A PRELIMINARY SURVEY OF THE DISTRIBUTION OF THE MALLOPHAGA ('FEATHER LICE') ON THE CLASS AVES (BIRDS).

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[With 2 plates and 3 text figures]

INTRODUCTION

The object of this survey is to summarise the present knowledge of the distribution of the Mallophaga on the class Aves, and to show where this distribution may throw light on the phylogenetic relationships of certain bird groups.

The Mallophaga are ectoparasitic insects living on birds and mammals. These parasites pass their complete life-history from egg to adult on one host, and in the majority of cases, each species of Mallophaga is restricted to one host species or a group of closely related host species. Their present distribution suggests that they became parasitic on birds at an early stage in the evolution of this latter class, and that they evolved with their hosts, but at a somewhat slower rate. This has resulted in the Mallophaga parasitising related hosts being themselves related, and thus, in the majority of cases, it is possible by examining a specimen of Mallophaga to say from which order of birds it was taken. Any host species may be parasitised by species of one to twelve or rarely more genera, some of which are restricted to definite ecological niches on the body of the bird where their general body form seems to be adaptive to the feathers of that niche. Two of the most striking examples (Pl. 1, figs. 1-2) are the short round species found on the head and neck; and the elongate, more flattened species on the wings and back. As the Mallophaga of any one ecological niche, have evolved in a more constant environment than have the birds, they have diverged from each other less. Thus, it is usual to find a genus of Mallophaga distributed throughout an order of birds. In the case of the Charadriiformes, for instance, the species found on the head of a gull (suborder Lari) and on that of a ruff (suborder Charadrii) both belong to the same genus (Grypsornis). This general principle that the Mallophaga of related hosts are themselves related suggests that the distribution of these parasites should be valuable evidence on the phylogeny of their hosts. However, there have been many factors operating during the evolution of the Mallophaga which may have obscured this initial relationship between host and parasite. These factors have been fully discussed elsewhere (Hopkins, 1942 and 1949; Clay, 1940 and in press), but may be summarised here once again:

Discontinuous Distribution. A genus of Mallophaga formerly widely distributed throughout the Aves may have become extinct on certain bird groups; its presence would not, therefore, denote relation-
ship between the host groups on which it is now found. The genus Colpoccephalus seems to be an example of such a genus; it has not been included in the Mallophaga faunas shown in the distribution charts, as its presence or absence seems to be of little significance.

Secondary Infestations. Although it is probably rare for the rise of one host order to be able to establish themselves on the host of another order, there is little doubt that such secondary infestation is the explanation of some of the cases of anomalous distributions of genera. The occurrence of the same genus (Sarcoptes) on the Charadriiformes (waders), gulls and auks), Procellariiformes (petrels) and the Gruiformes (cranes) is probably an example. Among the factors limiting the establishment of a host on a new host are the difficulties of transference and the strange environment for a species which is strongly host specific. Elsewhere (Clay, in press) the question of feather structure in relation to distribution of the Mallophaga has been discussed. Reference was made to a paper by A. C. Chandler (1910) in which this author puts forward a classification of the birds based on the minute structure of their feathers; and it was shown that the distribution of the Mallophaga in some cases supported Chandler's emendations to the usually accepted avian classification. It was suggested that this might either be a confirmation of the relationship between these groups, or that host groups with a similar feather structure might be parasitized by related Mallophaga because secondary infestation had been made possible by the similarity of feather structure—this character of the environment probably being one of the factors limiting the establishment of a host specific species on a new host.

Parallel Evolution. It is possible that parallel evolution may explain some of the cases of anomalous distribution found in the Mallophaga, although insufficient is known about the morphology and development for any certainty in these cases.

In spite of the limiting factors briefly summarized above there is no doubt that the distribution of the Mallophaga is a source of evidence, which, with careful evaluation, should be utilised by the ornithologist in considering the position of birds of doubtful affinities. It is important to note, as will be made clear below, that in those cases, where a bird has an anomalous mallophaga fauna there is usually a difference of opinion over its correct systematic position, and that the evidence from the Mallophaga usually supports the opinion of one school of ornithologists.

The Distribution of the Mallophaga on the Aves

Struthioniformes (Ostriches) and Rheiformes (Rheas). The distribution of the Mallophaga supports Chandler's conclusions from the feather structure and Lowe's (1928, 1935, 1942) from other anatomical features that these two orders are related and not the relics of independent unrelated stocks as is often stated. The ostriches and rheas are parasitized by closely related species of a specialized genus (Struthiodipetalus) of Mallophaga found on no other order of birds, and also by the same two species of mites (Paralges pacificus

Habitat forms of Mallophaga
and *Paralichthys bicaudatus* and subspecies of the same cestode (*Houttuynia struthiocamei*) (Eichler, 1918). Lowe (1928, 1935, 1938) from studies not only of the structure of the feathers, but of many other anatomical features concluded that the Struthiones (= Struthioniformes, Rheiiformes, Casuariiformes and Aepypterygiformes) 'represent a perfectly natural group descended from some common ancestor' (1938:244). The relationship between the Struthioniformes and Rheiiformes is simply confirmed by their parasitic fauna—a fauna difficult to explain except by postulating such a relationship.

**Casuariiformes** (Cassowaries, Emus). Chandler and Lowe (1928) believed that this order was related to the two already mentioned. The evidence from the Mallophaga is neutral: only one genus (Dahlemia) is known, which has no obvious relationship to any other. The fact that both this genus and that from the Struthioniformes and Rheiiformes show asymmetry of the head has encouraged some authors to deduce a relationship between the three host orders, but Dahlemia, as shown by its general morphology, is not closely related to Struthiocephalus, and asymmetry of the head is found in another unrelated genus (Hystrichosoma) parasitic on the Icteridae (Passeres). The presence of asymmetry of the head of the species found on the Struthioniformes and Casuariiformes may be a case of convergence in response to some common feature in the structure of the feathers.

**Aepypterygiformes** (Kiwi). Chandler on account of the feather structure and Lowe on other anatomical features placed this order near the three others already discussed. Although only one genus *Fallicola* (Aepypteryx) is known from this order and little, therefore, can be deduced from its presence, it is of some interest that *Fallicola* is found also on the Railidae. This distribution supports the belief of Färbringer (1888) that there is a relationship between aepyptes and the rails. However, this mallophagan genus is also found on some of the Passeriformes, although there is evidence that there it may be due to secondary infestation. This is an example of the possibility of error in using the distribution of the Mallophaga as evidence of relationships between the hosts.

**Tinamiformes** (Tinamous). Chandler states (1247): 'the structure of the down alone is sufficient proof that the tinamous are unquestionably far more closely allied to the Galli than to any other birds.' Färbringer (1888), Beddard (1890), and others have drawn attention to the apparent gallinaceous affinities of the tinamous. Lowe (1942:17) and most modern classifications place them in a different super-order, the Palearquantidae, together with the four orders already considered. Evidence from the Mallophaga is here of little ass-

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1 The evidence of relationship provided by one genus of Mallophaga is obviously less convincing than if more genera are involved, and in most cases should probably not be taken into account at all. Comparisons have therefore been made between the mallophagan fauna of host groups that is the genera of Mallophaga normally found throughout the host groups in question.
stance: the Tinamiformes are chiefly parasitized by the species of one family (Heptapogostiridae) found on no other orders of birds and which are presumably the descendants of a common ancestor parasite on an ancestral tinamou. The species have filled the different ecological niches on the body of the bird and taken on a superficial resemblance to the unrelated occupants of similar niches on other orders. Some genera of this family have retained the primitive type of head found also in the species parasitic on the Sphenisciformes, Galli, and Columbae; and also bear a superficial resemblance to these species in some other characters. The species on the Galli and Columbae by the characters of their external and internal morphology seem to be truly related; those on the Tinamiformes and Sphenisciformes differ from the former and from each other in some characters of their internal and external morphology. Hence, it is not possible to say on the available evidence whether the Mallophaga parasitic on the Sphenisciformes, Galli, Columbae, and Tinamiformes are relics of not closely related stocks—those on the last three groups appearing similar owing to the retention of certain generalized primitive characters due to the similarity of the feather structure—or whether they are the only descendants left of some common stock which once had a wider distribution. This might or might not denote relationship between the Galli and the Tinamiformes. The other genera found on the Tinamiformes show no relationship to any found on the Galli, with the exception of one (Tinamatorcida) which belongs to a subfamily (Degeneriellinae) found not only on the Galli but on many other orders.

Sphenisciformes (Penguins). The penguins are parasitized by two genera of Mallophaga which have the primitive type of head, but provide no evidence on the relationships of the hosts.

Gaviiformes (Divers) [Gaviiformes of European authors] and Columbiformes (Grebes) [Podicipediformes of European authors]. The Mallophaga of these two orders throw no light on the relationship of their hosts.

Procellariiformes (Petrels). This order is parasitized by a large number (13) of genera, the majority of which are peculiar to the order, and probably developed from a common ancestor on the order. One genus (Stenomastax) is also found on the Charadriiformes, and a second genus (Procellariphaga) either superficially resembles or is related to one (Austrinocompsa) also found on the Charadriiformes. The occurrence of these two genera may be due to secondary infestation (see Clay, 1949:292).

Pelecaniformes. This order is usually divided into three suborders: the Phaethontes (Tropic-birds), the Pelecan (Pelecans, Gannets, Cormorants) and the Fregatae (Frigate-birds). Figure 1 shows that

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1 The occurrence of one species of this family on the Carcinus is probably due to secondary infestation.
the Phaethontes do not have the mallophagan fauna characteristic of the Pelecaniformes, but have two genera of the fauna characteristic of the Charadriiformes. Chandler (1916:316) states, 'The third group, Phaethontidae, is so strikingly like the Laridae [i.e. in feather structure] that their affiliation with the steganopodes [=Pelecaniformes] seems very doubtful, and if feather morphology is considered, they should be looked upon rather as aberrant larid forms'. Mathews and Reedle (1921) basing their conclusions on the anatomy of the Phaethontes placed them as a family of the Laridae. Lowe (1936) on a consideration of the form of the quadrate and its tympanic relations believed that the associations of this family lay with the rest of the Pelecaniformes. Murphy (1936:792) although stating that 'there is no doubt about the place of the tropic-birds in the order Pelecaniformes' goes on to say that 'they differ much in habits from all the existing relatives, and share many superficial characters with the tropic-birds. These include form and size, the shape of the beak, the silky sheen of the plumage, the voice and the aerial grace. Furthermore tropic-birds hatch from the egg covered with down, instead of being naked like young boobies, cormorants, and pelicans.'

The mallophagan fauna supports the view of a relationship between the Phaethontes and the Charadriiformes. Alternatively, it can be argued that as members of these two groups live in the same habitat, the transference of Mallophaga could have taken place and the similarity of the structure of the feathers (if this does not denote relationship) might have enabled the immigrant louse to establish itself on the new host. The fact that one of thelice is question (Sauganiastrum) is a louse of the head, a form otherwise absent on the Pelecaniformes, would mean that the immigrant louse would have found an empty ecological niche to occupy. It must also be noted that the genus Sauganiastrum, which probably originated on the Charadriiformes, is found not only on Phaethontes, but also on the Procellariiformes and the Gruidae. Its occurrence on these latter host groups may be due to secondary infestations. Here, therefore, we have a case in which there is considerable doubt concerning the relationships of a group of birds. The evidence from the Mallophaga, as the evidence from any other single source, is not conclusive, but supports the views held by some ornithologists and should be taken into account in evaluating the total evidence.

Ciconiiformes (Herons, Storks, Ibises and allies). This order is usually divided into four suborders: the Ardeae, Balaeicpitae, Ciconiæ and Phoenicopecteri. Of the eight genera of Mallophaga (omitting Colopocephalum) found on the Ciconiiformes only two (Ciconiophilus and Ardeicola) are common to the Ardeae (Herons, Bitternæ) and Ciconiæ (Storks, Ibises, Spoonbills); only one of these (Ciconiophilus) is known from the Balaeicpitae (Whale-headed Stork), but little collecting has been done from this last suborder; the Phoenicopecteri (Flamingoes) have none of the genera found on the rest of the Ciconiiformes. The Scopodaea (Hammerhead), usually regarded as a superfamily of the Ciconiæ has (apart from a somewhat aberrant species of Colopocephalum) two genera (Linaeacea and...
Automenopon) found elsewhere throughout the Charadriiformes, a distribution which may or may not be of significance (see Hopkins, 1931:103). One genus (Ciconiophilus) found on the Ciconiformes is also found on Cygnus (Swans: Anseriformes) and another (Ibidocetus) characteristic of the Threskiornithoidae (Ibis) is also found on Aramus scolopaceus (Limpkin: Gruidiformes), a third genus (Laemobothrio) found on some of the Threskiornithoidae is again found on Aramus, but this genus has a wide distribution with species on the Railidae (Rails), Phasianidae (Trumpeters), Opisthocomus (Hoatzin) and less closely related species on the Falconiformes (Birds of Prey).

The distribution of these genera suggests that Ciconiophilus may be a straggler on the swans from the Ciconiiformes, Ibidocetus a straggler on Aramus from the Threskiornithoidae and Laemobothrio a straggler on this latter superfamily from the Railidae. Although Eichler (1949) suggests that the mallophagous fauna of Aramus (fig. 1) may indicate a position for this family between the Railidae and Threskiornithidae.

The Phoenicopteridae (fig. 2) are parasitized by three genera found elsewhere only on the Anseres (Ducks, Geese, Swans). Chandler (1916:210) stated: "that in the details of the minute structure of the feathers the Phoenicopteridae agree with the Anseres more closely than

\[ \text{ANSERIFORMES} \]

\[ \text{CICONIFORMES} \]

Fig. 2. Anseriformes (Mallopplagan fauna: 5 species.): A, black. Genera of Anseropodidae counted as one) and Ciconiiformes.

with the Ciconiidae. Opinions on the systematic position of the flamingoes based on the internal anatomy are divided. The general

\[ \text{ANSEFITEROMES} \]

characters of the bill and feet of the flamingoes, their habit of nesting on the ground and their call are all more duck-like than stork-like. Fossil flamingoes apparently show less elongation of the legs and have a stouter bill (Howard, 1930). On the other hand, the similarity of feather structure (I this does not denote relationship) might have allowed immigrant ice from one of the Anseres to establish themselves on the flamingoes; the common habitat in which the birds live would have made the initial transfer possible. But there are three mallophagous genera involved all suggesting anserine affinities for the flamingoes, a relationship supported by some of the evidence from ornithological sources.

Anseriformes. This order is usually divided into two suborders: the Anseres (Ducks, Geese, Swans) and the Anhimae (Screechers). The former have five genera of Mallopplagan, two of which (Holomenopon and Ornithokis and its closely related genera or subgenera) are found only on the Anseres and three others (Aulacocot, Anisocot and Trinemat) found elsewhere only on the Phoenicopteridae. The Mallopplagan of the Anhimae throw no light on the affinities of that suborder.

Falconiformes (The Birds of Prey). The main point of interest provided by the mallopplagan parasitizing this order is that a species of a genus found elsewhere in the Falconiformes only on the Catharinae (New World vultures) has been taken from Pseudepsiphrus africanaus, an Old World vulture. This suggests that the division into 'Old World' and 'New World' vultures is not so marked as indicated by the usually adopted classification, a presumption supported by the fossil record (Howard, 1930). The Falconiformes have other genera which show a somewhat inexplicable distribution and which are mentioned here without further comment. One genus (Kardin) is also found elsewhere only on the owls (Strigiformes) and another (Cuculophila) is found elsewhere only on the cuckoos (Cuculi).

Galliformes (Game Birds and Hoatzins) and Columbiformes (Sandgrouse, Pigeons, Doves). The possible relationship of these orders to the Tinamiformes has already been discussed. The distribution of genera (or closely related genera) comprising the mallopplagan fauna of the Galli (Game Birds) suggests affinities between the Galli and the Columbidae (Pigeons, Doves) and the Galli and the Musophaga (Plantain-eaters). The Opisthocomi (Hoatzins) usually considered as a suborder of the Galliformes, has five genera none of which is related to those found on the Galli: no information about the feather structure of Opisthocomus has been found. The presence of these five genera distinct from those on any other order (except in the case of one, Larmothrix, which has a wide distribution) suggests an isolated position for Opisthocomus within the Aves.

The Pterocletes have two genera from which no deductions of affinities can be made: one (Neomenopon) has no close affinities, the
other (Syrrhaptoferns) belongs to the widespread Degeerianella. The Columbidae have a number of genera a group of which (Coloeornis, Campmanulotes and related genera) have obvious affinities with two (Ganoides and Goniocole) found on the Galii. Chandler states that in feather structure the Columbiformes 'show more similarities to the gallinaceous birds than to any other group', and as the malleophagous genera involved have the primitive type of head the explanation discussed under the Tinamiformes might also be applicable in this case. However, the characters (both of the external and internal morphology) common to these genera are such that it must be assumed that all the genera are related. Hence, if this does not denote relationship of the hosts, the presence of these genera must be due to secondary infestation, made possible perhaps by the similarity of feather structure.

The Musophagii, with four out of five malleophagous genera either the same or closely related to those found on the Galii, seem to show a definite relationship to the Galii and none to the Cuculli. This relationship has been discussed elsewhere (Clay, 1947), but at that time the paper by Lowe (1943) had not been seen. In this paper Dr. Lowe, basing his remarks on a study of pterylography, osteology and myology, comes to the conclusion that the Cuculli and Musophagi cannot be placed in the same order. Chandler states that: 'The Musophagidæ do not differ in any important ways from the Cucullidæ in the structure of their feathers', but he continues 'the Cuculli (=Cuculliformes) especially the Musophagidæ come nearer the gallinaceous and columbid birds.'

Gruiformes (Cranes, Rails and allies) and Charadriiformes (Waders, Gulls and Aules). These two orders are taken together as both the anatomical evidence (Lowe, 1931; 1934, Chandler 1933) and the fossil record (Howard, 1930) suggest that they have arisen from a common stock, probably in the Eocene; further, certain families of birds are placed in the Gruiformes by some ornithologists and in the Charadriiformes by others.

The Gruiformes comprises an heterogeneous assemblage of suborders, the affinities of some still being a matter for discussion. Figure 3 represents the Gruiformes as arranged by Wetmore, 1940, and figure 4 shows a rearrangement based on the malleophagous faunas of the suborders.

The suborder Gruiformes is usually divided into two superfamilies: the Railloidea (Rails) and Gruidea. The former has a malleophagous fauna comprising five genera; two of these genera are found also on the Psophidiæ (Trumpeters) and three of them on the Aramidæ (Limpkins), both these families usually being included in the second superfamily, the Gruidea. The Gruidea (Cranes), the third family of the Gruidea, has a malleophagous fauna of four genera, none of which is found on the other families of the suborder Grues, nor on the Railloidea. From the Heliornithidæ (Sun-geese) and the Rhynchoehitæ (Kagus)—two other suborders of the Gruiformes—genera of the ratine malleophagous fauna have been recorded. The Jacanidæ (Jacanas), a group of birds with an obscure systematic position but usually placed with the Charadriiformes, have two genera belonging to the ralline fauna\(^4\). These facts suggest that the Railloidea, Aramidæ, Psophidiæ, Heliornithidæ, Rhynchoehitæ and Jacanidæ are more nearly related to each other than to the Gruidea. Evidence on the relationships between these groups from ornithological sources is conflicting. Chandler (1934) deduces from the feather structure a relationship between the Gruidae, Aramidæ and Railloidea and considers them offshoots from a primitive stem leading to the Charadriiformes; while the Otididæ, Psophidiæ (and possibly the Aramidæ) he considers are more closely related to each other and may be early offshoots from the stem leading to the Columbæ and Galii. This, as shown above, is in conflict with the evidence from the malleophagous faunas. Lowe (1931: 1940), however, considers that the Railloidea and the Heliornithidæ are an isolated group and should be removed from the Gruiformes to form a separate order, the Railloidea. This view is partly supported by the distribution of the Malleophaga, but the Railloidea would have to include some of the families which were retained in the Gruiformes by Lowe. This latter author (1945) considers that

\(^4\) Evidence has recently become available (Zimmermann, in press; and Tordoff, in press) that the Jacanidæ also have three genera (Quadrupus, Saramandusoria and Actornithophaga) characteristic of the Charadriiformes.
the affinities of the Jacanoidae are not with the Charadriiformes, but with the Gruiformes; later (1931) he places them with the Gruidae not with the Railidae in his new order the Railiformes. Evidence from the Mallophaga of the Jacanidae, however, suggests railing not gruiform affinities. Lowe (1931) considers that the Burhinidae (Stone-curlews)—placed by Wetmore, 1940 as a superfamily of the Charadrii, fig. 1—should also be placed near the Gruidae in the suborder Gruae of his order Telmatomorphae (which also includes the Charadriiformes). The Burhinidae have two genera characteristic of the mallophagan fauna of the Charadriiformes, thus confirming Wetmore's classification. Another family which has been bandied about between

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\begin{array}{ccc}
\text{OTIDES} & \% \setcounter{equation}{0} & \text{TURNCES} & \% \setcounter{equation}{0} & \text{Gruidae} & \% \\
\text{MESOCRATIDES} & \% & \text{HELIOdONITHES} & \% & \text{RUHEMOCHETI} & \\
\text{EURYPYGEAE} & & & & & \\
\text{CARIAHAE} & \% & \text{Rallidae} & \% \\
\end{array}
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Fig. 4. Gruiformes re-arranged according to the Mallophagan fauna. Scale as in fig. 3.

the Gruiformes and the Charadriiformes is the Rostratulidae (Painted Snipe). This family has an interesting mallophagan fauna: two genera, one (Quadriceps) of which belongs to the mallophagan fauna typical of the Charadriiformes (fig. 1) and the other (Pseudomenopon) to that of the Railidae. Little can be deduced from this distribution, the presence of one or other of the genera may be due to secondary infestation. Pseudomenopon, it should be noted, is also found on the Gaviiformes and the Colymbiformes.

The Mallophaga of the other five suborders of the Gruiformes are of little assistance in deducing relationships. The Orides (Bustards) [10]

have one genus (Otidoechus), the nearest relatives of which are found on the Galli (Cicologaster) and on the Scolopacidae—the snipe and woodcock—(Rheonomina). These genera are perhaps relics of a previously more widely distributed group of genera. The Mesocratides (Montes) and the Turnicles (Bustard-quails, Hemiproctes) are each parasitized by one genus of Mallophaga; these genera are related and probably derived from an ancestral stock widely distributed throughout the Aves, their present day representatives forming the Degaeria-liniae found on many unrelated host orders. Although such genera throw little light on the relationships of their hosts it may be mentioned that the genus (Turnicola) on the Turnicles seems to show affinities to one (Penneaureus) on the Passeriformes, the latter also most probably being derived from a Degaeria-like ancestor. This resemblance may be due to parallel evolution or relationship between the hosts, a point of interest as the Turnicles show some passerine characters (Lowe, 1923-1927). Only one genus (of doubtful affinities) has been seen from the Eurypygae (Sun-bitterna). The Cariamne (Carianaes) are parasitized by two genera (apart from Colpocephalum) found elsewhere only on the Tinamiformes, a distribution probably explained by secondary infestation on the Cariamne. As the Mallophaga of these five suborders are such that no certain deductions can be made as to the relationships of their hosts, there is no object in discussing the ornithological evidence bearing on the affinities of the host groups.

Psittaciiformes (Parrots). This order is parasitized by a number of mallophagan genera which throw no light on the relationships of the parrots within the class Aves. The parrots are probably an example of an order on which the Ichnoceran mallophagan fauna is derived from a primitive ancestral stock of a type found throughout the Aves, and which has evolved on the order itself into the different genera now found; these genera will, therefore, be more closely related to each other than to those on any other order.

Cuculiformes One suborder, the Musophagi (Plantain-eaters), has already been discussed under the Galliformes. The other, the Cuculi (Cuckoos), has a quite different mallophagan fauna comprising four genera, one (Cuculophaga) belonging to the widespread Degaeria-liniae, two of which the affinities are obscure, and one other (Cuculids), the affinities of which seem to lie with one found on the Falconiformes (see above). The significance of this distribution cannot at the present time be assessed.

Strigiformes (Owls). The Owls are parasitized by two genera; the affinities of one (Strigiphilus) are unknown, the other (Kerodonta) is found elsewhere only on the Falconiformes.

Caprimulgiformes (Nightjars) and Coliiformes (Colies) are each parasitized by distinctive genera which throw no light on the relationships of the hosts.

Apodiformes, Trogoniformes, Coraciiformes, Piciformes and Passeriformes. These orders can be considered together as some
members of all the orders are parasitized by elements of the passerine fauna. The order Apodiformes contains two suborders: the Apodidae (Swifts), the Mallophaga of which give no evidence as to relationship, and the Trochilidae (Humming-birds). The latter suborder is parasitized by one genus (or two closely related genera, Rizina and Trochilodes) found also on the Passeriformes (Perching Birds). Chandler (1:359) states that the structure of the feathers shows a striking likeness to those of the latter order. Lowe (1950) basing his conclusions on a study of other anatomical features considered that the humming-birds should be placed as a suborder of the Passeriformes.

The Trogoniformes (Trogonidae) are parasitized by two genera (Myiidae and Brudia) characteristic of the Passeriformes. Again, Chandler (1:358) on the basis of feather structure considered these two orders to be related.

The coraciiformes (as arranged by Wetmore, 1940) do not have a uniform mallophagan fauna. In the suborder Alectridae the superfamily Alectridinae (Kingfishers) is parasitized by two genera which throw no light on the affinities of their hosts. No Mallophaga have been seen from the Todidae (Todies); two genera (Brudia and Philopterus) have been taken from the Monotremata (Moles) both of which belong to the passerine fauna. In the suborder Meropiformes (Bee-eaters) one (Brudia) of the three mallophagan genera belongs to the passerine fauna. In the suborder Coracidae, the family Coraciidae (Rollers) is parasitized by two genera, one (Toronumops) which is found elsewhere only on the Monotremata, and the other (Cephalornis) is closely related to one on the Passeriformes (Picidae), but of a generalized type (the Degeerellinae) found elsewhere in the class Aves. No Mallophaga have been seen from the Lepidothecidae (Cuck-o-roosters). The Upupidae (Hoopoes) have two genera (Uropsila and Menarchus) belonging to the passerine fauna, but both belong to groups of genera found elsewhere. The Phoeniculidae (Wood-hoopoes) have two genera, one (Hippocannis) probably related to Uropsila on the Upupidae and the other (Odontophora) the affinities of which are not known. The Bucerotidae (Hornbills) have the genera, none of which belong to the passerine fauna, but the Ichneumonidae genera are all probably derived from a single ancestral stock which belonged to the Degeerellinae, a genus of which is found on the Passeriformes. Chandler shows that in feather structure the Alectridinae and the Bucerotidae are somewhat different from the rest of the order, a fact supported by the mallophagan faunas which may have evolved in a rather specialized way.

The Piciformes (Jacamars, Barbets, Toucans, Woodpeckers) (with the exception of the Galbuliidae from which nothing has been seen) have an entirely passerine mallophagan fauna which supports the evidence put forward by Chandler and Lowe (1940) based on the morphology of feathers, skeleton and muscles.

The distribution of the Mallophaga on these orders suggests, therefore, a close passerine relationship for the Picidae, Trogoniformes, and Monotremidae, and less close passerine connection for the Trochilidae, Meropidae and Rhamphastidae. The Mallophaga of the rest of the groups although not conclusive, do not preclude a passerine relationship, except perhaps in the case of the Alectridinae where the Mallophaga show no passerine affinities.

EXPLANATION OF THE DISTRIBUTION CHARTS

As the mallophaga have a host-wise not a geographical distribution the parasitologist has no method of demonstrating distribution graphically. These charts are an attempt to do so. They are based on Wetmore's classification of birds (1940) and the suborders are drawn as entire areas clustered together to form the order; the superfamilies, into which a suborder is divided are shown as contiguous areas. The size of each area is proportional to the number of species (as given by Mayr, 1949) in the division represented. Thus, the size of any area shows the number of species over which a parasite genus is distributed; and the number of distinct areas in an order and the irregularity of outline of an area representing a suborder gives some indication of the diversity of host species parasitized. Both these representations can only be approximate for owing to the difficulties of bird phylogeny the relation of the 'territories' to each other is often doubtful; and the size of the 'territories' shown will need adjustment as new species are discovered and as birds now considered as species are relegated to sub-specific rank. The names of orders are given in large capitals underlined, suborders in smaller capitals, superfamilies in lower case letters and families in small lower case letters.

Where two numbers are given with a name, the lower is the total number of genera recorded from the host group and the upper is the number of genera belonging to the mallophagan fauna. (shown in black) of the order illustrated. The mallophagan fauna is the number of genera characteristic of the host group in question. A genus found on only one small section of the group is not included in the faunal number, but is included in the lower number. Colpephalum, for the reasons given above, is omitted from all the faunal numbers and from both upper and lower numbers. Two genera on one host order, which are allopatric replacements of each other are counted as one genus: Bivarifrons and Starnidascus, for instance, are counted as one genus in compiling the mallophagan fauna of the Passeriformes, as the former genus appears to be the allopatric replacement of Starnidascus on the Icteridae (Troupials).

REFERENCES


...No attempt has been made to show the relationship between superfamilies within a suborder. [13]


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