

[*Extracted from the PROCEEDINGS of THE LINNEAN SOCIETY OF LONDON,*
Session 161, 1948-49, Pt. 1, 14 July 1949.]

**SOME FACTORS WHICH HAVE MODIFIED THE PHYLOGENETIC
RELATIONSHIP BETWEEN PARASITE AND HOST
IN THE MALLOPHAGA**

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The Mallophaga are all obligatory parasites of mammals and birds. Unlike most other ectoparasites of these groups of hosts, which undergo some portion of their life-history away from the host, the Mallophaga spend their whole life on the host, which they never willingly leave so long as the host is alive. Their eggs are glued to the hair or feathers of the host, their young stages are all passed on the host, courtship and provision for the next generation all take place on the host, and on the death of the latter many of its Mallophaga grip a hair or a feather firmly with their mandibles and die in this position, so that even in death, host and parasite are not divided. This very close association with the host has freed the Mallophaga from the necessity of having a very high rate of reproduction to guard against the probability that any given individual will fail to find a suitable host, and it has also resulted in these parasites being very poorly equipped for transfer from one host to another except during actual contact of these latter. It follows that so many of the opportunities to transfer from one host to another that are available to Mallophaga are within the host-species and so few are extra-specific that there would be little to be gained by retaining the ability to live on a wide variety of hosts and instead the Mallophaga have become extremely narrowly specialized for life on a very limited choice of hosts and are perhaps the most specific of all ectoparasites. In many groups of Mallophaga it is the normal rule that every host-species has its own species or sub-species of louse, and in certain groups of hosts (the Procaviidae among mammals and the Tinamiformes among birds) it is sometimes even found that each subspecies of host is infested by a different species or subspecies of Mallophaga.

Turning to higher categories of the hosts, we find that almost every major division (nearly always the order and often the family) has at least, one characteristic group of lice peculiar to itself, so that if one is given a series of collections of Mallophaga from different groups of birds or mammals (but not labelled with the names of the hosts) it is normally possible to say with a high degree of accuracy from what group of birds or mammals each lot was obtained.

What seems to have happened is that both birds and mammals were infested by Mallophaga very soon after their divergence from the reptiles, that there was an initial period of very rapid evolution of the parasites in their new environment, and that subsequently their evolution slowed down until it proceeded almost in step with that of their hosts but normally somewhat more slowly and only very exceptionally (in the groups occurring on Procaviidae and Tinamiformes) more rapidly than that of the host. As I mentioned, it is normally possible to deduce the group of hosts from which a given batch of Mallophaga was obtained, and I now add that the lag in the evolution of the lice as compared with that of their hosts is often so considerable that their relationships remain clear while specialization has rendered those of their hosts obscure. It follows that, if the systematic position of a bird or mammal is in dispute, examination of its Mallophaga may provide very valuable evidence as to which view is correct. To take a well-known instance, ornithologists disagree as to the position of the

flamingos, some (perhaps the majority) considering them to be related to the storks while others hold them to be an offshoot of the ducks and geese ; I think all specialists on Mallophaga would agree that the latter view is the correct one. It is very significant that there does not seem to be any instance in which the opinion of mallophagologists as to the systematic position of a group of birds is at variance with that of the majority of ornithologists without the louse-students being able to claim the support of at least some workers on birds.

As is usually the case when any new discovery is made, there has been a certain amount of exaggeration of the value of the approach to host-relationships by way of those of their Mallophaga, and in particular, mistakes have been made owing to a lack of understanding of certain factors that we are only now beginning to appreciate and that must not be overlooked if our deductions are to rest on a sound foundation. Among these factors are discontinuous distribution, which I prefer to call secondary absence, secondary infestations, convergent or parallel evolution, and bad taxonomic work.

Among instances of secondary absence on a large scale are the absence of Mallophaga of the family Trichodectidae from pigs, seals and hyaenas, though they occur not only on all other families of the Ferungulata (that is Carnivora, Artiodactyla and Perissodactyla), but also on various other groups that diverged from the common stock before hoofed mammals and Carnivora had split off from one another, and the very peculiar fact that the genus *Falcolipeurus* occurs on many large birds of prey belonging to very different groups but not on any small ones, the latter instance being particularly interesting because it seems obvious that size has been the limiting factor though we do not know in what way it has worked. I think it difficult to over-estimate the possible importance of secondary absence in accounting for differences in the Mallophagan fauna of two different hosts. There is, for instance, one particular species of hyrax which possesses no less than eight different species of Mallophaga belonging to six different genera or subgenera, whereas there are other species of hyrax in which fairly adequate examination has only revealed two species of Mallophaga. Let us suppose that two different sets of descendants of the hyrax with eight lice were each to lose six of their lice, but a different six, and it becomes obvious that any deductions from the lack of relationship between the two pairs of survivors of the original set of eight lice would be extremely misleading. I am absolutely convinced that something very similar has happened many times and that we must not put any great weight on lack of resemblances between the Mallophaga of two different hosts.

Secondary infestations are well exemplified by the occurrence of a genus otherwise strictly confined to the petrels and their relatives on the skuas, which are gulls that have taken to obtaining food by buffeting other birds until they force them to disgorge ; the louse was doubtless acquired when some ancestral skua was robbing an ancestral petrel. Another good example is the occurrence of indistinguishable forms of *Felicola* on such distantly related hosts as the domestic cat, the civet and the white-tailed mongoose.

Examples of convergent or parallel evolution are less well-known and we owe most of our knowledge of them to Miss Clay. She finds that there are indications that development of a rather characteristic form of sclerotized clypeus that has been used as a generic character is perhaps correlated with feather-texture and may be of little or no significance in tracing the relationships of the Mallophaga that have this character, and also that certain stout-bodied forms found on pigeons, for example, that have been considered to be fairly closely allied to the rather similar Mallophaga of other groups of birds, are in reality so closely related to almost linear forms also found on pigeons that one form has certainly been derived at no very distant date (geologically speaking) from the other.

Perhaps the less said about bad systematic work the better, and I will only remark that the quality of much of the systematic work on Mallophaga is as bad as that of any to be found in biology—which is saying a very great deal.

Having mentioned the factors that limit the way in which we can use infestations with Mallophaga as evidence for the phylogeny of their hosts, it may be useful to examine under what conditions the lice can give us valuable pointers. We must be sure, first, that the resemblances between the Mallophaga we are comparing are genuine and not the result of bad systematic work, including under that term the mistake of allowing ourselves to be misled by characters that are the result of convergent or parallel evolution into suggesting louse-relationships that do not really exist. Next we must be sure that the mallophagan genera we use as evidence are representative of one another on the two groups of hosts, since without this condition the absence of resemblance between the lice of the two hosts may merely be due to secondary absence in both cases. And there must be sufficient instances of resemblance to exclude the likelihood that we are dealing with secondary infestations. I have suggested elsewhere that one correspondence between the lice of two hosts whose hypothetical relationship to one another is under examination means very little, that two such resemblances establish a probability that the relationship is genuine, and that three correspondences come very close to a certainty. Going back to the flamingos as an example, they are known to be infested by four genera of Mallophaga, of which one is found on both storks and Anatidae so cannot help us. The three other genera found on flamingos are all found on ducks but not on storks, and two of them are what I have called 'representative', in the sense that very closely related (but different) genera represent them on the storks. In this instance the evidence for a close relationship between the flamingos and the ducks to the exclusion of the storks is so strong that I think it conclusive. On the other hand, the fact that the genera found on the Musophagidae or plantain-eaters, usually placed with the cuckoos, do not include any cuckoo-genera of Mallophaga but do include two that are characteristic of the game-birds, are no more than highly suggestive, because these two genera may have begun to infest plantain-eaters merely because in the very distant past an ancestral plantain-eater used a dust-bath just after a game-bird, and acquired the lice as a result.

Finally I want to mention one anomaly for which I am quite unable to find a satisfactory explanation, in the hope that someone here may be able to suggest one. As I mentioned before, among the Procaviidae—hyraxes or conies of the rocks—it is very commonly the case that a subspecific difference in the hosts is accompanied by a specific difference in one of the Mallophaga infesting them, a representative of the genus *Procavicola*. In most of the areas occupied by *Procapnia capensis coombsi* and *Procapnia capensis letabae* this holds good, *coombsi* being infested by *Procavicola pretoriensis* and *letabae* by *Procavicola mokeetsi*. But in one area, adjacent to the range of *letabae*, *coombsi* is infested, not by *pretoriensis* (as it ought to be according to our ideas) but by *mokeetsi*, the species characteristic of the other subspecies of host. This anomaly is so strange that I specially questioned the late Dr. Austin Roberts, an authority on the forms of *Procapnia capensis*, as to whether there could have been any mistake about his determination of these specimens, but he assured me that they really were *coombsi*. Can a mammal take on the physiological characteristics of another subspecies before acquiring its physical characteristics, and would this account for the observed facts? Frankly, I do not know, but that is the best hypothesis that has occurred to me, and if anybody present can suggest a better explanation I would be most interested to hear it.