THE MALLOPHAGA AS A POSSIBLE CLUE TO BIRD PHYLOGENY.

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In taking up a study of the Mallophaga, or Biting Lice, which are chiefly, though not entirely, parasitic on birds, after a number of years of study of the hosts themselves, my attention was very early directed towards a very remarkable correspondence betweeen the species-groups of these parasitic insects coming from definite host-groups. Thus I found that a species of *Philopterus* from the common Australian cuckoo *Cacomantis flabelliformis* was hardly specifically distinct from the parasite of the European cuckoo *Cuculus canorus*. Yet these two birds have widely diverged from one another in their progress from the common ancestral stock. In addition, these parasites, with others from other species of cuckoos distributed throughout the world, form a definite group within the genus *Philopterus*, which is easily recognisable on its structural characters; so that one may say at a glance that any one of the species has come from a cuckoo. Similarly, species of *Philopterus* obtained from Kingfishers of different genera, and of world-wide distribution, have definite features in common which enable them to be recognised both as showing close relation one to another, and as having come from Kingfisher hosts.

So far, I have only instanced two picarian families, but when the distribution of parasites among the orders of birds is studied, it is found that the same relation holds. Mallophagan parasites of hawks, ducks, pigeons, or shore-birds, all afford well-defined groups, the distribution of which is confined to, in most cases, a single host order. So much is this the case, that Piaget (1880), in his great monograph, has divided up the unwieldy Mallophagan genera into a number of sections; in the first place quite frankly upon host distribution, but he has nevertheless been able to give diagnoses for these groups based upon their structural peculiarities.

In seeking for an explanation of this condition of distribution, I was forced to the conclusion that the parasites, owing to the equable conditions of temperature and nutrition under which they lived, had not tended to differentiate at the same rate as their hosts. The Mallophaga do not voluntarily leave the body of their host, and cannot live away from it for more than a few hours. Their whole life is thus passed upon the body of the bird (or mammal), the temperature of which is constant. Similarly they feed upon barbules of feathers, epidermal scales, &c., which have a fairly constant chemical composition. And they undergo no particular struggle for existence, as they are rarely found upon any one host individual in such numbers as to render the obtaining of sufficient food a matter of difficulty. The stimulus to a rapid differentiation is therefore absent, and the usual fluctuating variations exist comfortably side by side, none tending to become dominant at the expense of the others. There are some other interesting points in the biology of the Mallophaga, which are admirably summarised by Kellogg (1913, pp. 130 sqq.).

The same author has also (1896, p. 51) come to the conclusion put forth at the beginning of the last paragraph. He writes:—"The occurrence of a parasitic species common to European and American birds, which is not an infrequent matter, must have another explanation than any yet suggested. This explanation, I believe, is, for many of the instances, that the parasitic species has persisted unchanged from the common ancestor of the two or more now distinct but closely allied bird-species." And again, less cautiously (1913, p. 157):—"Now, removing all cases of even an imaginable rare possible contact of bodies between these related but specifically distinct hosts, such as might occur in birds of circumpolar range, or in gregarious maritime kinds, meeting on common mid-ocean islands, or in kinds occasionally exported by man from their normal range, etc., there are still left many cases of this commonness of a parasite species to two or more usually rather closely related host species of quite distinct geographic range. How can this actual condition be explained?

"I can see but one answer. That is, that the parasite species has been handed down practically unchanged to the present specifically and even generically distinct several bird species from their common ancestor of earlier days. The parasite species dates from the days of this ancestor."

It will be noted that Kellogg refers only to the same parasitic species being found on allied bird forms in Europe and America, but the argument holds also for allied forms of parasites. Having come to the conclusion that we had, in the Mallophaga, to deal with a case of retarded evolution, the next question that naturally arose was—How far back does this retardation extend? In other words, would it be possible by a careful study of the Mallophaga, and of their host distribution, to gain any clue as to the inter-relationship of the hosts themselves. As the result of a little preliminary inquiry, I became convinced that there was some hope of such a result, and in September, 1911, read before the Sydney University Science Society, a short paper discussing this possibility, a summary of which was printed in the Annual Report of the Society for that year.

The propriety of attempting to indicate phyletic relationships by such means as a study of the distribution of parasites may be questioned. But in the case of birds, in attempts to satisfactorily classify which all the resources of morphology and embryology have been employed in vain, I would submit that nothing that is likely to throw a gleam of light should be lightly set aside. Birds are easily divided into a number of admittedly natural groups, but hardly any two systematists can be found in agreement as to the relationship of these groups among themselves. Professor Newton was so dissatisfied with all attempts at classification that he published his wealth of ornithological learning in the form of a "Dictionary of Birds," just to avoid a systematic arrangement. Embryology, which has helped to clear up so many phyletic difficulties, has only produced a series of results monotonous in their uniformity. Morphology, too, has merely confirmed the general sameness of bird structure, the efforts of Garrod, Forbes and others to establish a classification on the variation of this organ, or the presence or absence of that, all ending in failure. One has only to compare any of the recent attempts at classification of birds, to see how hopelessly at variance are their authors. Bevond a general agreement that the passerine birds constitute the highest and most specialised order, nothing is certain.

In view of the fact that all the ordinary biological means have failed, I think it quite justifiable that an attempt should be made to see what light may be thrown upon bird phylogeny by a study of bird parasites.

An examination of the literature to see whether the above idea had occurred to any other worker disclosed only one suggestive sentence, prior to a paper by Kellogg in 1913. Giebel and Taschenberg, two monographers of the *Mallophaga*, give no sign of having recognised any remarkable condition of affairs in the relation of parasite to host. Piaget, although he clearly exposed this condition, did so more or less accidentally, and has not indulged in any speculations on it. Kellogg, on the other hand, wrote (Kellogg & Kuwana, 1902, p. 458) :—

"It was hoped that the character of the parasites found on the strictly Galapagos Island bird hosts might throw some light on the relationships of these birds to continental genera and species, ..."

This hope was defeated by the extraordinary conditions obtaining on the islands, birds of different orders huddling together promiscuously on the bare rocks, and their parasites becoming hopelessly mixed. The germ, however, was with Kellogg in 1902, and in 1913 (p. 138) he writes much more definitely :—

"Of the other Mallophagan genera found on the tinamous two that specially characterize the pheasants and other gallinaceous birds are, by odds, the most commonly represented. And this condition suggests another interesting problem. Is it going to be possible to get suggestions regarding the phyletic affinities of hosts from the character of their parasitic fauna? Take, for example, an order of birds troublesome to the ornithological taxonomists. Will the evidence of the presence on members of this order of certain parasitic genera characteristic of another order, indicate their affinities to this second order? It does indeed seem, in the case of the Tinamiformes and Galliformes, as if the evidence from the Mallophagan distribution was in conformity with that suggested by certain structural similarities in the two groups."

. Seeing that Professor Kellogg has now put into words the concrete question which I had already been disposed to answer in the affirmative myself, nothing can be gained by any further diffidence on account of the unconventional nature of the suggestions put forward. I am of the opinion, after a careful preliminary study of the relationships between the Mallophaga and their hosts, that when a more complete study of these parasites has been made they will afford very considerable help towards solving the vexed question of bird phylogeny.

In the first place, I would suggest that the adoption of a parasitic habit by mallophagous insects occurred even as far back as late Mesozoic time. My reason for arriving at this conclusion I put forward with some hesitation, but I have not been able to suggest a better interpretation of the remarkable facts which follow. In each of the two sub-orders of Mallophaga occurs a family with a distribution confined to mammals. Each of these families is characterised, among other things, by the fact that the tarsus bears only a single claw, while all the bird frequenting forms have two claws upon the tarsus. One of these families, the *Gyropidae,* is an offshoot from the lowest and most generalised of the bird-frequenting forms; the other, the *Trichodectidae,* from the higher and more specialised bird-frequenting forms. But coming to marsupials in Australia, there is found upon them a family of Mallophaga with two claws upon the tarsus, of which the first-described species, *Heterodoxus longitarsus,* was included by Piaget, its author (1880, p. 504), in the common bird genus *Menopon.* Even at the present time Neumann (1912, p. 359) has seen no reason to remove it from the genus *Menopon.* Unfortunately no Mallophaga from American marsupials are known, but upwards of twenty species have now been taken upon Australian marsupials (most of which are still undescribed), all belonging to the family *Boopidae* of Mjoberg (1910, p 21), and all closely related to the lowest and most generalised bird-frequenting genus, *Menopon.* And with the exception of one or two cases which may yet be explained by straggling (Mjoberg, 1910, p. 22; Neumann, 1912, p. 364), the *Boopidae* are confined to marsupials, and they are also the only mallophagous parasites found upon them.

We find, then, upon the marsupial fauna which has been isolated in the Austro-Malayan region, what we might be justified in calling typical bird parasites. We also find in Australia, mallophagan species belonging to practically all the known bird-frequenting genera. But the marsupial parasites are most closely related to what is admittedly the most generalised bird infesting genus. It seems more reasonable to me to suppose that the migration upon marsupials was of ancient rather than recent occurrence: and I suggest, with some hesitancy, I admit, that the *Mallophaga* took to a parasitic mode of life at a time when they had not, as a group, progressed beyond the *Menopon* condition; and that they parasitised both birds and marsupials before the true mammals had differentiated out. This, however, has no very direct bearing upon the main question at issue beyond an indication, if my supposition be at all acceptable, that we have here a case of parasitism that has accompanied practically the whole phyletic history of birds.

The actual evidence which I have to offer upon the possible clues to bird phylogeny afforded by the parasites is, at present, slender enough, but one or two instances are extremely suggestive. The general relations of parasite to host have been briefly indicated above, and illustrated by one or two examples. It is not my intention to multiply these. They have been selected quite at random, and a hundred others might equally as well have been given, so repetition can serve no purpose. From this general condition, which enables us to recognise parasites of hawks or of any other order of birds at a glance, I wish to proceed to one or two special cases. The question of the relationship of parasites of, say, hawks to those of shore birds, or passerines, will have to be left until a much more complete study has been made of *Mallophaga* in general. If this relationship can ever be stated, as I believe it may, then we shall have a clue as to the interrelation of the hosts themselves.

Of the parasites of the Struthiones, *Degeeriella asymmetrica* is found upon the emu; *Lipeurus asymmetricus* upon two species of rhea; and *Lipeurus quadrimaculatus* upon the ostrich and also upon a species of rhea. These three species are undoubtedly congeneric, and should be included in a genus distinct from either of those mentioned above. The two latter species are distinguished by a peculiar asymmetry of the chitinous border of the clypeus, the precise form of which is best seen from the accompanying text figure, from all other Mallophaga. The young of *Degeeriella asymmetrica* exhibits a precisely similar structure, which in

the adult increases in extent and becomes folded on itself in a remarkable manner, forming a V-shaped cleft, the relation of which is again more easily seen from the figure. It is hardly possible to come to any other conclusion than that these three species have been derived from a common ancestor. And we find them on hosts which admittedly have had a common origin, and which are now widely separated upon three distinct continents.

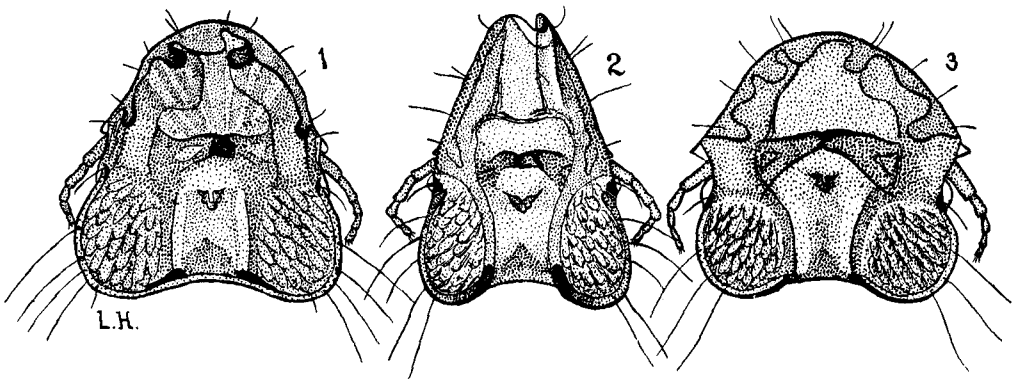

Fig. 1. *Lipeurus quadrimaculatus.* Fig. 2. *Degeeriella asymmetrica.* Fig 3. *Lipeurus asymmetricus*—after Piaget.

Next we may profitably expand the facts given by Kellogg in the paragraph last quoted p. 7). Upon tinamous and gallinaceous birds, two genera, *Goniodes* and *Goniocotes* are most commonly represented. We also find these two genera commonly upon pigeons; and a species of *Goniocotes* has been found upon *Opisthocomus.* The four bird groups here mentioned are, by some systematists, considered as closely related, and this relation is definitely supported by the distribution of parasites. But one more order of birds is concerned in the distribution of these two genera of parasites, and that is the Sphenisciformes, a fact that is noted without comment by Kellogg (1913, p. 141). No bird systematist has ever suggested any possible relation between the penguins and any of the other four bird-groups mentioned. Yet two mallophagan genera, characteristic of and otherwise confined to these four groups, are also found upon penguins. If the hypothesis that the five groups had origin in common be not admitted, how is the occurrence of these particular parasites on penguins to be explained? Penguins are marine, the other four groups terrestrial. I can scarcely conceive any circumstance by which penguins, with their Antarctic marine distribution, could come into sufficiently close relation with any of these other birds to allow of direct straggling to take place. Had there been a common occurrence of certain genera upon gulls or petrels and upon penguins, then straggling might be suspected. But these particular genera, *Goniodes* and *Goniocotes,* are not found upon gulls or petrels, or upon any other marine birds except penguins. And although only one or two species have been described from these last hosts, I have in my own collection other undescribed forms taken from Australian penguins, the only parasites I have taken from these birds belonging to these genera, so that the penguin habitat cannot be questioned.

In default of any better explanation, I submit that these facts of distribution point to the Sphenisciformes having an ancestral stock in common with the Tinamiformes, Galliformes, and Columbiformes. It would follow from this that the penguins have undergone a comparatively recent and rapid specialisation to an aquatic life, and are not such an ancient and lowly group as they have generally been considered. A suggestion such as this might possibly enable the morphologist to attack the problem in a new light. It could, of course, only be a suggestion. Bird phylogeny must be established upon definite morphological grounds. But if a study of the parasites gave us a reasonable series of indications of relationship, it seems probable that the morphologist, on a re-examination of his types, would be able to separate those characters of phyletic value from those which are useless from this point of view, and would be able to place our knowledge of bird relationships upon a surer footing.

I have cited these two special cases as examples of the indications which appear from a mere study of the distribution of mallophagan genera as at present constituted. Other examples might be quoted, but would serve no particular purpose. I merely wish to draw attention to certain features that exist, and to suggest the possibility of a valuable line of study. Before anything in the way of appreciable results can be achieved, a much more exhaustive examination of the Mallophaga will be necessary. Those of European and North American birds are pretty well known. Dr. T. Harvey Johnston and myself have fairly considerable Australian collections, not yet worked up. But for the rest of the world comparatively little has been done. Until more collecting, figuring, and describing has been done, it will be impossible to make satisfactory comparisons and to straighten out the inter-relationships of the Mallophaga themselves. Moreover, many of the present genera are really family groups, and until they are split up in accordance with more recent knowledge of structure they are of little use as a basis of comparison.

Work on the Mallophaga is being carried on continuously by various workers—Professor Kellogg at the Leland Stanford University; Professor Neumann at Toulouse; Dr. Mjoberg in Stockholm; Dr. Johnston and myself in Australia. I should like to suggest to those in a position to obtain Mallophaga, which are very easily collected from bird or mammal hosts, and simply preserved in tubes of alcohol, should collect these generally neglected insects, and forward them to one of the workers mentioned. By this means the gaps in our knowledge may gradually be filled.

When our knowledge of the parasites is more nearly complete, I believe that it will be possible to shed some light on bird phylogeny. There will, of course, be considerable difficulties to overcome, and some necessary precautions must be taken. The complete disappearance of important connecting links may prevent a proper understanding of Mallophagan inter-relations. And remarkable contrasts in the rate and direction of variation of Mallophagan species will have to be in some degree accounted for. Why, for instance, has the common *Lipeurus columbae* of pigeons persisted unaltered upon practically all the Columbiformes of the world, while species belonging to other genera found upon pigeons show a considerable amount of differentiation? Many such questions will arise, the explanation of which does not seem easy. And there is also the straggling difficulty. The genus *Laemobothrium* is found upon diurnal *Accipitres*, and upon a number of waterfowl which in the ordinary course might form the food of the larger hawks. The position of the *Accipitres* is entirely unknown. Possibly there is a phyletic connection between them and the waterfowl. Equally possibly, the genus *Laemobothrium* may have straggled from one to the other, when some primitive hawk was engaged in devouring a primitive waterfowl. This straggling would seem, however, to be fairly limited. Kellogg certainly found a condition of promiscuous straggling upon the Galapagos birds, but there the conditions are quite unusual. There does not appear to be much indication of it when conditions are normal. The evidence afforded by the cuckoos is distinctly against it. In the case of these birds, the parasites can only migrate from one host to another during the very brief time occupied in copulation. Young cuckoos are much more likely to be infested by parasites of the foster parents in whose nests they are reared. But no instance has been recorded of parasites of foster parents being found upon a cuckoo, and the cuckoo parasites manage to survive as a pure stock in spite of difficulties, although comparatively few individual cuckoos are parasitized.

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