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STUDIES ON THE EVOLUTION AND PHYLOGENY OF THE MALLOPHAGA (INSECTA) WITH SPECIAL REFERENCE TO THE RELATIONSHIPS BETWEEN THE PHYLOGENY OF HOST AND PARASITE.

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1. SUMMARY.

INTRODUCTION.

The Mallophaga, a suborder of the Pthiraptera, are a group of obligate ectoparasites living on birds and mammals which present interesting problems of evolution and phylogeny.+ The present distribution of the avian Mallophaga suggests that these insects became parasitic on the birds early in the evolution of the latter class and that they evolved with their hosts. In a group of related host species, each species may have allopatric species of a number of sympatric genera of Mallophaga common to the host group (1/: tables 4, 5, 6), and in addition, sympatric species of one or more of these genera.

+ This work is based largely on studies of the superfamily Ischnocera found on birds.

/ Numbers 1-12 refer to the printed papers following the summary.

In many cases, therefore, a single host species may have a considerable number of genera and species of Mallophaga (1:279). The problem is to find an explanation of the presence of often closely related genera and species in what is the equivalent of a restricted and isolated geographical area. A study of the morphology of the Mallophaga and their present distribution both on a single host individual and throughout the class Aves makes it possible to deduce some of the factors which may have influenced speciation in this group of ectoparasites and to compare these factors with those influencing groups of free-living animals.

Apart from the intrinsic interest of evolutionary problems in a group of ectoparasites, it is necessary when attempting to formulate a natural classification of the Mallophaga to have some understanding of the possible steps in the evolution of the group.

EVOLUTIONARY PROBLEMS.

Ecological Factors in Speciation.

The environment of the avian Mallophaga is formed by the chemical composition and physical structure of the feathers, the texture of the skin and certain physiological characters such as temperature and body secretions.

Feather structure. The Mallophaga live amongst the feathers and the size and form of these have influenced the general body shape (1:280-1) so that the species living on the head and neck of the bird, for instance, are easily distinguished from those living on the back and wings.

In the Ischnocera the regions round and anterior to the mandibles show considerable variation within the group and give those characters on which much of the classification is based. This variation is probably partly dependent on differences in feather structure as the majority of species take at least some feather parts in their diet and the mandibles are also used for clinging to the feathers to escape dislodgment. The main lines of evolution of the primitive Ischnoceran head seems to have been directed towards an increased mobility of the fore-part of the head by the development of sutures, and to a general lengthening of this part together with the development of secondary bars of thickening (the endocarinae 3:176) for its support. The modifications of the pulvinus (probably the clypeo-labral suture), which has an important function in directing and holding the feather parts are of especial interest (3:177-178). Modifications of the primitive head appear to have developed along rather similar lines independently in different groups (see parallel evolution (1:294)), the differences in the details of development being caused both by the isolation of the groups and by the differences in the minute feather structure of the different host groups (2:210-213; 3:185-191).

In one group of Mallophaga (Trochiloecetes) which has adopted an entirely blood diet, the normal chewing mouthparts characteristic of the Mallophaga have become adapted to piercing (5:617).

The general correlation found in some genera of Mallophaga between the size of the species and the size of the host (2:207-210; 4:3) may be dependent on feather structure. Other effects of the plumage on the Mallophaga are the frequent occurrence of pigmentless Mallophaga on white feathers, the greater sclerotization of species living on birds with iridescent feathers, and in one genus of Mallophaga some of the species have developed a similar type of endoskeleton supporting the pulvinus apparently independently, presumably in response to some similar character in the feather structure of their hosts (2:210, table 1.). This group has been separated as a genus, but the distribution suggests that the character is adaptive and not phylogenetic and the genus should not, therefore, be recognised.

Preening by the Host. This is an important factor in the control of the size of the Mallophaga populations and has probably affected body structure and egg laying sites (1:281).

Ecological Niches. The body of the host presents a number of ecological niches which have been colonized by the Mallophaga and to the characters of which the insect has become adapted (1:280-1); this adaptation is shown mainly by a change in the proportions of the head and body and of the secondary sutures and thickening of the head. These ecological types frequently form the basis of the generic separation of many of the sympatric species (1:281, table 1). The occupants of the same niche on different host groups sometimes have a superficial resemblance although quite distinct where they have been derived from different ancestral stocks. This superficial resemblance has been partly responsible for the present untenable suprageneric classification of the Ischnocera. Even when the ecological types were derived from the same ancestral stocks differences would have arisen through isolation (see below). Also the primitive birds presumably had a more uniform feather covering (1:291), and as the structure of the down barbules are now in many cases specific for the order or suborder (2:210-211) these must have undergone change during the evolution of the birds. There would, therefore, have been continuous adaptation by the parasite to the changing environment of the particular niche caused by the evolution of the birds themselves. There also seems to have been later changes of ecological niches so that a species has become secondarily adapted to a new niche (e.g. Sturnidoecus, 1:288-289). Thus, the adaptations and specializations for the different ecological niches on the body of the bird have been responsible for much of the diversity amongst the Mallophaga on one host species.

Isolation.

As in free-living animals isolation must have played an important role in the evolution of the Mallophaga. Normally the Mallophaga parasitic on one host species do not come into contact with those on other host species; this isolation of the populations has made possible the development of host specificity (1:284). During the evolution of the birds isolation of louse populations has been brought about by the divisions of their host species populations into non-breeding units, thereby forming new species of hosts which diverged into the families and orders now known; the isolated louse populations thus formed must have diverged from each other and became specialized for the new characters developed by their respective host species (1:283-4). This type of speciation is analogous to that on continental islands which have been formed by the disappearance of land connections. A louse population may also become isolated by the temporary isolation of parts of its host population (1:284-285), or by the extinction of a louse species in parts of its host's range (1:285-286) thus isolating the two populations on each side. If these periods of isolation were sufficient to enable the development of some sexually isolating mechanism (1:286-287) in one of the isolated populations the two populations would form non-breeding units even if re-united.

There is no doubt that the complete isolation of populations on one host species has been overcome and that secondary interspecific transferences have taken place. Transference from one host species to another, analogous to the colonization of oceanic islands in free-living animals, can take place between predator and prey, nestling and foster parent in brood parasites, by the use of common dust baths and by phoresy (1:293). As in free-living animals, it is necessary that at least a breeding pair or a fertilized female should be transferred, that the immigrant can live in the new environment and can overcome the competition of an already established and adapted resident louse population. The establishment of an immigrant louse would, therefore, be helped by the temporary absence in a given host population of the occupants of one of the ecological niches (1:285), thus providing an empty niche free from competition. This competition would also have forced immigrant lice to occupy new ecological niches on the body of the bird not previously occupied by any of the resident populations.

Interspecific infestations may account for the presence of closely related sympatric genera and species parasitic on one host species, for which sympatric speciation seems an unlikely explanation (1:290). The rather large number of sympatric genera and species parasitic on some host species may be explained by the host order being represented by a large number of living or extinct forms thus allowing for a greater amount of interspecific interchange of populations (1:291, table 9). Further, the characters of the plumage of the host species may provide a greater or lesser number of ecological niches (1:291) thus to some extent controlling the number of sympatric genera. Secondary interspecific infestations are more possible between related host species (1:284) than between host species belonging to different orders (1:284), and presumably were more possible before the development of strong host specificity and when the hosts themselves had not diverged to such an extent. Secondary infestations may also be helped by simularity of feather structure between two host groups (2:214).

THE PHYLOGENY AND CLASSIFICATION OF THE MALLOPHAGA.

The generic and suprageneric classifications of the Mallophaga present great difficulties (3:171) and it is necessary to have some understanding of the biology and possible evolution of the group in order to distinguish those characters likely to be of phylogenetic importance from those which are purely adaptive. There is some difficulty in the use of the terms phylogenetic and adaptive as applied to characters. Presumably the majority of characters are or have been adaptive and many of the orders in the animal kingdom are based on such adaptive characters, e.g. Pthiraptera adapted for an ectoparasitic life; Anseriformes for swimming; Ciconiiformes for life in swamps and marshes. Many of the problems of the classification of living animals is an attempt to relate forms to their primary adaptive group when they have become secondarily adapted to another habitat or mode of life (the flamingoes may be such a case, 11:435). The primary adaptive characters are called phylogenetic and the secondary characters - adaptive. Amongst phylogenetic characters are also those which may have been produced as by-products of an adaptive character by the pleiotropic effect of genes or by the establishment of neutral characters by genetic drift in small isolated populations.

In the superfamily Ischnocera the basic characters of the internal and external morphology are, in general, remarkably uniform throughout, while superficially there are considerable differences in the proportions of the body and the development of sutures and secondary lines of thickening. It is possible that the Ischnocera acquired these basic characters as adaptation by their particular ancestral stock to the general environmental factors provided by the body of the bird. This took place at a time when the primitive birds had a more uniform feather covering and before they diverged into the different groups with ensuing modification of feather structure. These later differences in the environment seem to have affected only the superficial characters of the parasite. In particular the head seems to have become better adapted for eating and clinging to the feathers, and the head and body to have become superficially adapted to the different ecological niches on the body of the bird. These adaptations would have been brought about in different ways in the different Mallophagan groups depending on the gene complex of the ancestral group, the isolation of the population, and the differences of the environment in the particular group of birds parasitized.

During this evolution there seems to have been much convergence and parallelism, changes of ecological niches with ensuing secondary modifications (1:288-289) and secondary interspecific infestations which has resulted in the original relationships being in many cases obscured. Although the classification must, of course, be based primarily on the morphological characters of the parasite, host distribution is frequently of importance as a secondary check on relationships and as an indication of which characters are of phylogenetic importance (3:173; 12:574). On the other hand, generic separation taking into account host distribution only leads to considerable errors (12:580).

Two types of genera or species groups based on their probable origins can be distinguished in the superfamily Ischnocera, one of these is the end product of the process of speciation which brought about the allopatric species, the other the sympatric species.

The allopatric genus (3:172-174) comprises a number of species, each one host specific to a host species or a group of closely related host species (1:283, tables 4-6), and probably formed as the result of the isolation and divergence of the species of the host group as already discussed. In the majority of allopatric genera the host order or suborder forms a clear cut line between groups of species and gives the limit of the genus (1:281, table 1). However, there are genera distributed over more than one host group (1:282, tables 2-3), the possible explanations for such distributions are discussed below under the relationships between the phylogeny of host and parasite.

The sympatric genera (3:174-175) present the more difficult problem in deciding on the limits of the genus. Sympatric forms are found in every stage of divergence from those which differ in one sex only to those which can now be separated generically on well-marked characters. The degree of divergence seems to depend partly on the age of the species and whether they now occupy different ecological niches. So common is the occurrence of these related sympatric genera that it is possible to accept as a general principle that throughout the avian Ischnocera the nearest affinities of a genus are usually to be found with the other genera parasitic on the same host order (2:211).

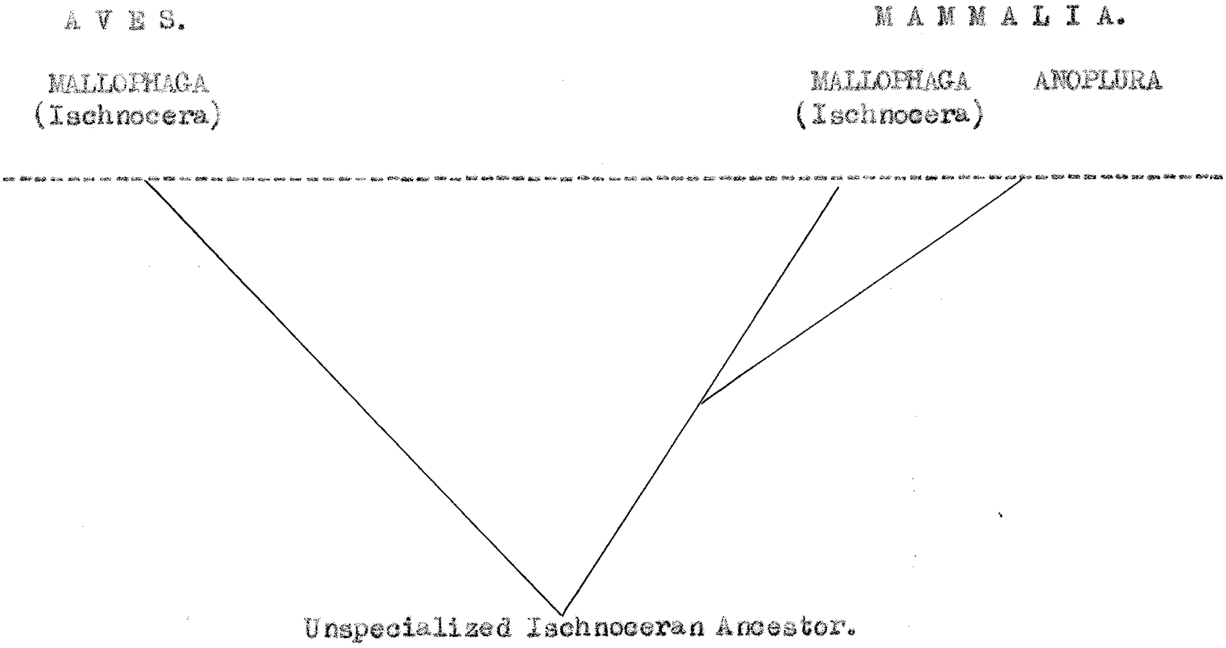
In an attempt to find characters of phylogenetic importance in the avian Ischnocera on which to base satisfactory generic and suprageneric classifications detailed studies have been made of the head (3) and of certain internal organs.

The Head. Symmons (1952, Trans. zool. Soc. Lond. 27:349-436) has shown the basic fundamental simularity of the Ischnoceran head. A study (3) of the exoskeleton of a large number of forms shows that superimposed on this basic simularity are many superficial variations. Many of the modifications seem to have taken place on parallel lines in otherwise unrelated groups, and in many related groups the species show all stages from the primitive head to the highly modified form (3:186). Thus, although in certain genera the head characters are diagnostic, in others the modifications of the head seem to be comparatively recent adaptive not phylogenetic characters (3:185-194). In no case do the characters of the head alone give an indication of suprageneric groupings.

Internal Male Genitalia and Alimentary Canal. A study (in preparation for the press) of the internal male genitalia of 143 species belonging to 73 genera has been disappointing in regard to finding characters of suprageneric importance. Only one case, and that not conclusively, suggests a basis for suprageneric division, but in other cases the characters of the internal genitalia may be of generic, subgeneric, or specific value. The gross morphology of the alimentary canal is again similar throughout the Ischnocera and the characters give no guidance for possible suprageneric divisions.

Suprageneric classifications of the Ischnocera have been attempted by various authors but no satisfactory system as yet evolved. The Ischnocera from mammals (with the exception of Trichophilopterus) can be distinguished from those on birds and can be included in a separate family the Trichodectidae. The opinion of the present writer, based on the examination of a large number of species belonging to all the recognised genera, together with studies of the gross internal morphology of representative examples, is that all the genera of Ischnocera parasitic on birds, together with Trichophilopterus from the mammals, should be included in the single family: Philopteridae. The other large superfamily, the Amblycera, has not yet been sufficiently studied for any decision on its suprageneric classification.

One further difficulty in the classification of the Mallophaga, a difficulty which is, of course, inherent in all classifications, but perhaps because of the evidence from the host distribution is more apparent in this group, is the impossibility in some cases of showing in a linear classification the phylogenetic relationships. It is held by many systematists that classification should be based on the relative time of evolution and not on the rate of evolution and that classification should be based entirely on phylogenetic relationships. The well known case of the birds which are phylogenetically nearer to the crocodiles than the crocodiles are to the turtles illustrates that at the Class level, at least, this principle cannot be followed. Is it in fact possible to apply it at any level? Recent work on the order Phthiraptera suggests that the suborder Anoplura (sucking lice) diverged from the mammal Ischnocera (suborder Mallophaga, chewing lice) after these had separated from the avian Ischnocera and had become established on mammals, and where the ~~former group~~ Anoplura followed a rapid morphological change in adaptation to the blood-sucking habit (5). This implies, therefore, that the Ischnocera of mammals, which retained their more primitive chewing habits and, therefore, changed less, are in fact, more closely related to the Anoplura than to the other superfamily of the Mallophaga, the Amblycera and to all the Mallophaga of birds (see fig. below). Thus, the present division of the order into the suborder Mallophaga for the chewing lice and the Anoplura for the sucking lice is phylogenetically incorrect (1:279).



This form of evolution, in which an ancestral stock has spilt into groups some of which have become adapted to a new way of life or a new habitat and thus diverged greatly, while the remaining groups are more similar to each other although in some cases less nearly related (1:295, fig. 3) must have happened at all levels continually in all groups.

It is apparent that in such cases a strict adherence to believed phylogenetic relationships would produce a completely unusable classification. The genus which is mainly a subjective concept, can be used as a convenient grouping of morphologically similar species of a common phylogenetic origin, but that where the phylogenetic history has produced subgroups morphologically different from their nearest related groups these morphological differences must be recognised by different generic names (3:174).

RELATIONSHIP BETWEEN PHYLOGENY OF HOST AND PARASITE.

In the great majority of cases the principle that the Mallophaga of related hosts are themselves related is true, evidence that the Mallophaga parasitized birds at an early stage of the evolution of the latter class. The lice living in a relatively constant environment have diverged to a lesser extent than their hosts, this being reflected in the many cases of a genus of Mallophaga being restricted to an order of birds (1:281, table 1). Hence, it can be accepted that, in general, the distribution of the Mallophaga can help in the elucidation of the correct systematic position of a bird (see nos. 6:2-4, 7, 8, 9, 10). It is rare to find evidence on the relationship between host orders from a distribution of their Mallophagan parasites (2:211), but within orders such relationships are the rule. However, there are cases of anomalous distribution of both genera and species of parasite indicating that the phylogenetic relationships of the Mallophaga cannot be used as infallible evidence of the phylogenetic relationships of their hosts. Some of these cases are illustrated by specially devised charts (11:442) which show host distribution of a parasite in a manner analogous to geographical distribution. Some of these cases can perhaps be explained by the incorrect placing of the host by the bird systematist, for example the Phoenicopteri (11:435), the Phaëthontes (11:434) and the Musophagi (11:437 and 8:654-656). Those cases of anomalous distribution which do not fit into this category can be explained by one of the following causes:

1. Discontinuous distribution of genera (1:293) or of one of a pair of a sympatric species (1:296, fig. 4).
2. Secondary infestations (1:294; 2:214).
3. Parallel evolution (1:294; 2:213).
4. Convergent evolution (1:293).
5. Retarded evolution (2:212).
6. Divergent evolution (2:213).
7. Human error in evaluation of the true systematic position of the parasite.

A detailed study (no. 12) of a genus, Rallicola, which has a wide and in some cases anomalous distribution illustrates some of the difficulties encountered in relating the phylogeny of host and parasite. This genus illustrates a possible error in the evaluation of the correct systematic position of the host (Jacanidae, 12:575-577); the possibility of parallel evolution (Brüelia and Furnaricola, 12:582); the possibility of convergence (Rallicola and Wilsoniella, 12:583); secondary infestation (the presence of a species of Rallicola on Corvus, 12:577-580) and as always the possibility of human error throughout the study.

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(Arranged chronologically).

1. New species of Mallophaga recorded from Asiatic birds. Proc. zool. Soc. Lond., 1936:905-914. 1936. (No copies available).

2. Mallophaga from the Tinamidae. Proc. zool. Soc. Lond., 1937:133-159. 1937. (No copies available).

3. Two new Mallophagan genera from the Columbidae. Entomologist, 70: 276-278. 1937. (With R. Meinertzhagen). (No copies available).

4. Two new genera of Mallophaga. Entomologist, 71:73-76. 1938. (With R. Meinertzhagen). (No copies available).

5. A revision of the genera and species of Mallophaga occurring on gallinaceous hosts. -- Part I, Lipeurus and related genera. Proc. zool. Soc. Lond. 108:109-204. 1938. (Two copies attached).

6. The Names of some Mallophagan genera. Entomologist, 71:206-207. 1938. (No copies available).

7. New genera and species of Mallophaga. Entomologist, 71:275-279. 1938. (No copies available).

\+ 8. New species of Mallophaga from Afropavo congensis. Amer. Mus. Novit., no. 1008:1-11. 1938.

\+ Denotes that the paper is referred to in the summary and a copy included.

9. Ectoparasites from captive birds. -I. Novit. zool., 41: 61-73. 1938. (With M. Rothschild). (No copies available).

10. Notes of some Mallophaga names. Novit. zool., 41:175-177. 1939. (No copies available).

11. Ectoparasites from captive birds. - II. Novit. zool., 41:305-315. 1939. (With M. Rothschild). (No copies available).

12. New genera and species of Mallophaga. Entomologist, 72:161-168. 1939. (With R. Meinertzhagen). (No copies available).

13. Three new genera of Mallophaga from the Charadriiformes. Ann. Mag. nat. Hist., (11), 4:450-454. 1939. (With R. Meinertzhagen) (Two copies attached)

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15. Mallophagan Miscellany. -- No. I. Ann. Mag. nat. Hist., (11), 6:427-433 1940. (No copies available).

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22. A Preliminary key to the genera of the Menoponidae (Mallophaga). Proc. zool. Soc. Lond. 117:457-477. 1947. (Two copies attached).

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24. List of Mallophaga collected from birds brought to the Society's Prosectorium. Proc. zool. Soc. Lond., 117:675-679. 1947. (With R. Meinertzhagen). (Two copies attached).

\+ 25. The systematic position of the Musophagi as indicated by their Mallophagan parasites. Ibis, 89:654-656. 1947.

\+ 26. Relationships within the Sterninae as indicated by their Mallophagan parasites. Ibis, 90:141-142. 1948.

27. Mallophaga Miscellany. -- No. 4. Ann. Mag. nat. Hist. (11), 14:540-552. 1947. (Two copies attached).

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+ 30. Species of the genus Saemundssonia (Mallophaga) from the Sterninae. Amer. Mus. Novit., no. 1409:1-25. 1949.

+ 31. Piercing mouth-parts in the biting lice (Mallophaga). Nature, 164:617. 1949.

32. Systematic notes on the Piaget collections of Mallophaga. -- Part I. Ann. Mag. nat. Hist., (12), 2:811-838; 895-921. 1949. (Two copies attached).

+ 33. Some problems in the evolution of a group of ectoparasites. Evolution, 3:279-299. 1949.

34. The early literature on Mallophaga. -- Part I. Bull. Brit. Mus. (Nat. Hist.) Ent. I: 221-272. 1950. (With G.H.E.Hopkins). (2 copies attached).

+ 35. A preliminary survey of the distribution of the Mallophaga on the class Aves. J. Bombay nat. Hist. Soc., 49:430-443. 1950.

+ 36. An introduction to a classification of the avian Ischnocera (Mallophaga): Part I. Trans. R. ent. Soc. Lond., 102:171-194. 1951.

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49. A new genus of Ischnocera (Mallophaga). Proc. R. ent. Soc. Lond., (in press).

50. Phthiraptera section of "The Taxononomists' Glossary of Genitalia in Insects". (in press).

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1. Some problems in the evolution of a group of ectoparasites. *Evolution*, 3:279-299. 1949.

2. The Mallophaga as an aid to the classification of birds with special reference to the structure of feathers. *Proc. Xth. Intern. Ornith. Congress June 1950.* 1951.

3. An introduction to a classification of the avian Ischnocera (Mallophaga) Part I. *Trans. R. ent. Soc. Lond.*, 102:171-194. 1951.

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