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A CLASSIFICATION OF RECENT BIRDS

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During the course of incorporating the Rothschild Collection of birds with the general collection of the American Museum of Natural History, an attempt was made to arrive at a natural arrangement for each family or other unit. This often led to rather detailed studies or to intensive efforts to determine the correct position of difficult genera. A number of publications growing from these studies are included in the bibliography (see titles by Amadon, Chapin, Delacour, Mayr, Vaurie, and Zimmer). They relate primarily to Old World families not yet included in Peters' "Check-list" for which no authoritative list exists comparable to Hellmayr's for the New World.

The principal purpose of this paper is to give these findings more general expression. We have of course incorporated the work of others whenever known to us and have included the non-passerine groups, although few changes are made from the now well-established sequence of Wetmore (1934, followed by Peters). Indeed we have throughout attempted to make no changes from the established sequence except when they are clearly indicated by recent evidence. Occasion is taken to give a corrected count of species in each family of birds; such a count proved a useful feature of a previous paper by the senior author (Mayr, 1946).

As a result of various discoveries and recent revisions the total number of species in the present list is 8590 as compared with 8616 in the previous one. The change within five years amounts to less than one-half of one per cent. Because of the large number of insular forms of doubtful status, the number of species of birds will always remain an estimate. The final figure may vary by several hundreds either way, depending on the point of view of the enumerator. The five "species" of *Todus* or the three of *Ryn-*

chops, for example, might be considered races just as have the former "species" of *Anhinga*. Further study of continental forms, on the other hand, often gives clear-cut answers as to the racial or specific status of forms previously of dubious status. The result of the two recent counts indicates, however, that the final figure will be within 2 per cent of 8600. For all practical purposes this figure will be satisfactory as a very close approach to the actual number of species of living birds.

We would like to express our appreciation to Mr. James L. Peters for providing revised figures for some of the families of South American mesomyodian song birds and to Dr. R. C. Murphy for up-to-date figures of the number of species in some of the sea bird families. We have profited greatly from a painstaking examination of our manuscript by Dr. J. Van Tyne.

Two important aims of any classification are to keep related groups as close together as possible and to put ancestral groups first, derived groups later. In a list that does not include fossil forms, the second of these principles can have only limited expression. Specialization is often a clue to relationship and phylogenetic sequence, but de-specialization may occur and much phylogenetically meaningless specialization exists. Cotingas, for example, appear more specialized than most of the Oscines, but the structure of the syrinx and tarsus, as well as other evidence, indicates that the Oscines are a later, more advanced group than the cotingas.

There is no particular difficulty in incorporating the above aims in a classification so long as a single, non-branching sequence is involved. Difficulties arise in a branching system, for it is impossible to pursue all avenues of descent simultaneously in a linear sequence of names. Inevitably one must follow each branch in succession to its most recent end twig and then go back to the main stem and repeat the process.

The problem of the relationship of the avian orders is an old one and one that will probably never be solved satisfactorily. One point that is frequently overlooked is that all living birds are exceedingly specialized in different directions and that this specialization had its beginning in the remote past. Perhaps the most specialized of known birds is *Hesperornis*, which lived in the Cretaceous. The Eocene *Diatryma* is perhaps more specialized than any bird that lives today. The connections between the living orders are lost in antiquity, and their analysis is further obscured by much convergent evolution of habitus type.

Predators, for example, evolve a hooked bill and sharp claws. It is now generally accepted that hawks and owls are not closely related, but Hudson (1948) supplies evidence that even the hawks may be a polyphyletic group. *Hesperornis* (Hesperornithes), the loons (Gaviae), and the grebes (Podicipedes) are often cited as forming a group of three related orders in view of the structure of their rear limbs, but as Stolpe (1935) has shown, the anatomical similarities that have been cited as evidence for relationship are actually functional convergences. A better known example of convergence is that of the "Ratites," a group which consists of at least five unrelated groups of birds, which have become flightless secondarily and attained large size. Many other cases of convergent evolution have been unmasked recently among the passerine birds, e.g., the "shrikes," "titmice," "finches," "warblers," and others (see below). In view of the frequency of convergence among birds, it seems mandatory that some of the other heterogeneous-appearing orders of birds (e.g., the Gressores, Grues, and Laro-Limicolae) be reëxamined to evaluate the authenticity of relationship of the included families and suborders. Some of them (e.g., the Thinocoridae, Turnicidae, and Mesoenatidae) have, of course, long been a puzzle to taxonomists.

The other extreme is provided by such groups as the Sphenisci and Tubinares, which appear exceedingly different but are clearly related, as first pointed out by Fürbringer and later confirmed by Simpson (1946). The relationship of the kiwis to the moas, and, if confirmed, the relationship of the turacos to the gallinaceous birds would also be illustrations of highly dissimilar but related groups.

The existing orders of birds are thus the terminal twigs of an exceedingly ramified phylogenetic tree, and it is rather immaterial in what exact sequence many of the orders are listed. Portmann (1938) is convinced that the gallinaceous birds are the most primitive of living birds. Stresemann (1927–1934) also placed them near the beginning, yet Wetmore lists them as the nineteenth order. In view of our scanty knowledge of relationships and the uneven rate of specializing trends, it is often impossible to decide which of two orders is the more primitive or ancestral.

The use of the ending "-formes" for ordinal names has met with considerable opposition among zoologists who are reluctant to see such a venerable name as, for example, "Lepidoptera" replaced by "Papilioniformes." We have followed Stresemann in

using the older ordinal names, but when those used by Wetmore have a different root they are given in parentheses.

RATITES

The problem of ratite phylogeny continues to receive much attention. The present consensus is that the main groups of these birds are of independent origin. Stresemann's suggestion that the kiwis (Apterygidae) be placed in the same order as the moas (Dinornithidae) is followed. McDowell (1948) may well be correct in believing the rheas to be allied to the tinamous, but we doubt whether they should be placed in the same order, pending further study.

In the literature one finds records of moas and kiwis from Australia and of elephant birds from Africa. In our opinion all of these records are based on such fragmentary material as to be subject to doubt. Oliver (1949) has recently written a volume called "The moas of New Zealand and Australia." The supposed Australian moa, "*Dinornis*" *queenslandiae* DeVis, is based on a femur head from "Post Tertiary" deposits. Two other giant extinct ratites, *Dromornis* and *Genyornis*, are known from the Pleistocene of Australia. Both are assigned to the Dromaeidae. Careful comparison of the published figures of the femur of "*Dinornis*" *queenslandiae*, made by McDowell at the suggestion of the authors, led him to the conclusion that the development of the trochanter is so different that it seems impossible that *queenslandiae* belongs in the Dinornithidae. There is no reason to suppose it could not represent a distinct ratite type allied to the emus rather than to the moas. According to McDowell (verbal communication) the supposed records of kiwis from Australia (*Metapteryx*) are also erroneous.

The presence of relatives of *Aepyornis* in fossil remains from Africa is based on even less satisfactory fragments and should not be accepted without much more evidence. We doubt if this will ever be forthcoming.

It is a curious fact that the male assumes all the duties of incubation in all the living ratites except sometimes in the ostrich but including the tinamous. Probably this is only a remarkable coincidence.

SPHENISCI; TUBINARES (PROCELLARIIFORMES)

As already noted, the penguins are related to the petrels and

less closely to the Steganopodes. Simpson (1946) has shown that the Miocene penguins were osteologically much like those of today. The metatarsals are less fused in the modern forms, an interesting example of "reversal of evolution" and "de-specialization."

LOONS: GAVIAE; GREBES: PODICIPEDES (COLYMBIFORMES)

The controversy as to whether the name *Colymbus* Linnaeus, 1758, applies to a loon or to a grebe is perhaps best resolved, as suggested in a paper by Dr. F. Salomonsen presented at the Xth International Ornithological Congress, by declaring the name indeterminable. The names *Gavia* will then be used for the loons and *Podiceps* for the typical grebes.

As already indicated, Stolpe (1935) concluded that there is little reason to believe that the loons and grebes are related to the Cretaceous *Hesperornis* (cf. Howard, 1950) or, for that matter, to each other. Since, however, the grebes have been thought to be remote allies of the petrels, and since McDowell (oral communication) thinks that the loons may be a specialized offshoot of petrel stock, it is possible that the grebes and loons have some distant or indirect relationship. It is permissible, therefore, to continue to keep them near each other in a classification.

STEGANOPODES (PELECANIFORMES)

Lanham (1947) has assembled anatomical data to show that the tropic birds (Phaëthontidae) and frigate birds (Fregatidae) share a number of apparently primitive characters with the Tubinares. These characters are often lacking in the third main group of the Steganopodes, which includes the pelicans, cormorants, anhingas, and gannets. *Phaëthon* is certainly further removed from *Pelecanus* and allies than is *Fregata*.

The resemblances between the tropic birds and the gulls and terns have often been pointed out, but until evidence of true affinity is brought forward they must be attributed to convergence. G. Timmermann (MS) has found certain of the Mallophaga of these two groups to be related, but it is possible that this is a result of secondary transfer of parasites in birds of similar size and habits. The case may be comparable to the occurrence on the skua (*Catharacta*) of an "endemic" species of Mallophaga of a genus otherwise restricted to the Tubinares (Hopkins, 1942, p. 100).

Anhinga is so much like *Phalacrocorax* that it would seem to

require no more than subfamily status. Stresemann did not give it even that.

ACCIPITRES OR FALCONES

The diurnal birds of prey are a highly differentiated group, thought by some to be related to the Gressores, and more distantly to the Steganopodes. Hudson (1948) and others have written on the classification of this order in recent years. The American vultures (Cathartidae) are very distinct and may not be related to the other Falcones. Perhaps they are representatives of some ancient American radiation which may even include some or all of such families as the Anhimidae, Cracidae, and Tinamidae (McDowell, verbal communication). The occurrence of a cathartid, *Pleseocathartes*, in the upper Eocene of France requires confirmation, in the opinion of Dr. A. Wetmore who has examined the specimens (verbal communication).

The African secretary bird, *Sagittarius*, resembles the gruiform Cariamidae of South America. Some would transfer the Sagittariidae to the Grues, others the Cariamidae to the Accipitres. Actually, the resemblance may be parallelism. Still, *Sagittarius* may not belong to the Accipitres.

Certain similarities in the pterylography and in the plantar tendons of the Pandionidae and Cathartidae (Compton, 1938) are apparently of no phylogenetic significance (Hudson, 1948).

GRESSORES (CICONIIFORMES)

The whale-head or shoe-bill stork, *Balaeniceps*, has often been placed in a monotypic family. Böhm (1930) thought its anatomy like that of a true stork, and Dr. James P. Chapin tells us that he believes it well placed in the Ciconiidae. It has the bill-rattling habit of storks. The hammerhead, *Scopus*, on the other hand, is more distinct and may be left in a separate family. Both genera share some characters with the Ardeidae.

The boat-billed heron, *Cochlearius*, appears to be a typical heron in all except its curious bill. It is even possible to point to the night herons as being probably its nearest relatives. We think this genus may properly be placed in the Ardeidae, just as the spoonbills, *Platalea*, are placed in the Threskiornithidae.

The trematodes of the Ciconiidae and Ardeidae are quite different (Szidat, 1942), but possibly study of those of some of the other families of Gressores will bridge this gap.

PHOENICOPTERI

Flamingos resemble the Anseres in some ways, though many of the characters involved, particularly the bill, are highly adaptive. The Mallophaga of the two groups are much alike (Hopkins, 1949), while those of the Phoenicopteri and Gressores (with which the flamingos are usually placed) are very different.

The flamingos have, however, many anatomical similarities with storks and ibises. Stresemann, after enumerating these similarities, stated that the resemblance of the flamingos to the waterfowl is superficial. In view of this conflicting evidence it seems best to place the flamingos as a separate order between the Anseres and Gressores. They may be related to both.

ANSERES

The waterfowl are a very distinct group but may be placed between the flamingos and gallinaceous birds. The two South American families Anhimidae (Anseres) and Cracidae (Galli) may be distantly related (Delacour, 1949). Delacour and Mayr (1945) wrote on the classification of the Anatidae, which they divided into two subfamilies and five tribes. Several genera are of doubtful allocation, and one in particular, the magpie-goose, *Anseranas*, deserves to be placed in a sixth tribe (von Boetticher, 1943).

GALLI

The gallinaceous birds are one of the primitive and basic orders. It is highly unlikely that they are related to the Tinami. We follow Delacour (1951) in considering the grouse and guineafowls as only subfamilies of the Phasianidae.

Stresemann placed the hoatzin, *Opisthocomus*, in a separate order, which, however, he considered to be "einen sehr nahen Verwandten der Galli." Some of the peculiarities of this bird, such as the large crop and the well-developed wing claws of the chick, are specializations for its peculiar diet and habitat and may not be primitive. Pycraft thought *Opisthocomus* to have significant resemblances to the genus *Centropus* (Cuculidae) and to the turacos (Musophagidae), as well as to the Galli. Stresemann considered the similarity to cuckoos and turacos as superficial.

For the time being, it seems best to retain the Opisthocomidae in the Galli as a suborder. In the opinion of McDowell the hoatzin has a large number of important resemblances to the Cracidae and Anhimidae.

CUCULI

There is a difference of opinion, first as to whether or not the turacos (Musophagidae) should be associated with the Galli, and second whether or not the cuckoos (Cuculidae) are related to the turacos. The Mallophaga of the turacos are said to be strongly indicative of relationship to the Galli, though Hopkins (1949) thinks this might be the result of accidental transfer in a dust bath. Pycraft and Fürbringer found morphological resemblances between turacos and the Galli, though Stresemann and others considered these superficial. We think, however, it is best to place the turacos tentatively near the Galli.

The turacos and cuckoos agree in most features of basic anatomy. Moreover, the cuckoos of the genus *Coua* of Madagafcar often resemble turacos in body form, presence of bare areas on face, coloration including even purplish or reddish tinge on tail, and general configuration of bill and nostrils. While they lack the full crest of the turacos, there is an incipient one. Turacos always perch with two toes back and two forward, though in death this functional zygodactyly is not always indicated by the position of the toes. Moreau (1938) has emphasized developmental differences between turacos and cuckoos, but the tendency towards peculiar nesting habits in the latter lessens the significance of this. It is entirely possible that the Musophagidae are somewhat primitive relatives of the Cuculidae, so we tentatively follow convention in associating the two families in the same order.

GRUES

This order has no obvious ties with the orders preceding it, though various links with the Falcones, Galli, or even the Gressores have been advanced at one time or another. The large number of relict families of a genus or two each in the Grues marks it as a declining and ancient order, as does its fossil history. The phorhoracids of South America and possibly the Eocene *Diatryma* are among the extinct relatives of the Grues.

LARO-LIMICOLAE (CHARADRIIFORMES)

This diversified order may be connected with the Grues through one or all of the Burhinidae, Jacanidae, and Thinocoridae. Several of the shore bird families currently recognized seem to require no more than subfamily status (cf. Stresemann).

COLUMBAE; PSITTACI

The Columbae may be tentatively placed near the Laro-Limicolae, but certain resemblances between pigeons and game birds may eventually prove to be of significance. It is unlikely that the sand grouse (Pteroclidae) are grouse-like except in superficial adaptations.

The Psittaci are a strongly differentiated group. Resemblance to the Accipitres is probably mere convergence, and relationship to the Cuculi, championed by Gadow, must be rather distant at best. McDowell has found similarities between the humeri of parrots and those of pigeons.

CAPRIMULGI; STRIGES

Hudson (1937) found a great difference between the thigh muscles of owls and those of Caprimulgidae, but perhaps examination of other families, such as the Aegothelidae, would bridge the gap. Certainly there are strong reasons to believe the two orders to be related, but the resemblance of goatsuckers to swifts is evidently superficial.

CORACIAE

The Madagascar cuckoo roller, *Leptosomus*, and the ground rollers have been placed in the same family by Sclater (1924–1930) and by Wetmore. Yet the ground rollers appear to be much closer to the true rollers than to *Leptosomus*, though some may prefer to recognize three families.

MACROCHIRES (APODIFORMES); COLII

Whether the swifts and hummingbirds are actually related to each other or not is an open question, but Fürbringer found much evidence that they are. He considered both to be rather closely allied to the Passeres. Since, however, the Pici seem to be even closer to the Passeres, the sequence Macrochires, Pici, Passeres is suggested. The very isolated Colii are closest to the Macrochires, according to Fürbringer, although there is some indication of relationship with the Coraciae, particularly the Alcedinidae.

PERCHING BIRDS: PASSERES

The subdivision of the Passeres on the basis of the muscles of the syrinx was made by Johannes Müller as early as 1847. About

1880 Garrod and Forbes published several papers establishing the position of such families as the broadbills and philepittas. These and other important references on the Order Passeriformes are given by Ridgway (1901, pp. 2–23; 1907, pp. 328–332) and by Stresemann (1927–1934, pp. 843–850). The following brief summary mentions only the more important or controversial points.

Suboscines

The broadbills differ from other Passeres and agree with some non-Passeres by having a vinculum or band connecting the deep muscles of the toes. They have 15 cervical vertebrae as compared to 14 in most other Passeres, as well as other distinctions. It thus seems justifiable to follow those authorities who place the Eurylaimidae in a separate suborder. Their resemblances to the Pittidae or even the Cotingidae have led some to give them lesser rank.

The remaining Passeres may be divided into two groups, as follows:

A. Mesomyodes or Clamatores: Those in which the intrinsic muscles (if any) of the syrinx are attached to one of the ends or to the middle of the bronchial half rings (the Eurylaimidae agree with this group).

B. Acromyodes: Those in which these muscles are attached to both ends of the bronchial half rings.

Group A, Mesomyodes or Clamatores, is further divisible into two main groups: (1) those in which the syrinx is tracheobronchial (Haploophonae), and (2) those in which it is entirely tracheal (Tracheophonae). Group 1 contains both Old World and New World families. The former are the Pittidae (Asia, Australo-Papua, and Africa), Philepittidae (Madagascar), and Xenicidae[1] (New Zealand). Recent study has shown that the genus *Neodrepanis* of Madagascar is a philepittid (Amadon, in press). These three families, through not very closely related, are very likely more nearly allied to one another than to the Neotropical members of this group.

The remaining families of the "Haploophonae" are exclusively or predominantly (Tyrannidae) Neotropical, viz., Tyrannidae (in which we include *Oxyruncus* as a subfamily), Pipridae, Cotingidae,

[1] Since the name Xenicidae has prior usage, as for example in the "Catalogue of birds" of the British Museum, it is unnecessary to replace it by the more cumbersome Acanthisittidae merely because the latter is based on an older generic name.

and Phytotomidae. The Pipridae and Cotingidae differ from other passerines in that the femoral, not the ischiatic, artery is the principal one of the thigh. This is probably a functional character reflecting the relative development of the thigh muscles. Hence we do not think it necessary to make a separate family for the cock-of-the-rock, *Rupicola*, because it has the ischiatic artery predominant. This aberrancy may be correlated with its terrestrial dances.

Garrod united the manakins and cotingas in a single family. Further study may show that this procedure, with subfamily rank for the two groups, is justified. Of the genera currently assigned to the Pipridae, *Schiffornis* appears somewhat like a cotinga. *Calyptura* of the Cotingidae has been placed by some authors in the Pipridae. Some of the genera of both of these families are very much like some genera of the Tyrannidae. This is true of *Tyranneutes* and *Sapayoa* of the Pipridae. *Xenopsaris* was placed in the Cotingidae by Ridgway, in the Tyrannidae by Hellmayr.

The Cotingidae recall in some ways the Eurylaimidae, even to the construction of large, bag-like nests by the broadbills and by some cotingas. Pycraft was especially impressed by these similarities, and he thought the two groups might some day be reduced to subfamilies That the relationship is this close seems more than doubtful, but further study is needed. The peculiar genus *Phytotoma* (plant-cutters) somewhat resembles the cotingas, though the ischiatic is the principal artery of the thigh. It must be retained as a monotypic family pending further study.

The second division of group A is peculiar in that the syrinx is entirely tracheal. There are four families of "Tracheophonae," all Neotropical, the Rhinocryptidae, Conopophagidae, Formicariidae, and Dendrocolaptidae (including "Furnariidae").

The usual subdivision of the Tracheophonae into these four families is not particularly satisfactory. We follow the earlier authors who left the ovenbirds (*Furnarius* and allies) with the closely related woodhewers (*Dendrocolaptes* and allies), but the two groups may be retained as separate subfamilies. This family, Dendrocolaptidae, differs from the remaining tracheophones by having two rather than one pair of tracheo-bronchial muscles.

The group with one pair of tracheo-bronchial muscles is usually divided into a large family, the antbirds (Formicariidae), supposedly characterized by a two-notched metasternum, and two smaller families (Rhinocryptidae, Conopophagidae) in which the

metasternum is four-notched. Dr. J. T. Zimmer has called to our attention that the late Waldron Miller (unpublished) found that the genus *Melanopareia*, comprising otherwise typical formicarians, has a four-notched sternum. It is possible that further study will show that the Rhinocryptidae cannot be separated satisfactorily from the Formicariidae. The former may prove to be a polyphyletic group composed of specialized ant birds. The genus *Conopophaga* lacks intrinsic syrinx muscles altogether and has an exaspidean tarsal envelope. Whether these characters are constant enough to warrant full family status for this genus or not must remain with the future.

The Xenicidae of New Zealand resemble some of the Tracheophonae, particularly the genus *Conopophaga*. Both are long-legged, short-tailed denizens of the undergrowth, and both happen to have a white supraocular stripe. We do not think the parallelism is any more indicative of close relationship than, for example, that between such formicariids as *Grallaria* and such thrushes as *Amalocichla* or *Zeledonia*. The similarity of the Australian scrub bird, *Atrichornis*, to some of the Rhinocryptidae, e.g., *Liosceles* or *Scytalopus*, is, to our minds, equally a matter of adaptation to similar habitats.

In regard to group B above (those passeres in which the syrinx muscles are attached to both ends of the bronchial half rings), it contains, in addition to the true song birds, two primitive Australian families, the Atrichornithidae and Menuridae. Each of the latter contains but a single genus. Although very dissimilar in appearance, they share a number of anatomical peculiarities and are probably nearer to each other than either is to any other group. Although the attachment of the syrinx muscles in these two Australian families is similar to that of the Oscines, only two or three pairs of such muscles are present, as compared to five to seven pairs in the Oscines proper.

Probably further study of some of the larger of the groups mentioned above, e.g., the tyrant flycatchers, will reveal that they should be divided into subfamilies or tribes equivalent to those used below for some of the families of song birds.

The various suboscine perching birds give every appearance of being in the process of replacement by the Oscines. Many of the families of the former group have a relict distribution in Madagascar, New Zealand, Australia, or South America. The last continent was of course isolated for a long time. It has few well-

differentiated families of indigenous song birds, although the subfamilies of the tanager-pyrrhuloxine finch assemblage are richly developed. An adaptive radiation of the wrens, mimids, and other song birds of South America might reduce the Suboscines of that continent to the subordinate position they occupy in the Old World.

Oscines or True Song Birds

Of the approximately 8600 species of living birds, 5100 belong to the Passeres, and about 4000, to the Suborder Oscines. The difficulty in finding good anatomical characters that besets the avian taxonomist at every level is particularly acute in this suborder. As a group song birds are the most advanced, successful, and apparently latest to evolve of the entire Class Aves. They have developed an infinite variety of types, and many annectant and intermediate forms are still in existence. The "phylogenetic tree" of the group, if it could be drawn accurately, would probably resemble a great flat-topped "umbrella" tree.

Added to the above difficulties is a large amount of parallelism, often in different continents. For example, the American orioles and blackbirds (Icteridae) are the ecological homologues of the Old World starlings (Sturnidae). So slight are the anatomical distinctions in this suborder that these two groups were once placed in the same family by competent anatomists, though they are probably quite unrelated.

The object of the following discussion of the families of Oscines is not to present entirely novel findings. Rather it is to summarize the results of investigations of numerous workers and particularly the results of field workers who have often produced better clues to relationship than the anatomists. Furthermore, it is intended to expose our abysmal ignorance of the relationships of most songbird families. In spite of their basic uniformity, there are certain minor anatomical differences as pointed out by Stonor (1937) and Beecher (MS). It would seem high time to investigate previously unexplored anatomical systems (as Beecher has for the jaw muscles) in an attempt to shed new light on oscinine classification.

The shape of the bill has been used with too much confidence in the past as a reliable basis for classification. Actually the bill is the most plastic of all the organs of a bird, and evidence is mounting daily that shrike-like bills, warbler-like bills, finch-like bills, and flycatcher-like bills have been acquired repeatedly and

polyphyletically by various unrelated groups of Oscines. The investigation of the true relationship of these groups will be a rewarding task.

Habits are often a better clue to relationships than structure. Nest-building habits, for instance, are diagnostic for the subfamilies of Paridae, and similarity in nests was a clue to Mayr and Bond (1943) in allying *Ptyonoprogne* with *Hirundo* rather than with *Riparia*.

Only two or three oscinine families are reasonably well defined. The larks (Alaudidae) differ from the others by having the back of the tarsus rounded and broken up into plates. They also lack the bony pessulus at the junction of the bronchi in the syrinx. The Hirundinidae have the bronchial rings more or less complete; in other Oscines they are "half rings," with a membrane across the inner face. But, from here on, consistent family characters are extremely hard to find.

These difficulties have led some anatomists to divide the Oscines into only three or four families. This serves to keep passerine families equivalent to those of other orders, but does not help in classifying the many obviously monophyletic groups of song birds that must be designated somehow, whether we call them families, subfamilies, tribes, or what not. Certain groups clearly connected by linking forms may be reduced to the level of subfamilies as has been done for the thrush-babbler-flycatcher-warbler assemblage. This will, however, inevitably lead to the use of "tribes" or other intermediate categories, as in Delacour's (1946) revision of the Timaliinae. For this reason we have retained, for the time being, family status for a number of groups which it may prove expedient to reduce to subfamilies later.

The arrangement of the passerine families in a linear sequence is a task involving many compromises. At best, one can seek only to keep related families together. The classification of Stejneger, followed in considerable measure by that of Wetmore, places much weight on the relative reduction of the tenth (outer) primary. This trend towards specialization is of some importance, especially since all, or almost all, of the Suboscines have a long tenth primary, longer than in any oscinine. On the other hand, reduction of the tenth primary is certainly subject to reversal and is a highly adaptive, plastic, and polyphyletic character. For example, the genus *Urocynchramus* of the fringilline finches has a relatively long tenth primary, though all other finches lack one.

Other families in which the tenth primary may be present or absent from genus to genus are the Bombycillidae (*sensu lato*), Dicaeidae, and Sturnidae. The seemingly primitive Alaudidae have the tenth primary quite reduced or even vestigial in a few genera. Some highly specialized families, such as the Nectariniidae, have a moderately developed tenth primary. It certainly does not follow that the nine-primaried families are necessarily the "highest" song birds. Other characters denoting specialization, such as a booted condition of the tarsus, are also of variable significance.

A number of authorities, including W. K. Parker, Macgillivray, Sharpe, and Alfred Newton (1893–1896, pp. 117–120), thought that the Corvidae are, all in all, the most advanced and "highest" type of bird. Studies of the avian brain by Portmann (1947) have tended to show that *Corvus* ranks above other birds in brain development. As Dr. J. P. Chapin has pointed out to us, however, were similar attention given to certain icterids, sturnids, ploceids, and perhaps others, they might prove just as "advanced." Nevertheless, we have thought it best to follow the school that would terminate the oscinine series with the Corvidae and allied families. It is the sequence adopted in Sharpe's "Handlist" and in many ornithological reference works throughout the world.

It will be all too evident from this discussion that no linear sequence for the Oscines can be adequate and that various lines of specialization must often be followed to their conclusion and then a fresh start be made.

Unlike the Suboscines, which have their richest present representation in South America, the Oscines have flourished and differentiated chiefly in the Old World tropics and Australia. In these areas literally dozens of genera present such a problem that they have been shifted from family to family or assigned to "scrap baskets" such as the Prionopidae, Timaliidae, etc. We hope that the following discussion of these difficult groups, often with a listing of the genera involved, will prove useful.

ALAUDIDAE

The larks are perhaps best left at the beginning of the oscinine series because of the reticulate posterior surface of the tarsus and the absence of an ossified pessulus in the syrinx.

HIRUNDINIDAE

The swallows are specialized, but since they are well dif-

ferentiated from all other Oscines they may be left near the beginning of the sequence, for the time being at least, pending definite proof of affinity to other families. The African flycatcher, *Artomyias*, is very swallow-like and shows how swallows may have evolved from perching insect catchers. This is probably not an indication of true relationship. For a discussion of the genera of swallows, see Mayr and Bond (1943).

The curious African river-martin, *Pseudochelidon*, is very doubtfully a member of the swallow family, though Lowe (1938) placed it there. On the other hand, there is still less reason to place it in the Artamidae, which have completely different nesting habits, possess powder downs lacking in *Pseudochelidon*, and are absent from the Ethiopian region. We have examined the syrinx of *Pseudochelidon* from plentiful material supplied by Dr. James P. Chapin. The bronchial rings are all half rings, with a large internal membrane running the length of the bronchial tubes. Likewise, the bronchidesmus connecting the bronchii seems to be present, as in most song birds, whereas in swallows the bronchial rings tend to be complete and the bronchidesmus absent, though the only hirundinids available to us were so poorly preserved as to make it somewhat difficult to confirm these details.

We leave *Pseudochelidon* as a subfamily of the Hirundinidae, but probably it belongs in a separate family, possibly near the Prionopidae, to the members of which the bill and texture of the plumage bear some resemblances.

BULBULS AND ALLIES

CAMPEPHAGIDAE

Of the vast group of Old World insect eaters the cuckoo-shrikes are perhaps among the more primitive. In most of them the shafts of the dense feathers of the back are stiffened and enlarged, but this is absent or but weakly indicated in the minivets, *Pericrocotus*, and in the genus *Chlamydochera* of Borneo. The recent transfer of the genera *Tephrodornis* and *Hemipus* to the Campephagidae by Delacour and others is thus not necessarily invalidated by the absence of such modified shafts in these genera. In habits and nidification these two genera resemble cuckoo-shrikes, but it is quite possible that they are only "shrike-billed flycatchers."

IRENIDAE (AEGITHINIDAE)

The leafbirds were formerly associated with the Pycnonotidae but seem not very close. They may, however, be left in the general vicinity of the cuckoo-shrikes and bulbuls. Since Oberholser (1917b) proposed a family for the genus *Irena*, this family should be called Irenidae, not Aegithinidae. The genera of this family are *Aëthorhynchus*, *Aegithina*, *Chloropsis*, and *Irena*.

PYCNONOTIDAE

Bulbuls are among the more primitive appearing of Old World song birds. They may be related to the Campephagidae, but a few, such as *Nicator*, resemble some of the bush shrikes (Laniidae: Malaconotinae), though perhaps only superficially. Delacour (1943) has recently revised the family. We would leave the African genus *Neolestes* in the Pycnonotidae (Chapin, 1921).

A few other aberrant genera sometimes associated with the bulbuls are best removed. *Hypergerus* of west Africa is more apt to be a giant sylviid. *Apalopteron* of the Bonin Islands differs markedly from bulbuls, particularly by reason of its very long legs. It may well be an aberrant, insular sylviid or timaliid. We have tentatively placed it in the Timaliinae, near *Siva*. The peculiar *Tylas eduardi* of Madagascar may, in the opinion of Chapin, be a member of the Oriolidae. Oberholser (1917a) set up a separate family for this genus, but this seems scarcely advisable pending further knowledge of its anatomy. Other Madagascan genera of difficult assignment are dealt with by Delacour in his revisions of the bush warblers (1942), bulbuls (1943), and babblers (1946). The genus *Malia* of Celebes is hard to place. It may, as Delacour has suggested, be a bulbul adapted for terrestrial life.

PRIMITIVE INSECT EATERS

MUSCICAPIDAE

The group embraced by the above descriptive term has sometimes been called the "Old World insect eaters," but it is impossible to separate the New World wrens and thrashers from it, while even the predominantly Old World warblers and babblers have a few New World representatives, and the thrushes are well represented there. The phrase "insect eaters" is not, of course, to be taken too literally, since many of the thrushes, in particular, feed to a considerable extent on earthworms, snails, and fruit.

The satisfactory association of many components of this group into families is virtually impossible. This was recognized by Hartert and many later authorities who have listed the Old World flycatchers and warblers, as well as the babblers and thrushes, as subfamilies of the Muscicapidae. The Mimidae and Troglodytidae seem to deserve similar treatment, some of the West Indian genera, in particular, being very thrush-like, while others seem intermediate between wrens and mockers.

The Turdinae include a number of aberrant genera that probably deserve the status of separate tribes or may even be wrongly placed with this subfamily. By no means all of the tropical thrushes have a "booted" tarsus. Among these difficult genera are *Henicurus* and *Cochoa* in the Old World and *Zeledonia* in the New World. The last-named genus was thought by Sharpe and by Pycraft (1905) to be an aberrant thrush, distantly related to such genera as *Catharus*. *Erythropygia*, sometimes placed with the Sylviinae, seems correctly assigned to the Turdinae (Chapin). Our listing of tribes is only tentative.

The babblers or Timaliinae have long been a "scrap basket" for genera that did not fit well into the Turdinae or Sylviinae. Delacour's (1946) revision brought a semblance of order into this group, but even so he was obliged to set aside a section for "aberrant genera." To the five tribes that he set up, a sixth, the Picathartini, including only the west African genus *Picathartes*, is to be added (Delacour and Amadon, in press). This genus has usually been placed in the Corvidae, where it surely does not belong.

We agree with Delacour in placing the wren-tit, *Chamaea*, of California in the tribe Chaemaeini of the Timaliinae. This bird appears to be very closely allied to the genus *Moupinia* of China.

A number of genera of the Australo-Papuan region (*Eupetes*, *Cinclosoma*, *Orthonyx*, *Psophodes*, *Ifrita*, *Androphobus*, and *Melampitta*) do not fit well in the Timaliinae but may for the time being be left as a tribe, the Cinclosomatini, of that subfamily. Some may consider them as nearer to the Turdinae. These seven genera probably do not comprise a homogeneous group; *Psophodes*, as noted elsewhere, may belong to the Pachycephalini. *Cinclorhamphus*, sometimes associated with this group, we tentatively place in the Malurinae.

The subfamily Sylviinae contains a large number of genera and species difficult to divide satisfactorily into major subgroups

(with the exception of the American gnatcatchers and allies which may be considered a tribe). A few genera, such as *Megalurulus* of New Caledonia, might be placed in either the Sylviinae or Timaliinae.

Another most peculiar "warbler" is *Lamprolia victoria* of Fiji; further study may show that it has nothing to do with this family (Mayr, 1945, p. 137).

Regulus agrees so well with some species of *Phylloscopus* as to leave little room for doubt that it is a sylviid adapted to boreal coniferous forests. More doubt exists as regards the central Asiatic *Lophobasileus* and *Leptopoceile*. These little birds suggest *Regulus*, but might be related to titmice, notably *Aegithalos*. We follow custom in leaving them near *Regulus* and *Phylloscopus*. Their mossy ground nest favors this assignment.

In Australia, New Guinea, Polynesia, and New Zealand there is a group of some 85 species of warblers which appears to be better differentiated than either the kinglets (*Regulus*) or the gnatcatchers (*Polioptila* and allies) and which deserves subfamily rank under the above name. It includes the birds grouped in the Acanthizidae in the 1926 "Checklist of Australian birds" of the Royal Australasian Ornithologists Union and comprise the following genera:

Malurus and its closest allies: *Clytomyias* (New Guinea only), *Chenorhamphus* (New Guinea only), *Todopsis* (New Guinea only), *Malurus*, and *Stipiturus*. The following are less closely allied to *Malurus: Dasyornis*, *Amytornis*, *Aphelocephala*, *Ephthianura* (including *Ashbyia*), *Smicrornis*, *Acanthiza*, *Pyrrholaema*, *Finschia* (New Zealand only), *Mohoua* (New Zealand only), *Pycnoptilus*, *Calamanthus*, *Eremiornis*, *Hylacola*, *Chthonicola*, *Gerygone*, *Hapolorhynchus* (New Zealand only), *Sericornis*, *Vitia*, *Origmella*, and *Crateroscelis*. *Cinclorhamphus* also may belong here.

The Muscicapinae are in need of a generic revision, but we have recognized as tribes the well-defined fantails of the genus *Rhipidura* (see Oliver, 1945, p. 143) and also the monarch-paradise flycatcher group (*Monarcha*, *Hypothymis*, *Terpsiphone*, and allies).

Of the Muscicapini proper, some of the African genera, such as *Fraseria*, have a great resemblance to thrushes. *Stizorhina*, formerly placed with the flycatchers, is considered by Chapin to be a thrush, very close to *Neocossyphus*.

The shrike-billed flycatchers (Pachycephalini) of the Australian region are often quite different from the average flycatchers in

appearance and manner of feeding but intergrade completely with them through such genera as *Pachycephalopsis* and *Heteromyias*.

Concerning the genera of the tribe Pachycephalini, *Coracornis* and *Hylocitrea* of Celebes and *Rhagalogus* of New Guinea are not far from *Pachycephala* proper. *Eulacestoma* of New Guinea, set apart by its large wattles, is intermediate in specialization of the bill between *Pachycephala* and *Falcunculus*. The peculiar *Pachycare*, which may not be a flycatcher at all, is best left near *Falcunculus*.

Another line leads to rather large, coarse-billed but otherwise unspecialized forms, from *Pachycephala* through *Oreoica* and *Colluricincla* (including *Myiolestes*) to *Pitohui*. *Turnagra*, the so-called New Zealand thrush, probably belongs here rather than in the Turdinae. Its skull is very different from that of *Turdus* (Oliver, 1945, p. 148). The Australian genus *Psophodes*, considered by Delacour to be an aberrant babbler, may belong near *Oreoica* in the Pachycephalini.

CINCLINAE

The dippers agree with the Turdinae in having a booted tarsus and (to some extent) in the mottled immature plumage of some of the Old World dippers, characters emphasized by Stejneger (1905). Other writers have been more impressed by their resemblance to wrens (Troglodytinae). The classification depends somewhat on the decision as to whether *Cinclus* is of New or Old World origin, but the distributional evidence is again somewhat equivocal. In either case, we do not feel that the characters of *Cinclus*, consisting chiefly of adaptations for its aquatic accomplishments, merit more than subfamily rank.

PRUNELLIDAE

The hedge sparrows resemble buntings (Emberizinae) in appearance and posture and also by living in part upon seeds and by having a true crop. On the other hand, the bill is more or less thrush-like, and the tenth primary is not vestigial as in the buntings.

The Heinroths (1924–1926, p. 34) suggest that *Prunella* may be a rather primitive genus related both to thrushes and finches. Since the Emberizinae are presumably of American origin and

Prunella is, at least at present, Palearctic, it is possible that the resemblance of the hedge sparrows to the buntings is parallelism.

MOTACILLIDAE

No one believes any longer that the pipits or "tit-larks" are related to the true larks, yet they are left in that vicinity in most classifications. The completely nine-primaried wing is correlated with their rapid sweeping flight and is merely paralleled by the tendency towards loss of the tenth primary in the Alaudidae. Probably the pipits are modified descendants of some group of turdids or sylviids, and they are best placed following this group of families.

SHRIKES AND ALLIES

This group appears possibly to represent somewhat specialized offshoots of the preceding large group of insect eaters. In the pachycephaline flycatchers of the Australian region, the intermediate steps leading from the Muscicapinae are unmistakable. The shrikes and their allies may have evolved similarly, but the intermediates are absent or can no longer be determined with confidence.

LANIIDAE

The Laniidae of early authors included distantly related genera that had only one feature in common, a hooked, *Lanius*-like bill. This functional adaptation has apparently arisen independently many times in birds with similar feeding habits. Various genera assigned to the Laniidae at one time or another have since been placed with the Pachycephalinae, Campephagidae (*Tephrodornis, Hemipus*), Vireonidae, Cracticidae, Vangidae, and Prionopidae.

The African bush shrikes (subfamily Malaconotinae) do not seem to be true shrikes either, but may be left in the Laniidae until more is known of their affinities. Of the 10 genera listed by Sclater (1924–1930, pp. 615–638) we would recognize only the following six, synonymizing those placed in parentheses: *Malaconotus* (*Chlorophoneus, Telophorus*), *Rhodophoneus, Tchagra* (*Antichromus*), *Laniarius, Dryoscopus* (*Chaunonotus*), *Lanioturdus*. As suggesting the possible relationships of this subfamily, one may note a similarity of *Malaconotus* to certain bulbuls (*Nicator*). *Lanioturdus* (which may not be a bush shrike itself) along with *Nilaus* (formerly considered a bush shrike but assigned by Mayr

[1943] to the Muscicapinae) suggests that the Malaconotinae in Africa may be allied to the Muscicapinae, notably to such Ethiopian genera as *Batis* and *Platysteira*, in somewhat the same way as are the Pachycephalinae in the Australian region.

In the Laniinae proper we leave only *Lanius* and the long-tailed African shrikes, *Urolestes* and *Corvinella*.

PRIONOPIDAE

The prionopids proper are reduced to three African genera (*Prionops*, *Sigmodus*, and *Eurocephalus*) after the removal of various unrelated genera (Mayr, 1943). There is a certain resemblance between the Prionopidae and some genera of African flycatchers and bush shrikes (Malaconotinae). It is therefore probable that this family should be associated with the primitive insect eaters and with the Laniidae.

On geographical premises it seems unlikely that the peculiar *Pityriasis gymnocephala* of Borneo (one of the strangest members of all the Oscines) is related to the Prionopidae. It was for this reason that Mayr (*op. cit.*) suggested that it be removed from that family. This bird does not seem to fit well anywhere else, however, and agrees with *Prionops*, and more particularly with *Sigmodus scopifrons*, in proportions, wing pattern, and other details. Moreover, one sees in these African Prionopidae a tendency towards specialization of the head feathers and presence of wattles that might be the forerunner of the bristle-like head feathers that suggested the name "*Pityriasis*" for the Borneo genus. Yet T. H. Harrisson (*in litt.*) is impressed by its "mynah-like" behavior.

VANGIDAE

The vangas are of somewhat uncertain affinities but may be related to the other shrike-like birds, particularly the Prionopidae. The Vangidae have become so diverse in the isolation provided by Madagascar that it is difficult to decide what the ancestor of the group was like.

The Australian "magpies" (Cracticidae) resemble shrikes and, even more, *Pityriasis* in the shape of the bill, but we think they are more likely to be related to the Australian corvid-like families, including the Grallinidae, Paradisaeidae, etc., and place them there.

ARTAMIDAE

The family contains but the one genus, *Artamus* (unless the African *Pseudochelidon* eventually is shown to belong here). The relationships of *Artamus* are doubtful, but there is a certain resemblance to some of the Vangidae and even to the Bombycillidae. It may be tentatively left in the vicinity of these families.

BOMBYCILLIDAE

The reasons for treating the American silky flycatchers, the West Indian palm chat, *Dulus*, and the Persian genus *Hypocolius* as subfamilies of the Bombycillidae have been given by Arvey (1949) and Delacour and Amadon (1949). The broader question of the relationships of the family are much more difficult. As pointed out to us by Chapin, *Hypocolius* shares with *Eurocephalus*, and to a lesser extent with *Prionops*, the peculiar feature of having the normally unbroken plates comprising the rear half of the oscinine tarsus divided weakly into a number of shields or scutes. This might mean that the resemblance of *Hypocolius* to other bombycillids is superficial. Another possibility is that the Bombycillidae belong in the general vicinity of the Prionopidae and related families. We here tentatively follow the latter alternative.

CREEPERS, NUTHATCHES, AND TITMICE

These birds are all primarily of Old World origin and may have evolved from generalized insect eaters.

CERTHIIDAE

The genus *Certhia* has had a long history of tree creeping, as shown by the spiny tail and specialized tail molt wherein the two central feathers are retained until all the others are replaced, thus giving continuous support. This adaptation occurs elsewhere only in the Picidae. All the other "creepers" sometimes placed in the Certhiidae are more like nuthatches, but we leave the Certhiidae near the Sittidae, should there be any relationship.

SITTIDAE

This family, as we conceive it, is admittedly something of a "scrap basket." We tentatively suggest the following subfamilies:

SALPORNINAE: *Salpornis*, *Rhabdornis*, *Climacteris*, and *Tichodroma*. The members of these genera all have a rather long, de-

curved bill. *Rhabdornis* (Philippines) and *Climacteris* (Australia) appear to be related, but whether or not they are allied to *Salpornis* (India, Africa) is a moot question. The wall creeper (*Tichodroma*) resembles in some ways the nuthatches (*Sitta*) and may be a specialized derivative of some such bird as the rock nuthatch (*Sitta tephronota*). The Heinroths (1924–1926) point out a number of differences between the two genera, and the true position of *Tichodroma* remains doubtful.

SITTINAE: *Sitta*, *Neositta*, and *Daphoenositta*. The Australo-Papuan tree-runners (*Neositta*, *Daphoenositta*) resemble in many ways some of the nuthatches such as *Sitta frontalis*. This may be misleading, since the open nests of the various species of *Neositta* are not at all like those of the members of *Sitta*. Perhaps *Neositta* is related to *Climacteris*.

HYPOSITTINAE: The coral-billed "nuthatch" of Madagascar is another puzzling bird. It suggests some of the nuthatches, but the proportions are those of the true creepers (*Certhia*), which it resembles in habits. The tail feathers are unmodified. Rand (1936a, 1936b) has written on the habits and position of *Hypositta*, *Neositta*, and *Daphoenositta*.

PARIDAE

The tits appear to be a polyphyletic group of genera placed together on the basis of superficial resemblance due to arboreal habits and a fine, more or less conical bill. Three groups can be distinguished:

1. The true titmice. This consists of the genus *Parus* and the closely related *Melanochlora* (sultan tits). *Sylviparus* is a dubious member of this group.

There is a remarkable resemblance between some of the jays, particularly the boreal *Perisoreus*, and the genus *Parus*. This similarity does not extend to the skull or the internal anatomy, and Ridgway (1904, pp. 253–254) stated that even the external features "when closely examined, show many points of difference." It is probable, therefore, that the like manner in which jays, titmice, and even nuthatches hold nuts or seeds in their feet while opening them or store them away in crevices for future use has no great phylogenetic significance. Kramer (1930) has published data on the occurrence of such habits in various groups of birds. A parallel case is the habit of the true shrikes (*Lanius*) and of the unrelated Australian "shrikes" (*Cracticus*) of impaling and dismembering small birds and rodents.

2. *Remiz-Auriparus* group. These birds may be distantly related to the Dicaeidae (flowerpeckers). They are characterized by the peculiarly shaped bill and the bag-like nest they construct. *Cephalopyrus* may belong to this group, though it is a hole nester.

3. *Aegithalos-Psaltriparus-Psaltria.* In their complete juvenal molt (Stresemann, 1923), cranial characters, and nest structure (Lucas, 1890), the long-tailed tits and bush tits differ radically from the Paridae. The young hatch naked, while young of the true titmice are partly downy. They share several of these characters with *Panurus* and *Paradoxornis* and are perhaps nothing but an offshoot of the Timaliinae. The fact that the parrotbills make a cup-like nest, while the nest of the present group is bag-like, is not, however, favorable to this suggestion.

It is now universally agreed that *Panurus* is a close relative of *Paradoxornis*. Delacour (1946) places it, together with *Chamaea*, in the tribe Chamaeini of the Timaliinae, along with the other "parrot-bills."

OLD WORLD NECTAR EATERS

DICAEIDAE

The primitive fruit-eating dicaeid genus *Melanocharis* of New Guinea has a great resemblance to certain genera of Meliphagidae (*Timeliopsis, Oedistoma*). Since the latter have a highly specialized tongue and that of *Melanocharis* is unspecialized (Mayr and Amadon, 1947), this resemblance may not indicate affinity.

Another moot affinity of the flowerpeckers is with the birds placed by us in the subfamily Remizinae of the Paridae. The genus *Cephalopyrus* of the Himalayas could be an intermediate.

Finally, one may mention, as possibly repaying study, the resemblance of certain flowerpeckers to the Bombycillidae in appearance, fondness for mistletoe berries, gregarious habits, and other details of behavior.

NECTARINIIDAE

The sunbirds, a very compact group (Delacour, 1944), are evidently relatives of the Dicaeidae, highly specialized for nectar feeding. The tongue is quite similar in sunbirds (Scharnke, 1932) and in the nectar-feeding kinds of flowerpeckers, and both build a similar pensile nest. Though more specialized as regards plumage and modification of the tongue, sunbirds do not show the progressive loss of the tenth primary culminating in the nine-

primaried condition of such dicaeid genera as *Pardalotus* and many species of *Dicaeum*.

The Dicaeidae are best represented in Australia, Papua, the East Indies, and the Philippines, and do not reach Africa; almost the reverse is true of the Nectariniidae.

The curious African genera, *Pholidornis* and *Parmoptila*, formerly associated with the Dicaeidae or Nectariniidae, are considered by Chapin (1917) to be aberrant, thin-billed Ploceidae, with which we agree.

The African species *Hylia prasina* has usually been placed in the Sylviinae and may be an aberrant member of that group. Bates (1930, p. 447) figured the hyoid bones of this species, which he found to be flattened like those of a sunbird. The tenth primary is rather larger than in typical sunbirds. He placed *Hylia* in a separate family but thought it was allied to the Nectariniidae. Serle (1949, p. 212), among others, found its habits and call notes to suggest those of a sunbird, though the song is more musical. The nest is more or less globular, not much like that of a sunbird. *Hylia* may be a primitive sunbird. Chapin considers this possible but not established.

MELIPHAGIDAE

The numerous members of this Australo-Papuan family have, with one or two exceptions, a highly modified suctorial tongue, unlike that of flowerpeckers or sunbirds and surely of independent evolution. Otherwise they are rather unspecialized Oscines, except for the frequent presence of ornamental tufts of yellow feathers or of bare areas or wattles around the eyes. As noted above, they may be distantly related to the Dicaeidae.

The curious nectar-feeding sugar bird, *Promerops cafer* of South Africa, has a stomach and tongue like those of the Australian meliphagids (Scharnke, 1932). Its external appearance is also similar. It seems definitely not to be a sunbird (Nectariniidae). *Promerops* feeds on flowers of trees of the genus *Protea*, plants also well represented in Australia. Salomonsen (1933) advanced the theory that *Promerops* was once much more widespread (along with *Protea*) and that both were gradually restricted to South Africa. The Meliphagidae are, however, so strictly Australian in distribution that it is difficult to believe that one genus wandered so widely while all the others failed to make their way even to Asia, much less to Africa. Also, many Meliphagidae are not

specialized as to food plants. The possibility of some South African-Australian transfer remains, of course, highly speculative.

We leave *Promerops* as a subfamily of the Meliphagidae, but we feel that its similarity may, after all, be parallelism.

ZOSTEROPIDAE

The relationships of the Zosteropidae remain to be discovered. Since some of them are somewhat specialized for feeding on nectar, they may continue to be left in the vicinity of the Meliphagidae and Dicaeidae. The nine-primaried wing indicates a considerable degree of specialization.

VIREOS, TANAGERS, FINCHES, AND ALLIES

The Vireonidae may be the most primitive family of this assemblage. Its members often have a functional tenth primary, and they are otherwise rather unspecialized, usually insectivorous birds. The shrike-billed vireos, *Vireolanius*, and pepper-shrikes, *Cyclarhis*, have the longest tenth primaries and may well be the most primitive of the vireos, despite their large size and bright colors. It seems best to place these genera in the Vireonidae and not to set up monotypic families for them (Zimmer, 1942).

The wood warblers (Parulinae) are perhaps most like the vireos. The warblers in turn are not far from the Coerebinae, while some of the latter have always been admitted to be very difficult to separate from many tanagers (Thraupinae). All of these groups (except the vireos) may best be considered subfamilies of the Thraupidae. Additional subfamilies are the plush-capped finch, *Catamblyrhynchus*, which is not aberrant enough to require a family, and the pyrrhuloxias and cardinal grosbeaks (Pyrrhuloxiinae). The latter, as is well known, are very difficult to separate from the tanagers. Such a genus as *Saltator* provides a transition. *Richmondena* seems to be congeneric with *Pyrrhuloxia*, so the subfamily takes its name from the latter genus.

The swallow-tanager, *Tersina*, has a very peculiar palate (Lucas, 1895). Its habit of nesting in holes in trees is also remarkable. It is best to leave it in a separate family for the present.

Whether the Pyrrhuloxiinae are closely related to the buntings and American sparrows (Emberizinae) or merely parallel them will remain uncertain until careful studies have been made of the numerous, chiefly Neotropical, genera. Until such time, it is

best to keep the buntings as a subfamily of the Fringillidae. The only other subfamily of this family will be the Fringillinae which includes the chaffinches, linnets, evening grosbeaks, and others. It is the only subfamily of the entire assemblage of families better represented in the Old World than in the New, but even this group is presumably of American origin. If the Ploceidae should be found to be related to the finches, which we doubt, the center of origin of the Fringillinae and perhaps other subfamilies must be viewed in a different light.

Sushkin (1924) separated the chaffinches, *Fringilla*, in a subfamily distinct from the goldfinches and their relatives ("Carduelinae"). He gave no reason for this separation, and we think it unnecessary.

A few puzzling genera may be mentioned. The extinct, huge-billed *Chaunoproctus* of the Bonin Islands is, in our opinion, related to *Carpodacus*, not to the Pyrrhuloxiinae (pair in Leiden examined in 1950). *Neospiza concolor* of San Tomé is now recognized to be a finch, not a weaverbird, and is to be placed in the Fringillinae next to *Poliospiza* (*fide* Chapin). The two species of *Nesospiza* from the Tristan da Cunha group seem to belong to the Fringillinae, perhaps near *Serinus*, although Lowe and others are correct in believing that the Gough Island finch, *Rowettia*, is not related to *Nesospiza* but was derived from the South American genus *Melanodera*. From the latter it is scarcely separable generically.

In the "Catalogue of birds of the Americas, part 11" Hellmayr (1938) lists no fewer than 28 genera in the Fringillinae and "Carduelinae." Of these only the following seem properly to belong there: *Fringilla*, *Coccothraustes*, *Hesperiphona*, *Pyrrhula*, *Carpodacus*, *Pinicola*, *Leucosticte*, *Chloris*, *Carduelis*, *Acanthis*, *Loximitris*, *Spinus*, and *Loxia*. The extraneous genera included by Hellmayr belong for the most part to the Pyrrhuloxiinae and perhaps, in a few cases, to the Emberizinae. This includes a few genera, such as *Sicalis*, which resemble goldfinches, *Spinus*, but apparently only superficially. In the Old World there has been less trouble in delimiting the Fringillinae, with the exception of the genus *Montifringilla*, which resembles *Leucosticte* but is actually a member of the Ploceidae.

The Hawaiian honeycreepers (Drepaniidae) while closely related to the families discussed above are rather difficult to align with any one of them (Amadon, 1950b). For this reason we leave

them as a family. An insectivorous and nectarivorous rather than frugivorous or granivorous type of bird seems most primitive in this family.

The Icteridae are a better differentiated and perhaps a somewhat older group than most of the other nine-primaried passerines. There is a remarkable amount of parallelism between the Icteridae as compared with the Ploceidae and Sturnidae, which might indicate distant relationship.

WEAVERBIRDS, STARLINGS, AND ASSOCIATED FAMILIES

Among the more important papers on the Ploceidae are those of Chapin (1917), Sushkin (1927), and Delacour (1943 and earlier). It is quite possible that the family is composite. Of the more typical weavers, the genera *Bubalornis* and *Dinemellia* seem the most primitive. They contain species that are rather large, coarse, heavy-billed birds suggestive of starlings (von Boetticher, 1931), and presumably may represent the stock ancestral to *Ploceus* and its relatives. On the other hand, the Estrildinae may well have evolved from thin-billed, small birds similar to the living species of *Pholidornis*, *Parmoptila*, and *Nigrita*. That *Pholidornis* is a weaver is still open to question, but Chapin considers it probable.

The parasitic Viduinae resemble their hosts, the Estrildinae, even to the mouth spots of the nestlings. Some consider this mimicry, as indeed it may be in part, but Chapin believes the two subfamilies to be closely allied, if, indeed, subfamily separation is necessary. The other parasitic weaver, *Anomalospiza imberbis*, belongs to the Ploceinae. It is parasitic on warblers, not upon other weavers. We think it unnecessary to recognize subfamilies for *Plocepasser* (Passerinae) or *Sporopipes* (Ploceinae).

STURNIDAE

The genera of the Sturnidae were revised by Amadon (1943).[1]

[1] A correction to that paper may be given here. *Speculipastor bicolor* Reichenow was placed in the genus *Spreo* and renamed *bicoloratus* to avoid conflict with *Spreo bicolor* Gmelin. Dr. H. von Boetticher has brought to my attention that Reichenow later (1914, p. 356) made his own genus *Speculipastor* a synonym of *Spreo* and used the name *speculiferus* for the species he had named *bicolor*. This was done in such a cryptic manner that the name was missed in all subsequent general lists. The name *speculiferus* Reichenow will stand, however, with *bicoloratus* and *bicolor* as synonyms, so long as this species is placed in the genus *Spreo*.—D. A.

Since then Chapin (1948) has shown that *Neocichla* belongs to this family.

The primitive buffalo-weavers (Bubalornithinae) bear a certain resemblance to some of the starlings (von Boetticher, 1931), and the two families may be related, although this cannot be taken as definitely established. Some of the Papuan glossy starlings of the genus *Aplonis* nest in colonies and build long, hanging nests similar to those of such species as *Ploceus philippinus*. Both *Passer domesticus* (Ploceidae) and *Acridotheres tristis* (Sturnidae) lay their eggs either in holes or in domed tree nests, according to local conditions. Whether this similarity in nesting habits is indicative of relationship or not is another question. The bill of the African ox-bird, *Buphagus*, and of the Celebesian starling, *Scissirostrum dubium*, are slightly like that of some weavers, but this is pure convergence. *Scissirostrum* is a specialized, not a primitive, starling as regards bill form and function (Amadon, 1943).

The long-extinct *Fregilupus varius* of the Mascarene Islands is not unlike some of the Vangidae in color pattern. Recent comparison of mounted specimens of *Fregilupus* in the museums at Leiden and at Paris convinced the junior author that it is correctly assigned to the Sturnidae. The outermost primary is much reduced as in most Sturnidae, not long as in the Vangidae. Presumably the same is true of *Necropsar leguati*, another long-extinct Mascarene species.

ORIOLIDAE; DICRURIDAE

The orioles and drongos parallel in degree of specialization some of the starlings, though they are not necessarily related to them. Indeed, it may be that both families are better placed in the vicinity of the Campephagidae and Irenidae, but more evidence is needed. For a revision of the Dicruridae, see Vaurie (1949).

As stated above, we tentatively place the genus *Tylas* of Madagascar in the Oriolidae.

CROWS AND AUSTRALIAN CORVID-LIKE FAMILIES

CORVIDAE

For a revision of the genera, see Amadon (1944). Lowe (1949) has since established a monotypic family for *Zavattariornis*, but this Abyssinian genus seems to be a generalized corvid. Our rea-

sons for following the earlier authorities who placed the crows at the apex of the Class Aves were mentioned earlier.

The jays are the most primitive of the Corvidae. From them evolved first the magpies and finally *Corvus*, a genus that contains what are in many ways the most adaptable and highly evolved of all birds.

The Australian families associated with the crows resemble the Corvidae and equal them in degree of specialization but may well be of independent evolution. They all have a tarsus that is weakly scutellated or even booted, a point of difference from the true corvids.

GRALLINIDAE

In this family we unite the three genera of so-called Australian mud-nest builders, *Grallina*, *Corcorax*, and *Struthidea*. The last two give many indications of relationship despite the difference in the bill (Amadon, 1944). *Grallina* (including the Papuan *Pomareopsis*) is a very peculiar genus, but the fact that it builds the same bowl-shaped mud nest as the other two suggests that it may, after all, be related to them. A preliminary study by the junior author, including comparison of the skulls of all three genera, has not brought to light any basic differences (Amadon, 1950a). Partly to avoid too many monotypic families, we place all three genera in the same family but keep *Grallina* in a separate subfamily. Should this course prove correct, the variation in the bill of these genera would parallel that in the three genera of the New Zealand Callaeidae. Indeed, the two families have much in common.

CALLAEIDAE

Stonor (1942) showed that *Callaeas*, *Philesturnus*, and *Neomorpha* [= *Heteralocha*] belong in a single group. He accepted Garrod's (1872) supposed evidence for the affinity of *Neomorpha* to the Sturnidae, but perusal of that paper does not indicate that Garrod himself meant to imply any close ties. At that time Garrod included the Icteridae in the Sturnidae, and he apparently found as much resemblance in the icterid as in the true sturnid skull to that of the Huia. The chief point of resemblance consisted of facets for the attachment of the large digastric muscles, which, as Lowe (1938) and Lorenz (1949) have shown, are an adaptation for operating a long bill that can be opened forcibly

against resistance. We do not think the Calleidae and Sturnidae are allied.

CRACTICIDAE

The bell magpies or piping crows of the Australian region, as mentioned earlier, resemble the Laniidae and associated families, but in our opinion their real relationship is probably with the Australian and New Zealand corvid-like families. The Cracticidae agree with these families by having the tarsus almost booted. Pycraft thought the Cracticidae to be very near to the bowerbirds and birds of paradise. There is a striking resemblance in color pattern between *Grallina* and some species of *Cracticus*, but *Grallina* is so aberrant that this cannot safely be used as a basis for comparison.

In the largest forms of *Strepera* (Cracticidae) the plumage is almost or entirely black, and the hook on the bill may be absent in adults. The result is a bird very much like a crow, *Corvus*, but this is parallelism, although the families to which these genera belong may not be very distantly related. For a further discussion and revision of the Cracticidae, see Amadon (in press).

PTILONORHYNCHIDAE; PARADISAEIDAE

Stonor (1937) found some consistent differences between the skulls of bower birds and birds of paradise so that the two groups may be placed in separate families. Similarities in behavior and in general morphology, however, indicate that they are not distantly related.

SYSTEMATIC LIST

All living or recent orders and families are given in the following list, but subfamilies and tribes have been introduced only as necessary to indicate new groupings. Suborders have been listed only in the Passeres. For the song birds, vernacular groupings are used also, to aid in associating related families.

The numbers of recent known species for each unit follow the names, those of subfamilies being in parentheses.

Order Struthiones
    Family Struthionidae, Ostrich, 1
Order Apteryges, Moas (fossil) and Kiwis
    Family Apterygidae, Kiwis, 3

Order Casuarii
- Family Casuariidae, Cassowaries, 3
- Family Dromaeidae, Emus, 2

Order Rheae
- Family Rheidae, Rheas, 2

Order Crypturi (Tinamiformes)
- Family Tinamidae, Tinamous, 33

Order Sphenisci
- Family Spheniscidae, Penguins, 16

Order Tubinares (Procellariiformes)
- Family Diomedeidae, Albatrosses, 13
- Family Procellariidae, 73
  - Subfamily Hydrobatinae, Storm Petrels, (20)
  - Subfamily Procellariinae, Shearwaters, etc., (53)
- Family Pelecanoididae, Diving Petrels, 4

Order Podicipedes (Colymbiformes)
- Family Podicipitidae, Grebes, 20

Order Gaviae
- Family Gaviidae, Loons, 4

Order Steganopodes (Pelecaniformes)
- Family Phaëthontidae, Tropic Birds, 3
- Family Fregatidae, Frigate Birds, 5
- Family Phalacrocoracidae, Cormorants, Anhingas, 31
  - Subfamily Phalacrocoracinae, Cormorants, (30)
  - Subfamily Anhinginae, Anhingas, (1)
- Family Sulidae, Boobies, Gannets, 9
- Family Pelecanidae, Pelicans, 6

Order Falcones or Accipitres
- Family Accipitridae, Hawks, Eagles, etc., 205
- Family Falconidae, Falcons, etc., 58
- Family Pandionidae, Osprey, 1
- Family Cathartidae, New World Vultures, 6
- Family Sagittariidae, Secretary Bird, 1

Order Gressores (Ciconiiformes)
- Family Ardeidae, Herons, etc., 59
- Family Threskiornithidae, Ibises, etc., 28
- Family Ciconiidae, Storks, 17
- Family Scopidae, Hammerhead, 1

Order Phoenicopteri
- Family Phoenicopteridae, Flamingos, 6

Order Anseres
- Family Anatidae, Swans, Geese, Ducks, 145
- Family Anhimidae, Screamers, 3

Order Galli
- Family Megapodiidae, Brush Turkeys, 10
- Family Cracidae, Guans, etc., 38
- Family Phasianidae, Pheasants, etc., 190
  - Subfamily Phasianinae, Pheasants, Quail, etc., (165)
  - Subfamily Numidinae, Guineafowl, (7)

Subfamily Tetraoninae, Grouse, (18)
Family Meleagrididae, Turkeys, 2
Family Opisthocomidae, Hoatzin, 1
Order Cuculi
Family Musophagidae, Turacos, 19
Family Cuculidae, Cuckoos, 128
Order Grues
Family Cariamidae, Seriamas, 2
Family Psophiidae, Trumpeters, 3
Family Gruidae, Cranes, 14
Family Aramidae, Limpkin, 1
Family Eurypygidae, Sun Bittern, 1
Family Heliornithidae, Sun Grebes, 3
Family Rhynochetidae, Kagu, 1
Family Otididae, Bustards, 23
Family Rallidae, Rails, 132
Family Mesoenatidae, Roatelos, 3
Family Turnicidae, Button Quails, 16
Subfamily Turnicinae, Typical Button Quails, (15)
Subfamily Pedionominae, Plains Wanderer or Collared Hemipode, (1)
Order Laro-Limicolae (Charadriiformes)
Family Jacanidae, Jacanas, 7
Family Thinocoridae, Seed Snipe, 4
Family Chionididae, Sheath Bills, 2
Family Dromadidae, Crab Plover, 1
Family Burhinidae, Thick-knees, 9
Family Haematopodidae, Oystercatchers, 6
Family Charadriidae, Plovers, Sandpipers, etc., 152
Subfamily Charadriinae, Plovers, (63)
Subfamily Scolopacinae, Sandpipers, etc., (77)
Subfamily Phalaropinae, Phalaropes, (3)
Subfamily Recurvirostrinae, Avocets, Stilts, (7)
Subfamily Rostratulinae, Painted Snipe, (2)
Family Glareolidae, Pratincoles, Coursers, 16
Family Laridae, Gulls, etc., 89
Subfamily Stercorariinae, Jaegers, Skuas, (4)
Subfamily Larinae, Gulls, (43)
Subfamily Sterninae, Terns, (39)
Subfamily Rynchopinae, Skimmers, (3)
Family Alcidae, Auks, etc., 22
Order Columbae
Family Pteroclidae, Sand Grouse, 16
Family Columbidae, Pigeons, 289
Family Raphidae, Dodos, 3
Order Psittaci
Family Psittacidae, Parrots, 316
Order Striges
Family Strigidae, Owls, 134
Subfamily Striginae, Typical Owls, (123)

Subfamily Tytoninae, Barn Owls, (11)
Order Caprimulgi
Family Aegothelidae, Owlet Frogmouths, 8
Family Podargidae, Frogmouths, 12
Family Caprimulgidae, Goatsuckers, etc., 67
Family Nyctibiidae, Potoos, 5
Family Steatornithidae, Oil Bird, 1
Order Trogones
Family Trogonidae, Trogons, 35
Order Coraciae
Family Coraciidae, Rollers, 17
Subfamily Leptosomatinae, Cuckoo Rollers, (1)
Subfamily Brachypteraciinae, Ground Rollers, (5)
Subfamily Coraciinae, Typical Rollers, (11)
Family Alcedinidae, Kingfishers, 87
Family Meropidae, Bee Eaters, 25
Family Momotidae, Motmots, 8
Family Todidae, Todies, 5
Family Upupidae, Hoopoes, 7
Subfamily Upupinae, Typical Hoopoe, (1)
Subfamily Phoeniculinae, Tree Hoopoes, (6)
Family Bucerotidae, Hornbills, 45
Order Colii
Family Coliidae, Mousebirds, 6
Order Macrochires (Apodiformes; Micropodiformes)
Family Apodidae, Swifts, 79
Subfamily Apodinae, Typical Swifts, (76)
Subfamily Hemiprocninae, Crested Swifts, (3)
Family Trochilidae, Hummingbirds, 319
Order Pici
Family Bucconidae, Puffbirds, 32
Family Galbulidae, Jacamars, 14
Family Capitonidae, Barbets, 76
Family Picidae, Woodpeckers, etc., 210
Subfamily Jynginae, Wrynecks, (2)
Subfamily Picumninae, Piculets, (29)
Subfamily Picinae, Woodpeckers, (179)
Family Ramphastidae, Toucans, 37
Family Indicatoridae, Honey Guides, 12
Order Passeres
Suborder Eurylaimi
Family Eurylaimidae, Broadbills, 14
Suborder Tyranni
Superfamily Furnarioidea (Tracheophonae)
Family Rhinocryptidae, Tapaculos, 26
Family Conopophagidae, Ant-pipits, 10
Family Formicariidae, Antbirds and Allies, 221
Family Furnariidae, Ovenbirds and Woodhewers, 259
Subfamily Furnariinae, Ovenbirds, (212)

Tribe Enicurini, Fork Tails
Subfamily Miminae, Mockers and Thrashers, (30)
Subfamily Troglodytinae, Wrens, (63)
Subfamily Cinclinae, Dippers, (5)
Family Prunellidae, Hedge Sparrows or Accentors, 12
Family Motacillidae, Wagtails and Pipits, 48

SHRIKES AND ALLIES

Family Laniidae, Shrikes, 67
Subfamily Laniinae, Typical Shrikes, (25)
Subfamily Malaconotinae, Bush Shrikes, (42)
Family Prionopidae, Helmet Shrikes, 14
Subfamily Prionopinae, Helmet Shrikes, (13)
Subfamily Pityriasidinae, Bornean Bristle-head, (1)
Family Vangidae, Vangas, 11

WAXWINGS AND WOOD SWALLOWS

Family Artamidae, Wood Swallows, 10
Family Bombycillidae, Waxwings, etc., 9
Subfamily Hypocoliinae, Hypocolius, (1)
Subfamily Dulinae, Palm Chat, (1)
Subfamily Ptilogonatinae, Silky Flycatchers, (4)
Subfamily Bombycillinae, Waxwings, (3)

CREEPERS, NUTHATCHES, AND TITMICE

Family Certhiidae, Typical Creepers, 6
Family Sittidae, Nuthatches, etc., 29
Subfamily Salpornithinae, Spotted Creepers, etc., (12)
Subfamily Sittinae, Nuthatches, etc., (16)
Subfamily Hypositinae, Coral-billed Nuthatch, (1)
Family Paridae, Titmice, 64
Subfamily Parinae, Typical Titmice and Chickadees (46)
Subfamily Remizinae, Penduline Titmice and Verdins, (8)
Subfamily Aegithalinae, Long-tailed Titmice and Bush Tits, (7)

OLD WORLD NECTAR EATERS

Family Dicaeidae, Flowerpeckers, 54
Family Nectariniidae, Sunbirds, 104
Family Meliphagidae, Honeyeaters, 160
Subfamily Meliphaginae, Australian Honeyeaters, (159)
Subfamily Promeropinae, Sugar-bird, (1)
Family Zosteropidae, White-eyes, 80

VIREOS, FINCHES, AND ALLIES

Family Vireonidae, Vireos, 41
Family Drepaniidae, Hawaiian Honeycreepers, 22
Family Thraupidae, Tanagers, etc., 474
Subfamily Parulinae, Wood Warblers, (109)

Subfamily Coerebinae, Honeycreepers, (36)
Subfamily Catamblyrhynchinae, Plush-capped Finch, (1)
Subfamily Thraupinae, Tanagers, (196)
Subfamily Pyrrhuloxiinae, Cardinal Grosbeaks, (132)
Family Tersinidae, Swallow-tanager, 1
Family Fringillidae, Typical Finches, 293
Subfamily Emberizinae, Buntings and American Sparrows, (171)
Subfamily Fringillinae, Chaffinches, Linnets, and Allies, (122)
Family Icteridae, Troupials, American Blackbirds, and Allies, 88

WEAVERBIRDS, STARLINGS, AND ALLIES

Family Ploceidae, Weaverbirds, 263
Subfamily Bubalornithinae, Buffalo-weavers, (3)
Subfamily Passerinae, Sparrow-weavers, (35)
Subfamily Ploceinae, Typical Weavers, (109)
Subfamily Estrildinae, Waxbills and Allies, (107)
Subfamily Viduinae, Widow-birds, (9)
Family Sturnidae, Starlings, 103
Subfamily Sturninae, Starlings, (101)
Subfamily Buphaginae, Tick-birds, (2)
Family Oriolidae, Old World Orioles, 34
Family Dicruridae, Drongos, 20

CROWS AND AUSTRALIAN CROW-LIKE BIRDS

Family Corvidae, Crows, Jays, Magpies, 100
Family Cracticidae, Bell Magpies, etc., 11
Family Grallinidae, Magpie-larks, etc., 4
Subfamily Grallinae, Magpie-larks, (2)
Subfamily Corcoracinae, White-winged Chough; Gray Jumper, (2)
Family Callaeidae, Wattlebirds, 3
Family Ptilonorhynchidae, Bowerbirds, 17
Family Paradisaeidae, Birds of Paradise, 43

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