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The application of syringeal morphology to the classification of the Old World Insect Eaters (Muscicapidae)

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Introduction

The assemblage of passerine birds sometimes known as "Old World Insect Eaters", and often considered to constitute a single large family, Muscicapidae, presents a number of vexing problems for the taxonomist. When taken in this broad sense, the family is usually divided into 12–15 subfamilies, the largest of which are Turdinae (thrushes), Sylviinae (warblers), Muscicapinae (typical flycatchers), Monarchinae (monarch flycatchers), and Timaliinae (babblers). The lack of clearcut taxonomic characters and disagreement among taxonomists as to how existing characters should be applied have left the relationships of many genera in doubt. Certain of the characters currently in use (e. g., bill shape, presence of rictal bristles) are obviously related to the general food niche and probably should be treated as a single character complex. Others, such as the presence of spots in the juvenile plumage and the number of annual moults, are less obviously food-related but have not proven to be regular in distribution. This paper introduces a previously unused taxonomic character for two major groups of the Muscicapidae, the thrushes and the typical flycatchers. This character, the pattern of syringeal muscles, bears no obvious relationship to the mode of feeding or to general body plan. It is as consistently distributed as any other character used in the classification of these groups and should prove useful in establishing relationships.

Few modern ornithologists are fully aware of the past importance of the morphology of the vocal organ in passerine classification. Of the four suborders of the Passeriformes usually recognized (e. g., Wetmore, 1960), three (Tyranni, Menurae, and Passeres or "Oscines") are defined wholly on the basis of the number and region of insertion of the syringeal muscles; the fourth (Eurylaemi) is defined on the basis of the presence of a connecting vinculum between the plantar tendons of the leg. Despite this strong reliance on syringeal structure in defining the higher subdivisions of the order, few attempts have been made to characterize oscine family or subfamily groups on the basis of syrinx. The two families (Alaudidae and Hirundinidae) that are defined partly on the basis of the syrinx are so

distinctive that syringeal structure serves merely to reinforce taxonomic conclusions based on more obvious characters.

The bases for the lack of application of syringeal morphology to family and subfamily divisions appear to be (1) that the syringeal morphology of most genera in most families had not been studied prior to 1965, and (2) that those oscine syringes that had been examined were sufficiently similar that it was apparent that only the examination of a substantial percentage of genera and species would reveal consistent similarities and differences among the various groups.

In a broad study of the syrinx of passerine birds (Ames, 1971), I examined more than 600 specimens of 550 species in 350 genera of oscines, representing all but two of the 54 oscine families recognized by Wetmore (1960). The exceptions were the families Callaeidae and Catamblyrhynchidae. The syrinx throughout the suborder was found to conform closely to the general pattern already described by many authors (Owen, 1866; Haecker, 1898; Shufeldt, 1898; Setterwall, 1901; Köditz, 1925; Miskimen, 1951; George and Berger, 1965, and others).

In all oscines the syrinx is of the tracheobronchial type, i. e., a specialization of the region of bifurcation of the trachea, involving cartilages with varying degrees of ossification, extrinsic muscles (inserting on the syrinx, but originating elsewhere), intrinsic muscles (originating, as well as inserting, on the syrinx), and vibrating membranes. The basic oscine pattern consists of two pairs of extrinsic muscles (M. tracheolateralis and M. sternotrachealis), two pairs of long intrinsic muscles (M. bronchotrachealis posticus and M. bronchotrachealis anticus), and two pairs of short intrinsic muscles (M. bronchialis posticus and M. bronchialis anticus). The last of these usually comprises two distinct fasciculi, often considered separate muscles. With the exception of the genus *Climacteris* (Ames, ms.), I have observed no deviations from the basic pattern of the above six muscles. The numerous reports of great variation in the number of oscine syringeal muscles have resulted from authors combining the figures from two or more earlier workers whose concepts of muscle nomenclature differed (myological "lumpers" and "splitters"). The main form of variation observed is in the points of insertion (rarely, of origin) of the above-named muscles. Occasionally one fasciculus of M. bronchialis anticus is lacking.

Although the same basic syringeal pattern prevails among oscines of body plans that vary from sunbird to raven, there are a few modifications of the pattern that appear to correspond to established taxonomic groupings. One such modification is found in the thrushes and typical flycatchers.

Taxonomic background

There has been a trend in recent years toward the use of the single family Muscicapidae to indicate the close relationships of thrushes, babblers, warblers, flycatchers and allies. The concept of treating these groups within

a single large family evidently originated with Seebohm and Sharp (1898—1902) and Hartert (1910), but received only scattered attention until the mid-1950s. As adopted by the Peters Check-list Committee (see Mayr and Greenway, 1956), Hartert's classification has been modified by dividing the Muscicapidae into 13 subfamilies. This raises to a higher relative taxonomic level certain groups, such as the gnatcatchers (Polioptilinae), rockfowl (Picathartinae) and crowtits (Panurinae), which are thus at a level equivalent to the thrushes, typical flycatchers, warblers and babblers. Of particular relevance to the present study is the treatment of the monarchs, fantails and whistlers as subfamilies (Monarchinae, Rhipidurinae and Pachycephalinae). Unlike the system that restricts the Muscicapidae to the so-called flycatching groups, this system does not imply that these three groups are more closely related to each other and to the typical flycatchers than to other groups of Old World Insect Eaters, except for the degree of relationship implied by placing them consecutively in the linear arrangement.

The more established classification, still in use by a number of authors and certainly in the majority of works on the average ornithological bookshelf, treats some of the groups mentioned above as separate families. Such a classification is employed by Wetmore (1960), who places the Timaliidae some distance from the other families in the linear order. An important aspect of this system, with regard to the relationships of the thrushes to the other groups, is the inclusion in the Muscicapidae of four subfamilies: Muscicapinae (typical flycatchers), Monarchinae (monarchs), Rhipidurinae (fantails) and Pachycephalinae (whistlers or thickheads). The muscicapines are thus considered more closely allied to the other flycatcher-like groups (especially the monarchs) than to the thrushes and warblers. Many authors separate the fantails and whistlers as separate families, while keeping the typical flycatchers and monarchs together.

The two basic systems of classification may be compared as follows:

Wetmore (1960)	**Peters Check-list**
Family Paradoxornithidae [= Panurinae]	Family Muscicapidae
Chamaeidae	Subfamily Turdinae
Timaliidae (incl. Picathartinae and Orthonychinae)	Orthonychinae
(Campephagidae, Pycnonotidae,	Timaliinae
Chloropseidae, Cinclidae,	Panurinae
Troglodytidae and Mimidae)	Picathartinae
Turdidae	Polioptilinae
Zeledoniidae	Sylviinae
Sylviidae (incl. Polioptilinae,	Malurinae
and Malurinae)	Muscicapinae
Regulidae	Platysteirinae
Muscicapidae (incl. Monarchinae,	Monarchinae
Platysteirinae, Rhipidurinae	Rhipidurinae
and Pachycephalinae)	Pachycephalinae

Although many authors have commented on the value of including all of the Old World Insect Eaters in a single family, few have undertaken revi-

sions of complete subgroups at the genus or species levels. Delacour (1946) revised the subfamily Timaliinae, Ripley (1952b) the Turdinae, and Vaurie (1953) the tribe Muscicapini. This tribe is roughly equivalent to the subfamily Muscicapinae, with the wattle-eyes removed as the subfamily Platysteirinae Sundevall 1872 (Traylor, 1970). In an important paper on passerine egg white protein patterns, Sibley (1970) discusses the interrelationships of the many groups of Old World Insect Eaters and reviews most of the earlier literature. He treats the Muscicapidae in the narrow sense, including only the traditional four "flycatching" subfamilies.

For the purposes of simplicity in the present paper, I will follow the classification adopted for the Peters Check-list unless otherwise stated. This is basically the scheme of Mayr and Greenway (1956), with the family Platysteirinae resurrected for the African genera *Bias, Pseudobias, Batis* and *Platysteira.*

Materials and methods

Syringes examined in this study were obtained almost exclusively from spirit specimens. The syrinx was removed by reflecting the skin on the neck and breast, severing the exposed trachea and esophagus midway up the neck, and making an parasagittal incision on the right side of the breast muscle and sternum. Cuts in the bronchi and esophagus allowed the syrinx to be removed while still attached to the esophagus. On reasonably large specimens the sternal cut was omitted and the syrinx extracted through the interclavicular space. Under a dissecting microscope the isolated syrinx, with a piece of esophagus still attached for ease of pinning, was further cleaned, with the removal of connective tissue and preserved blood. The syringeal muscles, thus clearly revealed, were studied and recorded, usually with little deeper dissection. This muscle complex is essentially one-layered, and the myology of the thrush-muscicapid syrinx is so distinctive that it usually may be distinguished with the naked eye.

Early in the broad study it became evident that the syrinx of thrushes had a distinctive pattern, and I made a special effort over a period of more than a decade to obtain representatives of as many genera and species as possible from all of the tribes and subfamilies of Muscicapidae. The list of species examined (Table 1) includes virtually every species of thrush and flycatcher available in the major spirit collections in the United States and Great Britain. Taken together, these collections comprise about 35,000 bird specimens, but they lack some 13 genera of thrushes and three of typical flycatchers. In seeking specimens representing the other muscicapid subfamilies I have placed emphasis more on morphological diversity than on the representation of all available genera.

With a few exceptions, the identification on the specimen label was assumed to be correct. In this respect, the anatomist is at the mercy of the field collector and must hope that the latter has correctly identified the specimen. In cases that produced anomalous results I usually attempted to

obtain additional specimens. A few specimens whose identity I questioned (the campephagid *Chlamydochaera jefferyi* and the three species of *Rhinomyias* flycatchers) were dried quickly with an air hose, compared with study skins, and replaced in alcohol.

In descriptions of syringeal muscles and cartilages I employ the nomenclature established by Owen (1866), slightly modified to provide broader applicability among oscines. The synonymy of muscles and cartilages has been discussed in detail elsewhere (George and Berger, 1965; Ames, 1971) and will not be repeated here.

Results

Within the Muscicapidae two basic syringeal patterns may be recognized, which I will call generalized oscine and turdine. These terms are used for sake of convenience only and should not be taken as indicative of taxonomic conclusions. The generalized oscine pattern is widely distributed among songbirds, occurring throughout virtually all non-muscicapid families, as well as most subfamilies of the Muscicapidae. It is distinguished by the configuration of the dorsolateral intrinsic muscles, M. bronchotrachealis posticus and M. bronchialis posticus, which usually insert on the anterior surface of the flattened dorsal end of element A-2 (the second of the three bony "intermediary bars"), or occasionally on A-1 (the most posterior bar). The two muscles taper toward their insertions, giving a pointed appearance to the posterodorsal corner of the syrinx. The generalized oscine syrinx varies in the relative shape, position and attachment

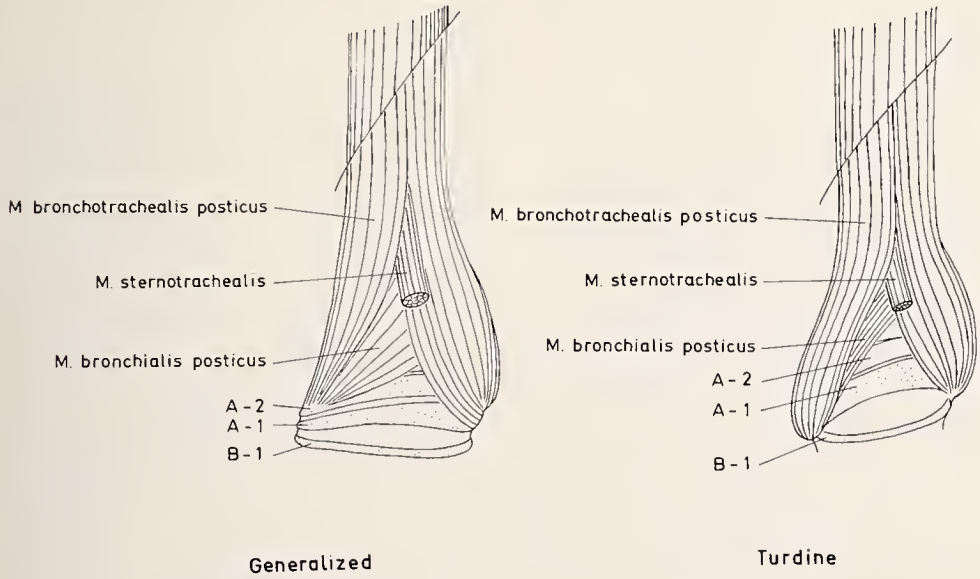


Fig. 1. Two types of oscine syrinx: generalized and turdine. Right side view.

of all of the muscles, and the extent to which the posterodorsal region is pointed varies considerably, depending largely on the degree of bulging of the muscles near their insertions. As will be seen, this bulging cannot be mistaken for the turdine condition, described below.

The turdine pattern is essentially limited to the Turdinae and Muscicapinae (see Table 1), but is not found throughout either group, as they are presently classified. The pattern is easily recognized by a thumb-like extension of the dorsolateral muscles, which is formed by a bending posteriad of the dorsal end of element A-1 and the envelopment of the end of the element by the two muscles. The resulting "turdine thumb" is easily visible to the naked eye, even in a small syrinx.

A second characteristic of the turdine syrinx is the thinness of M. sternotrachealis, a slender muscle that originates on the inner side of the sternum (usually on the coracoid process) and extends across the interclavicular air sac to insert on the lateral surface of the syrinx. This muscle is always rather narrow in oscines, its diameter in most preserved specimens being one-fifth to one-tenth the longer diameter of the trachea. In the turdine syrinx M. sternotrachealis is usually about half as thick as in a generalized oscine syrinx of comparable size. Muscle diameter is not a good meristic character in taxonomy, due to variation in the degree of contraction, but the small size of M. sternotrachealis is strikingly evident in this case.

The species of Muscicapidae, Prunellidae and Campephagidae examined, with the syringeal type found in each, are listed in Table 1. When more than one specimen of a species were studied the number is indicated in parentheses. Out of about 250 genera in the broad family Muscicapidae, I have examined 124. A list of most of the species of other oscine families examined is found in my earlier work (1971).

Of the 49 genera of thrushes (Turdinae) listed by Ripley (1964), I have studied representatives of 36, all but six of which have the turdine pattern. The exceptions are *Zeledonia, Modulatrix, Myadestes, Neocossyphus, Stizorhina* and *Phaeornis*. The range of body types with the turdine syringeal pattern includes chats *(Saxicola),* typical thrushes *(Turdus),* whistling thrushes *(Myiophoneus),* cochoas *(Cochoa),* the wagtail-like forktails *(Enicurus),* the swallow-like *Grandala,* and warbler-like forms such as the scrub-robins *(Erythropygia).* This broad range of body plans suggests that the turdine thumb is not adaptively linked to the general mode of life, but has been relatively conservative in the radiation of the ancestral thrush stock into the present diversity. The functional relationships between the number, shape and position of syringeal muscles and the characteristics of the vocal repertoire are as yet totally unknown. From the variety of songs and calls heard from birds with the generalized oscine type of syrinx, and the nearly equal variety from those with the turdine type, one must conclude that the functional significance of the turdine thumb is subtle and likely to remain unknown for some time to come.

Table 1. Species of Prunellidae, Muscicapidae and Campephagidae examined in this study, with their syringeal types.

	Turdine	Generalized
Family Prunellidae		
Prunella collaris		○
montanella		○
modularis		○
Family Muscicapidae		
Subfamily Turdinae		
Brachypteryx montana	×	
Zeledonia coronata		○
Erythropygia leucophrys	×	
barbata	×	
Pogonocichla stellata	×	
Erithacus		
[= Sheppardia] sharpei	×	
[= Sheppardia] gunningi	×	
rubecula	×	
[= Luscinia] megarhynchos	×	
[= Tarsiger] cyanurus	×	
Cossypha natalensis	×	
niveicapilla	×	
Modulatrix stictigula		○
Cichladusa guttata	×	
Alethe fuelleborni	×	
montana	×	
Copsychus saularis	×	
sechellarum	×	
malabaricus	×	
Phoenicurus phoenicurus	×	
frontalis	×	
auroreus	×	
Rhyacornis fuliginosus	×	
Hodgsonius phoenicuroides	×	
Cinclidium leucurum	×	
frontale	×	
Grandala coelicolor	×	
Sialia sialis	×	
currucoides	×	
Enicurus scouleri	×	
maculatus	×	
Cochoa viridis	×	
Myadestes townsendi (3)		○
genibarbis (4)		○
unicolor		○
ralloides		○
Entomodestes leucotis	×	
Neocossyphus rufus		○
Stizorhina fraseri		○
Cercomela familiaris	×	
sordida	×	
Saxicola rubetra	×	
torquata	×	
Myrmecocichla arnotti	×	
Oenanthe oenathe	×	
deserti	×	
hispanica	×	
leucopyga	×	
pileata	×	
Chaimarrornis leucocephalus	×	
Saxicoloides fulicata	×	
Monticola brevipes	×	
solitarius	×	
Myiophoneus caeruleus (2)	×	
Zoothera cinerea	×	
naevia	×	
pinicola	×	
dixoni	×	
dauma	×	
Phaeornis obscurus		○
Catharus gracilirostris	×	
occidentalis	×	
fuscescens	×	
minimus	×	
Hylocichla mustelina	×	
Platycichla flavipes	×	
Turdus litsipsirupa	×	
ruficollis	×	
aurantius	×	
plumbeus	×	
falcklandii	×	
leucomelas	×	
amaurochalinus	×	
ignobilis	×	
grayi	×	
migratorius (9)	×	
Subfamily Orthonychinae		
Orthonyx temminckí		○
spaldingi		○
Psophodes olivaceus		○
Cinclosoma ajax		○
Irrita kowaldi		○
Subfamily Timaliinae		
Pellorneum ruficeps		○
Trichastoma tickelli		○
Pomatorhinus erythrogenys		○
ferrugineus		○
Neomixis tenella		○
viridis		○
Stachyris pyrrhops		○
nigriceps		○
Macronus flavicollis		○
gularis		○
Timalia pileata		○

	Turdine	Generalized
Chamaea fasciata		○
Turdoides fulvus		○
gymnogenys		○
Garrulax delesserti		○
mitratus		○
canorus		○
Leiothrix lutea		○
Minla cyanouroptera		○
strigula		○
Heterophasia capistrata		○
Yuhina flavicollis		○
gularis		○
nigromenta		○
zantholeuca		○
Genera sedis incertae		
Malia gratia		○
Oxylabes madagascariensis		○
Subfamily Panurinae		
Panurus biarmicus		○
Paradoxornis unicolor		○
gularis		○
Subfamily Picathartinae		
Picarthartes gymnocephalus		○
Subfamily Polioptilinae		
Polioptila caerulea		○
dumicola		○
Microbates cinereiventris		○
Rhamphocaenus melanurus		○
Subfamily Sylviinae		
Tesia superciliaris		○
Cettia diphone		○
montana		○
Bradypterus castaneus		○
cinnamomeus (2)		○
Calamonastes fasciolatus		○
Melocichla mentalis		○
Cisticola chiniana		○
cherina		○
brachyptera		○
Camaroptera brevicaudata		○
Sylvietta brachyura		○
Prinia gracilis		○
atrogularis		○
Apalis flavida		○
Orthotomus atrogularis		○
sepium		○
Locustella ochotensis		○
Schoenicola brevirostris		○
Phragamaticola aedon		○
Acrocephalus schoenobaenus		○
scirpaceus		○

	Turdine	Generalized
Conopoderas caffer		○
familiaris		○
Cinclorhamphus cruralis		○
Hippolais icterina		○
pallida		○
Sylvia cantillans		○
borin		○
curruca		○
melanocephala		○
atricapilla		○
Phylloscopus sibilatrix		○
coronatus		○
trochilus		○
Regulus calendula		○
satrapa		○
Seicercus ruficapillus		○
bourkei		○
nouhuysei		○
Artisornis metopias		○
Abroscopus schisticeps		○
Genera sedis incertae		
Hylia prasina		○
Lamprolia victoriae		○
Subfamily Malurinae		
Malurus gouldi		○
Stipiturus malachurus		○
Gerygone flavolateralis		○
Sericornis magnirostris		○
Vitia ruficapilla		○
Subfamily Muscicapinae		
Bradornis pallidus	×	
Melaenornis edolioides	×	
pammelaina	×	
Rhinomyias olivacea	×	
ruficauda (2)	×	
gularis	×	
Ficedula hypoleuca	×	
albicollis	×	
narcissina	×	
monileger	×	
hyperythra (2)	×	
crypta	×	
westermanni	×	
cyanomelaena	×	
Niltava grandis	×	
macgrigoriae	×	
sundara	×	
rubeculoides	×	
rufigastra	×	
Muscicapa striata	×	
sibirica	×	
griseisticta	×	
latirostris	×	

	Turdine	Generalized
Muscicapa thalassina	×	
panayensis	×	
Newtonia brunneicauda		○
archboldi		○
Microeca leucophaea		○
Subfamily Platysteirinae		
Batis capensis		○
minor		○
Platysteira cyanea		○
Dyaphorophyia castanea		○
Pseudobias wardi		○
Subfamily Monarchinae		
Elminia longicauda		○
albicauda		○
Trochocercus cyanomelas		○
Terpsiphone rufiventris		○
corvina		○
Hypothymis azurea		○
Monarcha alecto		○
axillaris		○
barbata		○
guttula		○
telescophthalmus		○
Erythrocercus mccalli		○
Chasiempis gayi		○
Clytorhynchus nigrogularis		○
pachycephaloides		○
Myiagra caledonica		○
azureicapilla		○
Machaerirhynchus sp.		○
Peltops blainvillei		○
Monachella muelleriana		○
Peneothello sigillatus		○
Seisura inquieta		○
Petroica multicolor		○
cucullata		○
Melanodryas cucullatus		○
Eopsaltria georgiana		○
Ephthianura albifrons		○
Subfamily Rhipidurinae		
Rhipidura brachyrhyncha		○
albolimbata		○
rufiventris		○
hypoxantha		○
Culicicapa ceylonensis		○
helianthea		○
Subfamily Pachycephalinae		
Oreoica gutturalis		○
Pachycephala cinerea		○
philippinensis		○
pectoralis		○
schlegeli		○
Colluricincla rufiventris		○
rectirostris		○
Pitohui dichrous		○
Genus sedis incertae		
Turnagra capensis		○
Family Campephagidae		
Coracina pectoralis		○
azurea		○
montana		○
Chlamydochaera jefferyi	×	
Lalage maculosa		○
Campephaga phoenicea		○
Pericrocotus flammeus		○
Hemipus picatus		○
Tephrodornis pondicerianus		○

The 13 thrush genera that I have been unable to obtain are: *Namibornis* (1 sp., southwestern Africa), *Cercotrichas* (1 sp., central Africa, Arabia), *Pinarornis* (1 sp., Rhodesia), *Chaetops* (1 sp., South Africa), *Drymodes* (2 spp., Australasia), *Irania* (1 sp., eastern Africa and the Middle East), *Thamnolea* (3 spp., eastern and southern Africa), *Pseudocossyphus* (1 sp., Madagascar), *Geomalia* (1 sp., Celebes), *Amalocichla* (2 spp., New Guinea), *Cataponera* (1 sp., Celebes), *Nesocichla* (1 sp., South Atlantic Islands), and *Cichlherminia* (1 sp., West Indies). As might be expected, most of these (ten) are monotypic, restricted in distribution, and little studied. Perhaps the most interesting from the taxonomic point of view is *Drymodes*, the only thrush genus endemic to the Australian continent.

For the purposes of the present discussion, the subfamily Muscicapinae is considered synonymous with the tribe Muscicapini, as revised by Vaurie

(1953), except that *Culicicapa* is treated here in the Rhipidurinae, following the suggestion of Vaurie (op. cit.) and of Parker (1964). I have examined specimens of 28 species, representing eight of the 11 genera treated by Vaurie (excluding *Culicicapa).* Members of 25 species, in six genera, were found to be turdine in syringeal pattern, 19 of them in three genera *(Muscicapa, Ficedula* and *Niltava)* often grouped in *Muscicapa.* The three species with the generalized pattern are in the genera *Newtonia* (two) and *Microeca.* The range of body plans with the turdine syrinx is smaller than in the thrushes — the subfamily Muscicapinae is a less diverse group than the Turdinae — but many are far from typical flycatchers in the sense that *Muscicapa striata* is usually considered to be. In most muscicapines the turdine thumb is more pronounced than in many thrushes, such as *Copsychus* and *Myiophoneus,* in which it is shorter and slenderer.

Of the three muscicapine genera lacking *(Horizorhinus,* 1 sp.; *Fraseria,* 2 spp.; *Humblotia,* 1 sp.), *Horizorhinus* is the only one the taxonomic position of which is in doubt. It is listed by Deignan (1964) as sedis incertae, and Vaurie (1953) indicates that it is very likely a babbler (Timaliinae). Examination of the syrinx would throw some light on the matter.

My coverage of the remaining subfamilies of the Muscicapidae has been less complete than that of the Turdinae and Muscicapinae, but in all cases has covered a wide range of body plans. Numerical representation by subfamilies has been as follows:

Orthonychinae	4 out of	9 genera
Timaliinae	13 out of	44 genera
Panurinae	2 out of	3 genera
Picathartinae	1 out of	1 genus
Polioptilinae	3 out of	3 genera
Sylviinae	22 out of	ca. 60 genera
Malurinae	5 out of	ca. 25 genera
Platysteirinae	3 out of	4 genera
Monarchinae	18 out of	ca. 24 genera
Rhipidurinae	2 out of	2 genera
Pachycephalinae	4 out of	9 genera
Totals	80 out of	ca. 190 genera
Turdinae and Muscicapinae	44 out of	60 genera
Total Muscicapidae	124 out of	ca. 250 genera

Phylogenetic pathways

If the family Muscicapidae is taken to be monophyletic and its subdivisions based on some sort of cladistic scheme (axioms on which systematists are by no means agreed), two basic routes of syringeal evolution could have resulted in the present distribution of turdine and generalized oscine syringeal patterns within the currently accepted arrangement of subfamilies and genera. With its broad distribution among song-

birds, the generalized pattern may logically be assumed to represent the primitive condition.

One phylogenetic route (Fig. 2 a) assumes the acquisition of the turdine pattern (solid line) in a stock that produced both the Turdinae and the Muscicapinae, followed by a return to the primitive condition (dashed line) in at least three lines of thrushes (leading, respectively, to *Zeledonia*, to *Modulatrix*, and to the *Myadestes-Phaeornis-Stizorhina-Neocossyphus* group) and at least two lines of flycatchers (to *Newtonia* and to *Microeca*). To attain even this degree of monophyly, one must consider the Turdinae

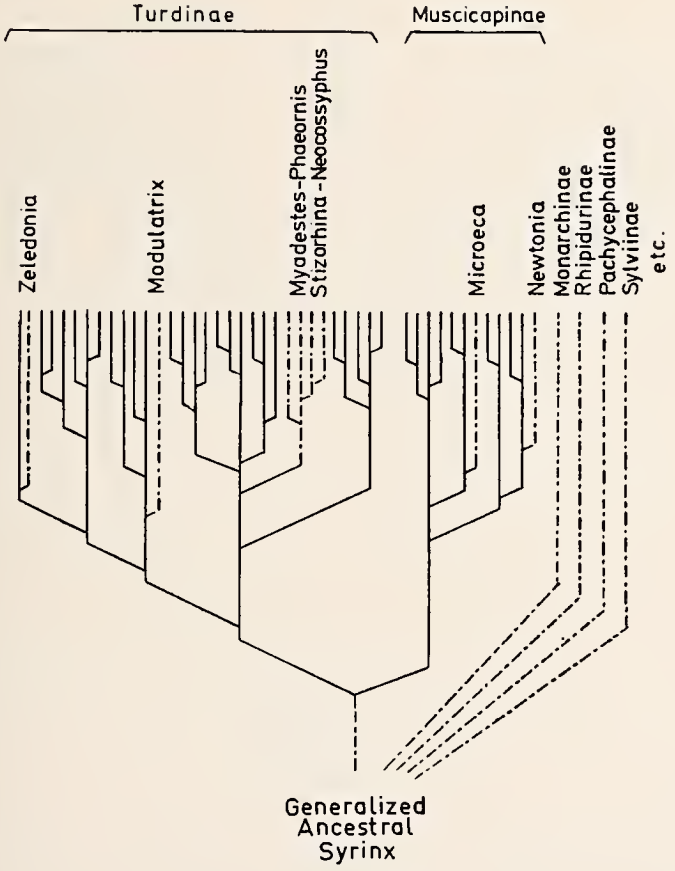


Fig. 2 a

Fig. 2. Dendrograms of possible phylogenies of the generalized and turdine syringeal types, within the framework of the prevailing taxonomic groupings. Dashed lines: generalized syrinx type. Solid lines: turdine syrinx type. a, Assuming that the turdine condition was acquired only once and then lost in lines leading to Turdinae and Muscicapinae with generalized syringes. b, Assuming that members of the Turdinae and Muscicapinae with generalized syringes have retained this type from the primitive condition. c, Assuming that the turdine condition was acquired only once in the evolution of the Turdinae and Muscicapinae and never subsequently lost.

and Muscicapinae to be more closely related than is indicated by their relative positions in the linear arrangement of the "Peters Check-List".

The second alternative (Fig. 2 b) is based on the premise that those genera exhibiting the generalized condition do so primitively and that, therefore, the turdine condition has evolved in several separate evolu-

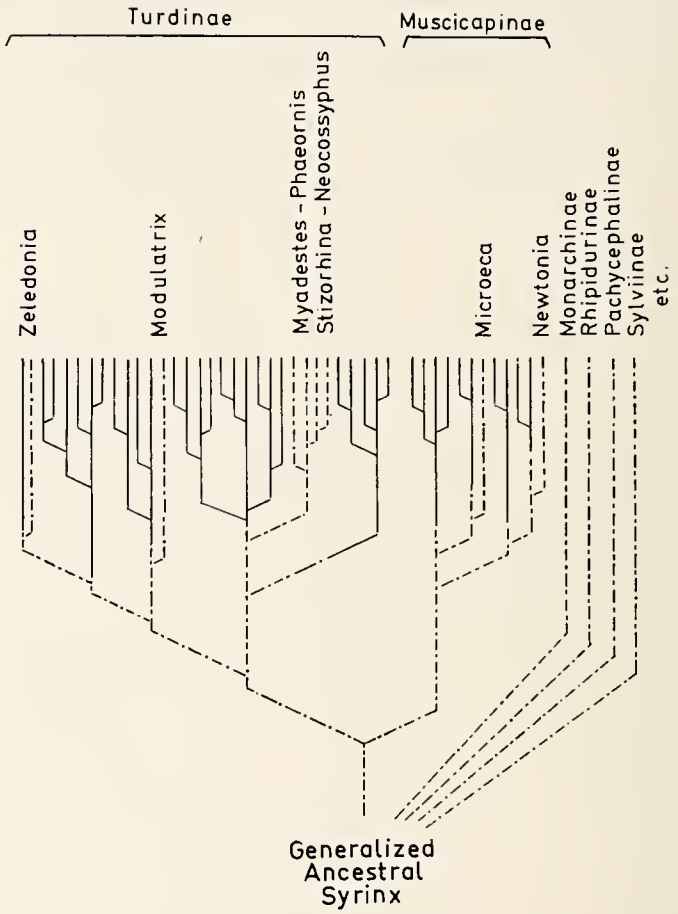


Fig. 2 b

tionary lines within the two subfamilies. The close relationship of the Turdinae and Muscicapinae, needed for the first scheme, is not necessary for this one, but the order of subfamilies is retained in the dendrogram for ease of comparison. An estimate of the number of separate appearances of the turdine patterns depends on just how distinctive the various lines of thrushes and flycatchers are considered to be.

The phylogenetic arrangement in Figure 2 c incorporates those changes that must be made in the other two dendrograms if one is to suppose that the turdine condition arose only once and was never secondarily lost. The

significant difference between this arrangement and the other two is, of course, that the generalized "twigs" have been pruned from the Turdinae and Muscicapinae.

Determination of which of the three arrangements, or what combination of them, most closely indicates the actual evolutionary pathways of the syrinx is difficult — many taxonomists would say impossible — especially with virtually nothing known about the adaptive significance of the various features of syringeal morphology.

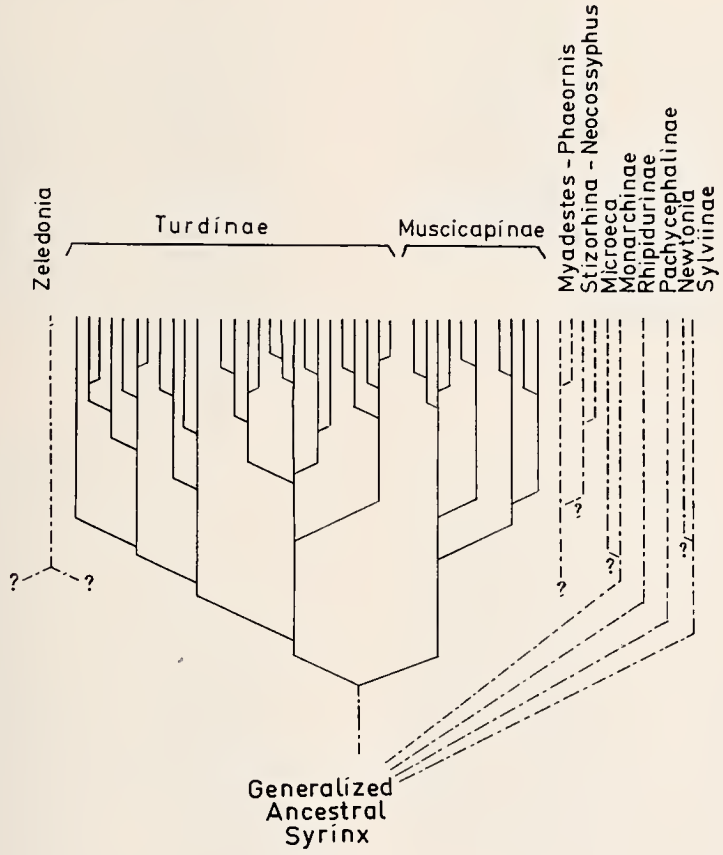


Fig. 2 c

The syrinx as a taxonomic character

The facts that the turdine pattern is restricted to two groups of the Muscicapidae (with the one exception noted below), and that it strongly prevails within these two groups, despite wide variation in vocalizations, suggest that the adaptive value of this pattern, if any still exists, is not directly related to vocalization patterns. In view of the paucity of information on the influence of syringeal structure on the nonvocal functions of

the respiratory system, it would be premature to speculate on the possible selective advantage conferred by one or the other type of syrinx. In evaluating the syringeal pattern as a taxonomic character, therefore, I rely entirely on the degree to which its distribution agrees with that of the other taxonomic characters that form the basis for the current classification.

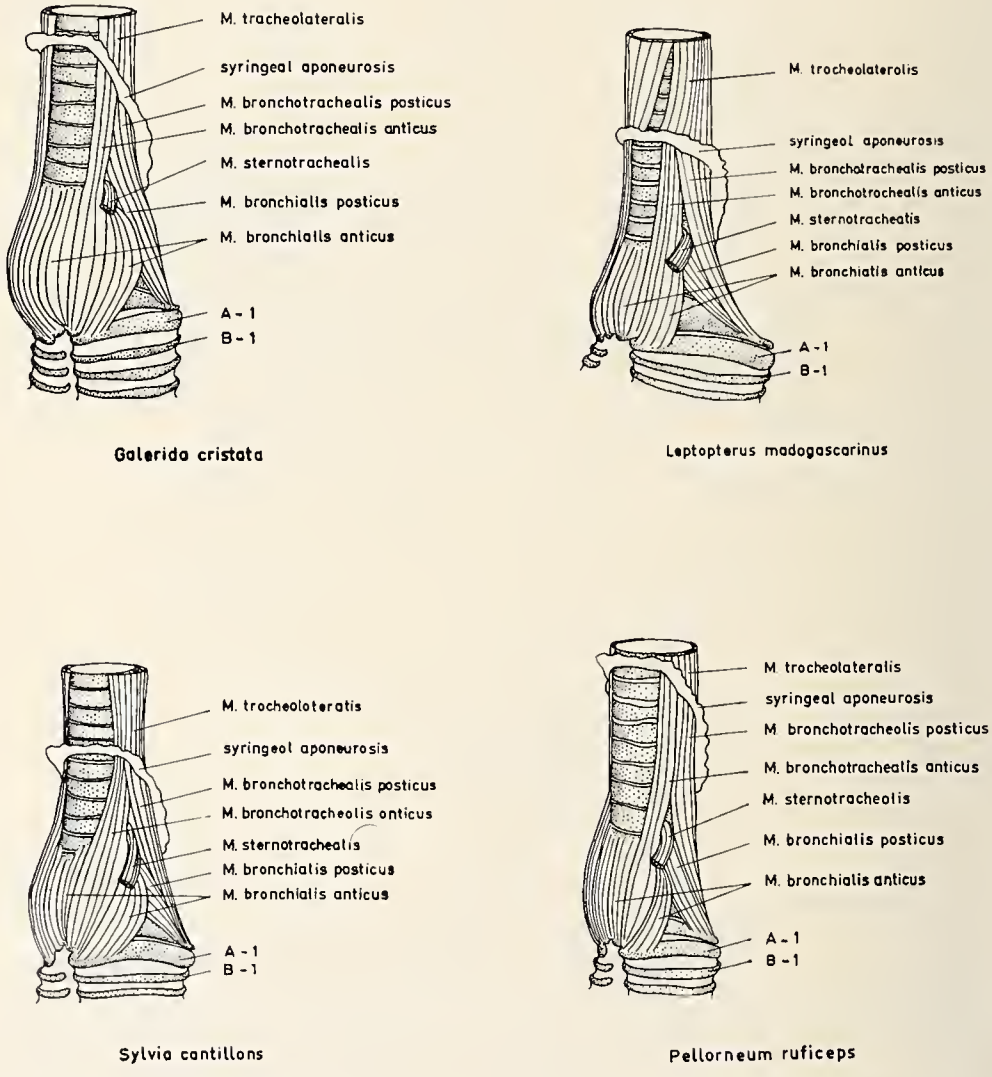


Fig. 3. Syringes of generalized oscine type, left ventrilateral view. Crested Lark, *Galerida cristata* (Alaudidae), x 5; Blue Vanga Shrike, *Leptopterus madagascarinus* (Vangidae), x 5; Subalpine Warbler, *Sylvia cantillans* (Muscicapidae: Sylviinae), x 7; Striped Jungle Babbler, *Pellorneum ruficeps* (Muscicapidae: Timaliinae), x 7.

Fig. 4. Syringes of turdine type, left ventrilateral view. Sharpe's Akalat, *Erithacus [= Sheppardia] sharpei* (Muscicapidae: Turdinae), x 5; Spotted Flycatcher, *Muscicapa striata* (Muscicapidae: Muscicapinae), x 5; Spotted Forktail, *Enicurus maculatus* (Muscicapidae: Turdinae), x 4; Olive-backed Jungle Flycatcher, *Rhinomyias olivacea* (Muscicapidae: Muscicapinae), x 7.

Cercomela familiaris

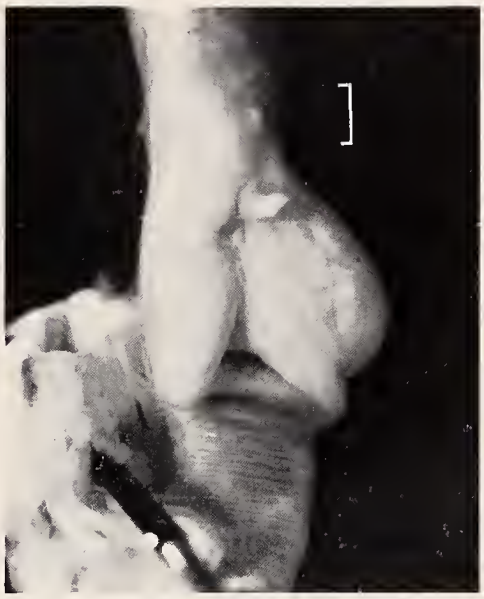
Grandala coelicolor

Alethe montana

Cochoa viridis

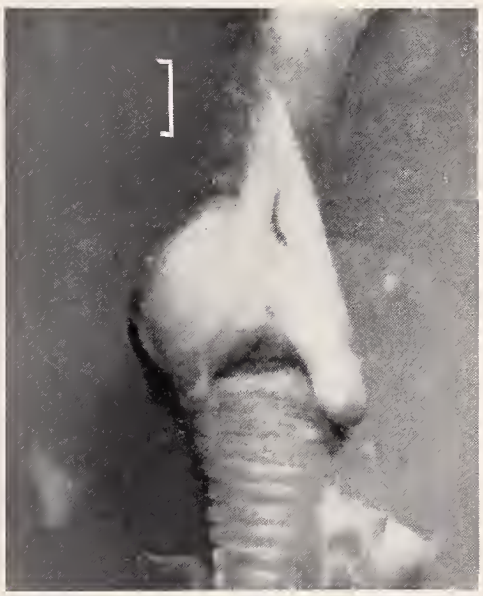
Figs. 5—6. Syringes of 8 species of Muscicapidae. All except Niltava are viewed from the right. The scale bar indicates one millimeter.

Entomodestes leucotis



Turdus ruficollis

Myadestes genibarbis



Niltava grandis

Departures from the expected distribution of turdine and generalized syringeal patterns

The distribution of the turdine and generalized patterns follows the established classification so closely that one might expect those few species in which the syrinx departs from the predicted distribution to be aberrant in other characters. Interestingly, five of the six exceptions in the Turdinae are atypical thrushes, and two *(Zeledonia* and *Stizorhina)* are considered by many authorities not to be thrushes at all. Of the two exceptions in the Muscicapinae, only one *(Newtonia)* has been widely considered to be doubtfully muscicapine.

In taxonomic applications of the syringeal pattern dichotomy, one must bear in mind that it merely separates most members of the Muscicapinae and Turdinae from other oscines. If the syringeal pattern suggests the removal of a species from the Turdinae, it equally excludes it from the Muscicapinae.

Zeledonia. The taxonomic history of the wrenthrush *(Zeledonia coronata),* sole member of this neotropical genus, has been thoroughly reviewed by Sibley (1968), with particular reference to the study by Pycraft (1905). From the time of its description by Ridgway in 1889 until Sibley's study, *Zeledonia* was generally considered to have close affinities with the thrushes. It has either been included in the Turdidae, or Turdinae, (Mayr and Amadon, 1951; Ripley, 1952 b, 1964; and many others) or placed in a monotypic family adjacent to the Turdidae in a linear arrangement (Ridgway, 1907; Wetmore, 1960; others).

In addition to reviewing earlier work on the affinities of the wrenthrush, Sibley presents evidence from the eggwhite protein patterns that the wrenthrush is related, not to the thrushes, but to the "nine-primaried oscines" (his Fringillidae). He goes on to point out that morphologically *Zeledonia* seems closest to the wood warblers (his tribe Parulini). Hunt (1971) provides the first detailed field information on the wrenthrush, but refrains from taxonomic comments, beyond comparing the wrenthrush with certain tropical wood warblers, and indicating that his findings support Sibley's. Austin (1971) and Storer (1971) recognize the family Zeledoniidae, but place it adjacent to the Parulidae.

The presence of the generalized oscine syringeal type in *Zeledonia* supports Sibley's conclusion that this bird is not closely related to the true thrushes. The syringeal pattern is not of great help in determining where the wrenthrush does belong, since the details of the syrinx serve primarily to separate *Zeledonia* from those families from which it would be excluded on other, more obvious, grounds. On the other hand, there is nothing in the syrinx of *Zeledonia* incompatible with inclusion in the Parulidae.

Modulatrix. This little-studied African genus was erected by Ripley (1952 a) for *Turdinus stictigula* Reichenow, previously considered a babbler (Timaliinae). Delacour (1946) excludes *T. stictigula* from the babblers, noting its resemblance to certain thrushes of the genus *Cossypha*, in which he places *stictigula*. Ripley defines *Modulatrix* on the basis of its narrow bill, long tarsi and toes, rounded wing, tail shape, and color pattern. The genus has been accepted as a thrush by most recent authors.

The presence of the generalized syringeal pattern in *Modulatrix* suggests that the genus may be wrongly placed in the Turdinae and may belong in the Timaliinae, after all. Only a thorough study of the characters of this genus, compared with thrush-like babblers and babbler-like thrushes, will settle the problem.

Myadestes and *Phaeornis*. The New World solitaires *(Myadestes)* and the Hawaiian thrush *(Phaeornis)* have a recent history free of taxonomic controversy. In the case of *Myadestes*, this was not always the case. Sibley (1973), with his usual thoroughness, has reviewed the taxonomic history of *Myadestes* in detail, noting that this genus (including *M. leucotis*, the type species of the genus *Entomodestes)* was placed with the silky flycatchers in the family Ptilogonatidae until 1864. Following a suggestion made by Baird in that year, more and more authors began to treat *Myadestes* as a thrush genus. Since the early 20th century, virtually all authors have unquestioningly considered the solitaires to be thrushes.

The *Myadestes* solitaires are quite flycatcher-like in appearance and feed on the wing more than most other thrushes. Enhancing the flycatcher appearance is the general body plan, with long tail, short legs and small feet, upright posture, and broad bill. These characters are even more pronounced in *Entomodestes*, which Ridgway (1907) felt might well belong in the Ptilogonatidae. *Phaeornis* is similar to *Myadestes* in general wing and tail proportions, but has distinctly longer legs and larger feet. Ripley (1952 b) implies that the two species of *Phaeornis* could well be placed in *Myadestes*, but he leaves them separate. In the Peters Check-List (1964) he separates them more widely, placing *Phaeornis* immediately before *Catharus*, near the end of the thrushes.

Sibley (1973) presents evidence in the eggwhite protein patterns that the three genera of silky flycatchers *(Phainopepla, Ptilogonys* and *Phainoptila)* are more closely related to the solitaires — *Myadestes obscurus* and *M. ralloides* were studied; *Entomodestes* and *Phaeornis* were not — than either group is to other genera. He considers that the silky flycatchers might deserve placement in the Turdidae (sic. Turdinae) or that *Myadestes* (and possibly *Entomodestes)* should be placed in the Ptilogonatidae. Taking the course least disruptive to the current classification, Sibley tentatively recommends the latter transfer.

While it is true, as Sibley reports, that the *Myadestes* syrinx is more like those of the silky flycatchers than like those of typical thrushes, the resemblance is not especially close when considered in respect to the full range of variation seen in the oscine syrinx. The syringeal musculature in ptilogonatids is conspicuously slender, as it is in the waxwings *(Bombycilla),* to which the silky flycatchers are usually considered related. In *Myadestes* the musculature is quite robust. This difference may be related more to selection for strong singing ability than to phylogeny. Although the *Myadestes* syrinx is of the generalized type, it has one feature that links it to the turdine type. M. bronchotrachealis posticus inserts on element A-1, a relatively unusual condition, but by no means unique to the turdine syrinx. In my one specimen of *M. ralloides* a few superficial fibres of M. bronchotrachealis posticus even extend over the end of A-1 to insert on the A-1/B-1 membrane. Although this could be viewed as an incipient turdine condition, the syrinx in even this specimen is basically generalized oscine, not turdine.

The syrinx of *Phaeornis obscurus* is typical of the generalized oscine type, with M. bronchotrachealis posticus inserting on the dorsal end of A-2. In the overall proportions of the syrinx the Hawaiian thrush resembles the myadestine solitaires. The syrinx is strongly muscled ventrally and rather weakly so dorsally, a situation found in a variety of unrelated oscines.

The syrinx of the white-eared solitaire *(Entomodestes leucotis)* is strongly turdine, the well developed "thumb" extending well posterior of the ventral muscles. In several other features, however, this syrinx is highly distinctive, an example of extreme modification within the turdine framework. The whole syrinx is unusually broad in the region of the intrinsic muscles, especially ventrally. The short ventral intrinsic muscles (M. bronchialis anticus) are broad and peculiarly squared-off at their origin, following the anterior edge of the drum. This squared-off appearance, although unusual in the Old World Insect Eaters, occurs in several other groups, notably the shrikes (Laniidae). I doubt that it has taxonomic significance in this case, and hesitate to speculate on its functional importance.

A second conspicuous feature of the syrinx of *Entomodestes* involves the bony rings that support the trachea anterior to the drum. On the ventral side of the trachea these rings are anteroposteriorly attennuated, leaving wide membranous areas between them. The same rings are also thickened dorsoventrally, presumably replacing some of the strength lost in the attennuation. The degree of attennuation decreases progressively anteriad from the drum. Attennuation of the tracheal rings, although the rule in the suboscine antbird-ovenbird complex (the superfamily Furnarioidea of Wetmore, 1960), is not known from any other oscine. In other respects, the syrinx of *Entomodestes* is unquestionably oscine, so the specialization of

the tracheal rings cannot be interpreted as indicating a relationship with the Furnarioidea. The attennuation may well have a nonvocal function, such as that of permitting extreme shortening of the trachea when the head is withdrawn.

The presence of the generalized oscine syrinx in *Myadestes* and *Phaeornis* strongly supports Sibley's conclusion that the relationships of *Myadestes* lie outside the Turdinae, as that group is presently defined. The turdine syrinx of *Entomodestes,* on the other hand, is an indication that this genus is correctly placed in the Turdinae. In respect to the degree of relationship between *Phaeornis* and *Myadestes,* and to the relationships of two genera with non-thrush groups, the syringeal evidence is inconclusive. It is evident, however, that exclusion from the Turdinae also means exclusion from the Muscicapinae. Exclusion from the Muscicapinae is also indicated by the zoogeography of the two genera. The syringeal evidence is presented here in the hope that other taxonomists will look critically at the established placement of *Myadestes* and *Phaeornis* in the Turdinae.

Stizorhina and *Neocossyphus.* The two species of *Stizorhina* are called rufous flycatchers in most works on African birds (e. g., Cave and Macdonald, 1955; Mackworth-Praed and Grant, 1960) and placed immediately before the platysteirines. Sharpe (1881) suggested that *Stizorhina* (then *Cassinia)* might be a thrush related to *Myadestes.* Chapin (1953) considers the close color similarity between *Neocossyphus* and *Stizorhina* to be taxonomically significant; he places the latter in the thrushes, following *Neocossyphus.* Ripley (1952 b, 1964) also includes *Stizorhina* in the Turdinae adjacent to *Neocossyphus,* remarking (1952 b, p .13) that *Stizorhina, Cochoa, Myadestes,* and *Phaeornis* "might be a group of relict forms of which only the solitaires of the New World have any large distribution and group of species".

The presence of the generalized syringeal pattern in *Stizorhina* supports the belief that it is not a thrush, but the same consideration must be given to *Neocossyphus.* The finding of the generalized syrinx in the latter is somewhat surprising, for it is universally considered a good thrush. Chapin points out that members of both genera have unspotted young, but there are other "undoubted" thrushes whose young lack spots. Of the six genera currently considered thrushes and possessing the generalized syringeal pattern, *Neocossyphus* is the only one whose position apparently has not questioned heretofore. Possibly a thorough study of the genus would reveal other characters that suggest relationships outside the Turdinae.

Turnagra. The New Zealand "thrush", or piopio, although once considered a true member of the Turdidae, is now usually regarded as non-thrush of uncertain affinities. It differs from the typical thrushes in most of the characters usually considered diagnostic: the tarsus is stout and scutellate

(instead of booted); the tenth (outer) primary is relatively long (instead of rudimentary); and the young are unspotted. Oliver (1955) notes that the palate of *Turnagra* differs from those of *Pachycephala* and of the true thrushes, but resembles those of *Gymnorhina* (Cracticidae) and *Manucodia* (Paradisaeidae). He places *Turnagra* in a separate family, Turnagridae, adjacent to the Callaeidae, a placement also employed by Falla et al. (1966). Mayr (1967) places this genus by itself after the Pachycephalinae as "Genus Incertae Sedis", noting that its affinities appear to be with the Pachycephalinae.

The syrinx of *Turnagra capensis* is representative of the generalized type as it occurs in a variety of oscines, except for the absence of the medial part of M. bronchialis anticus. This fasciculus is occasionally covered by M. bronchotrachealis anticus, but it is rarely lacking altogether. It is well developed in *Gymnorhina, Manucodia* and other members of their families, as well as in all of the Pachycephalinae that I have examined.

Newtonia. This endemic Madagascar genus is usually placed in the Muscicapinae (cf. Traylor, 1970) on the basis of the broad, flattened bill and prominent rictal bristles. Field observations on the five species of newtonias are scanty. Rand (1936, p. 429) notes that *N. brunneicauda* "flits from twig to twig, gleaning small insects more in the manner of a titmouse, than of a flycatcher, although occasionally it catches insects on the wing". Vaurie (1953) remarks on the uncertainty of the affinities of this genus, but indicates that it might be close to *Muscicapa.* He goes on to suggest, however, that if further study indicates that *Newtonia* should be removed from the Muscicapinae it might be placed in the Sylviinae near *Phylloscopus.*

The view that *Newtonia* should be removed from the Muscicapinae gains support from the presence of the generalized oscine syringeal pattern. Certainly the newtonias do not belong near the nucleus of the typical flycatchers, exemplified by *Muscicapa.* Placement in the Sylviinae is not incompatible with the syringeal pattern.

Microeca. Members of this genus appear to be typical muscicapines in habits and structure. Vaurie (1953, p. 527) refers to *Microeca* as "the geographical representative of *Muscicapa* in the Australo-Papuan region". He recognizes seven species, four of which (including *M. leucophaea* the type species) "seem to form a species group", and might be considered the core of the genus. It is unfortunate that these flycatchers are so rare in anatomical collections, for a more thorough study of the syrinx and other characters of the group would surely prove enlightening. The syringeal structure of *M. leucophaea,* considered in the light of that of other muscicapines, suggests that *Microeca* is not closely related to *Muscicapa.*

The Australian "robins". A group of thrush-like or flycatcher-like Australasian genera *(Petroica, Peneothello, Heteromyias, Eopsaltria, Melanodryas*

and *Ephthianura)* is usually placed at the end of the monarchs or between the monarchs and the whistlers (Serventy and Whittell, 1967; Rand and Gilliard, 1967; and others). Certain of them are sometimes included in the Malurinae or placed in a separate family, Ephthianuridae. Some of the group *(Peneothello ,Heteromyias)* are rather like *Muscicapa* and are usually called "flycatchers"; others *(Petroica, Eopsaltria, Ephthianura)* are more like *Erithacus* and are called "robins" or "chats". Storr (1958) considers the whole group, along with *Muscicapa* and its more obvious allies, to be "specialised derivatives of the thrush/robin/chat group" and includes them (and *Muscicapa)* in the Turdidae. Parker (1973) has examined the tongues of *Ephthianura* and *Ashbyia* and concludes that these "chats" are more closely related to the honeyeaters (Meliphagidae) than to the Sylviinae or Malurinae. As noted by Parker, the brush-tipped tongue has evolved, apparently separately, in a number of other nectar-feeding birds, so resemblances between the divided, brush-tipped tongue of *Ephthianura* and *Ashbyia* and that of the meliphagids must be considered with caution. Regrettably, Parker does not state which other members of the Australian "robin" group have brush-tipped tongues, if any.

The syringeal morphology provides only negative evidence for the placement of this enigmatic group. Although supporting Storr's belief that *Muscicapa* is close to the Turdinae, it indicates that *Petroica, Melanodryas, Eopsaltria* and *Ephthianura* are not. The syrinx of meliphagids has a distinctive feature (to be described in a later paper) not found in *Ephthianura.* In short, the syringeal structure of *Ephthianura* does not provide evidence of relationship to the Meliphagidae, but the sharing of the generalized type of syrinx with the other Australian muscicapids is not much stronger evidence of relationships.

Culicicapa. The two species of this genus, both of which were examined in this study, are strongly adapted for flycatching. The bill is flattened and the rictal bristles exceptionally well developed, consisting of two rows, instead of the usual one. Vaurie (1953), while including *Culicicapa* in the Muscicapini, suggests that it might better be placed in the Rhipidurini (Rhipidurinae of the present classification), a suggestion supported by Parker (1964) on the basis of other evidence. The behavior of *Culicicapa* is more like that of *Rhipidura* than like that of the typical muscicapines and includes tail-fanning (Smythies, 1940). The presence of the generalized syrinx provides additional weight to the view that *Culicicapa* should be removed from the immediate vicinity of *Muscicapa.*

Ifrita. This monotypic New Guinea genus is usually considered to belong in the Orthonychinae or the Timaliinae, but Desfayes (1967), after comparing its coloration and habits with various muscicapine flycatchers (especially the niltavas), has concluded that it should be placed in the Muscicapinae,

in fact, in the genus *Niltava* (which he merges with *Muscicapa).* Harrison (1967) reviews a number of taxonomic characters in disagreeing with Desfayes. The absence of the turdine syringeal pattern in *Ifrita,* taken in the light of the extreme homogeneity of the syrinx in *Muscicapa, Niltava* and allies, strongly supports the prevailing opinion that *Ifrita* is not muscicapine.

Chlamydochaera. The most surprising anomaly in the distribution of the turdine syringeal pattern is its presence in *Chlamydochaera,* a little-studied, monotypic genus limited in distribution to the mountains of North Borneo. Since its description by Sharpe in 1887, *Chlamydochaera jefferyi* has been assigned to the Campephagidae (cf. Peters, 1960). Its antomy apparently has never been studied in detail, and the little available information about its habits comes from Whitehead (in Sharpe, 1889).

Examination of the United States National Museum spirit specimen and study skins of *Chlamydochaera* revealed that it has booted tarsus, characteristic of thrushes but not limited to them. Its bill is slender, slightly hooked terminally, and slightly notched, certainly within the range of variation of both the Turdinae and Campephagidae. *Chlamydochaera* differs from most campephagids in the shape of the forehead. In *Coracina, Lalage* and *Pericrocotus* the forehead is noticeably low, almost in line with the culmen; in *Chlamydochaera* it rises more steeply, as it does in most other songbirds. The coloration, grey on the back and belly, with a broad, black breast-band and a buff throat, might occur in either group. Mayr and Amadon (1951) note that this species lacks the stiffened feathers of the lower back that characterize the cuckoo-shrikes *(Campephaga)* and greybirds *(Coracina),* but not the minivets *(Pericrocotus).* I can see nothing in Sharpe's description, in the scanty field observations, or in the museum specimens that relegates *Chlamydochaera* to one family or the other. In the absence of contradictory evidence, the turdine syringeal pattern, otherwise limited to two subfamilies of the Muscicapidae, must be considered a strong indication that *Chlamydochaera* is a thrush that has remained hidden in the Campephagidae for lack of adequate study.

Prunella. The hedge sparrows, or accentors, have certain thrush-like characters, primarily in the structure of the bill, that led Ripley (1952 b) to include them in the Turdinae. He cites similarities in structure and habits between *Prunella* and *Saxicoloides,* the latter generally acknowledged to be a good thrush. Most other authors (and Ripley in 1964) have retained the hedge sparrows as a separate group (Prunellidae) outside the Muscicapidae. The generalized oscine syringeal pattern found in the three species of *Prunella* supports the exclusion of this group from the Turdinae, but not necessarily from the Muscicapidae. *Saxicoloides,* on the other hand, has the turdine pattern, indicating that it is closer to the true thrushes than to *Prunella.*

Taxonomic suggestions

Several taxonomic assertions can be made when the syringeal data are considered in the light of other characters and of prevailing taxonomy.

1. The muscicapine genera *Bradornis, Melaenornis, Rhinomyias, Ficedula, Niltava* and *Muscicapa* constitute a cohesive group that appears to be more closely related to the thrushes than to any other members of the broad family Muscicapidae to which they are sometimes considered allied (Platysteirinae, Monarchinae and Rhipidurinae). The genera *Newtonia, Microeca* and *Culicicapa* do not appear to belong in this group.
2. Among the Turdinae, *Zeledonia, Modulatrix, Myadestes, Neocossyphus, Stizorhina* and *Phaeornis* do not fit in with the remainder of the genera currently placed in this subfamily. These exceptional genera probably should not be placed in a subfamily that excludes the muscicapines. Most of the six genera are anomalous in other characters and some have already been designated for removal from the Turdinae.
3. The separation of the piopio *(Turnagra)* from the thrushes is upheld.
4. The distinctness of the hedgesparrows *(Prunella)* from the thrushes is further demonstrated by the syringeal morphology.
5. The little-studied Bornean "campephagid" *Chlamydochaera jefferyi* is almost certainly misplaced at present; it appears to be a good thrush.

Acknowledgements

This study and the broader one on which it was based would not have been possible without the use of anatomical specimens from the following museums, the curators of which kindly gave me "carte blanche" in the selection of specimens: American Museum of Natural History (Dean Amadon); British Museum (Natural History), Tring (David W. Snow); Field Museum of Natural History (Melvin A. Traylor); Louisiana State University Museum of Natural History (George S. Lowery); United States National Museum of Natural History (Richard L. Zusi); and Peabody Museum of Natural History, Yale University (Charles G. Sibley). Paul Schwartz and Ben B. King deserve my thanks for providing, at my request, specimens of *Platycichla* and *Cochoa*, respectively.

It is a pleasure to acknowledge the assistance of the many colleagues who read this paper during its long genesis and offered suggestions for its improvement. Special thanks are due to P. J. K. Burton, Mary H. Clench, Lord Medway, Kenneth C. Parkes, S. Dillon Ripley, Charles G. Sibley, David W. Snow, Melvin A. Traylor, Charles Vaurie and H. E. Wolters.

Summary

The gross morphology of the syrinx was studied in 124 genera of the broad family Muscicapidae (Aves: Passeriformes) in comparison with about 225 genera in other oscine families. Two basic syringeal types were found: one, termed "turdine", in most thrushes (Turdinae) and muscicapine flycatchers (Muscicapinae),

the other, "generalized", in virtually all other oscines. Those members of the Turdinae, under the present (Peters Check-list) classification, with the generalized syrinx are mostly aberrant in other characters as well. The taxonomic implications of the study are as follows:

1. The Muscicapinae (including the genera *Muscicapa, Ficedula, Niltava, Bradornis, Melaenornis* and *Rhinomyias)* are more closely related to the Turdinae than to the other "flycatchers" of the Monarchinae, Rhipidurinae and Pachycephalinae.

2. The genera *Zeledonia, Modulatrix, Myadestes, Phaeornis, Stizorhina,* and *Neocossyphus* do not appear to be as closely related to the other Turdinae as are the Muscicapinae.

3. The genera *Newtonia, Microeca* and *Culicicapa* are not members of the thrush-muscicapine group.

4. The genus *Chlamydochaera,* long considered a cuckoo-shrike (Campephagidae) appears to belong in the thrushes (Turdinae).

Zusammenfassung

Bei 124 Gattungen der Familie Muscicapidae im weiteren Sinne (Aves: Passeriformes) wurde die Morphologie der Syrinx untersucht und mit der in etwa 225 Gattungen aus anderen Singvogelfamilien verglichen. Es zeigte sich dabei, daß wir die Ausbildung der Syrinx zwei Grundtypen zuordnen können: der eine findet sich bei den meisten Drosselartigen (Turdinae) und „echten" Fliegenschnäppern (Muscicapinae) („turdiner Syrinxtyp"), der andere, der undifferenzierte Syrinxtyp, bei praktisch allen anderen Singvögeln. Jene gegenwärtig zu den Turdinae gestellten Arten (s. Peters' Check-list, vol. 10), die den undifferenzierten Syrinxtyp besitzen, weichen in den meisten Fällen auch in anderen Merkmalen von den übrigen zu dieser Unterfamilie gerechneten Arten ab. Für die Taxonomie ergeben sich die nachstehenden Folgerungen:

1. Die Muscicapinae (mit den Gattungen *Muscicapa, Ficedula, Niltava, Bradornis, Melaenornis* und *Rhinomyias)* stehen den Turdinae näher als den anderen sog. „Fliegenschnäppern", d. h. den Monarchinae, Rhipidurinae und Pachycephalinae.

2. Die Gattungen *Zeledonia, Modulatrix, Myadestes, Phaeornis, Stizorhina* und *Neocossyphus* scheinen den Turdinae ferner zu stehen als die Muscicapinae.

3. Die Gattungen *Newtonia, Microeca* und *Culicicapa* gehören nicht zu der Gruppe der echten Fliegenschnäpper und Drosselartigen.

4. Die Gattung *Chlamydochaera,* lange Zeit zu den Campephagidae gerechnet, scheint zu den Drosselartigen (Turdinae) zu gehören.

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