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The Mallophaga as an Aid to the Classification of Birds with Special Reference to the Structure of Feathers

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Introduction

The object of this lecture is to bring to the notice of ornithologists both the use of the general principle that the phylogenetic relationships of the Mallophaga reflect those of their hosts and the limitations of the application of this rule; and further to discuss some of the problems with which the parasitologist is faced—problems which can be solved only by the ornithologist.

Evolution and present distribution of the Mallophaga

The present distribution and host relationships of the Mallophaga suggest that the evolution of this group must have taken place on certain lines (see Clay, 1949) resulting in related groups of birds being parasitized by related species of Mallophaga. The exceptions to this general rule can be explained by discontinuous distribution, secondary infestations, and parallel and convergent evolution (Hopkins, 1942; Clay, 1949).

The role of certain environmental factors in the evolution and distribution of the Mallophaga

The environment of the Mallophaga is formed by the external characters of the body of the bird and, hence, the evolution of the Mallophaga has been influenced by certain superficial characters of the hosts irrespective of whether these are of phylogenetic importance. The following are some general reactions, found throughout the Mallophaga, to certain characters of their environment.

1. **Size.** Harrison (1915: 96) was the first to point out that in a genus of Mallophaga distributed over a number of nearly related birds, the size of the parasite is roughly proportional to the size of the host. This principle

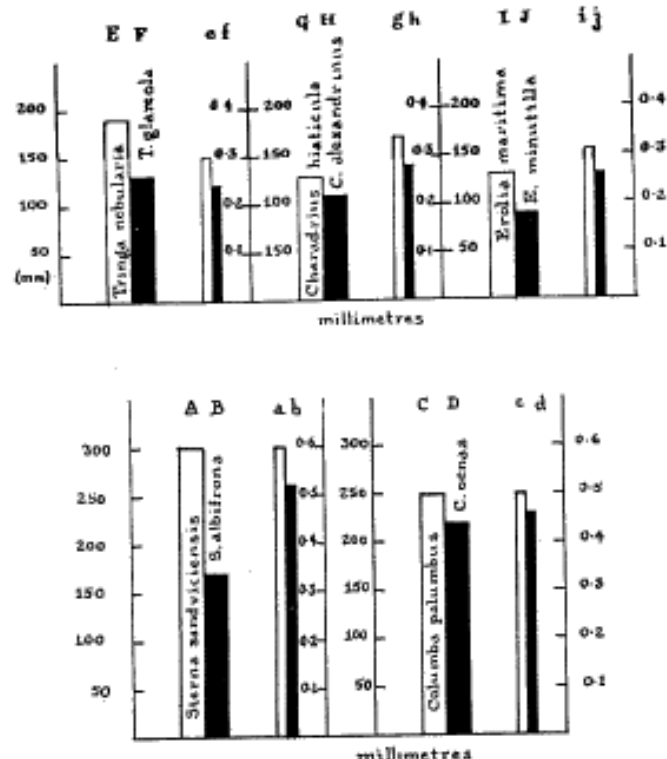


Fig. 1. Examples of the general relation in size between host species and parasite species. (Calculated from the mean of the lengths of wings of hosts and breadth of heads of parasites.) a-j, parasite species; a-b, *Saumundsonia* spp.; c-d, *Comptosoides* spp.; e-h, *Quadriceps* spp.; i-j, *Caraliceps* spp. A-J host species.

has a wide application throughout the Ischnocera and some examples are shown in figure 1. Although in these cases there is little or no overlap in measurements between the two Mallophaga species, in other cases the means of the measurements may be distinct, but there is an overlap in the range of measurements (fig. 2), or the difference in measurements may be

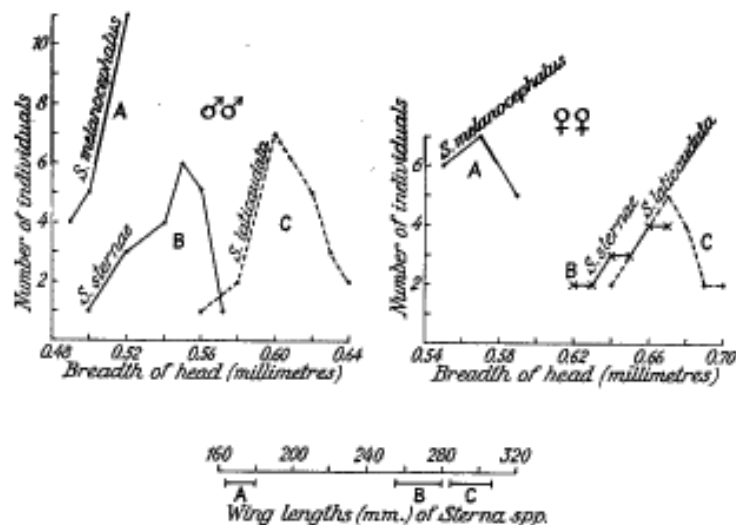


Fig. 2. Differences in size of male and female parasite (*Saumundsonia* spp.) in relation to size of host. A, *Sterna albifrons*, B, *Sterna hirundo*, C, *Sterna sandvicensis*.

shown in one sex only (fig. 2). Thus, measurements showing this correlation between size of host and parasite need careful analysis. It is not possible, therefore, to do more than make some suggestions of its cause: Size of parts of the feathers: Little seems to be known about the size of parts of the feathers in nearly related birds. Rensch (1924) has shown that the larger races of a species have a greater number of larger cells in the feathers than the smaller races of the same species, which presumably would mean an increase in the size of individual parts of the feather such as the barbules. Size of the barbules, as the latter are eaten by the Mallophaga, might directly affect the size of certain structures used in feeding, the increased or decreased size of which would be reflected in the size of the whole animal. The difficulties in accepting this theory is that the presumed optimum size appears to be different for males and females, and the range of size in some species seems rather large. Temperature of the body of the host: Wetmore (1922) has shown that larger birds in general have lower temperatures; if this is true for related species of birds, the occurrence of the

Table 1. The distribution of the "Clayella" group (+) of *Philopterus* on the *Momotidae* and the *Passeriformes*. Where no species of *Philopterus* has been seen from a family, this family is omitted from the list.

Momotidae.	+	Corvidae.		Muscicapidae.	
Formicariidae.	+	Paradisidae.	+	Prunculidae.	
Cotingidae.	+	Paridae.		Metacillidae.	
Tyrannidae.	+	Timaliidae.		Bombacillidae.	
Pittidae.	+	Pyrenonotidae.	+	Laniidae.	
Alcedidae.		Cinclidae.	+	Nectariniidae.	+
Hirundinidae.		Mimidae.		Dicaeidae.	+
Campephagidae.	+	Turdidae.		Ploceidae.	
Dicruridae.		Sylviidae.		Icteridae.	
Oriolidae.		Regulidae.		Fringillidae.	

larger parasite on the larger host might be explained by Bergmann's law—the larger species being found in the colder climate. Whether there is, in fact, a significant temperature difference between say *Columba palumbus* and *C. oenas* must wait for further work on the subject of birds' temperatures.

2. Colour. It is well established that, in many cases, there is a direct correlation between colour of the plumage of the host and colour of the Mallophaga species (Eichler, 1936; Clay, 1940: 33).

3. Texture of Feathers. There is some evidence that heavy sclerotization and sculpturing of the surface in certain Mallophaga is caused by iridescent feathers (see *Lagopoecus* from *Lophophorus impeyanus*, *Goniocotes* from *L. impeyanus* and *Tragopan satyra*; genera of Mallophaga found on the iridescent members of the *Paradisidae*). Feather texture may in some cases be responsible for the development of similar morphological characters of the head in a number of species belonging to the same genus parasitizing not closely related hosts. Table 1 gives the distribution of the "Clayella" group¹ of *Philopterus*; it is obvious that the families so parasitized do not form a natural taxonomic group, and it seems likely that they have some common feature in the structure of their feathers (some at least show iridescence of the feathers) which has resulted in modifications of their parasites on similar lines.

Feather structure

Chandler (1916) has shown that the details of the structure of certain parts of the feathers can be used in taxonomy. The down barbules espe-

¹ This group of species differs from the rest of the genus *Philopterus* in certain characters of the head, but as these characters have probably arisen independently in the species found on the different families and are adaptive and not phylogenetic, the group cannot be recognised as a genus.

cially show modifications and he states (387): "it is frequently possible by means of the down alone to identify the group to which a bird belongs." Chandler has also discussed the relationships of the class *Aves* using this one character of the minute structure of the feathers, admitting of course that no classification can be based on one character, but suggesting that it should be taken into account and may help to bridge the gaps left by other comparative studies. It is of interest that some of Chandler's suggested alterations in the usually accepted classification of the class are supported by evidence from the distribution of the Mallophaga. Are there, however, causes, other than relationship between the hosts, which might be responsible for the Mallophaga reflecting this similarity between the feather structure of their hosts?

Relationship between the genera of Mallophaga. It is obvious that unless the relationships between the genera of Mallophaga themselves are correctly evaluated any deductions of host relationships will be invalidated. The most important point to be emphasized is that in the largest superfamily of the Mallophaga (the *Ischnocera*), containing over a hundred genera, most of the genera are basically similar in both their external and internal morphology, and that there are many groups (say subfamilies) in which the genera are distinguished from each other by very minor characters. Some of these subfamilies, for example the *Degeeriellinae*, have a wide distribution throughout the class *Aves*, and further, probably formed the ancestral stocks giving rise to many genera, the affinities of which are now obscure. It is for this reason that only in a few cases does the distribution of the Mallophaga throw any light on the relationships between orders of birds as now recognised. It seems probable that no great divergence took place in the *Ischnoceran* Mallophaga until after the stocks giving rise to many of the modern avian orders had separated, possibly because until then there was no great divergence in feather structure. In many cases such ancestral avian stocks seem to have been parasitized by only one *Ischnoceran* genus—it being pure chance which of the few genera on the parent avian stock happened to be on that part of the population which was isolated and ultimately gave rise to the order as now known. This single Mallophagan stock diverged into several genera and filled the different ecological niches on the body of the bird; this has resulted in all such genera on one order being more closely related to each other than to those on any other order. The Mallophaga of the *Psittaciformes* are probably an example of such a case.

We can now consider what might have happened to such an ancestral Mallophagan stock isolated on a group of hosts and subjected throughout a long era of time to the different environments found on the bodies of the hosts:

a. **Cessation of Evolution.** The primitive type of Mallophagan head has a complete line of thickening (marginal band) round the anterior margin (the so-called circumfasciate head) and the thickening (ventral band) supporting the pulvillus (a structure of great importance in feeding) is complete. Specialization has taken place by the interruption of these bands of thickening. It would seem that these modifications are advantageous to the parasites on the majority of bird orders as there are only four host groups on which the parasite genera with unmodified heads are dominant. These are the Sphenisciformes, the Tinamiformes, the Galli and the Columbæ; the last three groups also have other parasite genera with modified heads. The Procellariiformes have one genus (*Episbatos*) in which the head is scarcely modified, but all the other genera on this order, and all other known genera from the rest of the Aves have Ischnoceran genera in which the head is in some way modified even if it is only the median interruption of the ventral band. Chandler has shown that the Tinamiformes, Galli and Columbæ (parasitized by Mallophaga with the more primitive heads) all have a similar type of down with a very typical structure. Without discussing whether this fact denotes a relationship between the Tinamiformes, Galli and Columbæ, it may prove that the primitive type of head is best suited to this feather structure and thus has a selective value which has prevented the modifications found in genera on other host orders. Further evidence that this may be true is given by the Mallophaga of other bird groups: Chandler (1916: 347) shows that the down of the Rhamphastidae is somewhat similar to that of the former three groups of birds, and it is therefore of interest that the head louse of this family (*Austrophilopterus*) is unusual in having the preantennal region not greatly modified. Chandler also shows that birds belonging to the Coraciidae, Trogoniformes, Momotidae, Meropidae and Upupidae show affinities in the structure of the feathers of the back to both the Cuculiformes and some of the Galliformes, and he also shows (1916: 377) that some of the Falconoidea show a feather structure similar to the Galli, although he does not suggest that this latter case indicates relationship. In all these bird groups, with the exception of the Momotidae and Meropidae, the dominant genera of body lice show the circumfasciate head. Thus, if the structure of the feathers favours the retention of the more primitive type of head, the genera concerned, because of the similarity of the rest of their morphology, will appear to be more closely related to each other than to those in which the head has become specialized, possibly in response to a different feather structure. This may be one of the causes of erroneous deductions of host relationships from those of their parasites.

b. **Parallel Evolution.** Alternatively to the cessation of evolution due to the similarity of feather structure, evolution of the members of one subfamily (with a wide distribution) may have taken place on parallel lines in response to the same feather structure (see Clay, 1949). Thus, two not closely related groups of birds with similarity in the structure of their feathers (not denoting relationship) might have apparently closely related Mallophaga.

c. **Divergent Evolution.** Some members of a host group might show divergence in feather structure, of no great phylogenetic importance, which might be responsible for modifications in the morphology of the louse populations. The latter would then appear not to be closely related to the populations on related host groups. Hence, a group of birds with a Mallophagan fauna which does not appear to be related to any other does not necessarily mean that the hosts occupy an isolated position in the class Aves; there are several groups, for example the Caprimulgiformes, Alcedinidae, Coliiformes and Apodi, where the Mallophaga give no clue to the affinities of their hosts.

Conclusions

The arguments for and against the use of the distribution of the Mallophaga as an aid to the classification of birds can be summed up as follows:

Arguments in favour

1. That in the great majority of cases the principle that the Mallophaga of related hosts are themselves related is true, and that it is possible to tell from the Mallophaga to what order a bird belongs. Hence, the distribution of the Mallophaga should carry a considerable amount of weight in those cases where the ornithologist is in doubt over the correct systematic position of a bird.

2. In most cases where a bird has an apparently anomalous Mallophagan fauna, there is found to be a difference of opinion over its correct systematic position, and in these cases the evidence from the Mallophaga usually support one of the opinions as to the relationship of the bird in question advanced by the ornithologists.

Arguments against

1. A great many of the genera of Mallophaga apparently confined to one group of related hosts, actually belong to subfamilies with a wide distribution throughout the class Aves, the differences between them being due,

most probably, partly to feather structure and partly to the time they have been isolated. Hosts with similar feather structure (if this does not denote relationship) might be parasitized by Mallophaga appearing to be related to each other because they had retained the primitive form of head or evolved on parallel lines. Again, hosts which had developed diverse characters in their feather structure might be parasitized by aberrant forms of Mallophaga.

2. Hosts with similar feather structure (if this does not denote relationship) might be parasitized by related Mallophaga because secondary infestation had taken place, this being made possible by the similarity of the environment—feather structure probably being one of the factors limiting the establishment of host specific species on a new host.

3. A genus of Mallophaga may show a discontinuous distribution either because it has become extinct on certain bird groups, or it may have been accidentally eliminated because it happened to be absent on the population which gave rise to a new bird group. These cases of the discontinuous distribution of once widely distributed genera will give a false idea of relationships between hosts.

These remarks on the influence of feather structure on the evolution of the Mallophaga must be of a tentative nature as too little is known both about the Mallophaga and the minute feather structure of many birds. It can be said, however, that although some cases of similarity between the Mallophaga species may be traceable to similarity of feather structure a study of Chandler's results will show that there are many exceptions: for example, the similarity of the down of the divers (*Gaviiformes sensu Wetmore, 1940*) and penguins is not reflected by the Mallophagan parasites; nor is the similarity of the down of *Eurypyga* to certain Ardeae. In the majority of cases where the evidence from the Mallophaga support Chandler's emendations to the usually accepted classification of the Aves, there is also supporting evidence from other anatomical features of the bird—presumptive evidence that the Mallophaga are showing phylogenetic relationships not adaptations to a similar feature of the environment.

Discussion:

G. Kramer asked if transplantation of Mallophaga from one host to another has been tried. This would be very important in order to prove or disprove the possibility of secondary infestation.

T. Clay: Few experiments of keeping Mallophaga on the feathers of strange hosts have been carried out. Except in the case of related hosts such

as chickens and guinea fowls the Mallophaga have died and been unable to breed.

R. Meinertzhagen: The young cuckoo has no contact with its parents and therefore is not infested with cuckoo-Mallophaga during the first few months of its life. But young cuckoos are often infested with Mallophaga from its foster parents and from air-borne infestation by Hippoboscid flies. But in no case have these stragglers been found on adult cuckoos, tending to show that natural straggling and successful acclimatization is a rare exception.

W. Yapp: Where there have been successful experimental transfer of Mallophaga, have there been any changes in form comparable to those which are alleged to have been produced by transfer of *Pediculus* from head to body and vice versa?

T. Clay: Too little is known about this subject to give an adequate answer.

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