

tip. Nine-primaried (tenth vestigial), world-wide aerial insect-eaters with plain or streaked (often iridescent) plumage and more or less spotted young. *Species dissected: Hirundo aethiopica, H. tahitica, Iridoprocne albiventris, Lamprochelidon sclateri, Petrochelidon fulva, Progne subis, Psalidoprocne fuliginosa, Pseudochelidon eurystomina, Pygochelidon cyanoleuca, Tachycineta thalassina. Discussion:* I agree with Lowe (1938) that *Pseudochelidon* is an aberrant swallow, the bronchial half-rings (instead of full rings) suggesting relationship with such a flycatcher as *Artomyias.* It has no connection with the Artaminae or Prionopinae. *Function:* The expansion of protractors *M1* and *M2* will permit wider opening of the mouth, especially by lifting the upper mandible. The forward-directed, black, loral feathers of swallows, starlings, and some flycatchers are under muscular control (Lorenz, 1949) and constitute a functional lens-shade associated with forward vision. In the same connection the ectethmoid plate of swallows and starlings falls short of the zygoma. The jaw musculature and associated characters suggest that both stem from the Muscicapinae along with Turdidae. Both have vestigial tenth and long ninth primaries like *Artomyias* as well as partial forward vision with specialized loral feathers. A few muscicapids, *Melaenornis* for example, have iridescent black plumage similar to that in some starlings and martins. Similar plumage patterns are seen in the following swallow-starling pairs: *Iridoprocne-Pholia, Hirundo-Cinnyricinclus, Progne-Aplonis, Hirundo-Saroglossa.* Streaked plumage occurs in some swallows and flycatchers (*Muscicapa, Artomyias*) and, as a rule, in juvenal starlings.

STARLINGS (STURNIDAE).—*Diagnosis:* Muscle pattern (figure 4) similar to that of the Turdinae in complex *M3b* and to that of the Hirundinidae in small *M6* and large protractors *M1* and *M2.* Bill varies from the un-notched wedge of *Sturnus* to the stout, notched, and arched beak of *Gracula;* nostril usually non-operculate; without rictal bristles. Palate generally vaulted and resembling that of the Turdinae, but flat in *Sturnus.* Ectethmoid winged. Tongue with bifid tip. Ten-primaried (short tenth and very long ninth) Old World fruit- and insect-eaters. *Species dissected: Acridotheres tristis, Aplonis grandis, A. metallicus, A. minor, Cinnyricinclus leucogaster, Gracula religiosa, Mino dumontii, Scissirostrum dubium, Sturnus contra, S. roseus, S. vulgaris. Discussion:* See Hirundinidae above. *Function:* Starlings, especially ground-feeders, have the protractors *M1* and *M2* extremely large in association with prying. *Sturnus* repeatedly parts the grass mat or probes by spreading the mandibles, at the same time directing the eyes between them. Birds with marked

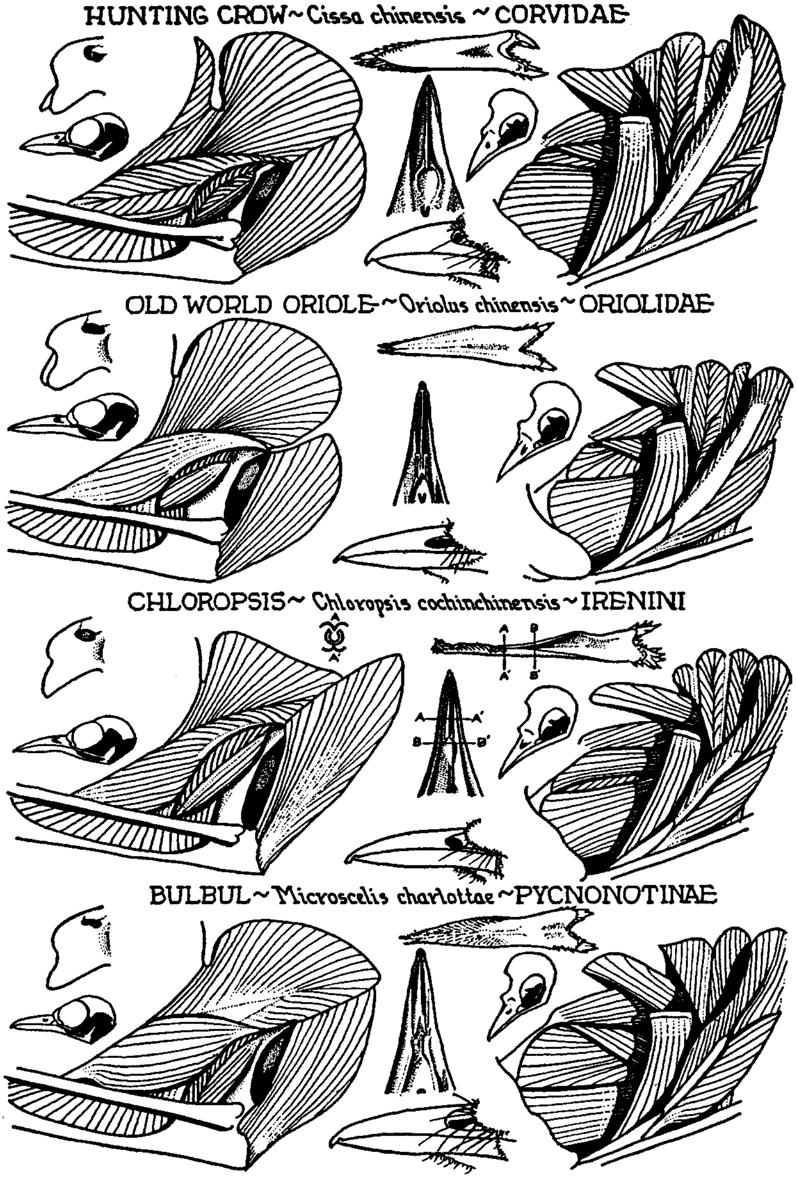


Figure 5. Characters in bulbuls, orioles, and crows.

forward vision of this sort have a temporal as well as the usual central fovea. The complex *M3b* may be for the same purpose noted in the Turdidae. Revision by Amadon (1943).

BULBULS, CORVINE BIRDS, WAXWINGS. CUCKOO-SHRIKES, AND NECTAR-FEEDERS.—All of these groups (families below) appear traceable to the bulbuls, here regarded as a specialized branch (Pycnonotinae) of the Sylviidae. *All have M7b very short,* its insertion on the inside surface of the mandible far posterior to that of *M7a* on the outside surface. Ectethmoid truncate. Single foramen becoming double in all terminal groups.

BULBULS (PYCNONOTINAE).—*Diagnosis:* Muscle pattern (figure 5) similar to that of the Sylviinae (especially *Macrosphenus*), the fibers of *M7a* (temporal slip) converging in an aponeurosis and *M7b* short (ventral slip of *M7c* not seen in figure). Outer slip of *M6* longer than the inner with a large gap between the latter and *M2.* Foramen single or pinched (double in *Andropadus*). Bill notched, slender to stout, generally decurved, operculate, with rictal bristles. Tongue generalized, but tendency for the horny papillae to be double-ranked. Palate as in the Sylviinae but posterior ridge reduced. Ten-primaried Old World (not Australian) fruit- and insect-eaters, usually with inconspicuous warbler-like plumage. *Species dissected: Criniger tephrogenys, Iole olivacea, Microscelis macclellandi, M. tickelli, M. virescens, Phyllastrephus strepitans, P. terrestris, Pycnonotus barbatus, P. cafer, P. dispar, P. finlaysoni. Discussion:* The characters distinguishing this subfamily from Sylviinae seem to link it to various derived groups below. *Function:* The more massive musculature agrees with a stronger bill while the expansion of *M1* and *M2* suggests added prying ability. Delacour's (1943a) "family" characters are weak; his assertion that the neck is short is not supported by skeletal material.

FAIRY BLUEBIRD, CHLOROPSIS (IRENINI).—*Diagnosis:* Muscle pattern (figure 5) pycnotine but *M3a* advanced, bifid *M6* (trifid in *Chloropsis*); *M1* and *M2* emphasized. Ectethmoid foramen double.' Tongue, bill, and palate pycnonotine, but *Chloropsis* with nectar adaptations (see below). *Species dissected: Chloropsis cochinchinensis, Irena puella. Discussion:* Many features of derived groups are forecast in this tribe of the Pycnonotinae, which does not include *Aegithina* or *Aethorhynchus;* the forward advance of *M3a* on the palatine clasp, trifid *M6,* reduction of rictal bristles, increased pinnate character of the muscles, expanded protractors, and the curled, whipped-out, nectar-adapted tongue (*Chloropsis*). *Function:* Vacuum is apparently created in this sucking tongue by catching its tubular part between the opposing ridges of upper and lower mandibles (A–A′) while the palatal boss engages the notch of the tongue (B–B′). In this position the brushy tip protrudes beyond the bill tip.

THE CORVINE ASSEMBLAGE.—This group, comprising the Ptilonorhynchidae, Callaeidae, Paradisaeidae, and Corvidae, is typified by double ectethmoid foramen, free lacrymal, advanced *M3a,* short *M7b,* tendency to pinnate adductors, loss of rictal bristles, and plumage specialization. The Oriolidae, a primitive group close to the Corvidae, has *M3a* not advanced as in jays.

BOWER BIRDS (PTILONORHYNCHIDAE).—*Diagnosis:* Muscle pattern (figure 6) similar to that of the Pycnonotinae but adductors *M7a* and

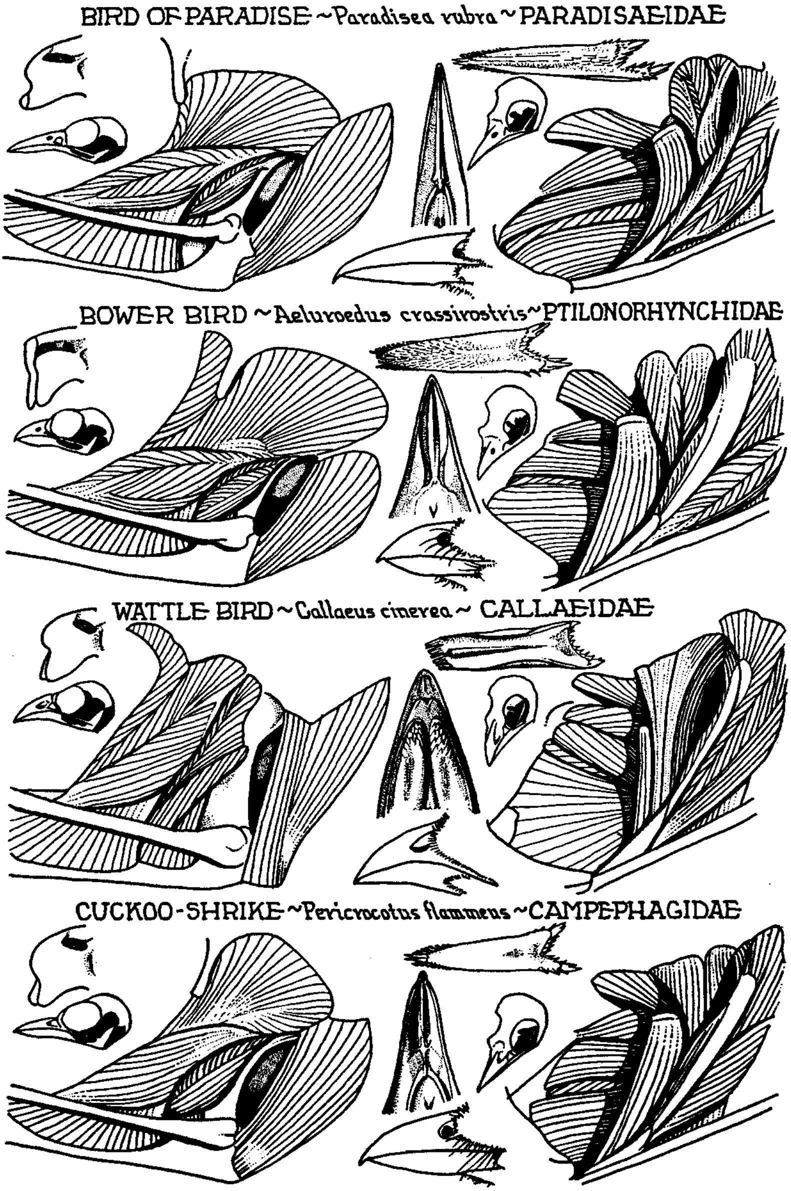


FIGURE 6. Characters in cuckoo-shrikes and Australian crow-like birds.

M7c pinnate, *M3a* advanced. Bill notched, arched, stout to slender; nostril operculate or feathered; without rictal bristles. Tongue with radiating surface-papillae and quadrifid, reedy tip. Palate (*Aeluroedus*) with posterior ridge joined to anterior or (*Prionodura*) with posterior ridge greatly reduced as in *Pycnonotus layardi.* Ten-primaried corvid-like fruit- and insect-eaters of the Australian region. *Species dissected: Aeluroedus crassirostris. Discussion:* Affinity to the Pycnonotinae is seen in the gap between *M2* and *M6* and in the characters of the corvine assemblage, even in the specialized *Aeluroedus,* but on the basis of external characters, the bulbuls are disjunct from their presumed descendant groups (cf. Delacour, 1943). The papillate tongue of *Aeluroedus* is approached by *Pycnonotus finlaysoni,* and partial resemblance in plumage is seen in bulbul-bowerbird pairs like *Trachycomus-Sericulus, Chloropsis-Xanthomelas.* Some members of both groups are mimics. But the Pycnonotinae do not reach the Australian region, and we are obliged to assume that the ancestral bulbul-like stock which reached there evolved into the endemic families treated here and below. *Function:* Adduction and palate retraction as throughout assemblage.

BIRDS OF PARADISE (PARADISAEIDAE).—*Diagnosis:* Muscle pattern (figure 6) similar to that of the Ptilonorhynchidae but *M6* trifid pinnate, *M7b* reduced, and *M1* and *M2* expanded. Bill notched (except in riflebirds), without rictal bristles; nostril operculate or feathered. Palate with long central ridge fused to posterior ridge. Tongue surface papillate with double-ranked horny papillae posteriorly. Lacrymal free in *Ptilorhis,* fused in *Paradisea. Species dissected: Paradisea rubra, Ptilorhis paradisea. Discussion:* If this actually is another corvid-like endemic group which evolved in the Australian region from ancestral pycnonotine stock, the tendency toward bare nape in bulbuls may be associated with often naked nape in the Paradisaeidae; the long nape "hairs" of the bulbul *Tricholestes* may be the "anlagen" of feather specialization, the red-throated mutant of *Pycnonotus dispar johnstoni* (de Schauensee, 1946: 53) the forerunner of the bright coloration in descendant groups.

WATTLE BIRDS (CALLAEIDAE).—*Diagnosis:* Muscle pattern (figure 6) nearest that of *Aeluroedus* but *M6* trifid, temporal slip of *M7a* reduced; *M7c, M4a,* and *M1* expanded. Bill un-notched, varying from the straight wedge of *Philesturnus* to the arched beak of *Callaeas,* operculate, without rictal bristles. Palate with lateral bosses papillate like the tongue of *Aeluroedus.* Tongue truncate with quadrifid tip and raised mid-rib suggested in *Aeluroedus.* Endemic New Zealand leaf- and insect-eaters. *Species dissected: Callaeas cinerea, Philestur-*

nus carunculatus. Discussion: A primitive corvid-like group most closely allied to bower birds (plumage pattern of *Callaeas* resembles that of the related cuckoo-shrikes). *Function:* the palate in *Callaeas* (raised as in *Phytotoma*) is adapted for leaf-eating. *Philesturnus* is convergent with *Sturnus* in having enlarged protractors *M1* and *M2*, otherwise like *Callaeas*.

OLD WORLD ORIOLES (ORIOLIDAE).—*Diagnosis:* Muscle pattern (figure 5) similar to that of the Pycnonotinae, but *M6* trifid and pinnate. Bill notched, of moderate strength, operculate, with rictal bristles. Tongue unspecialized. Palate with central ridge more or less confluent with weak posterior ridge. Ten-primaried Old World fruit- and insect-eaters. *Species dissected: Oriolus chinensis, O. xanthornus. Discussion:* Similar in plumage to some of the Pycnonotinae; in some ways, this unspecialized, anatomically primitive group also parallels the jays.

CROWS, JAYS, MAGPIES (CORVIDAE).—*Diagnosis:* Muscle pattern (figure 5) similar to that of the Oriolidae, but *M7a* and *M7c* pinnate and outer slip of *M6* advancing its insertion on the mandible (in *Corvus M3a* likewise is advanced). Bill seldom distinctly notched; rictal bristles present; nostril feathered. Tongue with horny papillae double-ranked. Palate usually with posterior ridge suppressed, but fused with central ridge in *Cissa*. Ten-primaried world-wide omnivores. *Species dissected: Aphelocoma ultramarina, Cissa chinensis, Cissilopha melanocyanea, Corvus brachyrhynchos, Crypsirhina temia, Cyanocitta cristata. Discussion:* The partly pinnate adductors of the Oriolidae are intermediate between the pinnate adductor musculature of the Corvidae and the mainly parallel musculature of the Pycnonotinae. The variable black and white plumage of the bulbul *Microscelis madagascariensis* suggests that of the Corvidae; anatomically, the bower birds are intermediate between bulbuls and crows. *Function:* In most of these omnivores, hammering plays a role in food-getting. Revision by Amadon (1944).

THE CUCKOO-SHRIKE, WAXWING ASSEMBLAGE.—The families of this assemblage seem to have arisen from the Pycnonotinae mainly with plumage and diet specialization and with the internal specialization of free lacrymals. Ectethmoid truncate. Foramen variable, but double in most advanced forms.

CUCKOO-SHRIKES (CAMPEPHAGIDAE).—*Diagnosis:* Muscle pattern (figure 6) as in the Pycnonotinae, but the insertion of *M3a* advanced and the gap lacking between *M2* and *M6*. Bill notched; rictal bristles present; nostril feathered. Palate vaulted with central ridge disappearing posteriorly (crow-like). Tongue with papillae double-ranked ventrally and "quadrifid" tip (bifid with lateral fringes). Ten-primaried Old World fruit- and insect-eaters. *Species dissected: Coracina lineata, C. melanops, C. papuensis, Edolisoma holopolium, Edolisoma sp., Lalage maculosa, L. niger, Malindangia sp. Discussion:* Delacour places *Tephrodornis* and *Hemipus* here, but the former agrees on every point with the Prionopinae, extending the range of this group into the Oriental region; the latter is a monarch flycatcher. *Function:* The advanced *M3a* increases the strength of palatal retraction in this group as in the assemblage.

WAXWINGS, SILKY FLYCATCHERS, PALM CHATS (BOMBYCILLIDAE).—*Diagnosis:* Muscle pattern (figure 4) similar to that of the Campephagidae but *M7c* pinnate and extended dorsally with gap between *M2* and *M6* as in the Pycnonotinae. Bill notched, short and broad, non-operculate, with rictal bristles. Tongue as in the Campephagidae (*Phainopepla* with papillate surface like *Pycnonotus finlaysoni* and *Aeluroedus*). Palate of *Phainopepla* like that of the Campephagidae; palate of *Bombycilla* like that of the Pycnonotinae. Ten-primaried, fruit- and insect-eaters, mainly of the New World. *Species dissected: Bombycilla cedrorum, B. garrula, Dulus dominicus, Phainopepla nitens, Phainoptila melanoxantha, Ptilogonys cinereus, Hypocolius ampelinus. Discussion:* Despite the close similarity of Campephagidae and Bombycillidae, they are thought to have arisen from the Pycnonotinae independently by specialization of characters incipient in that group. Both groups have the lacrymal free, similar internal characters throughout, and plumage specialization with crests. An examination of Col. Meinertzhagen's specimen of *Hypocolius* clearly establishes its position in the Bombycillidae, and the fused lacrymal may indicate that it is a little closer to typical bulbuls than the other bombycillids. See Delacour and Amadon (1949).

THE OLD WORLD NECTAR-FEEDER ASSEMBLAGE.—The sunbirds, flower-peckers, and white-eyes share many internal characters with the Pycnonotinae, lacking only the gap between *M6* and *M2* characteristic of the Pycnonotinae. They could have arisen from the Sylviinae close to the bulbul stem; but the serrate-tipped mandibles of sunbirds and flower-peckers may be forecast in such a bulbul as *Andropadus*, and it is relatively easy to derive the plumage types of the whole assemblage from bulbuls. All have the ninth primary long and the tenth short, the ectethmoid truncate, lacrymal fused, and a large palatine salivary gland.

WHITE-EYES (ZOSTEROPIDAE).—*Diagnosis:* Muscle pattern (figure 7) similar to that of the Pycnonotinae, but protractors *M1* and *M2* expanded, *M6* suppressed, *M4b* split to accommodate a palatine sali-

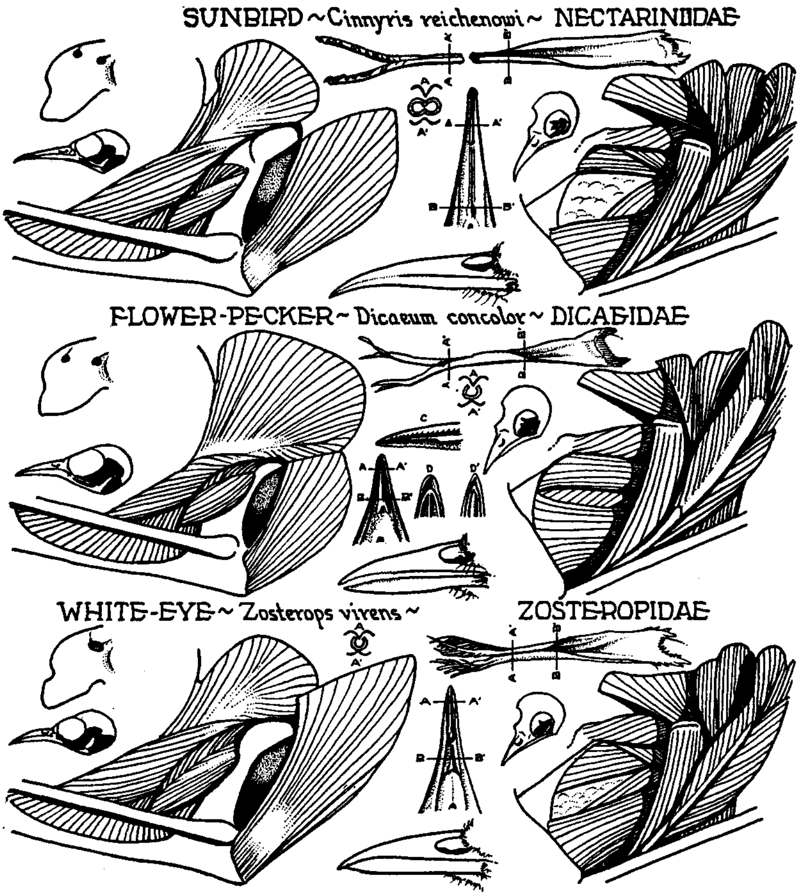


FIGURE 7. Characters in sylvioid nectar-feeders.

vary gland visible in the floor of the orbit. Ectethmoid foramen single. Bill slender, essentially un-notched, operculate, with rictal bristles. Palate similar to that of a sylviid or bulbul; tongue unspecialized, but that of *Zosterops virens* whipped out into quadrifid tip and tubular. Nine-primaried (tenth vestigial) insect- and nectar-feeders of the Old World. *Species dissected: Zosterops japonica, Z. lateralis, Z. palpebrosa, Z. virens. Discussion:* Regarding the pycnonotine origin, the bulbul *Phyllastrephus zosterops* resembles white-eyes in plumage. *Function:* Anatomically, white-eyes are nothing but warblers (or bulbuls) adapted for nectar-feeding by the expanded *M1* and *M2*, the loss of the bill-notch and rictal bristles, and the sometimes specialized tongue, which functions as described for the Irenini.

Sunbirds (Nectariniidae).—*Diagnosis:* Muscle pattern (figure 7) imilar to that of the Pycnonotinae, but protractors *M1* and *M2* expanded and inner slip of *M6* longer. Ectethmoid foramen double. Bill un-notched, slender, usually long, and decurved, serrate at tip, operculate, without rictal bristles. Palate with central ridge set in a groove and a raised boss far posterior. Tongue flat posteriorly with twin tubes separate anteriorly but fusing in the mid-portion. Ten-primaried (tenth short) nectar-feeders mainly of the Old World tropics. *Species dissected: Aethopyga gangliae, A. nipalensis, A. siparaja, Anthreptes collaris, A. malaccensis, Chalcoparia singalensis, Cinnyris jugularis, C. olivacea, C. oseus, C. reichenowi. Discussion:* The small size of sunbirds does not preclude derivation from larger bulbul-like ancestors, for size is adaptive; on the other hand the nest of the primitive sunbird *Arachnothera* suggests relationship to the warbler *Orthotomus* which has a "pinched" foramen intermediate between the single foramen of warblers and the double foramen of sunbirds. But the double foramen in sunbirds is matched in many groups diverging from the stem warblers. On such fine points of derivation we cannot be sure, and figure 18 expresses my best guess. *Function:* The expansion of protractors *M1* and *M2* indicates their use in prying into nectaries of flowers. The tongue functions as described for the Irenini, but the dorsal fusion of the twin tubes makes it more efficient. See revision by Delacour (1944) for tongue variants in *Arachnothera* and *Aethopyga.*

Flower-Peckers (Dicaeidae).—*Diagnosis:* Muscle pattern (figure 7) similar to that of sunbirds, but temporal slip of adductor *M7a* expanded and *M3a* advanced—protractors *M1* and *M2* reduced. Ectethmoid foramen double. Bill un-notched with finely serrate tip (notched in *Pardalotus*), operculate, without rictal bristles. Palate with central and posterior ridges fused. Tongue similar to that of sunbirds, but twin tubes each bifid terminally and not fused medially. Nine-primaried (tenth vestigial) fruit- and insect-eaters of the Australian and Oriental regions. *Species dissected: Dicaeum aeneum, D. concolor, D. cruentatum, Melanocharis versteri. Discussion:* The sunbirds and flower-peckers seem to have diverged from a common stock, the former as nectar-feeders with increased protraction, the latter as berry-eaters (mistletoe), with stronger adduction, but with above-average protraction for secondary nectar-feeding. *Function:* The tongue functions as in the Irenini, but the central palatal ridge has a sharp elevation (C), and the pattern of the tip of the upper mandible (D) is matched by that of the lower (D′). The serrate bill-tip, probably adapted for fruit-grasping, may be forecast in the multiple

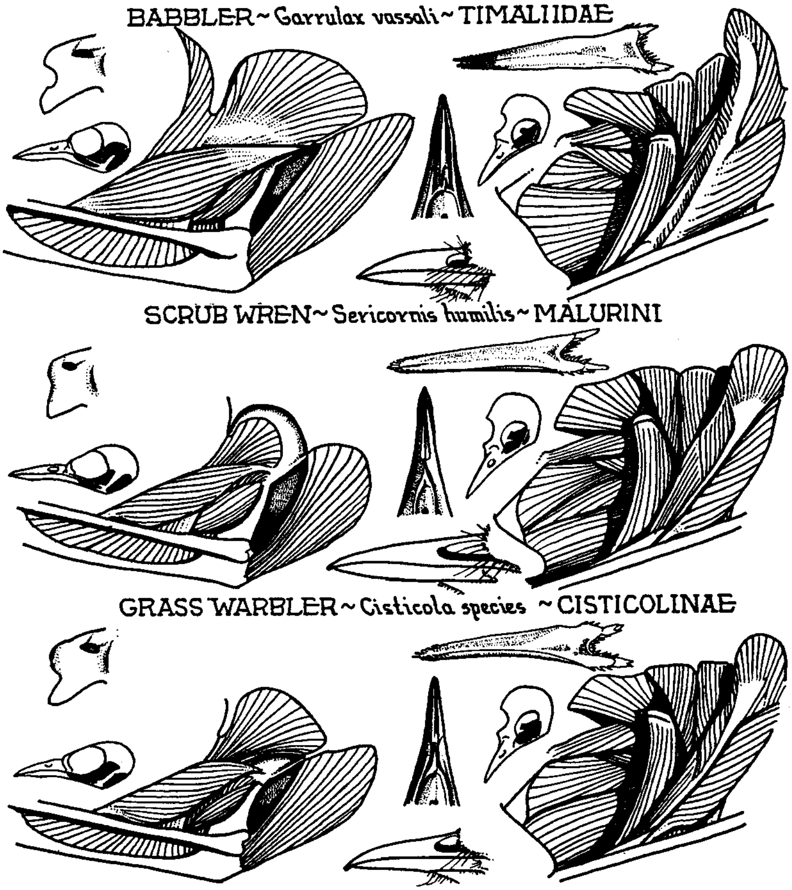


FIGURE 8. Characters in babblers and timalioid warblers.

bill-notches of the bulbul *Andropadus*. Revision by Mayr and Amadon (1947).

THE SUPERFAMILY TIMALIOIDEA

The Timalioidea form the larger of the two major divisions of the Oscines (figure 18). In the basic stock of this group, the capacity to evolve a pinnate *M7b* has permitted the development of shrike- and finch-like groups; the lack of this capacity apparently prevented the Sylvioidea from evolving similarly adapted forms. Two plumage types dominate this superfamily. One is a pattern of shaft-streaks, particularly on head and back. The other is a bold recognition pattern consisting of a black breast-crescent, auriculars, and crown, set off by light throat, forehead, and malar and superciliary regions.

This is evident in virtually all timalioid families, though often present only in part and sometimes apparently obliterated by extensive black or white. It is also found outside the Oscines, but within the suborder it is almost confined to the Timalioidea, only wheatears and jays among Sylvioidea showing it.

To trace timalioid origins, it is now necessary to return to the stem Sylviidae where warblers of the subfamily Cisticolinae exhibit pinnate *M7b* in its most primitive expression.

GRASS AND BUSH WARBLERS (CISTICOLINAE).—*Diagnosis:* Muscle pattern, etc. (figure 8) similar to that of the Sylviinae but *M7b* pinnate. Bill slender, notched, operculate, with rictal bristles. Ectethmoid winged, lacrymal fused. Tongue and palate similar to those of the Sylviinae but lateral ridges crowding center ridge posteriorly. Ten-primaried Old World insect-eaters. *Species dissected: Bradypterus castaneus, Cisticola galactotes, Cisticola sp., Horeites canturiens, Horornis montana, Locustella ochotensis, Megalurulus mariei, Megalurus palustris, Pnoepyga pusilla, Prinia atrogularis, Schoenicola brevirostris. Discussion:* This subfamily of the stem Sylviidae seems to be a key group from which the timalioid families all arise. The dark breast crescent of *Prinia flavicans* may foreshadow the recognition pattern mentioned above; *Cisticola* typifies the shaft-streak pattern. Revisions in part by Lynes (1930) and Delacour (1942–1943).

GRASS AND BUSH WARBLERS (MALURINI).—*Diagnosis:* Muscle pattern (figure 8) like that of the Cisticolinae but *M4b* tending to split into two slips. Ectethmoid plate truncate and falling short of zygoma as in true wrens. Tongue and bill similar to those of the Cisticolinae but nostril more broadly operculate. Palate with lateral ridges disappearing posteriorly. Ten-primaried Australian region insect-eaters, some with plumage specialization. *Species dissected: Amaurodryas vittata, Calamanthus fuliginosus, Gerygone magnirostris, Gerygone sp., Lamprolia victoriae, Malurus cyanea, Petroica multicolor, Petroica sp., Sericornis humilis, Stipiturus malacurus, Todopsis sp., Vitia ruficapilla. Discussion:* The colorful *Lamprolia* is definitely not related to the birds of paradise. The outer slip of *M6* is longer than the inner slip in *Vitia* and *Lamprolia* of Fiji; this suggests the origin of the latter from the former. *Todopsis* has the tip of the bill broadened.

MONARCHS, WHISTLERS, DRONGOS, AND VIREOS (MONARCHIDAE).—Internal characters are the basis for uniting these rather distinct shrike-flycatcher groups in a new family, the Monarchidae. All have, in common with Cisticolinae, a winged ectethmoid, a large, single foramen, fused lacrymal, and a prominent post-orbital process, but in their specialized bills show an advance over that group.

MONARCH FLYCATCHERS (MONARCHINAE).—*Diagnosis:* Muscle pattern (figure 9) similar to that of the Cisticolinae (but *M6* becoming trifid and pinnate in *Terpsiphone*). *M4a* with narrow anterior insertion on the slender transpalatine process.

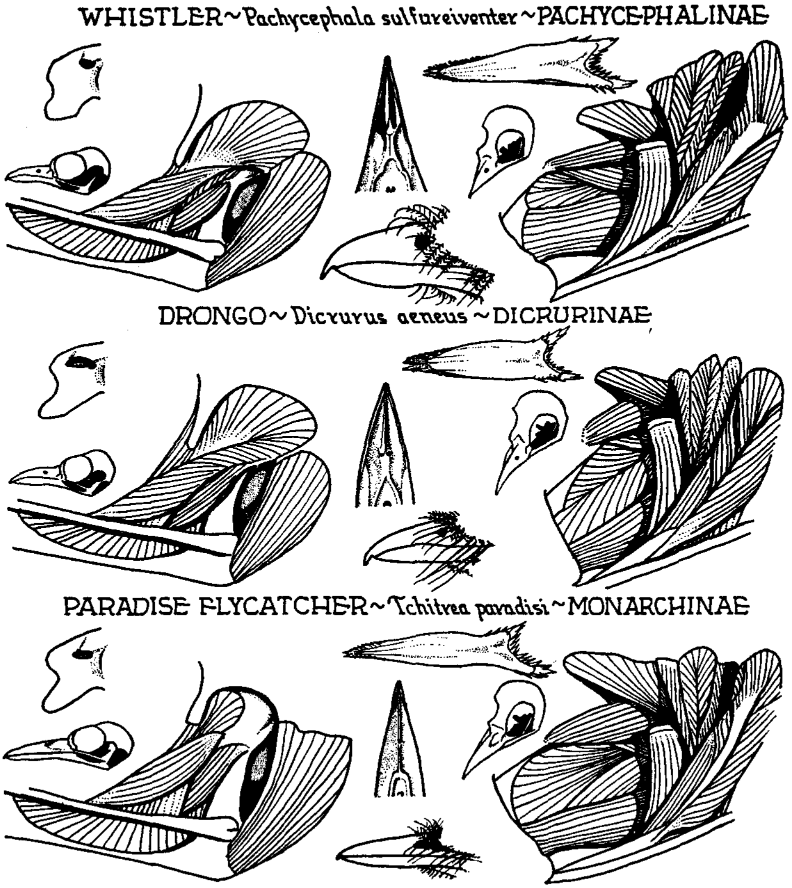


FIGURE 9. Characters in shrike-flycatchers.

Bill notched, broad and flat, semi-operculate to operculate, with nasal and rictal bristles. Posterior palatal ridge separated from anterior ridge only by the paired palatal nares. Tongue with prominent horny papillae posteriorly and quadrifid tip. Ten-primaried Old World shrike-flycatchers with plumage specialization culminating in the paradise flycatchers. *Species dissected: Batis poensis, Chasiempis gayi, Diaphorophyia castanea, Hemipus picatus, Hypothymis azurea, Lanioturdus torquatus, Monarcha castaneiventris, Myiagra ferrocyanea, Piezorhynchus sp., Platysteira cyanea, Rhipidura albicollis, R. cockerelli, R. leucophrys, Terpsiphone paradisi, T. rufiventris. Discussion:* As in the Malurini, a tendency for *M4b* to split with fusion of the lateral slip to *M4a* is seen in *Batis, Lanioturdus,* and *Platysteira.* But the small postorbital process and truncate ectethmoid with a small foramen in the Malurini, contrasted with the large process and "winged" ectethmoid with large foramen in the Monarchinae, suggest common cisticoline origin rather than direct relationship. These bony characters also distinguish the narrow-billed monarchs from the Malurini. The Monarchinae differ from the Muscicapinae also in having unspotted young and in behaving less like flycatchers and more like arboreal insect-gleaners (Delacour, 1947).

DRONGOS (DICRURINAE).—*Diagnosis:* Muscle pattern (figure 9) similar to that of *Terpsiphone*, but *M4a, M4b,* and the slips of *M7* fused (cf. monarchs); the temporal slip of *M7a* expanded. Bill notched, non-operculate with strong rictal and nasal bristles. Palatal pattern similar to that of the Monarchinae but more vaulted. Tongue similar to that of the monarchs but with a tendency for the horny papillae to be double-ranked. Ten-primaried (mainly black) Old World insect- and nectar-feeders with notable plumage specialization. *Species dissected: Dicrurus aeneus, D. balicasseus, D. coerulescens, D. hottentottus, D. sumatrana. Discussion:* Internal anatomy and plumage leave little doubt that this is a specialized group arising from the monarch flycatchers. *D. balicasseus* has a white belly like that of *Myiagra cyanoleuca*, and *Monarcha alecto* closely resembles unspecialized forms of *Dicrurus* in both black plumage and characters in the bill. *Function:* In *D. hottentottus*, the adaptive loss of the bill-notch and the nectar-adapted tongue indicate a strong approach to flower-feeding, though the persistence of rictal bristles suggests that insect-eating is still paramount. The similar quadrifid tongue-tips in this species and in the Meliphagidae suggest a common origin from the same timalioid stock. Revision by Vaurie (1949).

WHISTLERS (PACHYCEPHALINAE).—*Diagnosis:* Muscle pattern (figure 9) as in the drongos but without fusion. Palate and bill similar to those of drongos, but the latter always notched. Tongue also similar, but without double-ranking of papillae. Ten-primaried shrike-flycatchers of the Australian Region. *Species dissected: Colluricincla rectrirostris, Pachycephala pectoralis, P. sulfureiventer, Pitohui ferrugineus. Discussion:* This appears to be a specialized Austro-malayan line arising from the monarch flycatchers and generally with a deeper, narrower bill.

VIREOS (VIREONINAE).—Treated below under the American nine-primaried assemblage.

THE SHRIKE ASSEMBLAGE.—The world-wide, insectivorous Monarchidae may have existed before the origin of flowering plants. The primitive shrike groups of the several faunal regions, apparently stemming from it independently and with differential emphasis on its variations, suggest a Tethyan Upper Cretaceous or Eocene distribution pattern (see von Reichenbach, 1909). Anatomically, the Australian Cracticidae are close to the Vanginae of Madagascar and the Prionopinae of Africa and India (all having large postorbital processes), as well as to the Bornean Bald Shrike (*Pityriasis*). A separate and later origin of the Laniidae from the Monarchinae is suggested by their more advanced muscle pattern (pinnate adductors) and reduced postorbital processes. The members of the shrike assemblage, except the Laniinae, have the ectethmoid winged, free lacrymal, and a single foramen.

THE WOOD SWALLOWS, BUTCHER BIRDS, BALD SHRIKES, AND MAGPIE LARKS (CRACTICIDAE).—These four subfamilies are apparently the result of adaptive radiation from a single monarchine stock, mainly in Australia. The radiation of the Vangidae on Madagascar is a parallel example. Internal characters and the black-and-white plumage patterns unite the groups, even though the Artaminae are long-winged

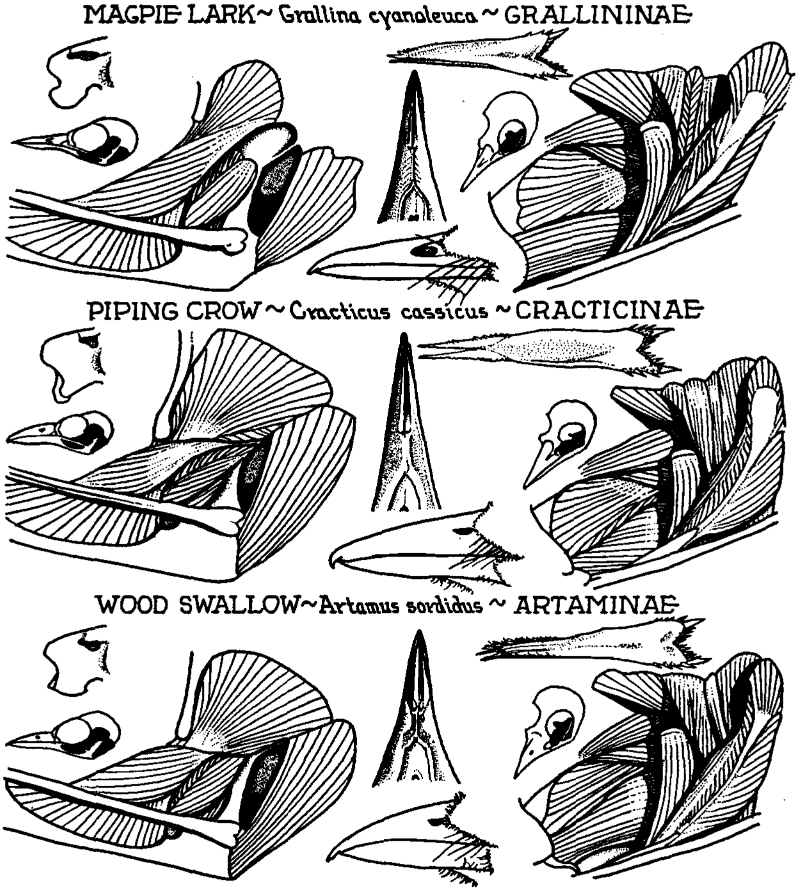


FIGURE 10. Characters in Australian shrikes.

fly-catchers, the Cracticinae and Pityriasidinae are shrike-like, and the Grallininae are ground insect-eaters.

WOOD SWALLOWS (ARTAMINAE).—*Diagnosis:* Muscle pattern (figure 10) similar to that of the Monarchinae, but *M6* trifid (not pinnate), ensheathed in an aponeurosis, with special development of the temporal slip of *M7a; M4a* and *M4b* tending to fuse (cf. monarchs, drongos). Other internal characters similar to those of the Monarchinae but lacrymal free (vestigial?). Tongue and palate also similar, but bill stronger, nostril approaching the slit-like aperture of the Prionopinae. Ten-primaried, aerial insect-eaters of the Australian and Oriental regions. *Species dissected: Artamus leucorhynchus, A. sordidus. Discussion:* (See under Vanginae). *Function:* The length of *M3b* suggests powerful palate retraction, as already evident in Monarchinae, hence, an unusually good grip at the tips of the mandibles. The swallow-like wing with short tenth and very long ninth primaries, is adapted for soaring flight.

BUTCHER BIRDS (CRACTICINAE).—*Diagnosis:* Muscle pattern (figure 10) similar to that of the Artaminae but *M6* quadrifid and no fusion of *M4a* and *M4b*; free lacrymal stronger. Tongue, palate, and bill also resemble those of the Artaminae but bill has a distinct shrike-like hook. Ten-primaried Australian shrikes with rounded wings. *Species dissected: Cracticus cassicus, Gymnorhina tibicen. Discussion:* The musculature is more massive than that of the Artaminae, reflecting the different feeding habits which mark these distinct adaptive lines. *Function:* The bill of the butcher bird (*Cracticus*) is adapted for tearing impaled animals; *Gymnorhina* does not feed in this manner.

BALD SHRIKE (PITYRIASIDINAE).—*Diagnosis:* Internally similar to the Cracticinae, these groups probably having a common monarchine origin. *Species dissected: Pityriasis gymnocephalus.*

MAGPIE LARKS AND MUD-NEST BUILDERS (GRALLININAE).—*Diagnosis:* Muscle pattern (figure 10) closer to that of *Terpsiphone* than to that of the other Cracticidae; but tongue, palate, and plumage support their inclusion in this family. (See Amadon, 1950a.) *Species dissected: Grallina cyanoleuca, Struthidea cinerea. Discussion:* The fused lacrymal may be an adaptation for lateral vision characteristic of some ground feeders, and the reduction in *M3b* with a trifid pinnate *M6* may be similarly explained.

THE VANGAS AND HELMET SHRIKES (VANGIDAE).—The radiation of the vangas (Vanginae) in Madagascar has produced forms adapted for many niches in addition to the shrike-niche. Although clearly distinct from the helmet shrikes (Prionopinae) of Africa in jaw musculature and other internal characters, the Vanginae show unmistakable relationship with that group; and both may have stemmed independently from monarch ancestors.

VANGAS (VANGINAE).—*Diagnosis:* Muscle pattern (figure 11) similar to that of the Artaminae (cf. Pycraft, 1907). Bill notched, with rictal bristles (except in *Falculea*); nostril non-operculate, feathered. Palate and tongue similar to those of the Artaminae and Monarchinae. Ten-primaried insect-eaters, confined to Madagascar. *Species dissected: Hypositta corallirostris, Schetba rufa, Tylas eduardi. Discussion: Tylas eduardi* appears to be a vangid; it is anatomically very far from the orioles or the bulbuls (Mayr and Amadon, 1951). *Hypositta* differs from typical vangids only in having the lacrymal fused and is not close to Sittidae internally. *Mystacornis crossleyi* (dissected) may also be a vangid. As is typical for endemic Madagascar groups (Rand, 1936), the vangids appear to have radiated into many food-niches from a common ancestral stock. *Function:* The species examined have a long *M3b*, suggesting strong palatal retraction as in the Artaminae, but *Schetba rufa* has a unique feature. In this species, the anterior end of the zygoma has a notch-like eminence dorsally (A)—buttressed by a similar one posteroventrally (B)—so that, when the palate is fully retracted and the tip of the mandible depressed in maximum adduction, this notch will fall in place behind the ethmoidal wing (C). Supposedly, the bird will thus be able to tear or to maintain a grip indefinitely with decreased muscular effort.

HELMET SHRIKES (PRIONOPINAE).—*Diagnosis:* Muscle pattern (figure 11) similar to that of the Vanginae but *M4a* and *M4b* not fused, the latter splitting into two slips in *Sigmodus* and *Tephrodornis*, but all three fused in *Prionops* (cf. monarchs, drongos).

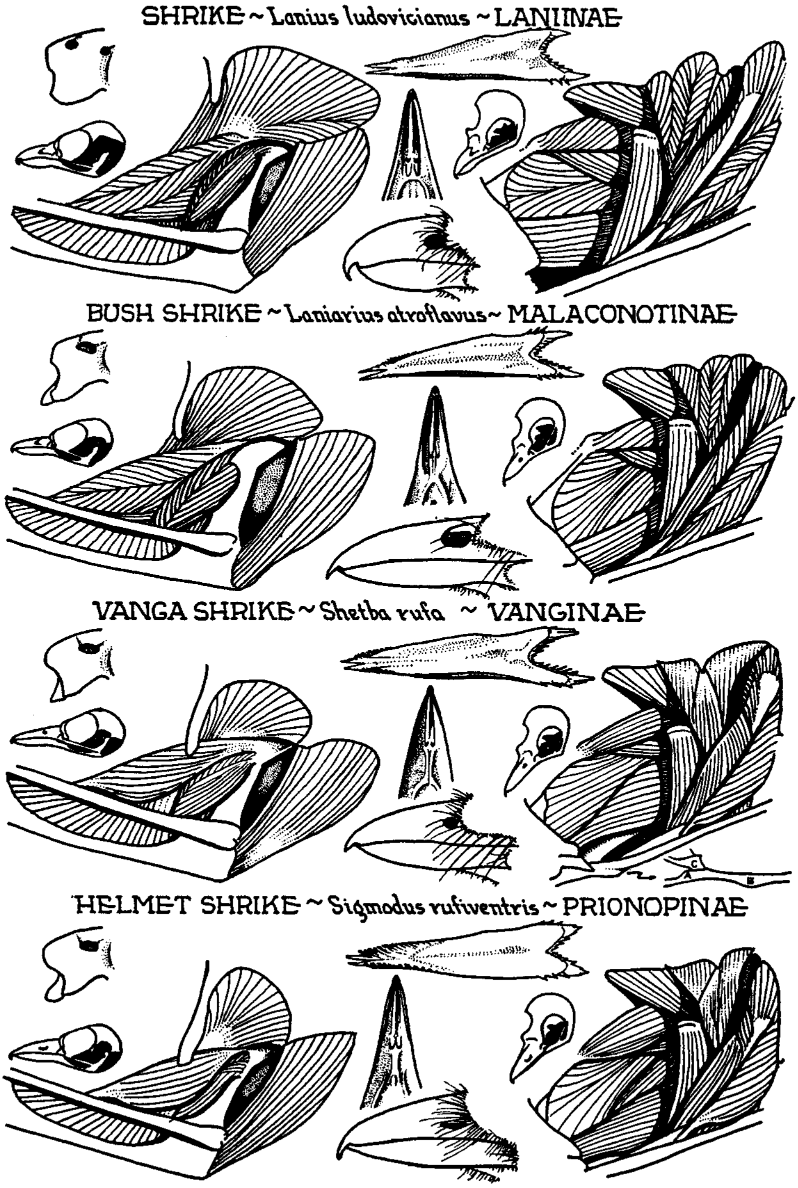


FIGURE 11. Characters in shrikes.

Tongue and palate similar to those of the Vanginae. Bill notched; rictal bristles present; slit-like nostril feathered. Ten-primaried African and Oriental insect-eaters. *Species dissected: Prionops poliocephala, Sigmodus rufiventris, Tephrodornis pondicerianus. Discussion: Tephrodornis* agrees with the Prionopinae in having pinnate *M7b*, split *M4b*, no advance in *M3a*, and free lacrymal—none of which ever occurs in cuckoo-shrikes, where Delacour has placed it. This extension of the range of this ancient African shrike group to the Oriental Region is not surprising. The early Tethyan distribution referred to above, which is *necessary* to explain shrike relationships, would have given the Prionopinae access to the Oriental Region (particularly southern India and Ceylon). Similarity of muscle pattern, bill, tongue, and palate (see figures) link the Prionopinae with the Vanginae and with the Pityriasidinae and Cracticidae. *Function:* In *Sigmodus, M3b* is even more strongly developed for powerful palatal retraction than in *Schetba.* This compensates for the lack of a notched zygoma as in *Schetba.* Review by Mayr (1943).

THE BUSH SHRIKES AND TRUE SHRIKES (LANIIDAE).—The Malaconotinae and Laniinae, ranging from the Ethiopian and Oriental regions into the Holarctic, may have arisen from the Monarchinae as a more successful shrike family that eliminated the less-advanced earlier shrikes (above) to a large extent in the Oriental Region. The more primitive shrikes appear to have survived best in sanctuaries like Australia and Madagascar.

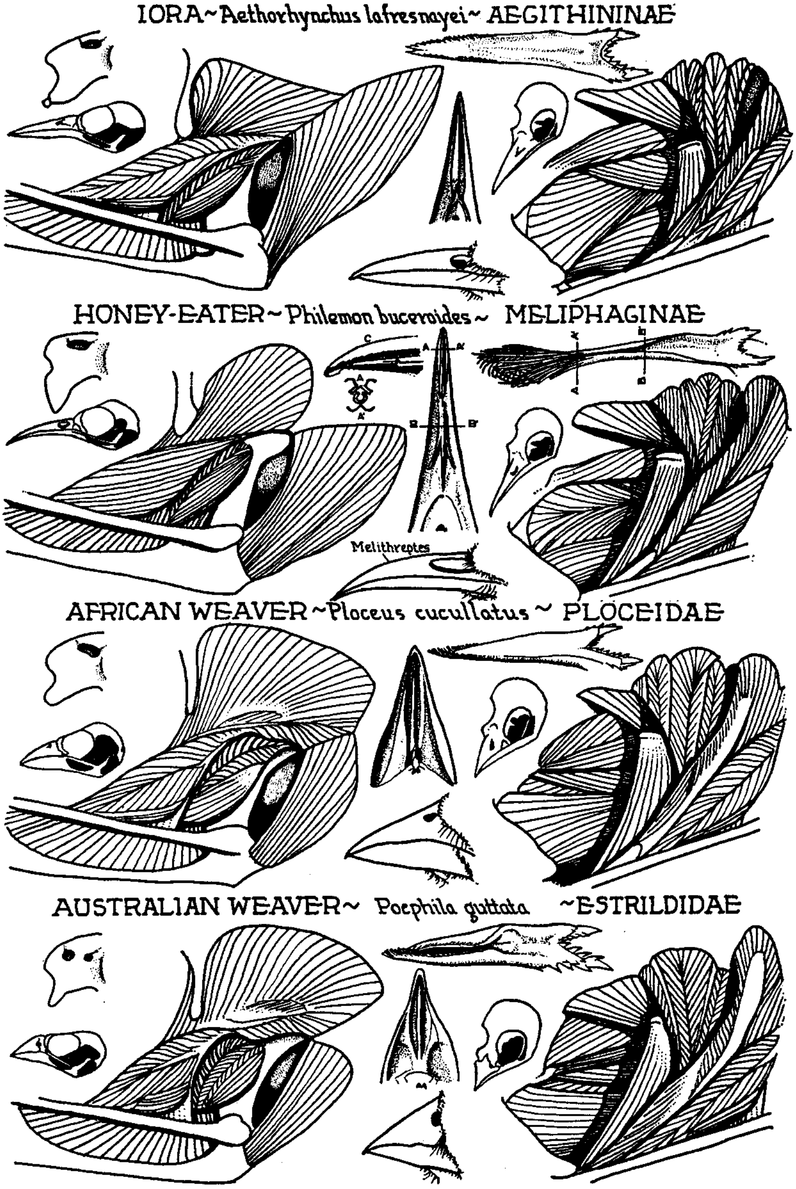
BUSH SHRIKES (MALACONOTINAE).—*Diagnosis:* Muscle pattern (figure 11) similar to that of the Monarchinae, but the trifid *M6* and *M7a* pinnate (temporal slip expanded) without splitting or fusion in *M4.* Ectethmoid foramen single. Post-orbital process reduced, compared with the more primitive shrikes. Palate and tongue similar to those of the Monarchinae but nostril semi-operculate and rictal bristles reduced. Ten-primaried (mainly forest) shrikes of Africa. *Species dissected: Chaunonotus sabinei, Dryoscopus affinis, D. gambensis, Laniarius atroflavus, L. ferrugineus, Nicator chloris, Tchagra senegala. Discussion: Nicator* is atypical with *M6* trifid and parallel and *M7a* parallel, but it fits best here. It is not related to the Pycnonotinae (*contra* Delacour, 1943a) and resembles *Malaconotus* externally.

TRUE SHRIKES (LANIINAE).—*Diagnosis:* Muscle pattern (figure 11) similar to that of the Malaconotinae but more massive and with different structure in *M6.* Bill stouter, with strong hook; nostril non-operculate, feathered; rictal bristles present. Ectethmoid truncate, foramen double; lacrymal fused or lost. Palate and tongue similar to those of the bush shrikes but the post-orbital process further reduced. Ten-primaried shrikes of the Old and New Worlds. *Species dissected: Cephalophoneus nasutus, Lanius excubitor, L. ludovicianus, L. schach, Urolestes melanoleucus. Discussion:* In all shrikes the lateral slip of *M6* tends to be advanced in its insertion anteriorly on the inner surface of the mandibular ramus, and this is pronounced in *Cephalophoneus. Function:* The loss of the lacrymal and resulting shortness of the ectethmoid, which does not reach the zygoma, may permit better forward vision as in the Starling (*Sturnus*).

THE HONEY-EATER, WEAVER ASSEMBLAGE.—Many lines of evidence suggest that primitive honey-eaters, which had evolved an angulated commissure (prominent in nectar- and seed-adapted groups) but had not yet lengthened the bill, were pre-adapted to evolve the weavers. *Aethorhynchus* (figure 12) is similar in muscle pattern to *Ploceus* (figure 12), and the two groups are similarly primitive in the large size often attained by the ectethmoid foramen. Palatal patterns are not far out of agreement, and plumage resemblances between the Australian honey-eaters and weavers may be significant. Some honey-eaters build domed nests, the dominant architectural form of weavers. There are parallel anatomical relationships between the nectar-feeders and finches of the nine-primaried American assemblage. In both of these cases the problem of deriving one specialized group from another is avoided by assuming that both come from a common unspecialized ancestor.

HONEY-EATERS (MELIPHAGIDAE).—Internal characters and the persistence of timalioid plumage patterns suggest a cisticoline origin for this timalioid family, though it is convergent with the Old World sylvioid group of nectar-feeders that may have displaced it from much of its former range. *Hylia* and *Pholidornis*, variously placed in the Ploceidae and Sylviidae, are unspecialized Meliphagids, wide-ranging in forested Africa. They may be combined with the specialized *Promerops* of the Cape region in the subfamily Promeropinae. This group is linked with the typical Australian subfamily (Meliphaginae), which it closely resembles, by the less specialized Oriental Aegithininae. All have the ectethmoid winged, foramen single, and lacrymal fused. The tongue is only weakly quadrifid in the Aegithininae.

AUSTRALIAN HONEY-EATERS (MELIPHAGINAE).—*Diagnosis:* Muscle pattern (figure 12) similar to that of the Cisticolinae in *Melidectes* and *Melipotes*, but *M7b* loses pinnate character in the typical, slender-billed forms. *M6* bifid (trifid and pinnate in *Philemon*), protractors *M1* and *M2* expanded. Bill un-notched, operculate, without rictal bristles. Tongue tubular, whipped out into long, quadrifid tip. Palate with central ridge often grooved and posterior ridge usually trifid. Ten-primaried nectar-feeders of the Australian Region. *Species dissected: Acrulocercus braccatus, Foulehaio carunculata, Melidectes fuscus, Meliphaga analoga, M. gracilis, M. versicolor, Melipotes gymnops, Myzanthe melanocephala, Myzomela cardinalis, M. melanocephala, M. sp., Philemon buceroides, Prosthemadera novaeseelandiae. Discussion:* The loss of the pinnate character of *M7b* in more typical meliphagids may be correlated with weaker adduction following stronger protraction (in *Acrulocercus, M2* crowds *M6* just as in starlings). Despite wide radiation in the Australian sanctuary, this subfamily was eliminated elsewhere. *Function: Philemon* (figured) is atypical, but its trifid *M6* (possibly quadrifid) suggests relationship to the Aegithininae and Estrildidae. In this and other specialized genera, vacuum for nectar-feeding is attained in a unique manner. The cross section A–A′ (also C) shows the grooved central ridge for closing the tubular section of the tongue, while pressure from the ridge of the lower mandible creates vacuum by a nibbling action observed in captive specimens. In *Melipotes* and *Prosthemadera* the central ridge is unspecialized. *Foulehaio, Myzomela, Prosthemadera,* and *Meliphaga* have *M4b* split to accommodate a large palatine salivary gland.



IORA~Aethorhynchus lafresnayei~ AEGITHININAE

HONEY-EATER~Philemon buceroides~ MELIPHAGINAE

AFRICAN WEAVER~Ploceus cucullatus~ PLOCEIDAE

AUSTRALIAN WEAVER~ Poephila guttata ~ESTRILDIDAE

FIGURE 12. Characters in honey-eaters and weavers.

AFRICAN HONEY-EATERS (PROMEROPINAE).—*Diagnosis:* Muscle pattern of *Promerops* is similar to that of the Meliphaginae (*M7b* parallel, *M6* bifid); the shorter-billed *Hylia* and *Pholidornis* have *M7b* pinnate as in the short-billed *Melidectes* and *Melipotes*. *Promerops* has the meliphagine trifid palatal boss. Tongue tubular with quadrifid tip in *Promerops;* grooved with truncate, quadrifid tip in *Hylia,* similar in *Pholidornis,* but tip not clearly quadrifid. Bill un-notched, long in *Promerops,* short in the others; operculate; without rictal bristles. *Promerops* and *Pholidornis* have rigid, scaly crown feathers, suggested by those of some Ploceinae, especially *Sporopipes*. Ten-primaried African nectar-feeders. *Species dissected: Hylia prasina, Pholidornis rushiae, Promerops cafer. Discussion: Pholidornis* is West African, *Hylia* widespread, both in forest; *Promerops* is confined to the Cape Region in ecological association with *Protea* flowers. The first two build pendant, roofed nests; that of *Promerops* is nearly roofed. *Gliciphila modesta* (one of the Meliphaginae of New Guinea) builds a pendant, roofed nest (Rand, 1942; 357).

ORIENTAL HONEY-EATERS (AEGITHININAE).—*Diagnosis:* Muscle pattern and other internal features (figure 12) as above with pinnate *M7b* (also *M7a* in *Aethorhynchus*), but nostril semi-operculate. *Aegithina* and *Erpornis* have *M6* bifid; *Aethorhynchus,* trifid and pinnate (like *Philemon*). Ten-primaried insect- and nectar-feeders of the Oriental Region. *Species dissected: Aegithina tiphia, Aethorhynchus lafresnayi, Erpornis xantholeuca. Discussion:* This timalioid group is not related to the pycnonotine Irenini. Though less specialized than African and Australian meliphagids, the semi-operculate nostril is close to that of the Australian *Manorina,* and the long tip of the tongue in *Aegithina* and *Aethorhynchus* shows an incipient quadrifid character. The whipped-out tongue of *Erpornis* is not clearly quadrifid, and the species is included here only until it can be checked thoroughly; it may be a babbler. *Function: Aethorhynchus* has a small, free lacrymal probably associated with forward vision in this prying group. The palate approaches that of the Ploceidae. The survival of this group in competition with the Oriental sylvioid nectar-feeders may hinge on its lack of specialization; except for the specialized *Promerops,* the same may hold for the African group.

WEAVERS.—Internal characters seem to confirm what Chapin (1917) and Delacour (1943b) suspected, that the Australian weavers originated independently of the African weavers. The Estrildidae seem, in fact, to have arisen from the Meliphaginae or Cisticolinae in Australia, while the Ploceidae arose from the Promeropinae or Cisticolinae in Africa. I am unable, on anatomical grounds, to agree with Chapin that the Viduinae are a subfamily of the Estrildidae; they seem to be a subfamily of the Ploceidae, parasitic on such estrildids as reached Africa and radiated throughout its grasslands. Their inability to reach Australia and their poorness in species suggest a relatively late origin from the Ploceidae.

WAXBILLS, MANNIKINS, GRASSFINCHES (ESTRILDIDAE).—*Diagnosis:* Muscle pattern (figure 12) derivable from that of the Cisticolinae, but adductors *M6* (trifid) and *M7* pinnate; palatal retractors, expanded, with large *M4* and complex *M3b* (as in Turdidae). Ectethmoid foramen double, lacrymal fused. Bill un-notched, broadly conical with nostril recessed below shield-like posterior border; rictal bristles virtually lacking. Tongue with ventral horn rolling inwards dorsally, frayed on sides and tip. Palate with lateral ridges compressed inward to fuse with central ridge, leaving posterolateral vaults. Ten-primaried Old World seed-eaters. *Species dissected: Estrilda angolensis, E. melpoda, E. nonnula, Lonchura castaneothorax, L. striata, Padda oryzivora, Parmoptila woodhousei, Pirenestes sanguineus, Poephila gouldiae, P. guttata, P. modesta, P. ruficauda, Pytilia afra, Sporopipes frontalis. Discussion:* The high origin of *M7* within the orbit and the trifid *M6* (quadrifid in the Ploceidae) are notable, as is the tendency for these adductors to have advanced insertions on the mandible. The double foramen, too, is not found in the Ploceidae. This group could logically have stemmed from the Cisticolinae. Both the Malurini and Estrildidae build similar domed nests in grass (neither woven nor pendant as in Ploceidae), lay similar eggs, and tend toward specialization in color of plumage—traits possibly reflecting a common ancestor. It is possible that the Australian weavers could have invaded Africa via Malaya because the grassland seed-niche there was open (the Ploceidae may have arisen as forest types); but the African grassland would not have been open to the Malurini because of competition with the Cisticolinae which were already there.

WEAVERBIRDS, WHYDAHS, ETC. (PLOCEIDAE).—*Diagnosis:* Muscle pattern (figure 12) similar to that of the Estrildidae, but *M6* quadrifid, *M7* shorter in both origin and insertion, and ectethmoid foramen single. Tongue not rolled and only the tip frayed out. Palatal ridges not fused and without posterolateral vaults. Bill un-notched without shield, semi-operculate, virtually without rictal bristles. Ten-primaried seed- and insect-eaters of the Ethiopian, Oriental, and Palaearctic regions. *Species dissected:* (Ploceinae) *Euplectes orix, E. progne, Malimbus nitens, M. sp., Ploceus bicolor, P. cucullatus, P. reichenowi;* (Viduinae) *Steganura paradisea, Vidua macroura, V. regia;* (Passerinae) *Dinemellia dinemelli, Passer domesticus, P. griseus. Discussion: Aethorhynchus* (Aegithininae) resembles the Ploceinae internally and externally, but each is considered a separate offshoot from the Cisticolinae. The internal (see *Diagnosis*) and external similarities suggest that the whydahs, etc. (Viduinae) have arisen from weavers (Ploceinae); in both there is an eclipse plumage, and young do not breed until the second year. The Viduinae are specific parasites of waxbills (Estrildidae), their young imitating those of that group in the marking of the mouth. *Anomalospiza* may belong to this group (Bannerman, 1949), its parasitization of members of the Cisticolinae paralleling that of some primitive neotropical cowbirds (Icteridae) which usually parasitize close relatives (Friedmann, 1929). *Dinemellia* is included in the subfamily Passerinae as a specialized rather than a primitive form, but this "lumping" may not be justified. Too few species have been dissected to consider seriously a detailed rearrangement of this complex group. The finely-woven retort-shaped nests of the Ploceinae may be an evolutionary elaboration on the clumsily-woven nests of *Cisticola,* that of *C. juncidis* approaching the retort shape. *Function:* Many weavers, particularly forest-dwellers, have weaker bills than the typical seed-eating forms.

THE AMERICAN NINE-PRIMARIED ASSEMBLAGE.—It seems particularly clear that the American nine-primaried families arose from the vireos (Vireoninae), a subfamily of the Monarchidae. On anatomical grounds, these primitive shrike-flycatchers appear to have given rise to insect-eating wood warblers (Parulinae) and fruit-eating tanagers (Thraupinae). The buntings (Emberizinae) apparently evolved from the Parulinae, and in turn gave rise to the blackbirds (Icteridae) and Galapagos finches (Geospizidae). The finches of the Pyrrhuloxiinae and Carduelinae and, on Hawaii, the highly adapted Drepanididae, apparently evolved from the tanagers. In addition, both warblers and tanagers independently produced nectar-feeders (Beecher, 1951b). Formerly these were included in a single family, the Coerebidae. Evidently the families of this assemblage radiated to fill the food-niches provided by flowering plants in the New World. The ectethmoid is usually winged, lacrymal fused, the single foramen becoming double in Parulidae.

VIREOS (VIREONINAE).—*Diagnosis:* Muscle pattern (figure 13) similar to that of the Monarchinae, but *M6* trifid, *M7a* with temporal slip pinnate, *M7b* parallel (except in *Vireo altiloquus* and *V. olivaceus*). Ectethmoid foramen large, single; lacrymal fused. Bill notched, semi-operculate with nasal and rictal bristles. Palate similar to that of the Monarchinae, tongue with bifid tip. Ten-primaried (tenth variable, ninth often long) insect-eaters of the New World. *Species dissected: Hylophilus decurtatus, H. hypoxanthus, H. olivaceus, H. poicilotis, Vireo altiloquus, V. flavifrons, V. griseus, V. olivaceus. Discussion:* Internal characters relate the vireos to the Monarchidae, but both these shrike-flycatcher groups are similar in behavior. Some monarchs occasionally nest in a horizontal fork like vireos. Plumage resemblances are less convincing; but the vireos have evidently been isolated from monarchs throughout the Tertiary, so close external resemblance cannot be expected. *M7b* is pinnate in only two species of vireos, but it is strongly pinnate in the Cyclarhini, which are strongly shrike-like. It is also pinnate in the Parulinae. The advance of *M3a* on the mediopalatine clasp is an assemblage character. *Hylophilus poicilotis* with pinnate *M6, M1,* and *M2* and un-notched bill is adapted to nectar-feeding, but its muscle pattern approaches that of the Cyclarhini.

SHRIKE-VIREOS (CYCLARHINI).—*Diagnosis:* Muscle pattern (figure 13) similar to that of *Hylophilus poicilotis* and *Vireo* but muscles more massive, *M1, M6,* and *M7* (including *M7b*) fully pinnate. Bill shrike-like; and horny palate relatively short,

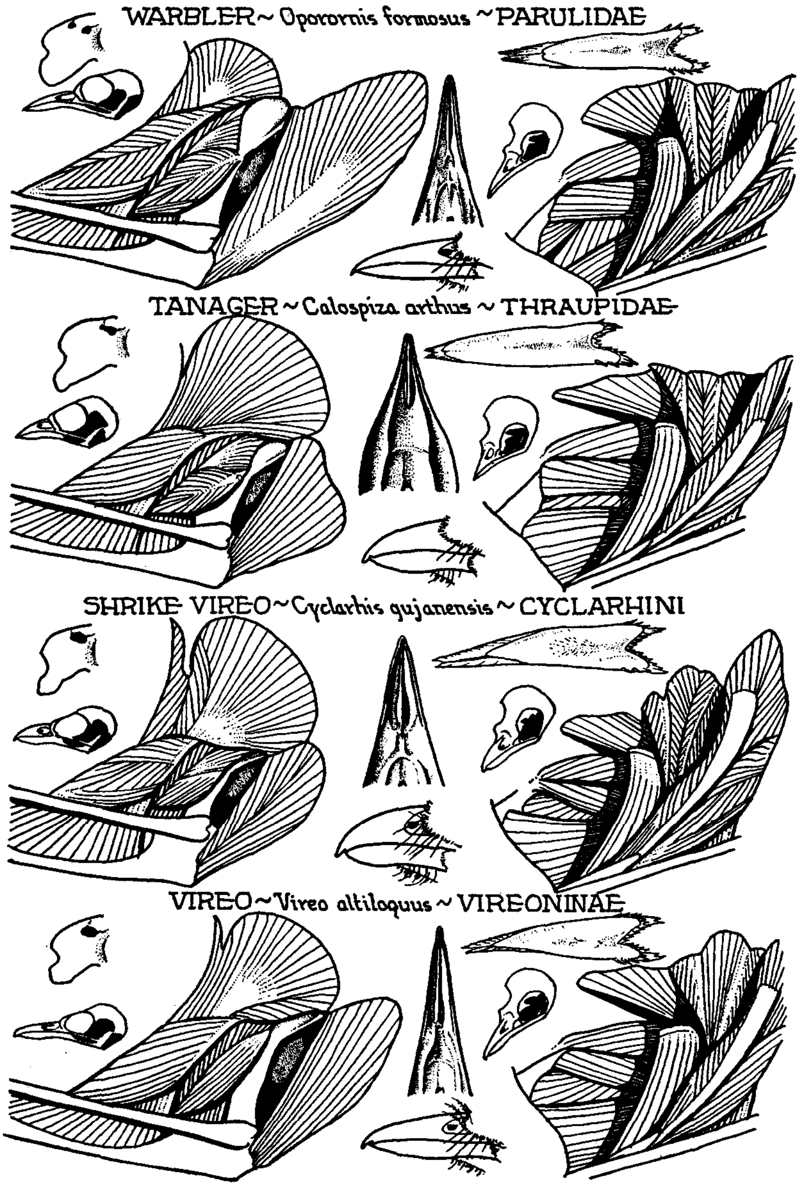


FIGURE 13. Characters in vireos, tanagers, and warblers.

narrow, and deep. *Species dissected: Cyclarhis gujanensis, Smaragdolanius pulchellus. Discussion:* This is a strongly shrike-like Neotropical group whose resemblance to the parallel Old World pachycephaline *Falcunculus* was shown by Naumburg (1925). It presumably includes *Vireolanius. Function:* Adductors and palatal retractors strongly developed as in other shrikes, but details betray vireo origin.

WARBLERS, BUNTINGS, ETC. (PARULIDAE).—The efficiency of the warblers in occupying insect-, fruit-, and nectar-niches is further reflected in the origin of the buntings from them; and in turn, the evolution of the adaptable blackbirds and Galapagos finches from the buntings.

WOOD WARBLERS (PARULINAE).—*Diagnosis:* Muscle pattern (figure 13) similar to that of the Cyclarhini, but less massive and *M3a* farther advanced. Ectethmoid foramen double or constricted; lacrymal fused. Bill un-notched (usually), narrow or broad, semi-operculate, with rictal and sometimes nasal bristles. Palate with conspicuous posterior ridge, lateral ridges disappearing posteriorly. Tongue with bifid tip. Nine-primaried (tenth small, rotated dorsally) insect- and nectar-feeders of the New World. *Species dissected: Basileuterus leucoblepharus, Dendroica aestiva, D. coronata, D. discolor, D. fusca, D. palmarum, D. pensylvanica, D. petechia, D. tigrina, D. virens, Geothlypis trichas, Granatellus venustus, Icteria virens, Mniotilta varia, Myioborus brunneiceps, Oporornis formosus, O. philadelphia, Parula americana, P. pitiayumi, Protonotaria citrea, Seiurus aurocapillus, S. noveboracensis, Setophaga ruticilla, Wilsonia pusilla. Discussion:* Broad-billed flycatcher-warblers like *Setophaga, Myioborus,* and *Basileuterus* appear to be primitive with parallel *M7a* and strong rictal and nasal bristles—in all of which they recall monarchs. *Function:* Wood warblers are the most slender-billed oscines with fully pinnate adductors. The efficiency of the pinnate adductors has permitted the reduction in mass of both muscle and bone in the head region, and this, I think, is responsible for their adaptive success. Segregation into adaptive tribes, aside from the Coerebini, calls for further anatomical study.

WARBLER HONEY-CREEPERS (COEREBINI).—I have elsewhere (Beecher, 1951b) given reasons for sinking the family Coerebidae and dividing its members between the warblers and tanagers. The present tribe agrees with warblers in all internal and external characters. *Species dissected: Ateleodacnis leucogenys, Coereba flaveola, Conirostrum rufum. Function:* Protractors *M1* and *M2* are expanded, an adaptation for prying in flowers. The tip of the tongue is whipped out.

BUNTINGS (EMBERIZINAE).—*Diagnosis:* Muscle pattern (figure 14) similar to that of the Parulinae, but the insertion of the median slip of *M6* advanced on the mandible at the expense of pinnate *M7b*. Large *M4a* overlying *M4b*. Ectethmoid foramen double or constricted; lacrymal fused (except in *Phrygilus* and *Lophospingus*). Bill un-notched, conical, semi-operculate, with rictal bristles. Palate with parallel anterior and lateral ridges terminating in a posterior boss for occlusion with the tomia of the lower mandible. Tongue slender, tapering to a short, bifid tip. Nine-primaried seed- and insect-eaters of the New and Old Worlds. *Species dissected: Amaurospiza concolor, Ammodramus savannarum, Arremon flaviventris, Atlapetes pileatus, Calamospiza melanocorys, Calcarius lapponicus, Chondestes grammacus, Coryphospingus pileatus, Cyanocompsa cyanea, Emberiza flaviventris, Guiraca caerulea, Junco hyemalis, J. oregonus, Melospiza georgiana, M. lincolni, M. melodia, Oryzoborus angolensis, Passerculus sandwichensis, Passerella iliaca, Passerina amoena, P. ciris, P. cyanea, P.*

leclancheri, Phrygilus fruticeti, P. unicolor, Pipilo chlorura, P. erythrophthalmus, P. fuscus, P. ocai, Plectrophenax nivalis, Pooecetes gramineus, Poospiza erythrophrys, P. nigro-rufa, Spizella arborea, S. passerina, S. pusilla, Zonotrichia albicollis, Z. capensis, Z. coronata, Z. leucophrys. Discussion: The North American buntings examined are specialized, with the insertion of *M6* advanced and the exoccipital inflated—and all except *Spizella pusilla* and *S. passerina* (which may not be close to *S. arborea*) tend to have a long hind claw for scratching. A primitive Neotropical group, containing the genera *Coryphospingus, Passerina, Phrygilus,* and *Poospiza,* has *M6* not advanced (unlike figure 14), approaching the paruline pattern. The insertion of *M6* is somewhat advanced in *Arremon* and *Ammodramus* as in the Holarctic or Palaearctic genera *Calcarius, Emberiza,* and *Plectrophenax.* All of these are likewise primitive in having the exoccipital uninflated or but slightly inflated, and none scratch for food. The American blackbirds are believed to have arisen from primitive Andean types like *Phrygilus* with the insertion of *M6* not advanced, thus similar to that of the cowbirds. *Phrygilus* also has plumage patterns paralleling those of the Icteridae. The advanced insertion of *M6* may be an adaptation for cracking seeds against the central boss.

Probably related to these Andean types are the primitive, mainly black "sporophiline" finches (Beecher, MS) which seem to be convergent with the Pyrrhuloxiinae, especially in bill form. *Species dissected: Catamenia analis, Sporophila aurita, S. moreletti, S. nigro-rufa, Tiaris bicolor, T. canora, T. olivacea, Volatinia jacarini. Oryzoborus* and *Cyanocompsa* (probably part of this complex) have the insertion of *M6* advanced. In *Catamenia* and *Sporophila,* as well as in *Amaurospiza,* the insertion is slightly advanced. The palate and external features suggest that *Melanospiza richardsonii* may belong here and may have come from the same stock as the Geospizidae.

GALAPAGOS FINCHES (GEOSPIZIDAE).—*Diagnosis:* Muscle pattern (figure 14) as in *Phrygilus* with the insertion of *M6* not advanced, *M7b* pinnate. Slot-like ectethmoid foramen single or double, lacrymal fused. Bill narrow, massive to slender, semi-operculate, with rictal bristles reduced. Palate emberizine, but with slight relief; tongue emberizine. *Species dissected: Camarhynchus parvulus, C. prosthemelas, Certhidea salvini, Geospiza assimilis, G. conirostris, G. fortis, G. fratercula, G. scandens, G. strenua. Discussion:* In the palate and externally *Melanospiza richardsonii* (Santa Lucia) is similar to *Geospiza,* and both may have been derived from a widespread Caribbean form like *Tiaris.* The Pliocene Gulf Stream could have rafted the ancestor of *Geospiza* through the Panama Water Gap to the Galapagos almost as readily as it might be airborne. I agree with Sushkin (1925) that *Certhidea* is an insect-eating Galapagos finch rather than a warbler. Adaptive radiation also has produced the nectar-feeding *G. scandens,* insect-eating *Camarhynchus,* and fruit-eating *G. crassirostris.*

AMERICAN BLACKBIRDS (ICTERIDAE).—Muscle pattern (figure 14) similar to above and to Andean Emberizinae but *M7b* complexly pinnate (not shown in Beecher, 1951a). Ectethmoid foramen constricted; lacrymal fused (except in *Sturnella* and *Pezites*). Bill un-notched,

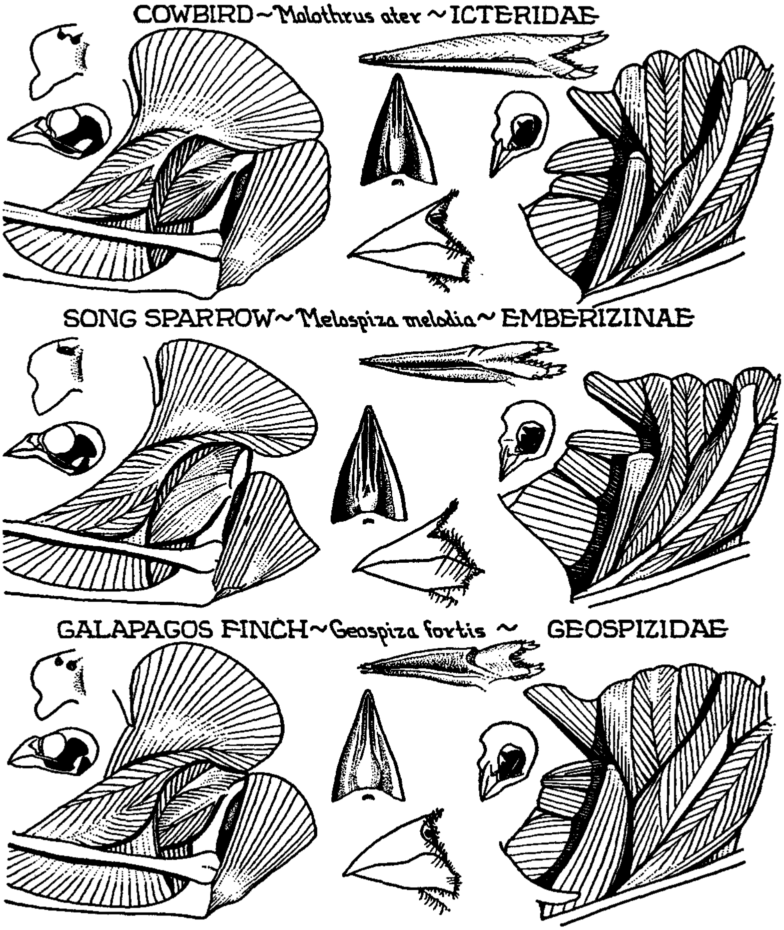


FIGURE 14. Characters in buntings, Galapagos finches, and American blackbirds.

conical to slender, semi-operculate (operculate in *Amblycercus*), generally without rictal bristles. Palate varying on emberizine pattern. Tongue similar to that of *Phrygilus* but often whipped out as an adaptation for flower-feeding (orioles, oropendolas, others). Nine-primaried New World seed-, fruit-, and insect-eaters. *All 38 genera* (including *Spiza*) *dissected. Discussion:* Bill un-notched, without rictal bristles, and the capacity to expand the protractors *M1* and *M2*, may have pre-adapted this group for radiation into virtually all the food-niches open to passerine birds in the New World.

TANAGERS, GROSBEAKS, SISKINS (THRAUPIDAE).—The tanagers seem to have arisen from vireos with parallel *M7b* and with specialization of plumage color similar to that noted in the Cyclarhini. Two subfamilies of finches, the Pyrrhuloxiinae and the Carduelinae, evolved from the tanagers in the New World with little disjunction and in a parallel fashion. In addition, the tanagers gave rise to a tribe adapted for feeding on nectar (the Dacnini, formerly included in the Coerebidae) and apparently provided the ancestral stock which radiated in Hawaii to produce the nectar-, fruit-, insect-, and seed-eating drepanidids.

TANAGERS (THRAUPINAE).—*Diagnosis:* Muscle pattern (figure 13) similar to that of the vireos but *M6* always pinnate, *M7* (not *M7b*) progressively becoming pinnate in advanced forms so that *Tanagra* is close to the Carduelinae in this and in the advance of the insertion of the median slip of *M6* on the mandible (Beecher, 1951b). Bill notched, generally broad, with rictal bristles; nostril semi-operculate or feathered. Ectethmoid foramen usually single, lacrymal fused (free in some species of *Thraupis* and *Calospiza*). Palate with central ridge short, posterior ridge almost lacking, and lateral ridges continuous posteriorly. Tongue similar to that of the vireos. Nine-primaried New World fruit- and nectar-feeders. *Species dissected:* (unspecialized, as figured) *Calospiza arthus, C. chilensis, C. cyanoptera, C. desmaresti, C. guttata, Ramphocelus bresilius, R. carbo, Thraupis bonariensis, T. cyanocephalus, T. palmarum, T. virens;* (approaching Carduelinae with advancing insertion of *M6*) *Chlorophoneus cyanea, Habia gutturalis, H. rubica, Nesospingus speculiferus, Stephanophorus diadematus, Tanagra chlorotica;* (approaching Pyrrhuloxiinae with insertion of *M6* not advanced) *Cissopis leveriana, Hemispingus frontalis, Hemithraupis guira, H. sp., Spindalis zena. Discussion:* The variability of tanagers parallels that of wood warblers, reflecting enormous adaptive potential, but the heavier bills and musculature suggest the crushing function of fruit-eaters.

SWALLOW TANAGERS (TERSININI).—*Tersina viridis* is anatomically close to *Calospiza,* and is a broad-headed fruit-eater nesting in holes in the ground. I regard it as a tribe of the tanagers.

PLUSH-CAPPED TANAGERS (CATAMBLYRHYNCHINAE).—In the absence of anatomical specimens this group is tentatively presumed different enough to merit subfamily status.

TANAGER HONEY-EATERS (DACNINI).—This tanager element of the "Coerebidae" is treated here as a tribe, convergent with the warbler tribe Coerebini. *Species dissected: Chlorophanes spiza, Cyanerpes cyanea, Dacnis cayana, Diglossa plumbea, Euneornis campestris, Hemidacnis albiventris, Iridophanes pulcherrima. Function:* The generally longer, un-notched bills are adapted for probing deeper flowers than the bills of the Coerebini. Apparently this is done without prying, since *M1* and *M2* are weak.

CARDINAL GROSBEAKS (PYRRHULOXIINAE).—*Diagnosis:* Muscle pattern (figure 15) massive with *M1, M6,* and *M7* (not *M7b*) pinnate. Oval ectethmoid foramen single, lacrymal fused. Bill massive, un-notched, generally with rictal bristles; nostril non-operculate. Palatal ridges continuous posteriorly, tongue cylindrical. Nine-primaried New World seed-, fruit-, and bud-eaters. *Species dissected: Loxigilla violacea, Melopyrrha nigra, Pheucticus ludovicianus, P. melanocephalus, Pitylus grossus, Pyrrhuloxia cardinalis, P. sinuata, Saltator atriceps, S. atricollis. Discussion:* The first two species are here considered convergent with the sporophiline group (Emberizinae) but may really belong in that group. The grosbeaks emerge so gradually out of the variable tanagers that even anatomically it is difficult to draw a

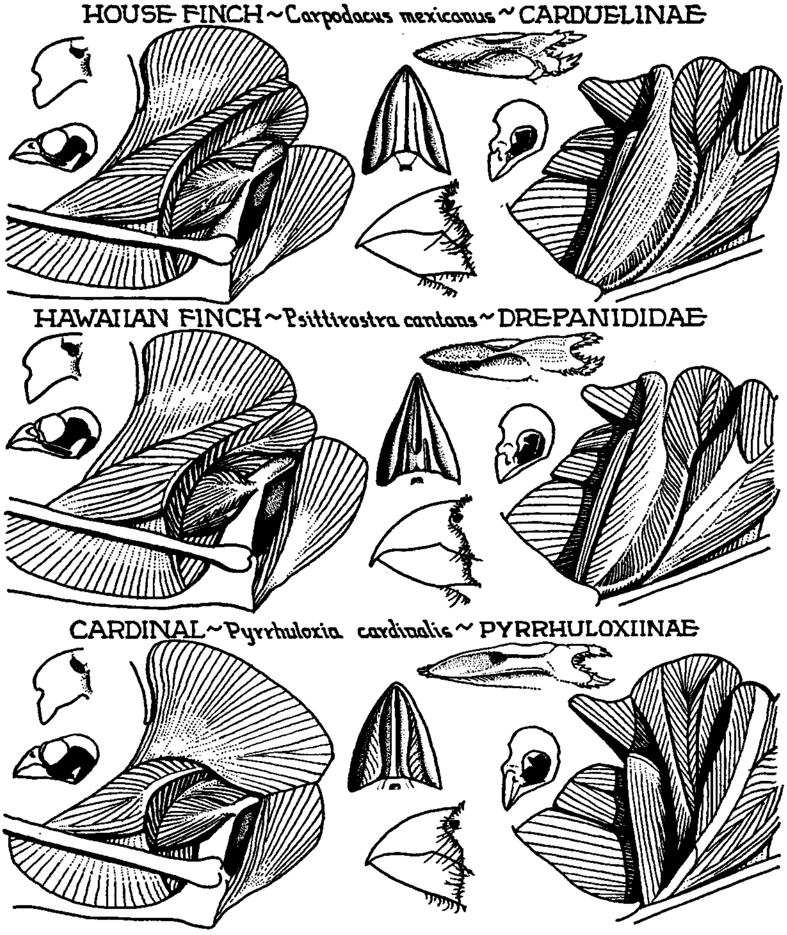


FIGURE 15. Characters in pyrrhuloxine, cardueline, and drepanidine finches.

boundary line. I agree with Mayr and Amadon (1951) that *Richmondena* is congeneric with *Pyrrhuloxia*. *Function:* The massive bill and musculature are the culmination of the crushing function suggested in the tanagers.

LINNETS, SISKINS, ETC. (CARDUELINAE).—*Diagnosis:* Muscle pattern (figure 15) similar to that of the tanager *Stephanophorus; M1, M6,* and *M7* (not *M7b*) pinnate, insertion of massive median slip of *M6* advanced on the mandible. *M3b* complex as in the Turdidae. Single ectethmoid foramen slot-like, lacrymal fused. Bill un-notched, conical, with rictal bristles; nostril feathered. Palate as in the Pyrrhuloxiinae but with short ridges between the central and lateral ones posteriorly. Tongue cylindrical, its horny sheath with edges nearly meeting in the mid-line dorsally. Nine-primaried fruit-, bud-, and seed-eaters of the New and Old Worlds. *Species dissected: Carduelis carduelis, Carpodacus mexicanus, C. purpureus, Coccothraustes coccothraustes, Fringilla coelebs, Hesperiphona vespertina, Leucosticte griseonucha, Loxia leucoptera, Loximitris dominicensis, Pinicola enucleator, Pyrrhula*

pyrrhula, Spinus pinus, S. tristis. Discussion: Sushkin's (1925) recognition of the subfamily Fringillinae for the chaffinch (*Fringilla coelebs*) is not supported; the modification of the bony palate from the cardueline pattern is the result of the enlarged palatine salivary gland probably in adaptation to more frugivorus habits. Mayr and Amadon's (1951) proposal to apply this name to the present group is not adopted because the term, Fringillidae, has been used for a polyphyletic family. Logically, it would be better to suppress the term and its root in formal taxonomic papers and to recognize the several finch groups as subfamilies of the warblers and tanagers as outlined above. I am not in favor of changes of family names on a purely nomenclatorial basis. Simpson (1945: 30) has pointed out that the International Rules do not call for observance of priority in forming supergeneric names. Had I constructed the names of the higher categories from type genera chosen by priority, the superfamily Timalioidea would become Passeroidea, the family Thraupidae would become Fringillidae, the subfamily Carduelinae would become Fringillinae. It would be impossible to use Monarchidae as a new family name, reducing older families to subordinate positions. Each of these changes would result in a name with confusing connotations and would serve no useful purpose whatever. In the case of the Monarchidae, taxonomy (so interpreted) would stand in the way of doing what must be done. I agree with Simpson that taxonomic principles for higher categories should be guided by general usage, common sense, and technical convenience. *Function:* The massive *M6*, with its advanced insertion in all genera except *Loxia*, insures maximum adduction. The hawfinches have posterolateral palatal vaults occluding with the posterior part of the tomia of the lower mandible in a mortar-and-pestle function.

HAWAIIAN HONEYCREEPERS, FINCHES (DREPANIDIDAE).—From what has been said of the fruit-, nectar-, and seed-adapted groups of the Thraupidae, we might predict the result of uncontested colonization of the Hawaiian Islands by an unspecialized tanager similar to *Piranga*. At any time between the Eocene and Pliocene such an ancestral form could have been rafted by the Gulf Stream through the Panama Water Gap and carried to Hawaii, though it was more likely airborne. If the islands emerged in the Pliocene (Stearns, 1946), radiation into the food niches could presumably take place rapidly in the virtual absence of competition, the special bill forms of the nectar-feeders reflecting the peculiarities of the Hawaiian flora. A generalized tanager stock similar to *Piranga* could evolve in two directions. The bill could become lengthened to produce nectar-feeders and probers (the counterpart of the Dacnini) or thickened for feeding on seeds and buds (the counterpart of the Carduelinae). Amadon (1950b) divides the Drepanididae into two such groups.

HAWAIIAN FINCHES (PSITTIROSTRINAE).—*Diagnosis:* Muscle pattern (figure 15) like that of *Carpodacus*, but more massive. Other internal features also similar, but central palatal ridge short as in tanagers, rictal bristles further reduced. *Species dissected: Psittirostra cantans, P. psittacea. Discussion:* The striking similarity of the Hawaiian finches to the cardueline finches in all but plumage suggests parallel development from isolated segments of the thraupine stock.

HAWAIIAN NECTAR-FEEDERS (DREPANIDINAE).—*Diagnosis:* Muscle pattern (Beecher, 1951b) like that of tanager nectar-feeders (Dacnini), but the longer, heavier bills and large *M1* and *M2* indicate prying. *Species dissected: Himatione sanguinea, Vestiaria coccinea. Discussion: Himatione* shows advanced insertion of the median slip of *M6* as in tanagers, a feature culminating in the condition in *Psittirostra.* I examined *Hemignathus lucidus* briefly and, without making direct comparison, thought it like *Himatione* and *Vestiaria.* But Amadon says it is close to *Psittirostra,* and I cannot say he is incorrect.

THE TIMALIID ASSEMBLAGE.—Although the term "assemblage" is usually applied to a group of families in this paper, it is here used to emphasize the adaptive potential of a single family. The existence of shrike-babblers, lark-babblers, and tit-babblers suggests the unprecedented number of adaptive "tribes" which evolved from it. These cannot be defined anatomically without dissecting many more species than exist in present spirit collections. The Timaliidae might be considered the stem group of the Timalioidea, since the Cisticolinae (somewhat more primitive) is a transitional group, as much a subfamily of this family as of Sylviidae. Revision by Delacour (1946).

BABBLERS (TIMALIIDAE).—*Diagnosis:* Muscle pattern (figure 8) similar to that of the Cisticolinae but outer slip of bifid *M6* longer than inner and *M7* with very high origin inside the orbit. Ectethmoid winged, foramen single, lacrymal fused. Bill notched, operculate or semi-operculate, with rictal bristles. Palate and tongue similar to those of the Cisticolinae. Ten-primaried Old World insect- and fruit-eaters. *Species dissected: Alcippe nipalensis, A. sp., Chrysomma sinensis, Cinclosoma ajax, Crateroscelis murinus, Daphoenositta miranda, Eupetes coerulescens, Garrulax leucolophus, G. vassali, Laniellus leucogrammicus, Leiothrix argentauris, Leioptila capistrata, Macronus rubricapilla, M. sp., Malia grata, Neomixis tenella, Orthonyx spinicauda, Pellorneum ignotum, P. tickelli, Picathartes oreas, Pomatorhinus montanus, Psophodes olivaceus, Siva cyanuroptera, S. strigula, Stachyris chrysaea, S. nigriceps, Turdinus brevicaudatus, T. crispifrons. Discussion: Picathartes* is unusual in its trifid pinnate *M6,* but I now agree with Delacour and Amadon (1951) as to its timaliine status. *Malia* clearly belongs here rather than with bulbuls or thrushes. *Cinclosoma* and *Eupetes* are slender-billed, narrow-skulled terrestrial forms with free lacrymal and, probably, forward vision; in them the pinnate character of *M7b* has virtually disappeared as it has in many honeyeaters and in the true wrens. *Leioptila capistrata,* reported by Deignan (1945) as investigating blossoms, has a tongue partially adapted to nectar-feeding. *Laniellus* of Java is a timaliine shrike; *Daphoenositta* of New Guinea is a timaliine tree creeper. Since the Laniidae and Sittidae are of timalioid origin, these attempts of Timaliidae to fill their niches in isolated regions are not strange. In fact it seems almost certain that many Australian forms which ornithologists have tried to link with groups occupying the same adaptive niche elsewhere (e. g. *Climacteris*, *Neositta*) are Timaliidae.

THE PIPIT, LARK, PARROT-BILL ASSEMBLAGE.—The pipits and larks seem to be parallel timalioid families arising from the Cisticolinae with the loss or reduction of the tenth primary and possessing plumage counterparts in the Monarchinae—a group of similar origin but different niche. *Alauda* and *Anthus* resemble *Cisticola* in their streaked pattern; *Eremophila* resembles *Motacilla*, *Rhipidura*, and *Platysteira* in recognition pattern. All four groups habitually wag or open and close the tail. The parrot-bills are basically similar to larks and pipits in muscle pattern, bill, palate, tongue, and (*Panurus*) reduction of the tenth primary. All have the ectethmoid winged, foramen single, and lacrymal fused.

PIPITS, WAGTAILS (MOTACILLIDAE).—*Diagnosis*: Muscle pattern (figure 16) similar to that of the Cisticolinae but *M6* becoming trifid, *M3a* advancing its insertion on the mediopalatine clasp, and the rather massive *M7* advancing its insertion on the mandible. Bill weak, slightly notched, with the culmen abruptly arched above the semi-operculate nostril; rictal bristles present. Palate similar to that of *Cisticola* but tongue trough-like, quadrifid at tip. Nine-primaried (ninth elongate) world-wide insect- and seed-eaters. *Species dissected: Anthus hodgsoni, A. pratensis, Motacilla alba, M. citreola, M. ocularis. Discussion: M. citreola* is very thin-billed, and its loss of pinnate character in *M7b* illustrates the same adaptive situation noted in Meliphagidae.

LARKS (ALAUDIDAE).—*Diagnosis:* Muscle pattern (figure 16) similar to that of the Motacillidae but *M6* bifid, *M3a* not advanced, *M4* and *M7* massive, the latter pinnate in all parts. Long postorbital process fused to suprameatic process. Bill un-notched, slender to conical with feathered nostril and rictal bristles. Palate as above but central ridge meeting posterior one in forms with a shorter bill. Tongue similar but with truncate, quadrifid tip. Ten-primaried (tenth reduced, ninth elongate) world-wide seed- and insect-eaters. *Species dissected: Alauda arvensis, Calandrella minor, Eremophila alpestris, Galerida cristata, Melanocorypha yeltoniensis, Mirafra assamicus. Discussion:* The larks seem to have originated from the Cisticolinae close to the pipits, monarchs, and parrot-bills. *Function:* Meinertzhagen (1951) observes that larks swallow seeds whole with grit, noting that the thick-billed *Rhamphocorys* does not have a very powerful "bite." Notably missing is the angulated commissure which in seed-cracking finches aligns the tomia or cutting edges of the bill more nearly at right angles to the pull of the palatine retractors so that they can assist the adductors. The weakness of *M6* in larks is compensated for by the intrusion of massive *M7* into the orbit, and the fusion of the postorbital and suprameatic processes may simply provide greater surface for its origin. The peculiar, scutellated tarsus of this group is regarded as a unique specialization and not accorded much weight. Apparently some members (e. g. *Eremophila*) have lost the tenth primary.

WREN-TIT, PENDULINE TIT, PARROT-BILL (PARADOXORNITHIDAE).—Delacour's (1946) proposal that the Wren-tit (*Chamaea*) is close to the parrot-bills is supported by internal characters, but I prefer to recognize the Paradoxornithidae as a family rather than reduce the group to a tribe (Chamaeini) of the Timaliidae. It may be practicable to recognize two subfamilies—the Paradoxornithinae for the parrot-bills and wren-tit and the Aegithalinae for the Bush Tit (*Psaltriparus*) and the Penduline Tit (*Aegithalos*). (cf. Mayr and Amadon, 1951).

PARROT-BILLS (PARADOXORNITHINAE).—*Diagnosis:* Muscle pattern (figure 16) and other internal features similar to those of the Alaudidae, especially in *Suthora*, but post-orbital process short. Bill un-notched, thin in *Chamaea* to parrot-like in *Paradoxornis*, the curved upper mandible notably heavy, with rictal bristles; nostril non-operculate, feathered (*Chamaea* semi-operculate, unfeathered). Palate with anterior and posterior ridges separate in *Chamaea*, fused in parrot-bills, but the posterior ridge trifid posteriorly in all. Tongue long in *Chamaea*, short and truncate in parrot-bills but always quadrifid at tip. Ten-primaried Old World insect- and seed-eaters represented by *Chamaea* in the New World. *Species dissected: Chamaea fasciata, Panurus biarmicus, Paradoxornis unicolor, Suthora verreauxi. Discussion:* The generic variations are on a gradient, and there is no doubt of the homogeneity of the group. As in larks, a lack of angulation in the commissure might prevent evolution of a true finch type, and traces of the black recognition pattern in parrot-bills suggest relationship with larks. They may belong in the same assemblage, but are here regarded as distinct adaptive branches arising from the Cisticolinae. *Function:* the parrot-bills are ecologically associated with great reed beds, and the bill is used particularly for tearing reeds apart to obtain insects (Caldwell and Caldwell, 1931).

LONG-TAILED AND BUSH TITS (AEGITHALINAE).—*Diagnosis:* Similar to above but *M5* pinnate and *M3a* advancing its insertion on the mediopalatine clasp. *Species dissected: Aegithalos caudatus* and *Psaltriparus minimus. Discussion:* In the habit of building roofed, pendant nests, unlike the cup-shaped nests of the Paradoxornithinae, these birds apparently converge with the Remizinae of the true titmice.

WREN, CREEPER, TITMOUSE ASSEMBLAGE.—These families have the protractors *M1* and *M2* expanded for bill prying, and seem to stem from each other in the sequence: Troglodytidae—Certhiidae—Sittidae—Paridae. *M7b* might be considered parallel but not in the same sense as in Sylvioidea. In the wrens and creepers with their slender bills this muscle seems to be just at the point of entirely losing its pinnate character, as has occurred in slender-billed species of

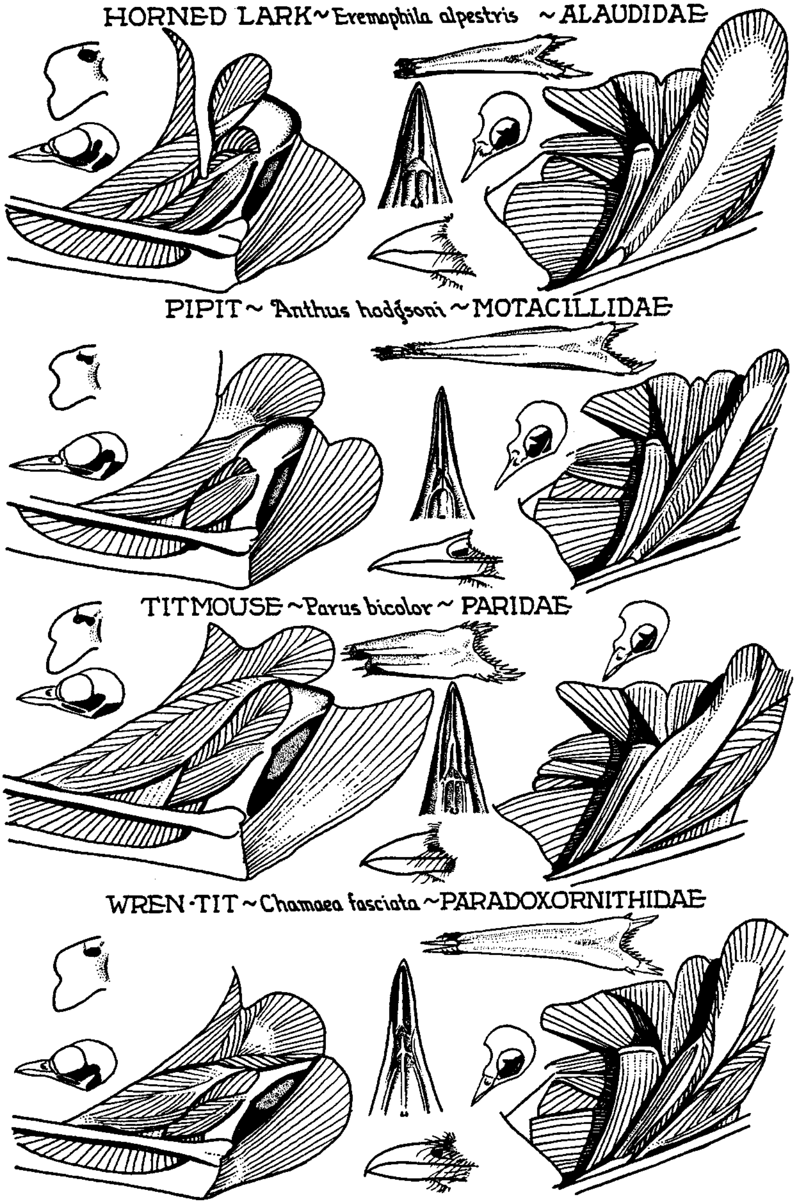


FIGURE 16. Characters in wren-tits, titmice, pipits, and larks.

Timaliidae and Meliphagidae (below). If so, according to Dollo's Law (Gregory, 1936), power would need to be re-acquired in a different way in the derived thicker-billed Sittidae and Paridae. It happens that in members of these latter families the fibers of *M7b* insert on a broad aponeurosis that is apparently the functional equivalent of a pinnate *M7b*, possibly the substitution product of new gene loci. In designating this assemblage as timalioid, I have been influenced by the split *M4b* (never found in Sylvioidea), horny palate (as in the assemblage above), and timaliid plumage type. The nervousness and habit of carrying the tail over the back would be weak evidence alone but tend to support the verdict of the other characters—along with grassland, desert, and brush habitat—that Troglodytidae and Malurini (Australian wrens) arose independently from the Cisticolinae. Competition with these other groups in the Old World could have largely eliminated the Troglodytidae there, while the open niches of the New World could have permitted wide radiation. The families of this assemblage are primarily hole nesters or dome-nest builders.

WRENS (TROGLODYTIDAE).—*Diagnosis:* Muscle pattern (figure 17) similar to that of the Malurini but *M7b* not clearly pinnate. Ectethmoid plate truncate and falling short of zygoma as in Malurini; foramen single, lacrymal fused. Tongue slender, with quadrifid tip. Palate with slight vault between central and posterior ridges in *Troglodytes;* these ridges continuous in *Heleodytes.* Bill slender, generally un-notched, operculate, without rictal bristles. Ten-primaried insect-eaters of the New World and the northern parts of the Old World, with streaked or barred plumage. *Species dissected: Cistothorus stellaris, Heleodytes fasciatus, Telmatodytes palustris, Troglodytes aedon, T. musculus. Function:* Narrow interorbital distance, taken with the short ectethmoid and lack of rictal bristles, suggests unusual forward vision in wrens, which feed in close quarters where lateral vision as used in "rapid peering" may be ineffective.

CREEPERS (CERTHIIDAE).—*Diagnosis:* Muscle pattern (figure 17) similar to that of the wrens but greater expansion of protractors *M1* and *M2.* Other internal characters as in wrens. Bill similar but decurved, un-notched. Tongue still more slender than that of a wren, quadrifid. Palate with posterior ridge "open" but in many ways intermediate between that of the wrens and that of the titmice. Ten-primaried tree-creepers, mainly Holarctic, with streaked plumage. *Species dissected: Certhia familiaris. Discussion: Certhia* with its stiffened tail feathers is apparently the most specialized form. *Rhabdornis, Salpornis,* and *Tichodroma* are considered primitive members of the group, but *Climacteris* is believed to be an endemic Australian

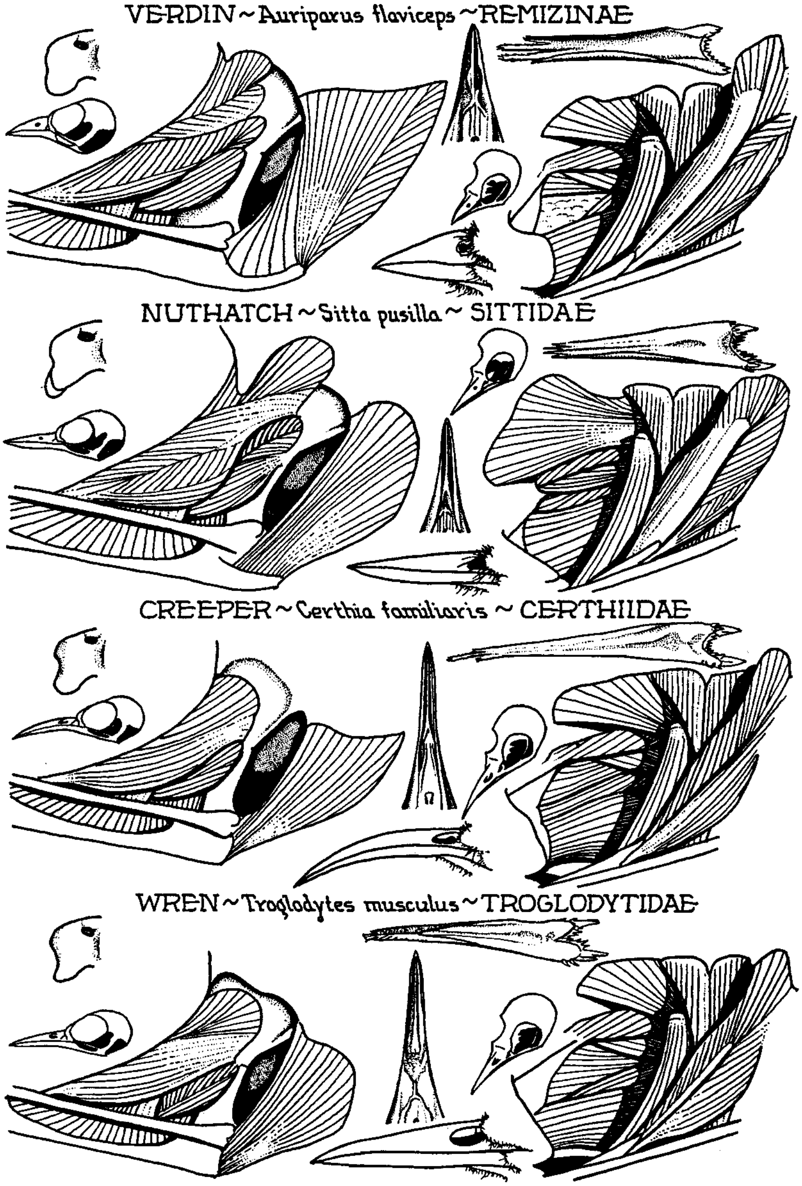


FIGURE 17. Characters in wrens, creepers, nuthatches, and verdins.

timaliid genus. Muscle pattern, modifications for forward vision, slender bill, and plumage seem to link the creepers to the wrens, and the wall-creeper *Tichodroma* suggests a transition between creepers and nuthatches. *Function:* The slender bill seems to act as a curved forceps for probing bark-crannies "roofed" from the weather, and the prying musculature is probably as strong as the bill structure will stand.

NUTHATCHES (SITTIDAE).—*Diagnosis:* Muscle pattern (figure 17) advanced over that of the Certhiidae, with protractor *M1* partly pinnate and *M2* expanded over the interorbital septum, *M3b* slightly advanced, *M4a* enlarged, *M7* pinnate, except *M7b* which is covered by an aponeurosis. Other internal characters similar to those of the Certhiidae but lacrymal free, reaching zygoma, bill slightly recurved with rictal bristles; nostril non-operculate. Tongue quadrifid. Palate similar to that of the Paridae. Ten-primaried trunk-foraging birds of world-wide distribution. *Species dissected: Sitta canadensis, S. frontalis, S. pusilla. Discussion: Hypositta* (see above) seems to be a vangid; *Neositta* and *Daphoenositta* are believed endemic timaliid genera of the Australian region. Because of adaptive changes, it is not certain that this group stems from Certhiidae. The palate, tongue, and plumage in *Tichodroma* suggest at least a common stock. *Function:* In addition to its prying function, the enormous *M2*, so like that of woodpeckers, may oppose the advanced *M3b* to snub the palate from both directions for a shock-absorbing function in hammering. The free lacrymal reaches the zygoma but may be moved aside for clearer vision at the tip of the bill.

TITMICE (PARIDAE).—*Diagnosis:* Muscle pattern (figure 16) similar to that of the Sittidae but *M2* less expanded, adductors more massive. Ectethmoid truncate, foramen becoming double (pinched); lacrymal fused. Bill un-notched, short, stout, with few rictal bristles; nostril non-operculate, feathered. Tongue short with truncate, quadrifid tip. Palate similar to that of *Sitta* but with flatter relief. Ten-primaried insect- and seed-eaters of world-wide distribution, plumage similar to that of the Sittidae. *Species dissected: Aegithaliscus annamensis, A. concinnus, Melanochlora sultana, Parus atricapillus, P. bicolor, P. carolinensis, P. gambeli, Sylviparus modestus. Discussion: Sylviparus* is typical despite its thin bill. *Function:* Adduction is greatly strengthened, and the broad ectethmoid suggests less forward vision than in *Sitta*.

PENDULINE TITS (REMIZINAE).—*Diagnosis:* Muscle pattern (figure 17) similar to that of the Paridae but protractors expanded (*M1* pinnate); *M4b* split to accommodate a large palatine salivary gland as in nectar-feeders. Ectethmoid foramen single, bill conical, without rictal bristles. Palate with boss at point of fusion of central and posterior ridges; tongue elongate but quadrifid at tip. Ten-primaried insect-, fruit-, and (I predict) nectar-feeders of world-wide distribution. *Species dissected: Anthoscopus sp., Auriparus flaviceps. Discussion:* Birds of this subfamily of Paridae are adapted for prying (Lorenz, 1949), and the pendant nest (convergent with Aegithalinae) culminates in the gauze-like bag of the African genus *Anthoscopus.*

EVOLUTIONARY IMPLICATIONS OF OSCININE RELATIONSHIPS

Comparison with Other Classifications.—Reviews of previous oscinine classifications by Newton (1893–1896) and Stresemann (1927–1934) show that earlier authors could not agree even as to which of the 60-odd families were generalized and which specialized. Few ornithologists appeared to realize that a linear series is no classification at all. Evolution is basically a process of divergence, and those who judged the thrushes, crows, or finches to be the most specialized groups were each right and each wrong. In a branching phyletic tree—the simplest expression of relationships so far as they may be inferred from morphology—all three, equally, are terminal groups. Lacking a phylogenetic tree, there was no classification, only a list of families. Modern ornithologists often show real insight into the relationships of these families, however, and Mayr and Amadon (1951) do a great service in "laying the cards on the table."

The present classification is based on the bird as a whole so far as we know it. Far from cutting across external characters (except bill form), the internal characters employed support and parallel them. Whereas the few available external characters offer multiple choices in deciding relationships, the anatomical characters offer limited choice—both pointing up relationships and ranging groups from simple to complex. The muscle patterns are not absolutely constant in every family—taxonomic characters rarely are. But the adaptive increase in the pinnate character of the jaw muscles in tanagers, for instance, links them to the finches which evolved from them, as supported by external lines of evidence such as color of plumage. These anatomical characters often relate families not previously linked by ornithologists but whose closeness on the basis of plumage is most convincing (cf. Beecher, 1951b). This is because the classifications based on superficial external characters laid great stress on bill resemblance, forgetful of the evolutionary prerequisite that new lines, diverging from an ancestral stock, must be *differently* adapted. Thus they failed as a rule to group families naturally and had no basis for detecting numerous cases of convergence. This gave an erroneous picture of oscinine evolution.

Adaptive Potential.—Evolution is dynamic (cf. Emerson, 1949; 640 ff.). The competing stem groups of Sylvioidea and Timalioidea seemed under constant pressure to evolve forms adapted for any food-niche insufficiently exploited; and success, aside from accidents of isolation, depended on adaptive potential. For instance, the babblers (Timaliidae) seem to be a microcosm of the Timalioidea as well as the stem group from which its specialized families arose (the transitional Cisticolinae is as much a subfamily of Timaliidae as of Sylviidae). The best check on the evidence that the Timaliidae has given rise to shrike groups is seen in the existence of timaliine shrikes (*Pteruthius, Laniellus*). A good check on timaliid origin for other groups is seen in the occurrence of timaliine larks (*Cinclorhamphus*) in Australia where true larks do not occur. Similar examples are seen in what I interpret as timaliine titmice (*Parisoma, Myioparus*), creepers (*Climacteris*), and nuthatches (*Neositta*). In the Sylvioidea, one of the best checks on the indicated origin of swallows from flycatchers may be the existence of the swallow-flycatcher (*Artomyias*). Similarly, the origin of dippers from thrushes is made more plausible by the existence of semi-aquatic chats, especially the forktail (*Enicurus*), internally adapted like *Cinclus* for holding slippery prey. These adaptive types are usually few in species and unspecialized when compared to major groups with the same adaptation, characteristically arising where the latter are absent.

Natural Assemblages.—It appears that the subfamilies of the stem Sylviidae may have been differently pre-adapted to seize initial advantages in the competition to fill food-niches made available by flowering plants. Each has apparently given rise to one or more natural assemblages of families with the adaptive potential to occupy all or most niches, and the mélange of species actually filling them in the present cross section of time is the result of a selection process (cf. Park, 1948).

The pinnate *M7b* of the Timalioidea may have conferred an initial advantage in the race to evolve massive, pinnate adductors, for the American finches and the Australian and African weavers all convergently occupy the seed-cracking niche. Their associated nectar-feeding groups may be a necessary link in the series leading to seed-cracking, for only the sylvioid nectar-feeders, the Nectariniidae, Dicaeidae, and Zosteropidae, with a very short, non-pinnate *M7b*, do not have an associated finch group. This reduction of *M7b* may be genetically deep-seated (in terms of pleiotropy) in all pycnonotine assemblages, the reason crows did not evolve a finch despite otherwise highly pinnate adductors. The shrike adaptation also calls for the added power of a pinnate *M7b*, and there are no sylvioid shrikes.

On the other hand, the tendency for *M3b* to expand into a powerful muscle with a distinct *M. retractor palatini* in the sylvioid thrushes and starlings may have given them the edge in exploiting ground-niches because of increased efficiency in securing slippery prey. A similar development of this muscle has adapted thrashers for digging (Engels, 1940), linnets and weavers for seed-cracking.

Niche Divergence without Plumage Divergence.—Natural assemblages always embrace groups differently adapted as to food-niche. A striking example is seen in the divergence of the starlings (Sturnidae) and swallows (Hirundinidae), which have very similar internal characters, from the flycatchers (Muscicapinae). These groups have evolved parallel plumage types, pointed wing, forward vision, and hole nesting, but are different in their feeding habits. The starling is a ground-feeder, the swallow an aerial feeder; yet forward vision and pointed wing pre-adapt the introduced starling in North America to take over the Purple Martin's niche when the latter flies south. On warm fall days, it feeds in the air, fluttering and gliding like the martin, but with frequent resting.

Again, the larks and pipits are ground-feeders, the monarchs and fantails are flycatchers, yet most of the plumage types of the one have counterparts in the other. There are many exceptions to this, but anatomical characters suggest that both have arisen from the Cisticolinae. The larks and pipits are streaked like the grass warbler *Cisticola* and often have the head and breast recognition pattern of *Prinia flavicans* or *P. pulchra.* The tail-opening trait of the grass warblers may have been transmitted genetically to these descendant groups also. The groups arising from the Cisticolinae may be regarded as a sort of super-assemblage, most of them with some suggestion of the recognition pattern mentioned earlier. Moreover, all are either differently adapted as to food-niche or, if not, appear to have arisen in isolation from each other.

Evolutionary Rates.—Wherever particularly favorable conditions of pre-adaptation, isolation, and niche-opportunity occur, a group may radiate into new major lines. The vireos, the stem group of the nine-primaried assemblage, are a good example of this. This group may have evolved at a higher rate when first isolated in America to produce the more adaptable warblers and tanagers whose success has narrowly limited the vireos' present niche. Despite supposed greater age, however, it remains a primitive "low rate" line with one-third as many species as the warblers and one-sixth as many as the tanagers. When we consider that each of the latter two has likewise given rise to several finch groups with still greater numbers of species, it appears that rate of evolution in this assemblage increases from the stem group to the terminal group. This is at least partly due to niche opportunities provided by flowering plants.

That rate of evolution is not merely a function of relative abundance of food types but actually signifies heightened adaptive potential in "high rate" terminal groups seems strongly indicated. The American blackbirds (Beecher, 1951a), originating from emberizine finches, were able to occupy virtually all passerine food-niches in a relatively short time, despite the competition of groups already occupying them. The Galapagos finches (Lack, 1947), of emberizine origin, and the Hawaiian Drepanididae, of tanager origin, have done similarly, while the (probably emberizine) finch *Nesospiza* (Lowe, 1923) seems to represent the early stages of such an evolution on Tristan da Cunha. Now there is no evidence that the Galapagos mockingbirds (*Nesomimus*) or Hawaiian thrushes (*Phaeornis*) reached these islands later than the finches, and I believe they were limited to relatively usual niches (Amadon, 1950b) because they represent low-rate lines. Though treated as a terminal group, the thrushes appear to be adaptively restricted by virtual inability to evolve pinnate musculature, and the history of oceanic faunas reveals no instance of such primitive colonizing groups embracing food-niches significantly "outside" their normal ones. The fact is that all of these explosive radiations were accomplished by "high rate" lines, particularly finches.

Validity of the Phylogenetic Tree.—The significance of the above may be that, through competition, the more recent, adaptable groups confine primitive groups to the few niches they fill efficiently. If so, the continued existence of the vireos and the entire sub-oscinine assemblage is the best evidence that for Oscines we can derive family from living family in the present cross section of time. The morphological tree may, therefore, approximate phylogeny—a tree in which dynamic branches are still growing out of a relatively static trunk.

Island Effect.—I do not see a special problem in the larger bill-size of island birds first noted by Murphy (1938: 538). The lesson of the Galapagos finches is that an emberizine stock, small-billed in competition with large-billed tanager finches on the mainland, could escape size restriction and could occupy *all* seed-niches in an island environment where competition is lacking. The larger-billed orioles of Caribbean islands are probably utilizing large fruits and flowers exploited by oropendolas on the mainland. Island forms, representing fewer groups, extend their adaptive range of bill form and size, and even low-rate groups can do the latter. Regarding the tendency toward small size in Rennell Island birds, Hamlin (Mayr and Hamlin, 1931) has commented on the stunted nature of the general vegetation

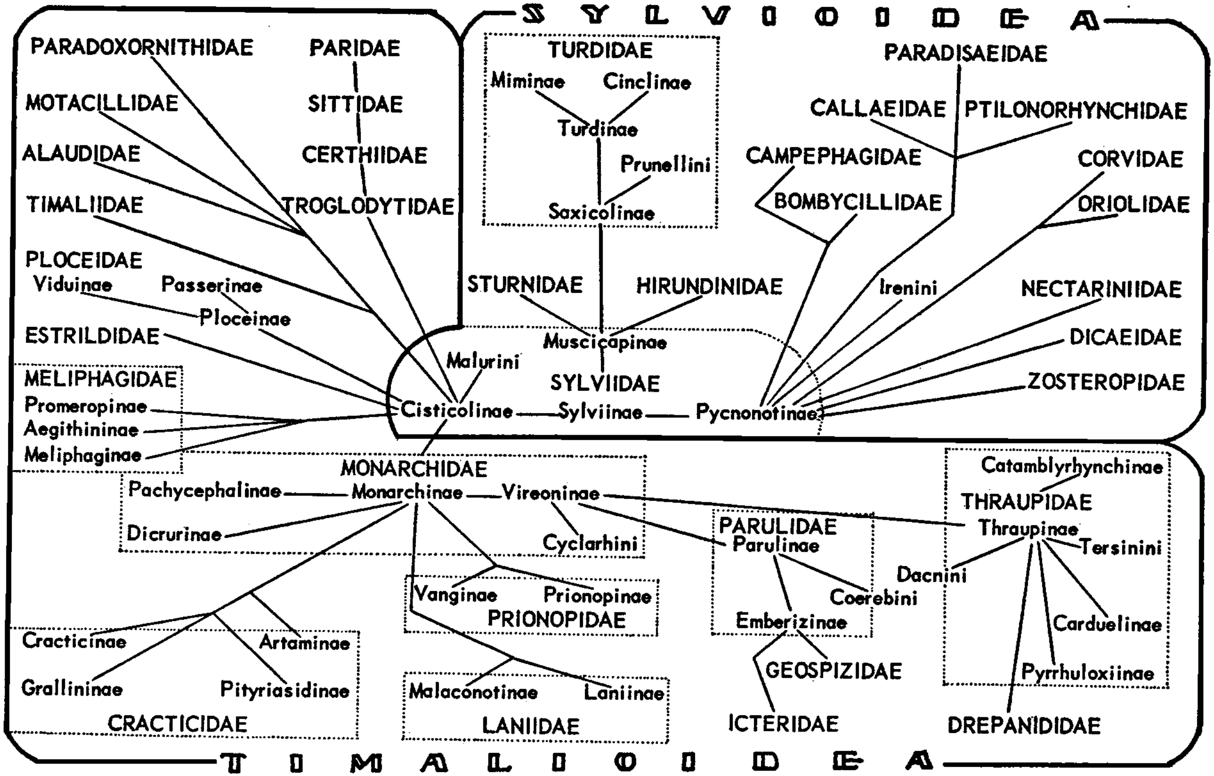


FIGURE 18. PHYLOGENETIC TREE OF THE OSCINES. This is not intended to include tribes. Only such tribes are shown as have been customarily treated as oscinine families—to indicate their reduction in rank. For practical purposes the families here recognized might be arranged in the following linear order with least violence to relationships: *SYLVIOIDEA:* SYLVIIDAE, STURNIDAE, HIRUNDINIDAE, TURDIDAE, ZOSTEROPIDAE, DICAEIDAE, NECTARINIIDAE, BOMBYCILLIDAE, CAMPEPHAGIDAE, ORIOLIDAE, CORVIDAE, CALLAEIDAE, PTILONORHYNCHIDAE, PARADISAEIDAE. *TIMALIOIDEA:* TROGLODYTIDAE, CERTHIIDAE, SITTIDAE, PARIDAE, PARADOXORNITHIDAE, MOTACILLIDAE, ALAUDIDAE, TIMALIIDAE, MELIPHAGIDAE, ESTRILDIDAE, PLOCEIDAE, MONARCHIDAE, CRACTICIDAE, PRIONOPIDAE, LANIIDAE, PARULIDAE, GEOSPIZIDAE, ICTERIDAE, THRAUPIDAE, DREPANIDIDAE.

there. If fruits and flowers are smaller, I would suggest that associated insects may also be smaller, reducing the size range of the whole food-chain.

The Reality of the Higher Groups.—Internal characters fully support the existence of the families as derived by ornithologists mainly through the study of external characters, and this mutual support is the best evidence that these two types of characters are not classifying different parts but the organism as a whole. The recent revisions of the Timaliidae and the Pycnonotidae by Delacour (1946; 1943a) are supported and no very great transfer of species from or into either is proposed on the basis of internal anatomy. The difficulty in distinguishing between the Sylviidae and the Timaliidae, experienced by taxonomists working with external characters, is somewhat borne out by internal characters; the grass and bush warblers (Cisticolinae) prove to be transitional between the two families and could be regarded as a subfamily of either. The value of internal characters is in showing group relationships, so that what were 60-odd equal families fall into a hierarchy of superfamilies, families, subfamilies, and tribes.

Complexity of Terminal Groups.—The terminal groups occupying the outer twigs of the phyletic tree (figure 18) are more complex than the stem group, both anatomically and in degree of behavioral elaboration (nesting, courtship, communal habits, etc.). These are primarily the weaver and finch groups (particularly the icterids), the crows, birds of paradise, bower-birds, and nectar-feeders—all of which, by virtue of special qualification or favorable isolation (or both), have undergone notable radiation. Primitive terminal groups which have also achieved adaptive success with structural and behavioral elaboration are shrikes (Vangidae, Cracticidae), isolated from competing advanced groups.

Evolutionary Relationships.—In a phylogeny expressive of evolution, the various sub-groups of seed-cracking birds are more closely related to primitive insect-eating groups than to each other. Their unusually wide dispersal made possible by their diet of seeds gave taxonomists a false impression of homogeneity not met with in fruit- or nectar-eaters, the Old and New World groups of which do not generally overlap in range. Such convergence between members of the various assemblages appears to be the rule. It may be very close as in finches or as between titmice and parrot-bills or superficial as between the corvine and shrike assemblages. Even where partial, however, convergence is probably always adaptive. The peculiar food-scratching behavior of North American buntings, with unusual development of the hind claw, occurs in African whydahs. Brood parasitism occurs in African weavers and American blackbirds (Friedmann, 1950) and forms of each, convergent in plumage, tend to occupy similar habitats (*Euplectes–Agelaius*). The long straight hind claw of larks, pipits, snow buntings, and longspurs may be an adaptation for locomotion on mud (or snow), and the coucal (*Centropus*) has similar equipment and inhabits muddy places. One hardly dares to propose that we see in all of these cases of convergence the effects of homologous genes (Spencer, 1949: 23), reflecting the close relationships of these passerine families.

I find myself in rather close agreement with Pycraft (1907) on the resemblances of shrike groups, though I draw different evolutionary implications from them. He marks the similarity of *Tylas* and *Xenopirostris*, both of which I include in Vangidae. He notes the resemblance of *Vireolanius* to what I call the primitive shrikes and of vireos to the Muscicapidae. I would say relationships of the vireos are with the Monarchidae, which I remove from Muscicapidae, and that the Vanginae, Prionopinae, Pityriasidinae, Cracticinae, Artaminae, and Cyclarhini (including *Vireolanius*) evolved separately from the Monarchidae as endemic shrikes in their respective faunal regions. I recognize Wetmore's (1951) contention that *Vireolanius* is a shrike but think it an endemic American shrike arising from the vireos. As in finches, it appears that each of the shrike families is more closely-related to the world-wide monarch-vireo group than to each other. Conversely, the Australian honey-eaters (Meliphagidae) must be expanded to include African and even Oriental groups. Taxonomically, relationships seem more complex than was assumed from external resemblance alone.

Origin and Dispersal.—Mayr (1946) stated the problem posed by related barbets, trogons, and parrots isolated in the tropics of the Old and New Worlds. It applies equally to the ancient suboscinine assemblage apparently displaced into the southern continents by a modern oscinine assemblage arising from it (cf. Matthew, 1915). The oriental Eurylaimidae, represented in Africa by the relict, *Smithornis*, is probably close to the New World Cotingidae (Pycraft, 1905). The Pittidae, Philepittidae, and Xenicidae show a notably disjunct distribution in the Old World tropics and must have been early separated from the closely related Furnariidae, Dendrocolaptidae, Tyrannidae, etc. of the New World tropics. Their sedentary habits virtually require that all of the latter groups must have been in South America before the Eocene Central American water gaps isolated it from North America until the end of the Tertiary. The problem applies also to primitive members of the oscinine assemblage. The nine-primaried American families arose to fill food-niches provided by the flowering plants in isolation from Old World groups, so the stem vireos may have reached America before the origin of flowering plants. The vireos arose from the Monarchidae, and these shrike-flycatchers, with the endemic primitive shrike groups arising from them (above), show a mainly tropical distribution pattern. This world-wide, pantropical pattern is often met in late Cretaceous groups (Beaufort, 1951). Sarasin (1910) notes 11 genera of reptiles and amphibians, 8 of land mollusks, and 6 of terrestrial flatworms with similar distribution. It is quite characteristic of skinks, iguanas, geckos, and boas, as well as of primitive insectivores and lemurs among mammals, though Simpson (1945) states that the relationships in these groups are still problematical.

The dilemma of zoogeographers seeking a former tropical exchange corridor at the north to account for these related, pantropical groups is that Bering bridge has not been even subtropical as far back as the Cretaceous (Stegmann, 1938; Chaney, 1940). Although Simpson (1947) finds it adequate to explain Tertiary mammal distributions, the above dispersals are believed to have occurred earlier—and even Simpson admits the bridge favored cold-adapted forms. On the other hand, there is a tropical angiosperm-gymnosperm flora in the Upper Cretaceous of Greenland, elsewhere met only in the American Potomac flora (Seward and Conway, 1935). This, with the subtropical floras of Western Europe and the London Clay in the Lower Eocene (Reid and Chandler, 1933), suggests a milder climate in the North Atlantic area. The latter flora, of Malaysian affinities, is thought to have occurred on the north shore of the Tethys Sea as a result of warm currents from the Indian Ocean (Brooks, 1926). The Potomac flora implies Cretaceous contact of North America with Greenland and possibly with the British Isles via Iceland, though not necessarily all at one time.

Geological evidence has not eliminated the possibility of Mesozoic drift of continents, and our understanding of faunal and floral relationships must be refined before this issue can be decided biogeographically. Since the velocity of the earth's rotation is 1000 miles per hour at the equator and 0 miles per hour at the poles, North America and northwestern Europe might have been in contact long after Africa and South America had drifted apart. If such a connection existed as recently as Upper Cretaceous, it would have been a tropical one, and the tropical flora would have retreated toward the equator in the several continents during the climatic deterioration following the regression of Tethys Sea into the present Mediterranean. In so doing it would have fragmented along with its faunas; and in Old and New World tropical regions, thus separated, parallel evolution of static, early-specialized groups (barbets, trogons, parrots) might be expected. But the generalized passerine insectivorous stocks might have tended to diverge rapidly in response to the available food-niches provided by the flowering plants, evolving different assemblages in the Old and New Worlds. However, most authors, like Darlington (1948), prefer the Bering bridge to its alternatives.

Other primitive insectivorous groups might have been expected to enter America along with the suboscines and vireos. *Polioptila*, *Microbates*, and *Ramphocaenus* may be relicts of a branch of the world-wide Sylviidae that did not survive well in competition with the American warblers. *Ramphocaenus* I regard as an American endemic only convergent with the African *Macrosphenus* and the oriental *Orthotomus* which it resembles. To have given rise to the Mimidae, thrushes would have had to arrive early, and so would swallows. Since wrens apparently are not related to thrashers, they may have evolved in the Old World, where competition with grass and bush warblers (Cisticolinae) early forced them into the grassland and desert niches of the New World. The initial presence of wrens and thrushes may have prevented extensive exploitation of the ground-niche by the insect-eaters of the nine-primaried assemblage. Considerable divergence of the Bombycillidae from the nearest Old World groups (bulbuls and cuckoo-shrikes) suggests early arrival. But most Tertiary interchange after this initial period would have been by cold-adapted species across the Bering bridge. Mayr's analysis of the North American bird fauna (1947) is admirable and makes further discussion here unnecessary, except that, since the "Old World" finches arose from tanagers in the New World, their Eurasian radiation is secondary. Its extent, however, suggests that the seed-cracking niche was vacant in Eurasia and that the Ploceidae reached the Palaearctic rather late.

Faunal relationships and geology both indicate that the Ethiopian and Oriental regions were in contact in the Upper Cretaceous when the Deccan volcanism devastated 250,000 square miles of peninsular India, isolating its southern tip and Ceylon. North of the Deccan, the Tethys Sea extended from Europe to Africa, divided into northern and southern components by a land mass extending from Africa to northern India (Lake, 1939). The distinctive African relicts of primitive groups like the Eurylaimidae, Pittidae, and Timaliidae (*Picathartes*) and oriental relicts of the African Prionopinae (*Tephrodornis*) suggest the early closure of this faunal bridge. Since the Timaliidae are scarce and the Pittidae absent on Ceylon today, these groups may have survived in a semi-isolated northern India, caught between the rising Himalayas to the north and the Deccan to the south with a receding Tethys on the west. Otherwise it is hard to account for the species- and niche-radiation there. The smaller number of species in the Australian Region may indicate isolation at the same time, but their importance in occupying its niches cannot be over-emphasized. The Pycnonotidae may also be an old Oriental group.

Faunal exchange was again possible in Miocene-Pliocene times when forest covered most of Africa with a belt across Arabia to the Oriental Region (Lonnberg, 1936; Beaufort, 1951). This accounts for the similarity of the Ethiopian and Malaysian forest bulbuls, babblers, and cuckoo-shrikes noted by Chapin (1932), who also thinks most African savanna birds arrived via a savanna belt north of this forest. I agree with him that the Malaconotinae and Laniinae could have arisen in Africa and that the Ploceidae, Viduinae, and *Cisticola* may have arisen in savanna south of the forest barrier, but I consider the last three closely related. The Estrildidae, arising in Australia, first entered the savanna north of the forest, in my opinion, and their parasitization by the Viduinae may, thus, date from the joining of the northern and southern savannas with regression of the forest in late Tertiary times. The Viduinae are the only weaver group confined to Africa.

CONCLUSIONS

The direct correspondence of all very early, world-wide distribution patterns with just those insectivorous passerine groups judged primitive on anatomical characters, the major assumptions of this work are confirmed. The fruit-, nectar-, and seed-eating groups, judged later in origin and more advanced, are of limited distribution, and this agrees with the separation of the faunal regions as the Tertiary unfolded. By their existence, these world-wide, primitive groups—confined mainly to insectivorous niches by the more advanced groups that apparently arose from them—make it less necessary to postulate extinct common ancestors for which we have no evidence and which probably were similar to modern sylviids.The morphological tree for the rapidly evolving Oscines may be a fair approach to a phylogenetic tree.

The working method, therefore, seems to be valid, and this arrangement of oscinine higher groups may be permissible as a first approximation. Allowance must be made for subjective judgements as to relationships between closely related groups in a still-evolving complex; but this is implicit in any classification, and we may hope for refinement as our understanding grows. This first attempt at a phylogenetic arrangement of the Oscines is offered for appraisal in terms of present and future ornithological facts.

SUMMARY

An attempt is made to clarify the relationships of the higher groups (families) of oscinine birds and to erect a phylogeny based on the methods of comparative anatomy. Several independent lines of anatomical evidence in the head region, particularly the jaw musculature, are used, but external characters are also considered. The working method assumes that structurally simpler characters are primitive and an initial separation of the suborder into the superfamilies Sylvioidea and Timalioidea is based on a simple but constant muscle difference. Within each of these, the families are arrayed in a hierarchy of increasing general complexity as they become adapted to the fruit-, nectar-, and seed-niches provided by the evolution of flowering plants. Most complex are the groups forming the terminal twigs of the phylogenetic tree, and here, especially, much convergence is noted. For example, the various finch sub-groups are found to be more closely related to insectivorous stocks in the same assemblage than to each other. The result is a classification more complex than one based on external characters which would place all finches together. Groups judged to be primitive anatomically all prove to have a worldwide distribution pattern believed to date from Upper Cretaceous time. The original assumption that more advanced groups were restricted in distribution by the separation of faunal regions in more recent periods is confirmed by anatomical relationships. The method seems, therefore, to be valid, and the morphological tree is believed to approximate phylogenetic relationships.

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