

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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C O N T E N T S.

1. Summary.
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1. S U M M A R Y.

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.<sup>+</sup> 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<sup>f</sup>: tables 4, 5, 6), and in addition, sympatric species of one or more of these genera.

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

<sup>f</sup> 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 similarity 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 similarity of the Ischnoceran head. A study (3) of the exoskeleton of a large number of forms shows that superimposed on this basic similarity 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.

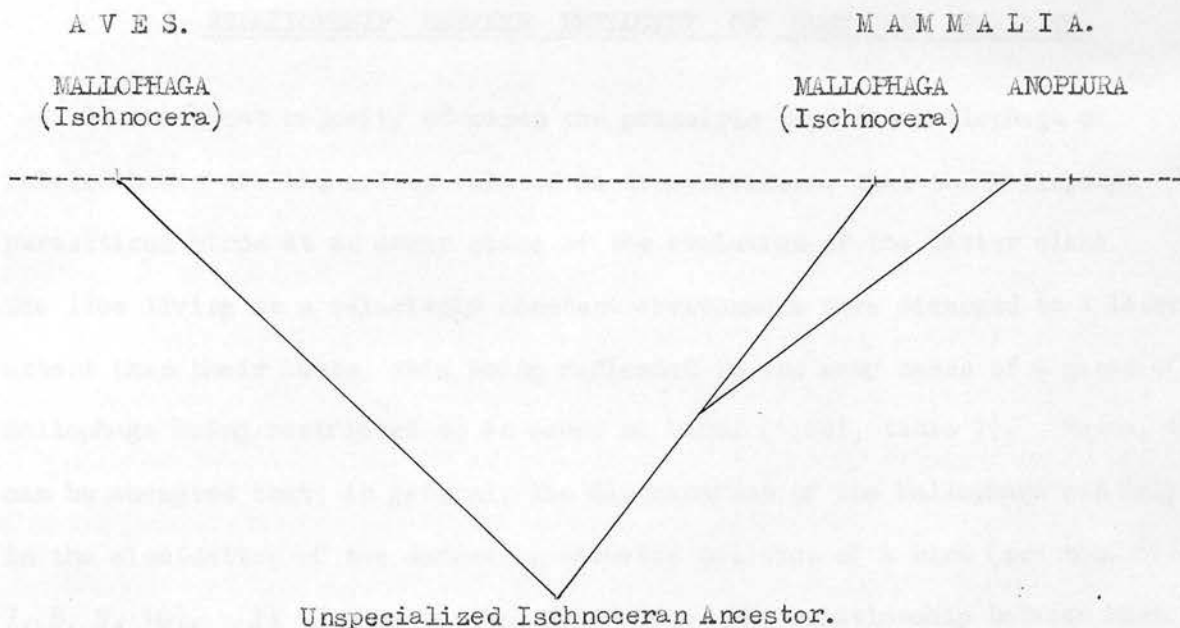
Internal Male Genitalia and Alimentary Canal. A study (in preparation for the press) of the internal male genitalia of 143 species belonging to 73 genera has been disappointing in regard to finding characters of suprageneric importance. Only one case, and that not conclusively, suggests a basis for suprageneric 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 <sup>Anoplura</sup> ~~former group~~ 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.

## LIST OF PUBLICATIONS.

(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.

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+ 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.  
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10. Notes of some Mallophaga names. Novit. zool., 41:175-177.  
1939. (No copies available).
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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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1940. (No copies available).
16. Anoplura. Brit. Graham Land. Exped., 1934-37, I:295-317. 1940.  
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1943. (Two copies attached).
- + 21. The Mallophagan parasites of the Passeriformes. Ibis, 88:403-405.  
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Proc. zool. Soc. Lond. 117:457-477. 1947. (Two copies attached).
23. Mallophaga Miscellany. --No. 3. Ann. Mag. nat. Hist. (11), 14:355-358.  
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24. List of Mallophaga collected from birds brought to the Society's  
Prosectorium. Proc. zool. Soc. Lond., 117:675-679.  
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- + 25. The systematic position of the Musophagi as indicated by their  
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- + 26. Relationships within the Sterninae as indicated by their Mallophagan  
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- + 30. Species of the genus Saemundssonina (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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- + 39. 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.
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- + 41. The Mallophaga and relationships within the Falconiformes. Ibis, 93:628. 1951.
42. A check list of the genera and species of Mallophaga. British Museum (Nat. Hist.), London. 1952. (With G.H.E. Hopkins). (2 copies attached).
43. Fleas, flukes and cuckoos. A study of bird parasites. Collins, London. 1952. (With M. Rothschild). (Two copies attached).
44. Additions and corrections to the check list of Mallophaga. Ann. Mag. nat. Hist., (12), 6:424-448. 1953. (With G.H.E. Hopkins). (Two copies attached).
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- + 46. Revisions of the genera of Mallophaga. -- I. The Rallicola-complex. Proc. zool. Soc. Lond., 123:563-587. 1953.

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(in press).
50. Phthiraptera section of "The Taxonomists' Glossary of Genitalia in  
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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.
4. Species of the genus Saemundssonina (Mallophaga) from the Sterninae. Amer. Mus. Novit., no. 1409:1-25. 1949.
5. Piercing mouth-parts in the biting lice (Mallophaga). Nature, 164:517. 1949.
6. New species of Mallophaga from Afropavo congensis. Amer. Mus. Novit., no. 1008:1-11. 1938.
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## SOME PROBLEMS IN THE EVOLUTION OF A GROUP OF ECTOPARASITES

TERESA CLAY

*British Museum (Natural History)*

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The Mallophaga are a group of ectoparasitic insects found on birds and mammals. Their complete life-cycle from egg to egg is spent on the same host form, away from which, under natural conditions, they cannot feed nor live for more than a short time. This group is of especial interest in that a large number of species may be found on one host. Most bird groups have five or six species of Mallophaga and some many more. Twelve species of Mallophaga belonging to eight genera and three families have been recorded from one species of Tinamidae (Tinamous), *Crypturellus obsoletus punensis*, and fifteen species belonging to twelve genera and three families from another, *Tinamus major*. In this paper the various factors which may have been responsible for speciation in this group of parasites are discussed and comparison made with the process of speciation in free-living animals.

### I. THE PRESENT DISTRIBUTION AND HOST RELATIONSHIPS OF THE MALLOPHAGA

The Mallophaga or chewing lice are placed as one of the sub-orders of the Phthiraptera, the other being the Anoplura or sucking lice of mammals. It is commonly assumed that the order is derived from a primitive Psocid-like ancestor which became parasitic first on birds. Both Harrison (1914, 3) and Webb (1946, 100) agree that the Mallophaga of mammals were derived from bird Mallophaga after these were already specialized for the parasitic habit; Webb (*loc. cit.*) suggests that migration from bird to mammal took place more than once. Hopkins (*in press*) considers this assumed avian origin of the Mallophaga

not improbable but unproved and by no means certain. Webb also suggests (1946, 101) that the Anoplura or sucking lice, found only on mammals, were derived from one of the Ischnocera (the more specialized superfamily of the Mallophaga further discussed below); this ancestral Ischnoceran is presumed to have migrated from bird to mammal where it gave rise to two branches, the descendants of one being the Anoplura, and of the other the Ischnoceran Mallophaga found on mammals. This implies that the Ischnocera (Mallophaga) on mammals are more closely related to the Anoplura than to the other superfamily of Mallophaga (the Amblycera) found on mammals and to all the Mallophaga of birds, and, of course, makes the present division of the order into two suborders—the Mallophaga or chewing lice and the Anoplura or sucking lice—phylogenetically incorrect.

The Mallophaga are separable into two, extremely distinct, superfamilies—the Amblycera and Ischnocera. The Amblycera (fig. 1a) have retained more of the habits and morphological characters of the ancestral free-living insect than have the Ischnocera (fig. 1b-f), and, in general, are probably not so restricted to definite habitats on the body of the host. This lesser degree of specialization for particular habitats has resulted in fewer and less extreme ecological types on any one host species—of the fifteen species found on *Tinamus major*, only one is a member of the Amblycera. This is reflected in the classification, the Amblycera being contained in about fifty homogeneous genera, while the Ischnocera are divided into nearly a hundred genera (the conception of large genera being adopted here),



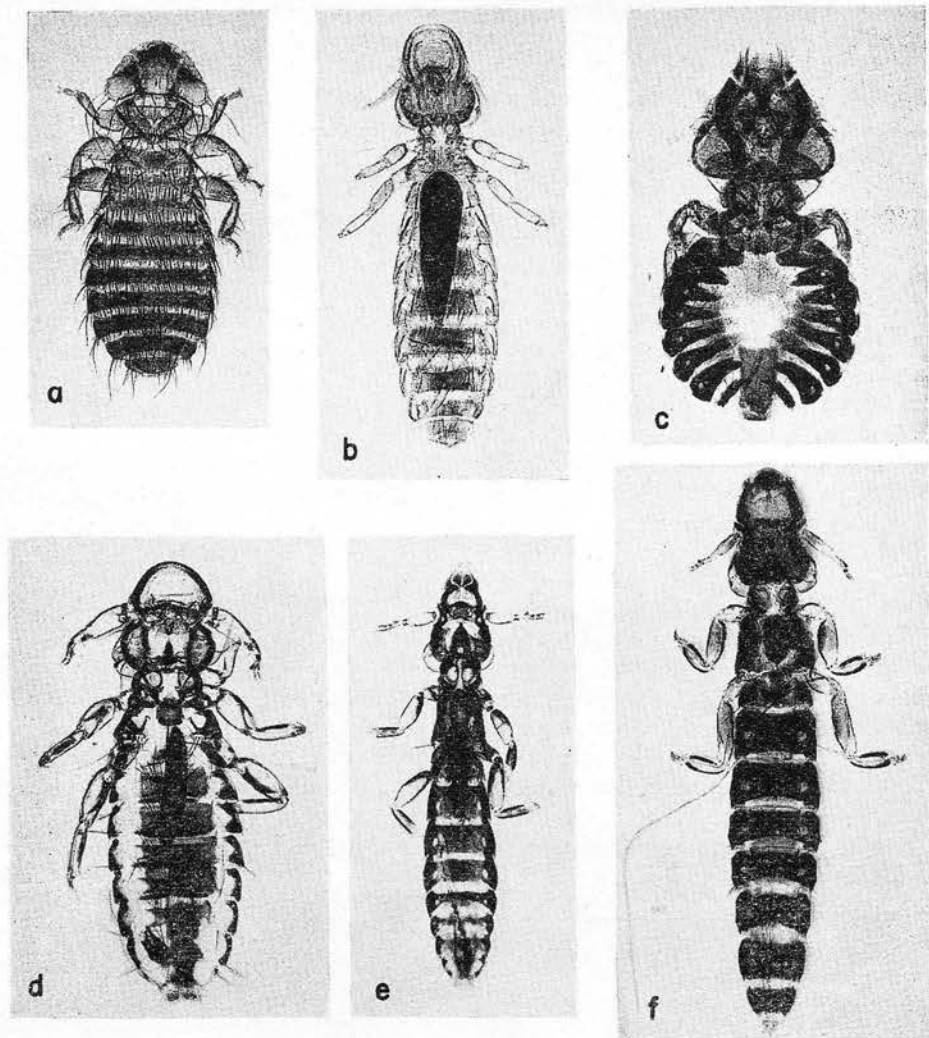


FIG. 1. a. Species of the superfamily Amblycera from the Anseriformes. b-f. Species of the Superfamily Ischnocera. b. *Degeeriella* species from the Falconiformes. c. *Craspedorhynchus* species from the Falconiformes. d. *Cuclostogaster* species from the Galliformes. e. *Fulicoffula* species from the Rallidae. f. *Perineus* species from the Procellariiformes.

many of which are divisible into well-marked species-groups. Hence, the problem of the multiplicity of forms in the Mallophaga is better illustrated by the Ischnocera, and examples from this superfamily will mostly be used, and as the groups living on avian hosts are better known to the present writer than those on mammalian, no examples will be taken from the latter.

The Ischnoceran population of any one host species belonging to the majority of avian orders is separable into a number of morphological types which occupy the different ecological niches found on the body of the bird. On the head and neck of the bird, for instance, is found a short, round-bodied type, not greatly flattened dorso-ventrally, and with a large head to accommodate the enlarged mandibles and

their strong supporting framework (fig. 1c). This type is adapted to movement on the shorter, narrower feathers of the head and neck, and, because its habitat is out of reach of the bird's bill during preening, it could develop the larger mandibles which meant an increase in head size; this type found on any other part of the bird would be easily picked off or crushed by the bill during the preening of the plumage. On the longer, broader feathers of the back and wings there is found a flattened elongate type (fig. 1e-f) which can slip sideways across the breadth of the feathers with great rapidity. The enlarged mandibles with the correlated increase of head size are not found in any of the typical wing-lice. Examinations of freshly killed birds show that these habitat forms are not found outside their own territories, except sometimes in the case of abnormally heavy infestations; the eggs of the head louse are laid on the feathers of the head and neck and those of the wing-louse on the wings and their axillary feathers. Apart from these two ecological types there are others, differing in size and body form, which either inhabit different parts of the plumage or are of the more primitive type (fig. 1b) and may not be so closely restricted and specialized for any one habitat; unfortunately there is little information available on the normal location of many of the species of Mallophaga.

That there is a general correlation between size and shape of the Mallophaga and size of feathers is suggested by the absence of the typical wing lice genera (that is with the elongated body and ventral genital opening in the male, fig. 1e-f) on those orders containing the smaller birds, for example, the Passeriformes (Perching birds); or on the smaller members of an order. Thus the wing louse genus *Falcolipeurus* of the Falconiformes (Birds of Prey) is not found on the smaller hawks. Where the typical wing louse is absent its place is taken by a narrow form with shortened abdomen and with the male genital opening in the dorsal

position (fig. 1b) as in *Bruelia* of the Passeriformes and *Degeeriella* of the Falconiformes. On any one host species there may be two or more related genera derived from each ecological type, and each of these sympatric genera may have two or more sympatric species.

The development of feathers by the ancestral birds or hair by the ancestral mammals provided a new type of habitat—an empty ecological niche—and it might be expected on the analogy of other groups, that the colonization of a new habitat, where food was plentiful and competition lacking, would result in the rapid evolution of the ancestral Mallophaga; the different ecological niches on the host's body, as these were formed during the evolution of the birds, would be occupied, with the ensuing adaptations of the louse. Superimposed on this process, which might be called evolution in space, was evolution in time caused by each habitat type having to adapt itself to the changes of its own particular ecological niche, these changes being brought

TABLE 1. *Examples of host groups with specific genera of typical head and wing lice*

Position on the bird of starred genera not recorded.

Host group	Genus of head louse	Genus of wing louse
Tinamiformes (Tinamous)	* <i>Pseudophilopterus</i>	<i>Pseudolipeurus</i>
Procellariiformes (Petrels)	<i>Trabeculus</i>	<i>Naubates</i>
Pelecaniformes (Pelicans, cormorants and allies)	—	<i>Pectinopygus</i>
Ciconiiformes (Herons and storks)	<i>Ibidocetus</i>	<i>Ardeicola</i>
Anseriformes (Ducks, geese, and swans)	<i>Analoecus</i>	<i>Anaticola</i>
Falconiformes (Birds of prey)	<i>Craspedorrhynchus</i>	<i>Falcolipeurus</i>
Rallidae (Rails)	<i>Incidifrons</i>	<i>Fulicoffula</i>
Momotidae (Motmots)	* <i>Clayella</i>	—
Meropidae (Bee-eaters)	<i>Meropoecus</i>	—
Rhamphastidae (Toucans)	* <i>Austrophilopterus</i>	—
Passeriformes (Perching birds)	<i>Philopterus</i>	—

about by the evolution of the birds themselves. The environment of the Mallophaga is formed by the chemical composition and physical structure of the feathers, the texture of the skin and certain physiological characters of the host such as temperature and body secretions. Thus, each ecological type, as the result of changes in these characters of their hosts, evolved with their hosts, but, in general, at a slower rate (that is after the initial period of rapid evolution); this is reflected in the general correlation found between the classification of host and parasite. It is usual to find a genus of Mallophaga restricted to an order of birds (table 1) [there are, however, a considerable number of exceptions (tables 2 and 3), the reasons for which will be

TABLE 2. *Examples of genera or groups of closely related genera of Ischnocera with unspecialized heads, or Amblycera, found on more than one host group*

Names in brackets will, in many cases, probably prove to be congeneric with the preceding genus. Starred genera belong to the superfamily Amblycera

Genus or closely related group of genera of Mallophaga	Host group on which found
<i>Otidocerus (Otilipeurus), Rhyonirimus and Cucitogaster</i>	Otides (Bustards) Charadriiformes (Shore-birds) Galliformes (Game birds) Musophagi (Plantain-eaters)
<i>Goniodes, Gonicotes, Colocerus, and Campanulotes</i>	Galliformes Columbae (Pigeons and Doves)
<i>Lagopoecus and Tinamotocola</i>	Galliformes Tinamiformes (Tinamous)
<i>Degeeriella (Cuculicola, Trogonirimus, Capra-iella, Upupicola and Picicola)</i>	Falconiformes (Birds of prey) Cuculi (Cuckoos) Trogoniformes (Trogons) Coraciidae (Rollers) Upupidae (Hoopoes) Pici (Woodpeckers) Passeriformes (Perching birds)
* <i>Colpocephalum (sens. Clay, 1947 (1))</i>	Pelecaniformes (Pelicans, cormorant and allies) Ciconiiformes (Herons and storks) Anseriformes (Ducks, geese, and swans) Galliformes Cariamae (Cariamias) Columbae Strigiformes (Owls) Pici Passeriformes
* <i>Menacanthus (sens. Clay, 1947 (1))</i>	Tinamiformes Galliformes Musophagi Upupidae Capitonidae (Barbets) Rhamphastidae (Toucans) Pici Passeriformes

TABLE 3. *Examples of genera or closely related groups of more specialized genera of Mallophaga found on more than one host group*

Explanations of these cases of anomalous distributions of Mallophaga genera given in the text. Names in brackets will, in many cases, probably prove to be congeneric with the preceding genus

Genus of closely related group of genera of Mallophaga	Host Group on which found
a. <i>Apterocola, Wilsoniella, Rallicola (Parricola, Furnaricola)</i>	Apterygiiformes (Kiwis) Opisthocomi (Hoazin) Rallidae (Rails) Charadriiformes Cuculi Passeriformes
b. <i>Saemundsonia</i>	Procellariiformes Gruidae (Cranes) Charadriiformes
c. <i>Ibidoecus</i>	Ciconiiformes Aramidae (Limpkins)
d. <i>Oxylipeurus, Splendoroffula</i>	Galliformes Musophagi
e. <i>Anatocerus (Ischnocera, head louse)</i>	Anseriformes Phoenicopteridae (Flamingoes)
f. <i>Anaticola (Ischnocera, wing louse)</i>	
g. <i>Trinoton (Amblycera)</i>	

discussed below], and within the parasite genus each species will usually be restricted either to one host species or subspecies (tables 4 and 5 and see Eichler, 1946, 10-11 for other examples), or to a group of related host species (table 6).

If it is assumed that the above outline gives a general picture of the course of evolution in the Mallophaga, can this be explained by the theory of speciation by geographical isolation as applied to free-living animals? The possible factors responsible for speciation and for the present distribution of the genera and species of the Mallophaga will be discussed below under three main headings: Isolating factors, Ecological factors, and the Origin of sympatric species. The word "speciation" is used for the process of bringing about any new form, whether the present product is now a species, genus or family.

## II. ISOLATING FACTORS IN MALLOPHAGA SPECIATION

### 1. Isolation by species formation in the hosts

The host distribution of the Mallophaga is the equivalent of the geographi-

cal distribution of the free-living animal. If the populations of any host species are in continuous contact then potentially the parasite can move throughout the species, but if the host species is divided into isolated or semi-isolated populations it follows that the louse population will be likewise divided. If one of these isolated populations of the bird species gives rise to a new species and even if later becomes sympatric with its parent population there

TABLE 4. *Examples of related host species or subspecies each with an allopatric species of a Mallophaga genus*

Some of the Mallophaga species will probably prove to be subspecies. Percentage of host species in the genus *Crypturellus* (*C.*) (Tinamiformes) from which *Strongylocotes* (*S.*) is known is 52.2%, *Austrokelloggia* (*A.*), 43.5% and *Pectenosoma* (*P.*), 47.8%

Host species from which Mallophaga known	Mallophaga species
<i>Crypturellus cinereus</i>	<i>Strongylocotes abdominalis</i> <i>Austrokelloggia heterurus</i>
<i>C. o. obsoletus</i>	<i>S. complanatus</i>
<i>C. o. ochraceiventris</i>	<i>S. intermedius</i>
<i>C. o. punensis</i>	<i>Pectenosoma punensis</i> <i>A. obsoletus</i>
<i>C. soui nigriceps</i>	<i>A. nigriceps</i> <i>P. nigriceps</i>
<i>C. s. mustelinus</i>	<i>S. perijae</i>
<i>C. s. albigularis</i>	<i>S. albigularis</i>
<i>C. s. inconspicuus</i>	<i>S. subconiceps</i> <i>A. inconspicuus</i> <i>P. inconspicuus</i>
<i>C. s. meserythrus</i>	<i>P. meserythra</i>
<i>C. u. undulatus</i>	<i>A. undulatus</i>
<i>C. u. yapura</i>	<i>P. yapurae</i>
<i>C. b. boucardi</i>	<i>S. boucardi</i> <i>A. boucardi</i> <i>P. boucardi</i>
<i>C. garleppi affinis</i>	<i>S. interruptus</i> <i>P. angusta</i>
<i>C. v. variegatus</i>	<i>A. coniceps</i> <i>P. verrucosa</i>
<i>C. v. salvini</i>	<i>S. variegatus</i>
<i>C. c. cinnamomeus</i>	<i>S. fimbriatus</i>
<i>C. c. idoneus</i>	<i>A. idoneus</i>
<i>C. c. sallaei</i>	<i>P. cinnamomea</i>
<i>C. n. noctivagus</i>	<i>S. noctivagi</i>
<i>C. t. talaua</i>	<i>S. glabrous</i> <i>A. genitalis</i> <i>P. parva</i>
<i>C. parvirostris</i>	<i>A. n. sp.</i> <i>P. n. sp.</i>

TABLE 5. *Examples of host groups where ratio of known species of Mallophaga is to host species as 1:1*

Host group	Percentage of host species in the group from which Mallophaga species of the genus is known	Mallophaga genus
Charadriiformes (Shore birds)		
<i>Chettusia</i>	100%	<i>Quadraceps</i>
<i>Hoplopterus</i>	100%	<i>Quadraceps</i>
<i>Charadrius</i>	45%	<i>Quadraceps</i>
<i>Tringa</i>	77.8%	<i>Quadraceps</i>
<i>Actitis</i>	100%	<i>Quadraceps</i>
<i>Heteroscelus</i>	100%	<i>Quadraceps</i>
Pterocletes (Sand-grouse)		
<i>Syrhaptes</i>	100%	<i>Syrhaptoecus</i>
<i>Pterocles</i>	81.2%	<i>Syrhaptoecus</i>
Anseriformes (Ducks, geese, and swans)		
Cygninae	71.4%	<i>Ornithobius</i>
Galliformes (Game birds)		
<i>Alectoris</i>	100%	<i>Cuculogaster</i>

would be no further interchange of lice owing to the discontinuance of interbreeding between the two bird populations, now distinct species. Here, therefore, is

TABLE 6. *Examples of groups of related host species each with an allopatric species of a Mallophaga genus*

Hosts	Percentage of host species in group from which Mallophaga known	Mallophaga species
Galliformes, Tetraonidae (Grouse)		
<i>Tetrao urogallus</i> <i>T. parvirostris</i>	100%	<i>Goniodes bituberculatus</i>
<i>Lyrurus tetrix</i> <i>L. mlokosieviczi</i>	100%	<i>G. tetraonis</i>
<i>Dendragapus obscurus</i>	100%	<i>G. simoni</i>
<i>Lagopus scoticus</i> <i>L. lagopus</i> <i>L. mutus</i> <i>L. leucurus</i>	100%	<i>G. lagopi</i>
<i>Canachites canadensis</i>	100%	<i>G. corpulentus</i>
<i>Bonasia umbellus</i>	100%	<i>G. bonasus</i>
<i>Tympanuchus cupido</i>	50%	<i>G. cupido</i>
<i>Centrocercus urophasianus</i>	100%	<i>G. centrocerci</i>
<i>Pediocetes phasianellus</i>	100%	<i>G. nebraskensis</i>
Charadriiformes, Sterninae (Terns)		
<i>Chlidonia hybrida</i> <i>C. leucoptera</i> <i>C. nigra</i>	100%	<i>Saemundssonina lobaticeps</i>
<i>Sterna aurantia</i>		<i>S. hopkinsi</i>
<i>S. hirundo</i> <i>S. paradisaea</i> <i>S. vitatta</i> <i>S. albifrons</i>	22.6%	<i>S. sterna</i> <i>S. lockleyi</i> <i>S. melanocephalus</i>
<i>Thalasseus bergii</i> <i>T. bengalensis</i> <i>T. sandvicensis</i>	42.8%	<i>S. laticaudata</i>

the exact analogy of the situation found on a group of continental islands, the populations of which have become isolated by the disappearance of land connections. Within each ecological niche on the body of the bird, these isolated populations of lice would have become modified through adaptations to the changing environment brought about by the changes in the evolving bird, as does a free-living animal to the climatic and other changes acting in its ecological niche (further discussed below under section III).

### 2. Isolation by the development of host specificity

In the Mallophaga dispersal can take place during brooding of the young birds (the case of brood parasites will be discussed below), during copulation, and during roosting in gregarious birds; all these interchanges of lice are between individuals of the same host species. Movement of Mallophaga individuals from one host species to another must be rare, as normally birds of different species do not come into close enough contact for such transference. Interchange can, however, take place between predator and prey, nestling and foster parent in brood parasites, by the use of common dust baths (Hoyle, 1938) and by phoresy (discussed below). In addition to the difficulty of transport from one host to another, the migrant louse must be able to establish itself on the new host. This may be prevented not only by the competition of the already established and better adapted resident louse population, but the immigrant louse may be strongly host specific, so that it is unable to feed or its eggs and nymphs develop on any but its own host species (Wilson, 1934, 308). The transference either of individuals of both sexes or of a fertilized female must of course take place. That establishment is not only a question of transference and lack of competition is shown by the cases of brood parasites, where there is ample opportunity for transference during brooding of the young, and no competition from

an established population on the new host. The European cuckoo (*Cuculus canorus*), a brood parasite, has species of three genera of lice found on the Cuculidae throughout the world which are distinct from those of the Passeres, the sub-order to which the foster-parents belong; thus, in spite of optimum conditions for transference the lice of the latter have never been able to establish themselves on the cuckoo. It is not known to what degree host specificity is carried and it is possible that lice could and do establish themselves on related hosts, the rare occurrence of this being due more to the difficulties for the louse of passing from one host species to another than to its establishment on the new species. The many cases of established populations of *Lipeurus caponis*, a normal parasite of the chicken, on pheasants, partridges, and guinea fowl, the eggs of which have been hatched under chickens, show that it is possible (see Eichler, 1940, for other examples), and will be further discussed below. The normal isolation of the populations of Mallophaga of any one host species, due to the difficulties of a louse passing between hosts of different species, has allowed the close adaptation of the parasite to the environment provided by its particular host, and has thus led to the development of host specificity. This host specificity will increase the isolation of the louse populations by making it more unlikely that an immigrant louse will be able to establish itself on a new host and thus interbreed with the resident louse population. This isolation has led, as in the case of island populations, to the formation of species—each restricted to the island in the case of the free-living animal and to the host species in the case of the parasite.

### 3. Isolation and reunion of host populations

During the evolution of the birds there must have been frequent geographical isolation of parts of the population of a bird species which reunited before any repro-

ductive isolating mechanism had developed. The reunion of the bird populations would mean the merging again of their louse populations, but it is possible that during the period of isolation one of the louse populations might have developed some character which prevented free interbreeding with the parent population, thus forming two species. These species would gradually spread throughout the combined host populations until the host species was parasitized by two sympatric species.

#### 4. Extinction of louse populations

The potential range of each species of Mallophaga is that of its host species, but collections of Mallophaga from one host species in different parts of its range show that there is a true geographical distribution superimposed on the host distribution. Such a geographical distribution may be found over quite small areas: for instance, in the British Isles populations of the chaffinch (*Fringilla coelebs*) or the robin (*Erithacus rubecula*) in one locality may be found with a high incidence of individuals infested with *Ricinus*, whereas in another locality infested individuals seem to be absent. Numerical data are scanty owing to the disinclination for the slaughter of large numbers of birds in one locality, but the following records suggest a geographical distribution for the parasite species concerned: *Laemobothrion* species from the coot (*Fulica atra*) never recorded from Great Britain (42\*), but known from Morocco (two infested individuals out of six examined) and India (two out of ten); *Laemobothrion* species from the moorhen (*Gallinula chloropus*) not recorded from Great Britain (75\*), but known from the Sudan (only one specimen examined); *Ricinus* species from the crested lark (*Galerida cristata*) not known from Egypt (one locality only, 13), nor Khartoum, Sudan (9), but found on five out of seven individuals from Atbara, Sudan; *Picicola* not known from the green woodpecker in the British Isles (11), but found in the only two in-

dividuals examined from Sweden; *Philopterus* species from the European robin known only from two records in the British Isles (147\* examined from Europe and N. Africa).

This type of discontinuous distribution of species may have had two important effects on speciation: (1) the isolation of populations by an intervening area of absence and (2) the emptying of a particular ecological niche enabling either another species on the same host or an immigrant louse from another host species to occupy it. If a host species, for instance, is spread across a continent and for some reason one of its louse species has become extinct in the middle of its range, then the two louse populations at either end of the range will be isolated. In time the louse species may again spread throughout the population of its host, but it is possible that in one of the populations some kind of sexual isolating mechanisms may have developed. Even where there is no temporary absence of a louse species the Mallophaga population of polytypic host species with a wide continuous range will tend to form distinct populations, potentially of subspecific value, as is found in free-living animals (Mayr, 1942, 180). Even the small amount of work done on this subject shows that this has happened: in the case of one of the louse species (*Cuclotogaster cinereus*) of the quail, specimens from the European quail (*Coturnix c. coturnix*) differ from those from the Far Eastern subspecies (*C. c. japonica*) in the proportions of the head, thorax, abdomen, and male genitalia (Clay, 1938, 149). No work has been done on the statistical examination of populations from different parts of the range of a polytypic species, which might show that such subspecies or microsubspecies are commoner than is now apparent.

Not only will some lice be absent in part of a bird's range but the population size of any given louse species may vary

\* Numbers in author's own records only, the actual numbers examined would be greater.

enormously: for instance, a curlew (*Numenius a. arquata*) from Ireland had over 1,800 lice of three species; other specimens have been found with all but one of these species absent, and reduced to 10 or 20 in number. Examples of equivalent differences in population numbers of a single louse species could be quoted for almost any host species from which Mallophaga have been collected. This suggests that fluctuation in population sizes with the concomitant increased speed of genetic change may also play an important role in speciation in the Mallophaga.

There are two characters found in the Ischnoceran Mallophaga which, amongst others, may have been developed during these periods of isolation and have been responsible for sexual isolation between daughter and parent populations: these are (a) the proportions of the abdomen and (b) sexual dimorphism of the antennae.

(a). As already shown there is a tendency towards a shortening of the abdomen in certain of the ecological types; this shortening must affect the method of copulation. It is probable that the majority of the Ischnocera take up the same position in copulation (Sikora and Eichler, 1941), that is the male dorsal surface under the female ventral surface, the male clasping the female either with the antennae or forelegs. The more primitive position of the male genital opening is ventral or ventro-terminal and during copulation the end of the body is recurved so that the genitalia can enter the ventrally placed vulva of the female (Werneck, 1936. Pl. 1); this recurving of the body would obviously be difficult in the short, round-bodied forms, and it is found that in these the genital opening of the male lies on the dorsal surface. This dorsal position of the male genital opening is found in unrelated families and has probably been developed independently more than once. Only one genus (*Labio-cotes*) is known of short, round-bodied forms in which the male genital opening is ventral, and it is possible that these

take up one of the other positions in copulation as described by Sikora and Eichler (1941). It might happen that in an isolated population of birds the Mallophaga population had occupied the favorable habitat of the head, and the shape of the abdomen became slightly modified; any modification in this region might lead to a difference in mating behavior and hence on the reunion of the louse populations there would be definite preferential mating resulting in the continued isolation of the two populations. The process, of course, may have been reversed: a slightly shortened body form being produced by the random fixation of mutations in a small isolated population; this form would not only be sexually isolated from the parent population, but would be pre-adapted for the occupation of the head niche.

Sometimes it seems to have happened that in a form in which the male genital opening had moved to the dorsal surface because of the shortening of the abdomen, there was a secondary lengthening of the body. This may be the case in the wing louse (*Columbicola*) of the Columbiformes (Pigeons and Doves), which, unlike other long-bodied forms, has the genital opening on the dorsal surface; it may have become modified for the head niche in isolation, but on the colonization of other host populations found this niche already occupied and was forced to adapt itself to the wing habitat.

(b). The second character which may have played a considerable part in speciation is the sexual dimorphism of the antennae. This character may be found in species belonging to all the families of the Ischnocera; in some genera such as *Degeeriella* from the Falconiformes it has only been found in one species (undescribed), in others such as *Goniodes* from the Galliformes (Game birds) it is present in the majority of species. It is not a generic character and there are instances of two species in which the females are very similar, but the males of one have enlarged and modified antennae.

As the antennae are used to clasp the female during copulation even incipient dimorphism might lead to a difference in mating behavior.

If this character, non-adaptive in its incipient stages, was developed in a small isolated population by random fixation it would probably lead to a difference in mating behavior and, hence, to sexual isolation of this population on reunion with its parent population. When a host species has two sympatric species of an Ischnoceran genus it is commonly found that these differ in the presence or absence of sexual dimorphism of the antennae, or in the degree of sexual dimorphism (table 7). This character may also have been responsible for the formation of species which gave rise to some of the sympatric

TABLE 7. *Examples of host species parasitized by two related species of Mallophaga, in one of which the antennae are similar in the two sexes and in the other dimorphic*

Starred species show slight sexual dimorphism of the antennae in contrast to the related species in which the male antennae are considerably enlarged

Host species	Mallophaga species	
	Antennae dimorphic	Antennae similar
Tinamiformes (Tinamous)		
<i>Tinamus tao septentrionalis</i>	<i>Kelloggia mirabilis</i>	<i>K. taoi</i>
<i>Rhyncotus r. rufescens</i>	<i>Heptapsogaster sexpunctatus</i>	<i>H. rotundatus</i>
Sphenisciformes (Penguins)		
<i>Eudyptes c. cretatus</i>	<i>Austrogoniodes hamiltoni</i>	* <i>A. macqueriensis</i>
Procellariiformes (Petrels)		
<i>Pterodroma m. mollis</i>	<i>Trabeculus</i> sp.	<i>T. sp.?</i>
Galliformes (Game birds)		
<i>Numida meleagris major</i>	<i>Goniodes perlatus</i>	<i>G. gigas</i>
<i>Afropavo congenis</i>	<i>G. chapini</i>	<i>G. afropavo</i>
<i>Arborophila r. rufogularis</i>	<i>G. processus</i>	* <i>G. indicus</i>
<i>Lophortyx californica</i>	<i>Lagopoecus docophoroides</i>	<i>L. sp. n.</i>
Rallidae (Rails)		
<i>Porphyrio madagascariensis aegyptiacus</i>	<i>Rallicola</i> sp?	* <i>R. sp?</i>
Strigiformes (Owls)		
<i>Bubo b. bubo</i>	<i>Strigiphilus heteroceras</i>	<i>S. sp?</i>
Passeriformes, Corvidae (Crows)		
<i>Corvus corax lawrencei</i>	<i>Bruelia</i> sp?	* <i>Bruelia</i> sp?

TABLE 8. *Examples of host groups, the members of which are parasitized by two related genera of Mallophaga, in one of which the antennae are similar in the two sexes, and in the other dimorphic*

Starred genera have a few species in which the antennae are similar in the sexes

Host order	Genera of Mallophaga	
	Antennae dimorphic	Antennae similar
Tinamiformes	<i>Nolhocotus</i> * <i>Heptapsogaster</i>	<i>Megaginus</i> <i>Discocorpus</i>
Procellariiformes	<i>Pseudonirmus</i>	<i>Episbates</i>
Galliformes	* <i>Goniodes</i> <i>Chelopistes</i>	<i>Goniocotes</i> <i>Labiocotes</i>
Columbae	<i>Coloceras</i>	<i>Campanulotes</i>

genera now found on some host orders (table 8). Again the fact that in all the genera of true wing lice (table 1) the majority of species show sexual dimorphism of the antennae, whereas in all the true head lice (table 1) it is rare, suggests that this character may have been the initial isolating factor in the formation of these ecological types. The less common occurrence of sympatric species and genera in the Amblycera may be partly due to the absence of sexual dimorphism of the antennae, which in most species of this superfamily, anyhow, can play no part in mating.

### III. ECOLOGICAL FACTORS IN MALLOPHAGA SPECIATION

#### 1. *Intrinsic changes in each ecological niche*

Under this heading are discussed the changes brought about in each habitat type by adaptation to the changes in its particular ecological niche, and which have been mainly responsible for the production of the allopatric genera and species. This is Simpson's "phyletic evolution" (1944, 202) and, as he shows, it consists of changes of populations as a whole, the new species replacing the former species. The processes involved in this mode of evolution differ in no way in the case of the Mallophaga from those of a group of free-living insects.

Once the Mallophaga had been able to adapt themselves to life in general on the body of the bird, the main selecting fac-



tors were, presumably, both interspecific and intraspecific competition and attack by the bird; this latter factor would make the head and neck the most secure place and may have been responsible for the production of the specialized type found on the wings. (Although the head and neck niche is the safest place in respect to preening by the host, it may have certain disadvantages in some birds; a sparse covering or the complete absence of feathers might make this niche uninhabitable in hot, dry climates, or on those birds which spend much time under water.) It seems probable that it is in these two habitats, that of the head and of the wing, that competition is the most severe, as the Mallophaga of these niches have developed the most extreme specialization of the head to the feather structure of the particular host. The production of a new species by a change of the whole population through adaptation to a changing environment is dependant mainly on the selection pressure, which here must have been competition between the Mallophaga. Chandler (1914) has shown that the minute structure of the feather is usually an ordinal character, and it is, therefore, of interest that the specialized head lice and the similarly specialized wing lice are divisible into genera, each of which is restricted to an order of birds (table 1); there are certain exceptions to this (table 3), the reasons for which will be discussed below. Further three host groups, the Momotidae (Motmots), Meropidae (Bee-eaters) and Rhamphastidae (Toucans) which have genera (*Bruelia* and *Menacanthus*) of less specialized lice also found on the Passeriformes, each have a specialized head louse different from that of the latter order (table 1). Such genera, restricted to certain orders of birds, show differences in the characters of the head framework and sutures which give support and mobility, and which, presumably, allow the most efficient application of the mandibles and of the *pulvinus* (*sens.* Cope, 1940, 120) [which serves an important function in feeding and

holding to the particular feather structure of the host order concerned.

The chief factor, therefore, influencing the production of the allopatric species and genera of the Mallophaga has been the successive splitting of the host populations during the evolution of the birds, thus leaving isolated louse populations. Within these isolated "islands" each ecological type diverged from those on other "islands" by specialization for the changing environment of its own niche and by the random fixation of non-adaptive characters made possible by the isolation. Within an order of birds the environmental differences between the same ecological niche are, in general, slight, and this has led to any one genus of parasite confined to an order of birds having a large number of allopatric species, one on each host species (tables 4 and 5) or one on a group of related host species (table 6); in the case of some of the Tinamidae, an ancient group of birds where presumably the louse populations have been isolated for a greater time, different species or subspecies of lice are found on the subspecies of a polytypic host species (table 4). These allopatric species do not usually differ greatly from each other, and are separable mainly on the characters of the external sclerotization and measurements (probably correlated with feather texture and feather size) and on nonadaptive characters such as the male genitalia. Such species are comparable to those allopatric species of a genus of free-living animals found on continental islands and in other isolated habitats.

## 2. Change of ecological niche on the same host species

Although any one host species may have a number of genera and species of Mallophaga recorded from it, any individual bird does not necessarily have them all. As shown above, a louse species may become extinct throughout parts of its host's range; this would mean that one of the ecological niches would be empty of

its specialized louse type, and might, especially if it was such a favourable niche as the head, be occupied by another species which would become secondarily adapted to the new habitat. This seems to have happened in the head niche of the Sturnidae or starlings: in this family the specialized head louse, *Philopterus*, characteristic of the suborder Passeres (Song birds), is absent, but the starlings have a genus *Sturnidoecus* (fig. 2d) which superficially resembles *Philopterus* (fig. 2e). *Sturnidoecus* has the large head with the complicated arrangement of sutures and sclerotization, and the short, round abdomen characteristic of the occupants of the head niche. But the char-

acters of the female genital region, the shape of the alimentary canal, the internal male genitalia and spermatheca show that it is more closely related to another genus *Bruelia* (fig. 2b) also found on the Passeres, which has the smaller head and more elongate body form. The fact that the genus *Sturnidoecus* has also been found on species of *Passer* (Ploceidae) and *Turdus* (Turdidae) in various parts of the world lends support to the theory of secondary interspecific infestations discussed below. It seems probable in these cases that populations of the *Passer* and *Turdus* species concerned, lacking the head louse, became secondarily infested by *Sturnidoecus* from one of the Sturni-

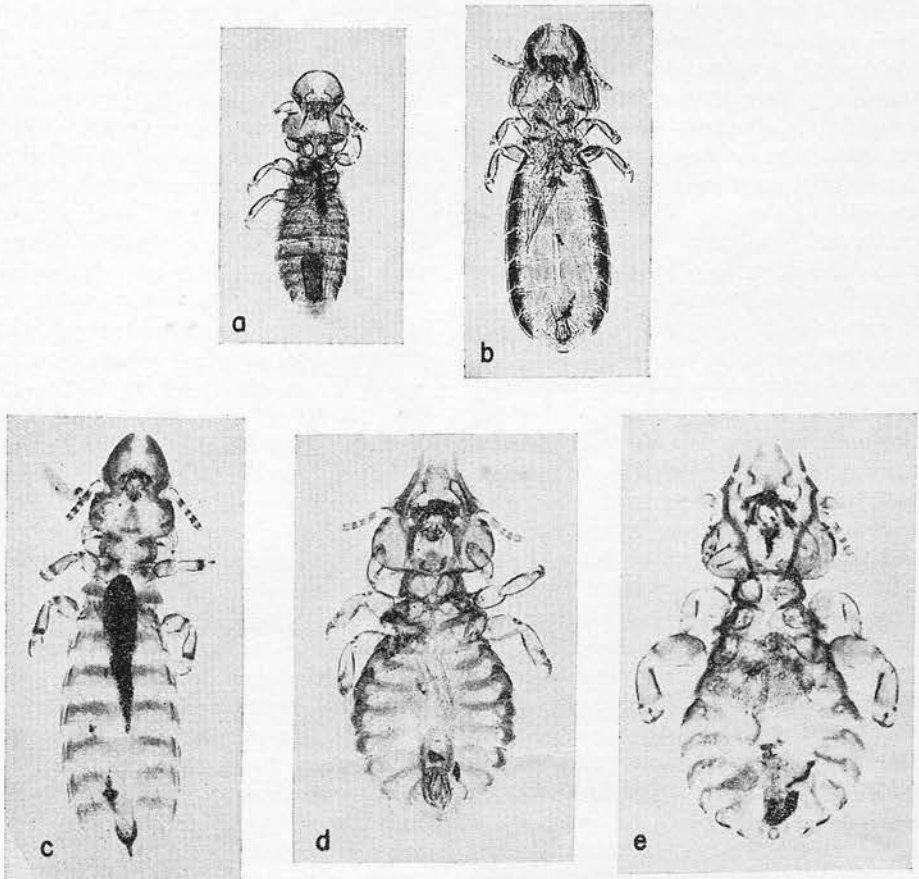


FIG. 2. Mallophaga of the Passeriformes. a. *Bruelia biguttata*.  $\times 35$ . b. *B. daumae*.  $\times 35$ . c. *B. nebulosa*.  $\times 65$ . d. *Sturnidoecus sturni*.  $\times 56.5$ . e. *Philopterus* sp.  $\times 60$ .

dae, and these in the absence of competition were able to establish themselves on the head. *Sturnidoecus*, unlike true *Philopterus*, is not so closely restricted to the head and may be found on other parts of the body.

#### IV. THE ORIGIN OF SYMPATRIC SPECIES

1. *Sympatric speciation*.—At first sight this would seem to be the most likely explanation of the presence of closely related species and genera found in a restricted and isolated geographical area. Mayr (1947) has summarized the arguments against the theory of sympatric speciation in general and these need not be repeated. In the case of the present group it seems unlikely, in the light of modern knowledge of genetics, that speciation could have taken place in an area such as the external body surface of a bird where there are no extrinsic isolating barriers, the plumage of one area grading into the next or in close contact with it. Even if the theory of conditioning is accepted, so that the Mallophaga hatched on the head and neck would tend to remain in that area, there would seem to be nothing to prevent interbreeding between individuals on the neck and those conditioned for the adjacent zone of the back and wings; such interbreeding would ensure the maintenance of gene flow between the two populations. However, the non-uniform distribution of plumules found in some orders might form isolated areas for populations conditioned to this type of feather, analogous to the isolation of free-living populations by intervening desert areas. If this feature had been responsible for speciation it would be expected that those orders in which there is a uniform distribution of plumules would have fewer sympatric genera. Only two examples of such orders need be taken to show that this is not so: the Procellariiformes (Petrels) which have ten Ischnoceran genera, some of which are divisible into two or more species-groups found on the same host, and the Falconiformes (Birds of Prey) which

have four Ischnoceran genera. Finally the available evidence suggests that the problem can be explained by the process of speciation through geographical isolation.

2. *Isolation*.—It has already been shown under section II, 3 and 4 how the isolation of parts of the louse populations of a host species and their subsequent reunion may have been responsible for some of the sympatric species now found on one host.

3. *Secondary interspecific infestations*.—Host specificity which may prevent the establishment of a louse transferred to a host of a different species has been discussed above; it was shown that although, in general, the Mallophaga are host specific there are cases of immigrant parasite species establishing themselves on a new host. It can also be presumed that establishment on a new host was more possible at a time in the evolution of the louse before it had developed extreme host specificity and when the hosts themselves, less divergent during the earlier stages of their evolution, offered a more uniform environment. This colonization of a new host by a species of Mallophaga is analogous to the transoceanic colonization of oceanic islands by free-living animals, and, as in this latter case, may have contributed to the presence of sympatric species and genera in the parasite. There is some evidence in support of this supposition. Eichler (1942, 78) has drawn attention to the fact that those orders of birds which are represented by a small number of species are those which have one, rarely two genera of Mallophaga, while those with many species usually support a number of sympatric genera and species (table 9). Although, in general, this statement is correct there are a number of exceptions which must be considered, as well as possible alternative explanations to that of secondary infestation as the cause. Some orders of birds now represented by a few species are, presumably, the relics of once numerous and widely spread groups. As

TABLE 9. Number of species in each host group with the number of sympatric genera and species-groups of Mallophaga

The Phoenicopteridae are omitted from the Ciconiiformes as their Mallophaga in no way resemble those of this order. For the same reason the family Opisthocomidae (Hoazin) is omitted from the Galliformes. The whole of the Gruiformes and certain other orders are omitted for reasons given in the text under "Note on Tables." The Todidae, Leptosomatidae, Galbulidae, and Bucconidae are omitted as no Mallophaga have been seen from these groups. Although all the genera and species-groups given will not be found on all the bird species throughout the order, an attempt has been made to list only those which could be sympatric; thus *Bisarrifrons* is not included in the number of genera found on the Passeriformes as it is the allopatric replacement of *Sturnidoecus* on the Icteridae (Troupials)

Host group	Number of species in group	Number of Mallophaga genera and species groups
Struthioniformes (Ostriches)	1	1
Rheiformes (Rheas)	2	2
Apterygiformes	3	2
Casuariiformes (Cassowaries)	3	1
Gaviiformes (Loons)	4	2
Coliiformes (Collies)	6	2
Phoeniculidae (Wood-hoopoes)	6	2
Pterocletes (Sand-grouse)	16	2
Sphenisciformes (Penguins)	17	2
Colymbiformes (Grebes)	20	2
Musophagi	20	5
Tinamiformes	32	21
Bucerotidae (Hornbills)	46	7
Pelecaniformes	54	6
Apodi (Swifts)	77	2
Alcedinidae (Kingfishers)	87	2
Caprimulgiformes (Goatsuckers)	92	2
Procellariiformes	93	15
Ciconiiformes	111	10
Cuculi	127	7
Strigiformes	134	3
Anseriformes	148	7
Galliformes	241	19
Falconiformes	271	9
Columbae	300	10
Charadriiformes	308	10
Psittaciformes (Parrots)	315	7
Passeriformes	5093	11

already shown any one species or genus of Mallophaga is not necessarily found throughout the range of its hosts; for instance, *Piagetiella*, which lives in the gular pouch of the Pelecaniformes, has been recorded amongst the Phalacrocoracidae (Cormorants) only in the New World and Antarctic species. It follows therefore, that the extinction of many genera and species of an order of birds may result in the fortuitous extinction of some of the genera of Mallophaga normally found on the order.

Many of the orders of birds now represented by a few species are those in

which the feather covering is of a uniform and homogeneous character, Struthioniformes, Rheiformes, Casuariiformes, Apterygiformes, and Sphenisciformes. On these birds there will be no well differentiated ecological niches and this will limit the number of ecological types of Mallophaga and hence the number of genera. If such a homogeneous feather covering is primitive (Lowe, 1928) then it is probable that the members of these bird orders never had more than a few genera of Mallophaga, or if secondary, then the extreme ecological types might have been eliminated with the degeneration of the feathers. In the case of the Tinamiformes, a primitive order but without the homogeneous feather covering found in the bird orders mentioned above, the number of sympatric genera and species of Mallophaga is the highest known, although the number of host species is not large (table 9). However fossil Tinamous, belonging to the modern family Tinamidae, are known from the Pliocene of S. America, and it is probable that this family was represented by a greater number of species between the time that it lost its primitive homogeneous feather covering and the present day. In addition its later evolution has taken place within one continent, the genera are well defined, most of the species are represented by many subspecies and many of the species are sympatric. During the long evolution of this family, then, there must have been ample opportunity for the interchange of lice between the host forms at all stages of differentiation; this may explain, at least in part, the unusually large number of sympatric genera and species of Mallophaga found in the Tinamiformes.

The unusually large number of genera and species of Mallophaga found on some bird orders may also be due to the individual birds being able to support a greater number of parasites. Features of the feather covering or physiological characters of the body may provide a greater number of ecological niches and, in general, make the body of these birds a more

favorable habitat for the lice, resulting in a greater number of immigrant lice being able to establish themselves. The opportunities for the transference of lice between different host species should also be taken into account—both the Tinamiformes and Galliformes which show a high number of sympatric genera and species are birds which make frequent use of dust baths, a method of lice transference already mentioned.

Those bird orders with a large number of species but with few genera of Mallophaga (table 9) may, in contrast to those above, either have a feather covering which gives few ecological niches (already discussed under the primitive orders), or the body may in general be unsuitable as a habitat for lice, so that their survival has always been precarious, resulting in the frequent extinction of forms and the infrequent establishment of immigrant lice.

In spite of the reservations discussed above it would seem that the presence of at least some of the sympatric genera found on any one order of birds may have been brought about by the interchange of lice populations between different members of a bird order, after the former had diverged sufficiently to prevent interbreeding. The factors, already discussed, such as the preadaptation for a certain niche by the immigrant louse population, the necessity of the absence of competition in that niche, or the presence of competition which might force the species, partly adapted for one niche, into another, would all affect speciation. The advantages of interspecific exchange of lice populations over intraspecific is that the two lice populations, having usually diverged to a greater extent, are more likely to be reproductively isolated.

Apart from secondary infestations by louse populations within one host order where it would be expected that environmental conditions and host specificity would not be strongly preventive factors, there has probably also been a number of cases of a louse species establishing itself

on a host of another bird order. The presence of one species of *Perineus* (a genus elsewhere restricted to the Procellariiformes and related to other genera on that host order) on several species of the bird family Stercorariidae (Skuas) of the order Charadriiformes, must be a case of a relatively recent colonization of a new host. In this case the louse has become specifically but not generically distinct from those on its original host order, but where this type of colonization took place at an earlier stage in evolution divergence might have proceeded further, and the two lines would now be included in higher categories, each having given rise to one or more genera differentiated and specialized for each host order. It is possible that some of the inexplicable cases of distribution and relationships of the Mallophaga are due to this cause. The widespread occurrence of the genus *Saemundssonina* (which probably originated on the Charadriiformes) on the Procellariiformes may also be another case of a comparatively recent secondary infestation. This example of two genera common to the Procellariiformes and Charadriiformes, together with species of Amblycera on the two host orders which are either related or superficially alike, suggests that the environment provided by the Procellariiformes and Charadriiformes may be similar (perhaps due to the specialization of superficial characters to a similar environment) and that this has made a limited exchange of lice between the two host orders possible.

Further evidence that the origin of sympatric species may be traced to secondary infestations is provided by the present distribution of certain species. An analysis of the distribution of the species of a genus of Mallophaga parasitic on a group of related birds shows that, in general, each bird species or group or related species has one louse species peculiar to it; in addition some of the host species may have a second sympatric species which is also found on another, but not closely related, species

of the host group in question. An example of this is found in the species of *Quadraceps* parasitic on the Sterninae (Terns): *Sterna paradisaea*, *S. hirundo* and *Chlidonias nigra* each have a distinct species of *Quadraceps*; but the species normal to *Chlidonias nigra* may also be found, occasionally, but apparently established, on *Sterna hirundo*. This suggests that the latter species has become established on a new host and may be found living normally together with the indigenous species. In other instances it may actually take the place of the original species; this would explain such cases as the occurrence of the same species of *Saemundssonina* on the two, not closely related, host species, *Sterna hirundo* and *Gelochelidon nilotica* (see Clay, 1948, 142).

Perhaps some mention should be made of the possible role in speciation played by phoresy. There are now (Thompson, 1937; Clay and Meinertzhagen, 1943) a considerable number of records of flies of the family Hippoboscidae (themselves parasitic on birds) being found with Ischnoceran Mallophaga attached. It is possible that transference by Hippoboscid flies is one of the normal ways in which the cuckoo obtains its louse population, as, except during copulation, there is no contact between individual cuckoos. The flies frequently carry more than one louse: two specimens of *Ornithomyia avicularia* recently taken from a young blackbird (*Turdus merula*) in England had respectively three males and one female, and one male and four females of *Bruelia merulensis* attached to the abdomens. Either of these batches taken to a new host could have given rise to a new louse population. At other times single specimens may be carried; if a fertilized female, bearing a character of an incipient isolating mechanism, was transferred to an individual of a louseless host population (of the type discussed above), it might give rise to a population in which this character, merely by the process of genetic drift, would become established and thus reproduc-

tively isolate this population if the hosts were later recolonized by the original parent population. It may be relevant that the Amblycera, showing fewer sympatric genera and species, have never been recorded attached to Hippoboscid flies.

#### V. CAUSES OF ANOMALOUS DISTRIBUTION

In conclusion it may be useful to summarize the causes for cases of anomalous distribution of genera and species found in the Mallophaga:

1. Related species of Mallophaga found on unrelated hosts may be descendants of a common ancestor evolved before the bird groups in question were separated, and which have remained relatively unchanged since. Examples of this type of genus (table 2) probably either belong to the less specialized Amblycera or to those Ischnocera (fig. 1d) which have not developed the modified head specialized for the particular feather structure of a host group. Extinction in most bird orders would explain their present discontinuous distribution.

2. Such species may be descendants of unrelated forms which have acquired similar characters in response to a similar environment. Although the cases of such convergence which misled the earlier workers on Mallophaga have now been recognized as such, it is a cause which should be considered in any case of apparent anomalous distribution of a genus. There is no doubt that many of the families as now recognized contain genera which are not related, but resemble each other through adaptation to the same ecological niche on different bird orders. In the Heptapsogastridae, a family of the Ischnocera found on the Tinamiformes, the genera have assumed a superficial resemblance to the different ecological types found on other orders of birds (information on the habitats occupied by most of the genera of the Heptapsogastridae is unfortunately not available). The Heptapsogastridae are an interesting example of adaptive radiation in one family which

became the chief occupants of a territory where there was probably little competition.

3. The species may be descendants of a common ancestor which have evolved on similar lines, that is parallel evolution. The term "parallel evolution" is used here for the evolution of the descendants of a common ancestor which, although divided into isolated populations, evolved on similar lines resulting from the identical mutations of identical genes; and because of the similarity of the environment in any one ecological niche, these genes would have similar selective values and produce a similar phenotype. Some of the cases of apparently anomalous distribution and relationships of Mallophagan genera may be explained on similar lines to those suggested by Wood (1937 and 1947) for the rodents. All the Ischnocera are basically rather similar in both their internal and external anatomy—it seems doubtful whether the hundred or more Ischnoceran genera should be divided into more than four or five families. The characters common to all the Ischnocera were probably the result of an early and rapid period of evolution specializing them for life on the bird; these initial modifications (as Wood, 1947, suggests in the case of the rodents) would largely predetermine the direction of further evolution, so that within each of the four or five families the possible mutations would tend to be the same and to have the same survival value when subjected to a similar environment. The Ischnocera are a most successful group which have branched out into a great many lines occupying the different ecological niches on the body of the bird. There is in this group a genetic predisposition towards increased mobility and strengthening of the parts of the head capsule by the formation of secondary sutures and lines of thickening, and in many cases these seem to have developed on parallel lines. Such specialization can be seen within the genus *Bruelia*, where there is an almost complete transition from the unmodified cir-

cumfasciate head (e.g., *B. biguttata*, fig. 2a), through the species with partially interrupted anterior margin (e.g., *B. nebulosa*, fig. 2c), to those with well marked anterior sutures and "signature" (e.g., *B. daumae*, fig. 2b); the extreme form of this development is seen in the related genus *Sturnidoecus* (fig. 2d). On most orders of birds there are one or more genera (e.g., *Degeeriella* (fig. 1b), *Cuculicola* and *Picicola*) which have never developed the more specialized head and are, therefore, naturally more similar to each other than are the forms with specialized heads, although not necessarily more closely related.

Parallel evolution on the above lines may have been responsible for the *Rallicola*-complex (table 3a) found on hosts belonging to many orders; as these species show specialization of the head it seems unlikely that they are the unchanged descendants of an ancestor developed in this form before the Apterygiformes had split off from the main stem of the evolving birds. The diagnostic characters of this group of species are the presence of spine-bearing tubercles each side of the female genital region and the general characters of the male genitalia. *Bruelia* found on the Passeriformes is also related to this group—there are species of *Bruelia* which are only separable from "*Furnaricola*" (table 3a) by the absence of the spine-bearing tubercle and characters of the male genitalia. It is possible therefore that the whole of this complex of genera is descended from a stock which had this genetic predisposition of the head to develop its secondary sutures and thickening on certain lines and to the formation of the spine-bearing tubercles. This might mean that both *Bruelia* and *Furnaricola* developed from a common ancestor on the Passeriformes, the spine-bearing tubercles being lost or never developed in the former genus. "*Furnaricola*" then, although generically indistinguishable from *Rallicola*, would be phylogenetically more closely related to *Bruelia* and its related genus *Sturnidoecus*. It

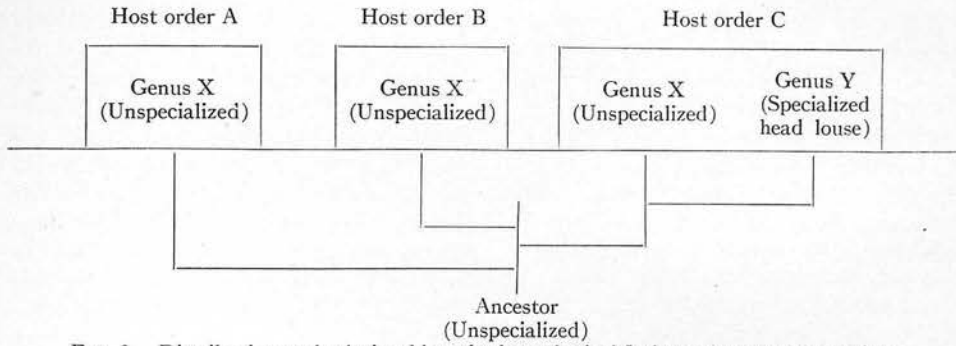


FIG. 3. Distribution and relationships of a hypothetical Ischnoceran genera complex.

seems likely that this type of parallel evolution has taken place more than once in the evolution of the Ischnocera, and is one of the likely sources of error in the formulation of a natural classification. Another source of error may be found among the unspecialized Ischnocera (table 2). Such a complex of genera and species-groups as *Degeeriella*, for instance, probably contains the relatively unchanged descendants of an ancestral stock which gave rise to the species now found on the different host orders; but on some orders such an ancestral stock may also have given rise to the specialized head or wing lice, either because these niches were empty through secondary absence, or because it is the case that all the Ischnoceran genera found on one bird order are derived from a common ancestor on that order. A hypothetical case of such relationships is shown in figure 3. It is difficult to demonstrate in a linear system the natural relationships between such groups of species (fig. 3, genus x) which are generically indistinguishable although from different host orders, and another group of species (fig. 3, genus y) derived from a common ancestor of (and hence more closely related to) one of the former groups on one of the host orders concerned; this derived group, because it occupies a different ecological niche, may now be so distinct that it is usually placed in a different family. The only method available to represent the actual phylogenetic relationships is either to split up

the species-groups from the different host orders into genera, which is often virtually impossible because of the overlap of characters; or to include the whole complex (genus x and y) in one genus, although apart from the characters shared by the family, they may have few others in common. Such a classification although phylogenetically correct soon ceases to be a convenient one.

Hopkins (1943, 16) has also emphasized the difficulties in the generic classification of the Trichodectidae (Mallophaga) of mammals caused by the amount of parallelism which has apparently taken place in their evolution.

4. That the species are descendants of an ancestor which became established on another host order by secondary infestation; this has been discussed above, and is the most likely explanation of the example in table 3, b.

5. Human error in the evaluation of the systematic position both of the host and parasite must be taken into account. This may be the explanation of the classic case of the Phoenicopteridae (flamingoes), usually placed with the Ciconiiformes, which have three genera of Mallophaga found elsewhere only on the Anseriformes (table 3, e, f, g); this distribution supports the inclusion of the flamingoes in the latter order instead of in the Ciconiiformes. It may also explain the genera common to the Galliformes and the Musophagi (table 3, d, Clay, 1947 (2)). It is of course not always possible to dis-



tinguish the cases caused by secondary infestations from those due to incorrect classification of the hosts, but, as Hopkins (142, 100) suggests, the number of species involved serves as a clue to the cause. The case of the Gruidae with one genus also found on the Charadriiformes (table 3, b) and three distinctive genera of its own, does not suggest any relationship between the Gruidae and the Charadriiformes; whereas the three genera common to the Phoenicopteridae and the Anseriformes suggest that the affinities in this family lie with the latter order. An example where the Mallophaga give no conclusive evidence of the affinities of the host is *Aramus*: this genus, usually placed with the Gruiformes, has one genus of Mallophaga also found on the Ciconiiformes (table 3, c), and two (*Rallicola* and *Pseudomenopon*) also found on the Rallidae, and one (*Laemobothrion*) found on a number of host groups, including the Rallidae and Ciconiiformes.

The above paragraphs deal with the anomalous distribution of genera, but it may also be of interest to mention briefly the distribution and relationships of the species within a genus of Mallophaga restricted to one host group. As in the case of the genera, and as is inherent in this theory of their evolution, the relationships between the species of Mallophaga reflect those of their hosts (table 4-6). The degree of difference between related species of Mallophaga will be dependent not only on their own age and plasticity, but on the differences in their environments which are formed by the external characters of their hosts species; the latter differences being dependent on age, plasticity and environment of the host species. There are three factors which may confuse the normal relation between classification of host and parasite: *Convergence*. A particular character of the feather covering found in a number of not closely related birds, which is due to convergence and not, therefore, of phylogenetic importance, may be reflected in the species of Mallophaga found on the hosts

concerned. In the genus *Philopterus* parasitic on the Passeriformes, for instance, a certain type of thickening of the anterior margin of the head and framework supporting the mouth parts has been developed in species from hosts belonging to different families; the available evidence suggests that this is a modification in response to feathers showing iridescence and hence a different physical structure. *Sympatric pairs*. Three related host species, x, y, z, may have been parasitized by three pairs of sympatric species, a<sup>1</sup> and b<sup>1</sup> on host x, a<sup>2</sup> and b<sup>2</sup> on y,

Host species	x	y	z
Parasite species	a <sup>1</sup> (b <sup>1</sup> )	(a <sup>2</sup> ) b <sup>2</sup>	a <sup>3</sup> (b <sup>3</sup> )

FIG. 4. False deduction of host relationships through the extinction or ignorance of some of the sympatric species. All the parasite species belong to the same genus. Those in brackets are now extinct or unknown. a<sup>1-3</sup> and b<sup>1-3</sup> are, respectively, closely related allopatric species.

and a<sup>3</sup> and b<sup>3</sup> on z (fig. 4); species a<sup>1-3</sup> and species b<sup>1-3</sup> are, respectively, closely related allopatric species. If some of these species become extinct (or have not been collected) so that host species x appears to have only parasite species a<sup>1</sup>, and y to have only b<sup>2</sup> and z only a<sup>3</sup> (fig. 4); then, from a consideration of the parasites, host species x and z will appear to be more closely related to each other than either is to y because the parasite species a<sup>1</sup> and a<sup>3</sup> are in fact more closely related to each other than to b<sup>2</sup>. *Secondary infestations*. This has already been discussed above, and it was shown that the occurrence of a species of *Saemundssonina* common to the two terns, *Sterna hirundo* and *Gelochelidon nilotica*, did not necessarily mean close relationship between the two hosts, but could be explained as a case of secondary infestation.

These many cases of anomalous distribution of both genera and species show clearly that the phylogenetic relationships of the Mallophaga cannot be used as in-

fallible evidence of the phylogenetic relationships of the hosts as is implied by some writers on the subject. The relationships of the parasites must be considered as useful sources of contributory evidence in elucidating the systematic position of birds of doubtful affinities, but such evidence must be interpreted in the light of the above discussion and assessed together with fossil, morphological, and biological evidence of the birds themselves.

#### CONCLUSIONS

It has been shown that in the particular case of a group of obligate ectoparasites speciation can be explained by the normal process of geographical isolation; and that factors similar to the formation of the populations of continental islands, the colonization of oceanic islands and the isolation and reunion of populations—which have contributed to speciation in free-living animals—have acted likewise in the evolution of the Mallophaga, if host distribution is equated with geographical distribution. It should be emphasized that the birds themselves underwent a rapid period of evolution: by the Upper Eocene most of the modern families were established; this was followed by a period of little morphological change so that Miocene birds, for example, can often be assigned to modern genera (Howard, 1947). During this period of rapid evolution the lice populations must have been subjected to conditions of great evolutionary stimulus. Not only had the ancestral louse colonized a new and empty habitat, but this was constantly being modified by the evolution of the birds. The louse populations were frequently being divided into many partially isolated local populations—through the isolation of their hosts and through the extinction of louse populations in parts of the range of their hosts; and this, as emphasized by Sewall Wright (1945, 416), has been one of the factors responsible for rapidity of evolution. It is probable that by the Upper Eocene, when most of the modern bird families were established, the ma-

ajority of the genera of Mallophaga had been established, and as the evolution of the birds slowed down, and thus lessened the stimulus, so also did that of the lice. The lice living in a more constant environment than their hosts have, during that time, probably changed to a lesser extent than the latter; this being reflected in the many cases of a genus of Mallophaga being restricted to one order of birds. The course of evolution and the present distribution of the Mallophaga supports "the evolutionary role of accident" (Mayr, 1947, 271). The apparently successful occupation of most of the available niches—including the inside of the shafts of the wing feathers on some birds and the gular pouch of the Pelecaniformes—on such a small area as the body of a bird can be explained by the normal process of natural selection: a louse arriving on a new host, if it is unable to compete with the established population, must either occupy an empty ecological niche or face extinction; this latter fate was presumably frequent.

It has not been possible to include in a paper of this kind all the available evidence for some of the statements made; much of this evidence will be included in a paper now in the course of preparation. The criticism may be made that there is as yet insufficient knowledge of the group as a whole on which to base the arguments used here; this is partly true, but it is hoped that such a paper will encourage further work on the biology and morphology of the Mallophaga. Further, any worker attempting a natural classification of this difficult group is forced to formulate some conception of its evolution, without which the classification will become even further divorced from a natural representation of relationships than it is at the moment.

#### NOTE ON TABLES

It has not been possible to reduce the data given in the tables to a numerical form because there are still a very large number of birds in most orders of which the Mallophaga are not fully known; the tables, therefore, contain only examples of the points mentioned in the text.

It is considered that these examples, which have been taken from a wide range of hosts and Mallophaga, support the general arguments used, and suggest that as further information becomes available it will not be greatly at variance with such examples.

Some difficulty arises over the category of host group to be used. Although, in general, the genera of Mallophaga follow the orders of birds, as usually arranged (Wetmore, 1940), this is not invariably the case. There are suborders or families of birds, the Mallophaga of which are quite different from those of the rest of the order (examples of these have been mentioned above); where the inclusion of these would affect the argument (as in table 9) they are omitted. In the Gruiformes, the families fall into at least six groups, each of which have distinctive genera of Mallophaga; in this case the suborder or family of which the Mallophaga form a related group is used. The Mallophaga of the Trochili (hummingbirds) and of all the orders (with the exceptions given in table 9) from the Trogoniformes to and including the Passeriformes (Wetmore, 1940, 8-11) suggest that these orders should be considered as a single complex; except for the Passeriformes, therefore, they have been omitted from table 9 as being misleading.

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#### SUMMARY

1. The Mallophaga, a group of obligate ectoparasitic insects found on birds and mammals, may have a large number of genera and species occurring on one host species. In a group of related host species, each species may have allopatric species of a number of sympatric genera of Mallophaga common to the group, and, in addition, sympatric species of these genera.

2. During their evolution, the Mallophaga branched out to fill the different ecological niches found on the body of the host, and for which they became spe-

cialized. The occupant of each niche has changed with the changing environment of its particular niche caused by the evolution of the hosts themselves.

3. Host isolation, the equivalent of geographical isolation, may explain speciation in the Mallophaga. Factors which have been responsible for the isolation of louse populations are: 1. The divisions of their host populations into non-breeding units—forming new species of hosts which diverged into the families and orders now known; the isolated louse populations thus formed diverged from each other and became specialized for the new characters developed by their respective hosts. This type of speciation is analogous to that on continental islands formed by the disappearance of land connections. 2. The development of host specificity; this would increase the isolation of the populations of any one host species. 3. The temporary isolation of parts of a louse population by the temporary isolation of parts of its host population, or by the extinction of a louse species in part of its host's range, thus isolating the two populations on each side. If these periods of isolation were sufficient to enable the development of some sexually isolating mechanism in one of the isolated populations a new species would be formed.

4. The ecological factors influencing the speciation in Mallophaga have been the intrinsic changes in each ecological niche and the migration of a species from one niche to another on the same host. These factors have affected mainly the proportions of the body and the secondary thickening and sutures of the head, which are important characters in feeding and in clinging to the feathers or hairs of the host.

5. The frequent occurrence of sympatric genera and species on any one host species may be explained by the isolation and later reunion of parts of a louse population as discussed under 4; and by secondary interspecific infestations.

6. Although in general the relationships of the Mallophaga reflect those of their

hosts, these basic relationships have now become confused, and the many cases of anomalous distribution make it impossible to use the evidence from the Mallophaga as an infallible guide to the phylogeny of the host. The factors responsible for these cases of anomalous distribution are discontinuous distribution, excessive convergent and parallel evolution making a reliable evaluation of phylogenetic relationships difficult, and secondary interspecific infestations.

7. In conclusion it is possible to say, if the host distribution of these parasites is equated with the geographical distribution of free-living animals, that the same general factors have been responsible for speciation in both cases.

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

*Theresa Clay*

*British Museum (Natural History), London*

## **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

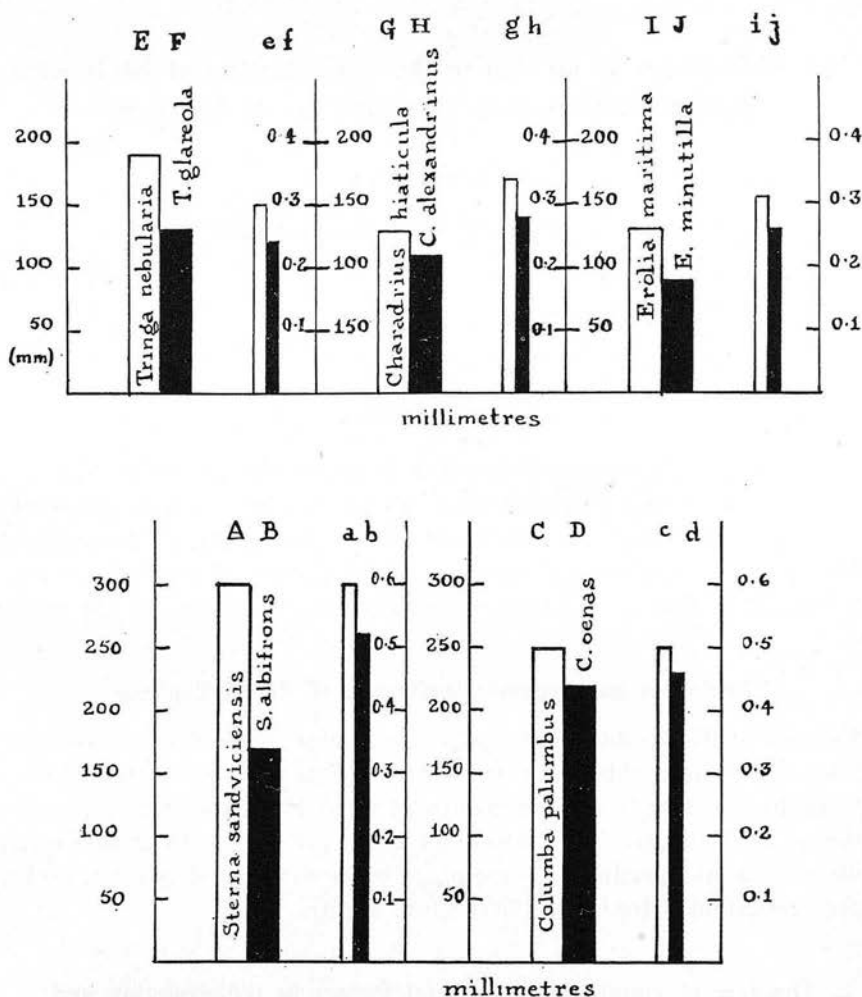


Fig. 1. Examples of the general relation in size between host species and parasite species. (Calculated from the mean of the lengths of wings of hosts and breadth of heads of parasites.) a-j. parasite species: a-b. *Saemundssonina* spp.; c-d. *Campanulotes* spp.; e-h. *Quadriceps* spp.; i-j. *Carduceps* 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

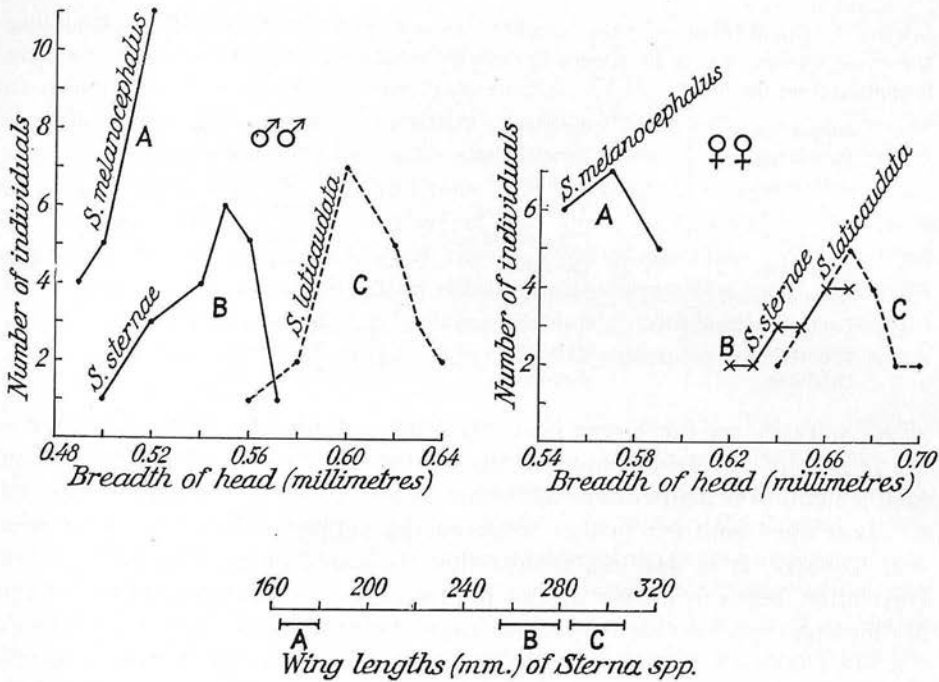


Fig. 2. Differences in size of male and female parasite (*Saemundssonina* spp.) in relation to size of host. A. *Sterna albifrons*, B. *Sterna hirundo*, C. *Sterna sandvicensis*.

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

Momotidae.	+	Corvidae.		Muscicapidae.	
Formicariidae.	+	Paradiseidae.	+	Prunellidae.	
Cotingidae.	+	Paridae.		Motacillidae.	
Tyrannidae.	+	Timaliidae.		Bombycillidae.	
Pittidae.	+	Pycnonotidae.	+	Laniidae.	
Alaudidae.		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 Paradiseidae). 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 I gives the distribution of the "Clayiella" group<sup>1</sup> of *Philoaterus*; 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-

<sup>1</sup> This group of species differs from the rest of the genus *Philoaterus* 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 pulvinus (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 Columbidae; the last three groups also have other parasite genera with modified heads. The Procellariiformes have one genus (*Episbates*) 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 Columbidae (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 Columbidae, 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 acclimatisation 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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## AN INTRODUCTION TO A CLASSIFICATION OF THE AVIAN ISCHNOCERA (MALLOPHAGA): PART I.

By THERESA CLAY.

(*British Museum (Natural History).*)

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With 1 Plate and 26 Text-figures.

### INTRODUCTION.

AN attempt to make a key for the genera of the Ischnocera on the lines of that made for the Amblycera (Clay, 1947) has presented many difficulties. These are mainly caused by the amount of convergent and parallel evolution which has taken place in this superfamily, resulting in those characters which could be used in such a key being found in unrelated genera. It is necessary, therefore, to make a more thorough study of both the external and internal anatomy with a view to finding reliable characters on which to base a classification, and to review the distribution and variability of those characters on which the genera have previously been based. The basic characters of the internal and external morphology are, in general, remarkably uniform throughout the Ischnocera, but superficially there are considerable differences in the proportions of the body and the development of sutures and of secondary lines of thickening. These differences are reflected in the large number of genera (over 130) which have been described, many of which grade into each other, or can hardly be regarded as more than well-marked species groups. Elsewhere (Clay, 1949) it has been suggested that the Ischnocera acquired these basic characters early in their evolution, possibly while the birds had a more uniform feather covering and before their divergence into different groups with the ensuing modifications of the feather structure. The more superficial characters on which the genera of the Ischnocera are based are mainly those which are adaptive to the different ecological niches on the body of the bird, and possibly to the different feather structure characterizing the particular group of hosts. During this evolution there was much convergence and parallelism, resulting in the original relationship between the genera being in many cases obscured. Thus an attempt to arrange these genera in families on the characters usually employed gives groups containing a heterogeneous collection of genera and obviously of polyphyletic origin.

*The genus.*—Since there will be frequent references to characters being of generic importance and as the generic concept is mainly a subjective one, it is necessary to state the principles on which genera have been recognized or discarded in this series of papers. The generic category is used for a convenient grouping of similar species of common phylogenetic origin. It is inherent in the generally accepted theory of the evolution of the Mallophaga that similar species from related hosts are themselves related. Throughout the great majority of the Ischnocera this fact is so obvious that it needs no emphasis—the exceptions to this general principle have been summarized and discussed elsewhere (Clay, 1949). This secondary check on the relationships of species



of Mallophaga based on the relationships of their hosts is naturally of the greatest value, but where the principle is applied indiscriminately it may lead to considerable errors in classification. Thus, genera are now being erected for groups of species morphologically indistinguishable from the remaining species in the genus merely because they parasitize a distinct group of hosts.

Two types of genera based on their origins can be distinguished in the Ischnocera. These are the end-products of the processes of speciation which brought about one, the allopatric species, and the other, the sympatric species; the origin and evolution of these have been discussed elsewhere (Clay, 1949).

The allopatric genus comprises a number of species formed as a result of the isolation and divergence of their hosts (Clay, 1949 : 288); this has resulted in the parasites of an order, family or genus of hosts resembling each other more closely than the corresponding species of a different order, family or genus of hosts. It is, therefore, a matter of opinion whether the genus should include the small group of similar forms from the genus of hosts (frequently a polytypic species), or the larger group of less similar forms from the host family (superspecies or sometimes polytypic species), or the still larger and more diverse group of species from the host order. Naturally the cases of all parasitic groups and all host divisions are not analogous. Parasitic groups, which seem either to be more plastic or to parasitize ancient orders of birds where the hosts have been longer isolated and are more divergent, tend to show a greater amount of divergence between the species, or to contain aberrant species, or species with exaggerated dimorphism of the secondary sexual characters. Such groups of species encourage the erection of a large number of small genera, many of which are monotypic; and although these genera come within the definition of a group of similar species of common phylogenetic origin, they cannot be considered as convenient groupings. This erection of genera for polytypic or superspecies merely burdens the memory with names which give no clue to relationships, in many cases makes it impossible to place a species if only one sex is known, and probably means the future erection of further monotypic genera for the inclusion of new species.

The present writer agrees with Mayr and Delacour (1945 : 5): "We believe in large genera, since it is the function of a generic name to express relationship (as an aid to memory), not distinctness, which is expressed by the species." Unfortunately many workers on Mallophaga seem to be concentrating on obscuring as many natural relationships as possible, superspecies, polytypic species and even aberrant members of a superspecies being made into genera. This results in the subspecies being called a species, a polytypic species a genus, a genus a family, with the ensuing multiplication of the higher categories. There would seem to be no advantage, for instance, in dividing *Degeeriella* from the Falconiformes into two genera as has been done, nor in separating the *Philopterus* species found on the HIRUNDINIDAE (a family of the Passeres) from those parasitizing the remainder of the Passeres. *Goniodes* from the Galli contains a number of species groups, and these have been used as a basis for erecting unnecessary genera (Kéler, 1940). On the other hand, *Anatoecus*, from the Anseriformes, possibly a less plastic group of parasites, shows little divergence throughout the genus. It is only by realizing that both these groups comprise forms which (with the exception of the sympatric species) are geographical (or host) replacements of each other, and in the case of some groups could be included in one polytypic species or a

superspecies, that one can get a satisfactory generic concept in the Mallophaga.

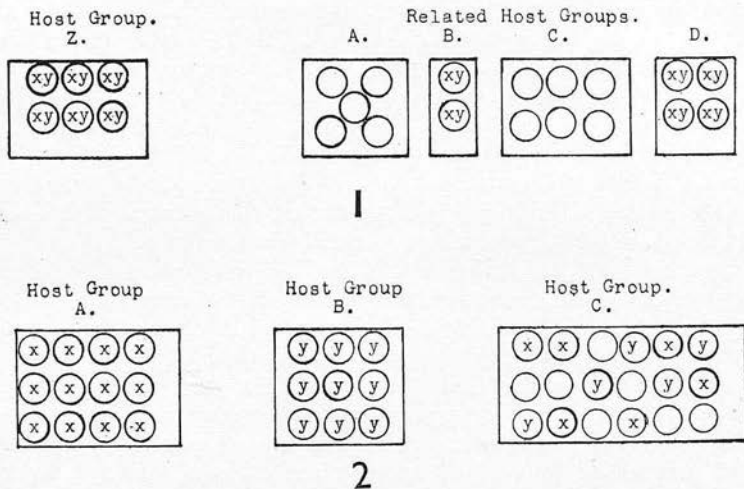
Host distribution is of importance as a secondary check on the relationship between species and on the delimitation of genera. If, for instance, a genus is erected for species from a certain host group, but is based on characters which means the inclusion also of some of the species parasitizing not closely related hosts, then such a group does not contain a natural association of related species and does not come within the above definition of a genus. Such a case is illustrated graphically in fig. 1: *z* is one host group; *A*, *B*, *C* and *D* are four host groups related to each other. The species on all groups are similar, but those on *z*, *B* and *D* can be separated from those on *A* and *C* by certain characters (*x* and *y*). It is not permissible to use these characters to erect a genus to include the species found on *z*, *B* and *D* because the species on the *A-C* group of hosts must be more closely related to each other than any of them are to those on *z* (it is assumed that secondary infestations from *z* to *B* and *D* have not taken place). All the species on the five host groups must be included in one genus. The separation of *Clayiella* from *Philopterus* and some of the genera based on colour pattern (*Koeniginirmus* and *Docophorulus*) are such cases. The host distribution of the only two species included in *Kodocephalon* by K  ler (1940), namely *Goniodes suborbiculatus* from a species of COLUMBIDAE and *Goniocotes discogaster* from a species of the MEGAPODIDAE (Galliformes), suggests that this is not a natural association and is not, in fact, supported on morphological grounds.

On the other hand, a consideration of the host distribution of species alone, ignoring morphological characters, also results in the erection of untenable genera. An example of such a case is illustrated in fig. 2: three unrelated host groups *A*, *B* and *C* are parasitized by similar species of Mallophaga. The species on *A* show a certain character *x*, and those on *B* a character *y*, and of those on *C* (a much larger group of hosts with a greater number and diversity of species) some show character *x*, some *y*, and some neither of these characters. It is not permissible to use characters *x* and *y* as a basis for separating generically those species found on host groups *A* and *B* even though all three host groups are unrelated to each other. The separation of *Furnaricola* from *Rallicola* is such a case.

#### ALLOPATRIC GENERA.

In the majority of allopatric genera the host order or suborder forms a clear-cut line between groups of species and gives the limits of the genera—for example *Anaticola* on the Anseriformes, *Ardeicola* on the Ciconiiformes, *Falcolipeurus* on the Falconiformes. Where a genus is found on more than one host order (*Saemundssonina*, for instance, on the Charadriiformes, the Procellariiformes and the Gruidae) the species found on each host order cannot be segregated into genera unless there is a morphological basis for this. However, there are some cases of such groups of related species with a wide host distribution which raise the most difficult problem in the classification of the Ischnocera. It seems possible that in these—the *Degeeriella* complex may be used as an example—the immediate ancestor of the species groups on each host order gave rise not only to the *Degeeriella* type of species, but to others which occupied different ecological niches, and have now evolved into groups of species very different from the *Degeeriella* type to which they are most nearly related. Therefore, to include the whole *Degeeriella* complex,

comprising *Lagopoeus*, *Cuculicola*, *Picicola*, *Upupicola*, *Capraiella*, *Trogoni-nirmus*, *Acutifrons*, and another group from the BUCEROTIDÆ, in one genus would be correct on morphological grounds, but there is a possibility that *Picicola* for instance is more closely related to another genus (*Penenirmus*) on the Passeres than to *Degeeriella*. In all cases where the distribution of a genus covers more than one host group there is the possibility that the species on one of the host groups are more closely related to another genus on that host group, although generically inseparable on morphological grounds from the species on the other host groups. This has been discussed elsewhere (Clay, 1949: 295), and has been raised by Wood (1950: 96) with reference to the geographical distribution of a group of rodents. It must be admitted that the present system of classification cannot satisfactorily represent such relation-



Figs. 1, 2.—Distribution of species of Mallophaga on unrelated host groups. Explanation in text. Circles denote species of Mallophaga.

ships. However, unless there is good evidence to the contrary, genera must be based on morphological criteria and not on hypothetical speculations of their evolution based on distribution. Each of such cases must, of course, be judged individually—the wide distribution of *Saemundssoni* is most probably due to secondary infestations, whereas that of the *Degeeriella*-complex may be due to the discontinuous distribution of a once universally distributed genus.

#### SYMPATRIC GENERA.

The genus which is the end-product of the sympatric species presents a more difficult problem. Sympatric species are found in every stage of divergence, from those which differ only in the details of the male genitalia (the females being very similar or indistinguishable) to those which can be separated generically on well-marked characters. The degree of divergence will depend mainly on the age of the two sympatric species and whether they have taken up different habitats on the host—in the latter case such forms may now be placed in different families. Where the two species have been

subjected to the same environmental factors degree of divergence is presumably dependent on the length of time they have been separated. The question of good generic divisions in these cases is an extremely difficult one. All these sympatric species groups will come within part of the generic definition given above, that is, a group of related species, so that the question to be decided is that of convenience. Other factors being equal it is convenient to have two distinct species on one host contained in different genera, but it is not convenient to have a position where species cannot be placed if only one sex is known, nor is it convenient if the two genera grade into each other to such an extent that there are no criteria for placing some of the species in one genus rather than another. The original species of *Soricella* were so distinct from *Columbicola* that a generic division seemed justified, but a large series of species from the COLUMBIDAE shows that these two groups grade into each other to such an extent that a generic division is now impossible. If the *Goniodes-Goniocotes* complex of species are examined from a large number of host species, even the apparently well-defined genera *Goniodes* and *Goniocotes* seem to grade into each other. On the TINAMIDAE, where there is a wealth of sympatric species and genera, generic separation becomes an almost insoluble problem.

The complexity and difficulty of generic separation in these sympatric forms has led to the erection of a multiplicity of genera, either owing to the small amount of material examined, or to the fact that the alternative to a great number of small genera seems to be the inclusion of a large number of species (for example all *Goniodes* and *Goniocotes*) in one genus.

While a correct evaluation of such genera is probably not possible without a more complete series of species than is usually available, it would seem to be more satisfactory to keep the generic divisions fairly wide to include as many related forms within the same genus as possible.

#### MATERIAL AND METHODS.

Whole specimens have been examined after treatment by caustic potash and mounting in Canada balsam, by mounting in polyvinyl lactophenol and by staining with lignin pink or mercurochrome. Both the internal and external anatomy has been studied by dissections, and sections of examples of a small number of genera have been examined.

Although it has been possible to examine specimens of practically all the known genera, the amount of suitable material available has limited the dissection of examples of all these genera, and time has limited the number of different species of each genus dissected. However, any such attempt at the classification of the Ischnocera must be considered as tentative due to the great amount of work still necessary, not only on the morphology but also on the biology of this group, together with the limitations involved by the number of genera and species still unknown.

#### ACKNOWLEDGMENTS.

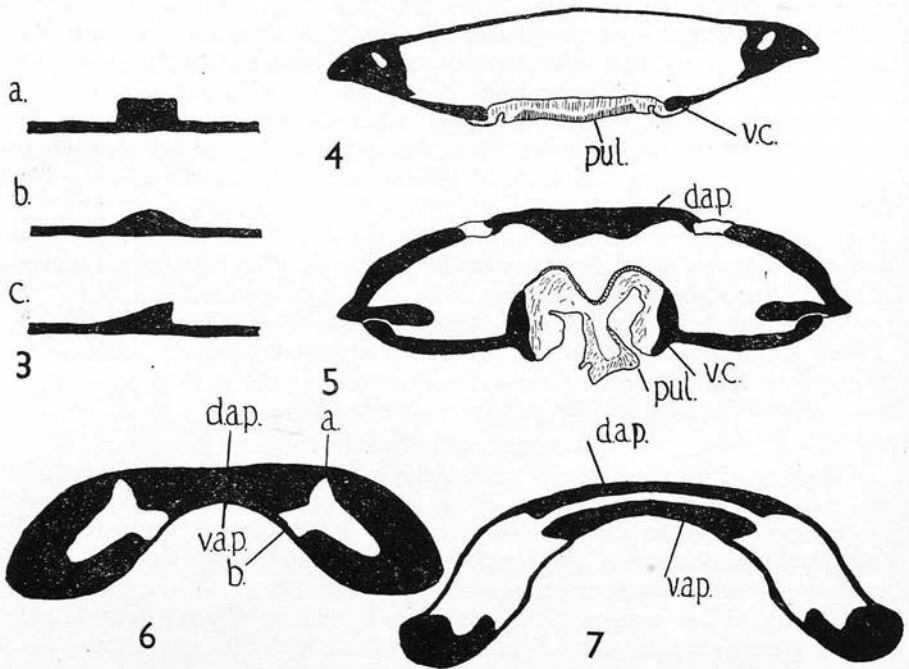
I am greatly indebted to Dr. S. Symmons and Dr. J. E. Webb for the loan of sections and to the following for providing material: Messrs. M. A. Carriker and G. H. E. Hopkins and Dr. L. R. Guimarães and Dr. H. Sick of the Fundação Brasil Central. Also to Mr. G. H. E. Hopkins for much helpful advice and criticism.

#### A. THE HEAD.

##### *Terminology.*

Scornful references (Cope, 1941: 72) have been made to the terminology

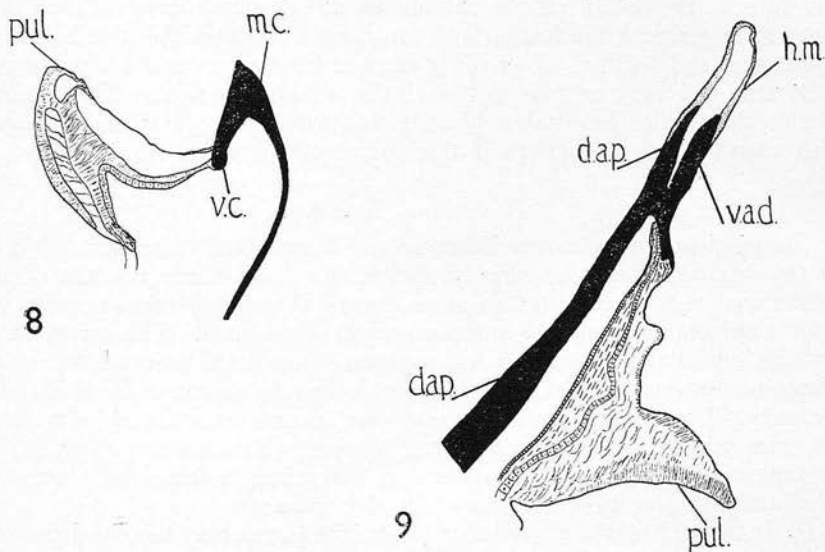
used to designate parts of the head in the Mallophaga, and a suggestion made that these should be replaced by terms with a morphological significance. This criticism would be more impressive if those working on the morphology of the Mallophagan head could agree on the homologies of the various sutures and lines of thickening which are used in the classification of the group. Until this has been achieved it seems more satisfactory to retain the names which can be understood by all workers than to follow the various ideas and theories of the homologies of different parts of the head put forward by recent morphologists. Even in the terms now in use there is little conformity, however, and it has been necessary to adopt some new names and to define and restrict those already in use. Two terms as used here must first be defined :



FIGS. 3-7.—Transverse sections of preantennal region of head. (3) Endocarinae (diagrammatic). (4) *Coloceras* sp., at level of pulvinus. (5) *Philopterus* sp., at level of pulvinus. (6) *Brüelia* sp., at level of anterior plate. (7) *Philopterus* sp., at level of anterior plate. Explanation of lettering as in figs. 10, 11.

*Endocarina*.—One of the most characteristic features of the Ischnocera is the presence of various dark bands running across the head. These so-called bands are internal ridge-like thickenings of the cuticula. The conspicuousness of the band is due to the thickness of the cuticula, and, as the "edges" of the band as seen in the surface view of the mounted insect are the lateral sides of the internal thickening, the definition of the band is dependent on the angle the thickening makes with the normal inner surface of the body wall. Thus a ridge which in transverse section shows these angles as right angles (fig. 3A) will appear as a very distinct band, but one in which the sides slope gently into the inner surface of the rest of the body wall (fig. 3B) will appear externally as an indistinct band. In some cases one side of the ridge may be at right

angles, and the other merge imperceptibly into the general surface (fig. 3c) so that the band is only delineated on one side. Sometimes this thickening may become less in certain areas so that portions of the bands become indistinct or apparently absent. All these types of internal thickenings are here called endocarinae or carinae. In many instances the form of some of the endocarinae are useful generic characters, but their apparent absence in other cases may have no significance—the presence or absence of the whole or part of the temporal carinae is a case in point. In some heads there may be dorsal and ventral endocarinae as well as those projecting from the lateral walls. It is not surprising, therefore, that considerable difficulty is experienced in tracing these carinae in mounted specimens, and that so many figures of Ischnoceran



FIGS. 8, 9.—Longitudinal sections of preantennal region of head. (8) *Lipeurus* sp. (9) *Philopterus* sp. Explanation of lettering as in figs. 10, 11.

heads give a composite picture partly dorsal and partly ventral. The section of a head of a species of *Philopterus* a little way anterior to the origin of the mandibles (fig. 5) illustrates the complexity of the endocarinae in the more specialized forms.

*Sutures.*—The term suture is used here in the sense of the second definition given by Snodgrass (1935 : 53), that is, "Lines where the sclerotization of the cuticula has become secondarily discontinuous in order to give flexibility." These thinner areas are again a characteristic feature of the Ischnoceran head, and are frequently constant throughout groups of related species and may form reliable generic characters. The term is used for all such areas which appear unsclerotized in the whole insect, although in some cases (only discernible in sections) the sclerotization is thin, not actually interrupted; in mounted specimens the points (a) and (b) on fig. 6, for instance, will appear as sutures.

#### *The General Structure of the Primitive Head and its Modifications.*

It is generally assumed that the primitive Ischnoceran head had the marginal carina complete—the so-called circumfasciate type of head now

found in such genera as *Goniodes* (fig. 10), and that the sutures and form of endocarinae found in such genera as *Saemundssonina* (fig. 11) are secondary. This view is supported by the fact that in some genera in which the adults show the anterior sutures, the nymphal stages have the circumfasciate head. The more primitive type of head capsule<sup>1</sup> has the following general characters: The preantennal region is enclosed by a thickened rim which turns inwards immediately anterior to the antennae to form a thickening dorsally, and to fuse with the framework supporting the mandibles ventrally. Passing anteriorly from this framework each side is an endocarina which forms a semicircle in front of the prestomum and to which is attached the pulvinus, (*sensu* Cope). The pulvinus, which is a membranous lobe of characteristic structure, is present in all the Ischnocera, and seems to have an important function in grasping the feather and directing it towards the mandibles for attachment and feeding. Posteriorly the mandibular framework is prolonged backwards and may or may not reach the occipital margin. The various modifications which have taken place in this primitive type of head together with a terminology for those parts of importance in classification follows:

#### *Preantennal Region.*

*Marginal carina* (epistoma, Kéler, 1938; frontal band, Harrison, 1937).—In the primitive forms, as already shown, this band forms the rim of the preantennal region (fig. 10); in some genera (*Episbates*) there may be no definite thickening round the anterior margin of the head. This carina turns inwards immediately anterior to the antenna each side to form the thickened preantennal nodus dorsally, and to fuse with the articulation of the mandibles ventrally. Dorsally the thickening may pass inwards from the nodus to form the transverse carina, either interrupted medianly (*Saemundssonina*, fig. 11) or continuous across the head (*Columbicola*). The primitive form of the marginal carina may become modified in the following ways:

1. In the mid-part of the anterior margin the carina may become depressed to a greater or less extent; at the place of this depression the anterior margin of the head is hyaline (the hyaline margin). Example: *Brüelia brachythorax* fig. 19.

2. The marginal carina may be divided into two or more parts by interruptions of its sclerotization as follows:

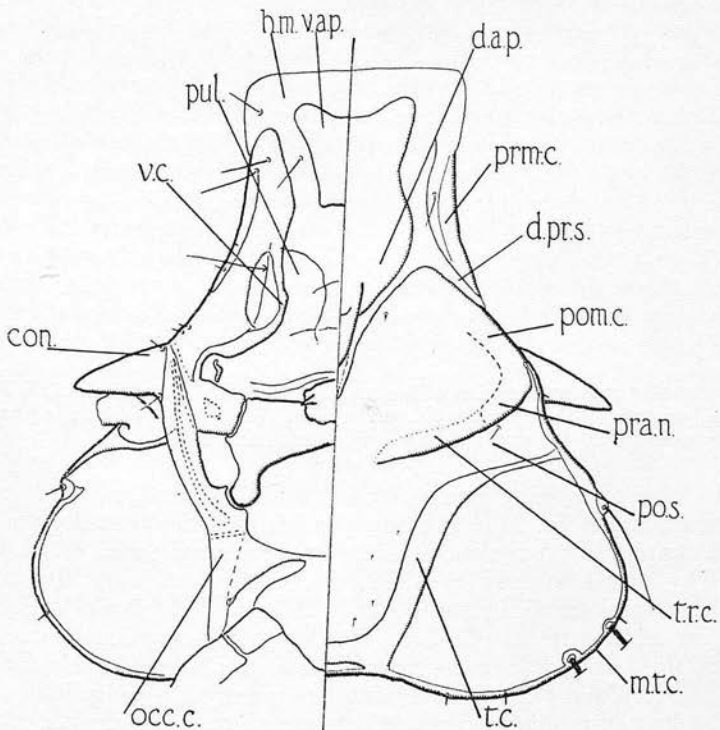
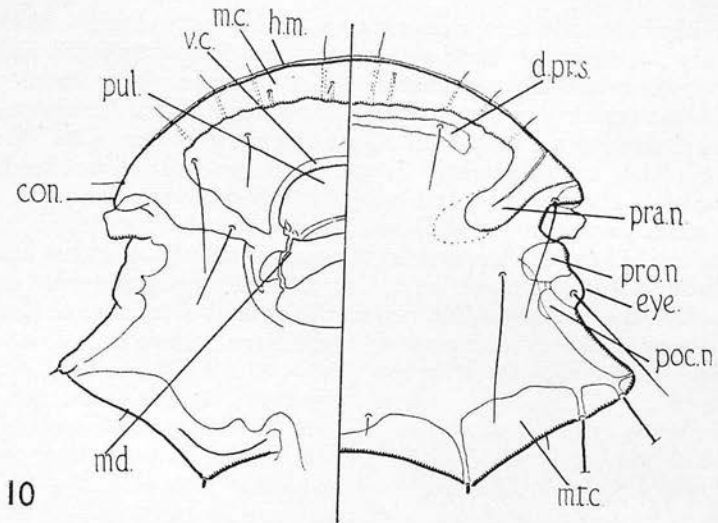
A median interruption in the anterior part of the carina giving a marginal carina each side of the head. Example: *Aptericola* (fig. 12, *m. c.*).

A lateral interruption each side giving a postmarginal carina (antennal band Piaget, 1885) running from the preantennal nodus to the interruption, and the premarginal carina (clypeal band, Piaget, 1885) running from the lateral interruption to the median anterior interruption (fig. 11, *pom. c.* and *prm. c.*).

In some species the marginal carina may be interrupted medianly and continued forward as the hyaline margin dorsally, but ventrally shows a further pigmented and sclerotized portion which fuses with the prolonged ventral carina. Example: *Meropoecus*, *Rallicola* species.

*The dorsal preantennal suture and the anterior plate* (clypeal signature, *auctorum*).—The dorsal surface of the preantennal region may have a suture

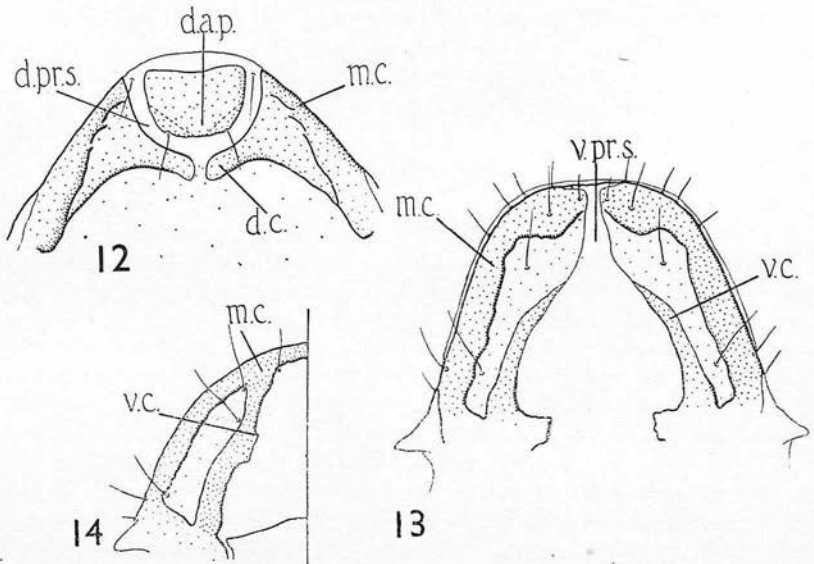
<sup>1</sup> Kéler has given a full account of the morphology of two Ischnoceran heads (1938 and 1939), so that details of the structures need not be repeated.



Figs. 10, 11.—(10) *Goniodes* sp., head. (11) *Saemundssonina* sp., head. *con.*, Conus; *d.a.p.*, dorsal anterior plate; *d.p.r.s.*, dorsal preantennal suture; *h.m.*, hyaline margin; *m.c.*, marginal carina; *md.*, mandible; *m.t.c.*, marginal temporal carina; *occ.c.*, occipital carina; *poc.n.*, postocular nodus; *pom.c.*, postmarginal carina; *po.s.*, postantennal suture; *pra.n.*, preantennal nodus; *pr.m.c.*, premarginal carina; *pro.n.*, preocular nodus; *pul.*, pulvinus; *t.c.*, temporal carina; *tr.c.*, transverse carina; *v.a.p.*, ventral anterior plate; *v.c.*, ventral carina.



which either does not reach the marginal carina (some species of *Goniodes*, fig. 10, *d.pr.s.*), or reaches but does not interrupt it. A suture such as is found in *Lagopoeus* cuts off a semicircular area of the dorsal surface; if the marginal carina is now interrupted medianly a distinct area of the dorsal surface will be cut off, forming the so-called "clypeal signature" (here called the dorsal anterior plate), a characteristic feature of many Ischnoceran heads. The anterior plate also has a ventral component (ventral anterior plate, fig. 11, *v.a.p.*) which may be fused to the dorsal plate throughout its length, and thus forms a solid block of sclerotization throughout the depth of the head as in *Brüelia marginalis* (fig. 6), or it may be fused only at its proximal end as in *Philopterus* (figs. 7 and 9). The ventral plate may be a narrow rim across the anterior part of the anterior plate as in *Haliperus*, where it is striated, or it



FIGS. 12-14.—Preantennal region of heads. (12) *Aptericola* sp., dorsal. (13) *Degeeriella* sp., ventral. (14) *Tinamotaecola* sp., ventral. *d.c.*, Dorsal carina; *v.p.r.s.*, ventral preantennal suture; explanation of other letters as in figs. 10, 11.

may be longer, narrowing proximally, and with a flattened, rounded or pointed proximal margin (fig. 11). It seems possible that the ventral plate in some genera represents the median portion of the marginal carina which has been cut off by sutures from the lateral part of the carina each side. In its simplest form the dorsal anterior plate is merely an area of the dorsal surface of the head cut off by a suture (*Rallicola*, *Brüelia*), but it may become modified by internal thickening, and in some genera has a single (*Saemundssonina*, *Philopterus*) or double (*Ibidoecus*) heavily sclerotized backwardly directed point.

The dorsal preantennal suture, which cuts off the anterior plate posteriorly, arises in the more modified forms either at the distal ends of the interrupted marginal carinae (*Aptericola*, fig. 12, *Meropoeus*), or at the distal ends of the postmarginal carinae (*Saemundssonina*, fig. 11, *Philopterus*, *Quadriceps*). In some genera the dorsal suture is not continued across the head and is represented by two lateral sutures each side of the dorsal plate, the posterior part of this plate thus being continuous with the rest of the dorsal surface

of the head (*Brüelia* species and *Craspedonirmus*). Some adults which show no dorsal suture have nymphs in which a dorsal suture is present (with which the anterior dorsal setae (see below) are associated). It is possible, therefore, that the adult suture represents part of this nymphal suture and that its absence in some adults is secondary. This also applies to the postantennal suture.

The proximal edge of the dorsal suture may have a line of thickening (fig. 12, *d.c.*)—the dorsal carina (internal bands, Harrison, 1937). This thickening may be continuous across the head (*Pseudonirmus*), or turned posteriorly in the midline and prolonged as two parallel bands. In *Halipeurus* the ends of these two bands actually lie free in the head cavity. Other parts of the dorsal surface of the preantennal region may have various areas of thickening, either proximal to the dorsal suture (some species of *Columbicola*), or anteriorly where there is no dorsal suture.

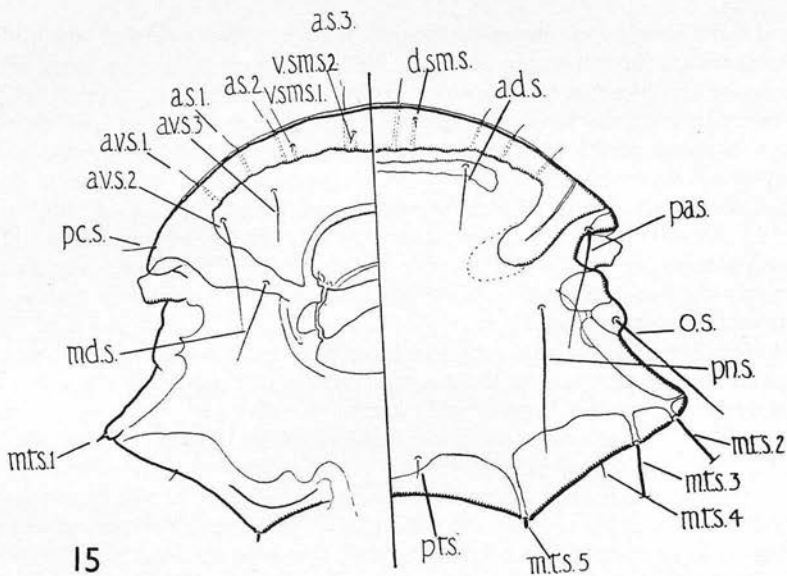
*The pulvinus and ventral carina* (Zygoma, Kéler, 1938; ventral bands, Harrison, 1937; internal bands, Piaget, 1885).—The ventral carina is continuous with the marginal carina and the mandibular framework, and is the thickening to which the pulvinus is attached. This latter structure, as already mentioned, is of importance in feeding and attachment, and the form of the ventral carina seems to be closely correlated with that of the pulvinus. In *Lipeurus* the pulvinus is a simple lobe attached to the complete semicircular ventral carina (fig. 8), and similarly in *Perineus* (Plate I, fig. 1), although in this genus there is no definite carina medianly. In *Coloceras* (Plate I, fig. 2), in which the ventral carina is complete, the pulvinus has a lateral lobe each side, giving a broad median groove (the mouth-channel, Kéler, 1938: 403). In the most highly modified forms, where the ventral carina is interrupted medianly and each carina has a thickened flattened surface lying parallel to the one on the other side, the pulvinus has a well-developed lateral lobe each side attached to this parallel part of the ventral carina (Plate I, fig. 4). In these forms the piece of feather being eaten lies in a central groove, held in position by the lateral lobes, and the pulvinus thus forms an efficient holding organ. The central portion of the pulvinus is also extrusible, and may be blown out as a lobe like structure (fig. 5, *pul.*). In such forms as *Philoceanus becki* and *Trabeculus* the pulvinus reaches its greatest development and has caused distortion of the preantennal region: in the latter genus the ventral carinae are pushed outwards proximally, where they fuse with the marginal carina. The surface of the pulvinus may be smooth or slightly sculptured and in some genera (*Austrogoniodes*, *Anaticola*, Plate I, fig. 3) the central groove has a median line of sclerotization.

The ventral carina, which in the more primitive forms passes forward from the mandibular framework each side to form a complete semicircle (Plate I, fig. 2 and fig. 10), may be modified in the following ways:

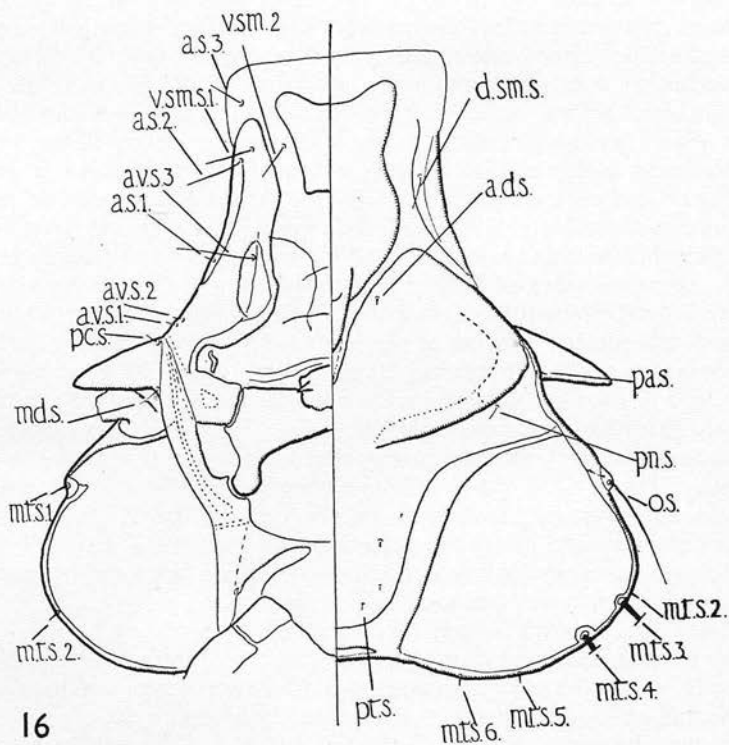
It may be interrupted medianly so that the thickening is only visible laterally, the pulvinus being attached to the edge of the sclerotized surface of the mid preantennal region. Example: *Episbates*.

It may be interrupted medianly with a suture—the ventral preantennal suture—running forwards from the two ends of the carina to, or nearly to, the complete marginal carina. Example: *Degeeriella* (fig. 13).

The edge of the ventral preantennal suture may be thickened each side (thus becoming a continuation of the ventral carina), and fused distally with the complete marginal carina. Example: *Tinamotaecola* (fig. 14).



15



16

FIGS. 15, 16.—Heads to show setae. (15) *Goniodes* sp. (16) *Saemundssonina* sp. *a.d.s.*, anterior dorsal seta; *a.s.*, anterior seta; *a.v.s.*, anterior ventral seta; *d.sm.s.*, dorsal submarginal seta; *md.s.*, mandibular seta; *m.t.s.*, marginal temporal seta; *o.s.*, ocular seta; *pa.s.*, preantennal seta; *pc.s.*, preconal seta; *pn.s.*, postnodal seta; *pt.s.*, posttemporal seta; *v.sm.s.*, ventral submarginal seta.

Part of the ventral carina each side may form a thickened flattened surface, lying parallel to that of the opposite side, to which the lobes of the pulvinus are attached. The ventral carinae may or may not reach the complete marginal carina, or the marginal carina may be interrupted medianly and the ventral carina fused to its edge each side (Plate I, fig. 4). In many genera the ventral carina does not form a distinct band anteriorly as in *Tinamotaecola* (fig. 14), but has a thickened inner edge only. Example: *Saemundssonina* (fig. 11).

In the more specialized heads the area between the proximal part of the ventral carina and the marginal carina has various modifications which may form useful generic characters.

In some of the genera (e.g., *Halipeurus*) parasitizing the Procellariformes there is a line of demarcation running anteriorly from the interrupted ventral carinae each side, giving a similar appearance to a ventral preantennal suture, but the surface of this area is sclerotized and sculptured (possibly secondarily). In *Halipeurus* and other genera from the Procellariformes the ventral carinae merge with the inner ventral surface of the head shortly after their proximal point of origin, but distally there is an isolated band of thickening along each side of the line of demarcation, which may be called the ventral carina. Another modification found in one of the genera (*Naubates*) from the Procellariformes is the presence of a more dorsal posterior prolongation of the ventral carina, which probably gives some extra support to the pulvinus.

As the preantennal region becomes more modified the ventral carinae become thicker and the attachment of the pulvinus more specialized. A comparison of fig. 4 (*Coloceras*) and fig. 5 (*Philopterus*) demonstrates this increase in complexity of the pulvinus and ventral carinae.

#### *Postantennal Region.*

*Temporal carina* (temple band, of some authors; occipital band, Piaget, 1885; zügel, Kéler, 1938).—This endocarina, when present, runs from the occipital margin of the head across the temples, and becomes continuous either with the preantennal nodus (*Philopterus*, *Cummingsiella*), or with the temple margin just above the eye (*Saemundssonina*, fig. 11, *t.c.*). In many species it merges with the inner surface of the dorsal sclerotization, and is only apparent near its point of origin at the occipital margin.

*Marginal temporal carina.*—The temples are usually enclosed by a thickened rim—the marginal temporal carina, which may be enlarged into irregularly shaped patches of thickening round the eye—the preocular nodus and the postocular nodus—and on the occipital margin—the occipital nodus.

*The postantennal suture.*—This suture either passes across the temples (*Lagopoecus*) or appears as two lateral sutures (*Quadriceps*).

*The occipital carina* (tremse, Kéler, 1948).—This runs backwards each side from the mandibular framework and may or may not fuse with the occipital margin; the posterior tentorial pits are always associated with this occipital thickening.

#### *The chaetotaxy.*

The setae of the head are remarkably constant in position and number throughout the Ischnocera, and can frequently be used as guides to certain parts of the head. There are five pairs of setae which are always present and approximately in the same position throughout the superfamily; these are:

A ventral seta arising just anterior to the conus—the preconal seta (*pc.s.*, figs. 15 and 16).

A ventral seta, on, or near the outer surface of the mandibular framework, the mandibular seta (*md.s.*). In some species (e.g., *Pectinopygus* sp.) this seta has become pushed out laterally and actually arises on the lower margin of the conus.

A seta on the dorsal, usually anterior, edge of the antennal socket, the preantennal seta (*pa.s.*).

A dorsal seta posterior to the preantennal nodus, the postnodal seta (*pn.s.*). Where there is a postantennal dorsal suture this seta lies in or near the suture (fig. 16, *pn.s.*).

A seta arising on the dorsal surface of the lens of the eye, the ocular seta (*o.s.*).

The remaining setae are also found throughout the superfamily, but their position, and sometimes number, is not so constant. In the primitive type of head (e.g., *Goniodes*, fig. 15) there are four or five setae arising on the anterior margin each side of the midline; in other genera (e.g., *Trogoninirmus*), also with a complete marginal carina (or circumfasciate head), they may originate submarginally on the dorsal surface. In the modified type of head (fig. 16) the outer of these marginal setae is associated with one of the anterior ventral setae (see below), and is here called the first anterior ventral setae (*a.v.s.* 1). As the remaining three or four may be marginal or submarginal on the dorsal or ventral surface they are called the anterior setae (*a.s.* 1-3).<sup>2</sup>

Where the dorsal preantennal suture interrupts the marginal carina the first anterior seta is often (but not invariably) associated with the point of interruption, either marginally or submarginally on the dorsal or more rarely on the ventral surface. In those species where the dorsal suture does not interrupt the marginal carina though they belong to a genus in which the majority of species show the interruption, as in *Philopterus*, then the first anterior seta will be found at the lateral edge of the dorsal suture, that is, near the point where the interruption of the marginal carina usually occurs in species of *Philopterus*.

Arising on the ventral surface of the marginal carina in the primitive type of head, each side of and near the midline is a pair of setae—the ventral submarginal setae (*v.sm.s.* 1-2). In other genera (e.g., *Lipeurus*, *Degeeriella*, *Labicotes*, *Otidococcus*) these may arise on the ventral surface below the marginal carina. In the most specialized type of head (fig. 16) the outer of this pair (*v.sm.s.* 1) usually lies on the marginal carina and the inner (*v.sm.s.* 2) just lateral to the ventral anterior plate. In *Anatococcus* this latter seta is minute and difficult to see.

Lateral and posterior to the ventral submarginal setae are two ventral setae each side—the anterior ventral setae (*a.v.s.* 2-3). In specialized forms where the ventral carina is modified these two setae, together with the first of the marginal setae (*a.v.s.* 1), often form a characteristic group associated with the ventral carina and the area between it and the lateral margin of the head—these three setae are called the anterior ventral setae (*a.v.s.* 1-3). In some genera (e.g., *Philopterus*, *Saemundssonina*, *Degeeriella*) the outer two (*a.v.s.* 1-2) are close together and arise just anterior to the preconal seta; in others (e.g., *Naubates*, *Halipeurus*, *Anaticola*, some species of *Pectinopygus*) all the

<sup>2</sup> All setae are counted from the lateral margins of the head towards the midline, and those on each half of the head are counted separately.

anterior ventral setae may be grouped much nearer the front of the head, or (e.g., *Degeeriella*, *Rhynonirmus*) *a.v.s.* 1-2 may arise near the conus and *a.v.s.* 3 near the anterior margin of the head. Their position seems to be mainly dependent on the shape of the head.

On the dorsal surface of the preantennal region there is a single submarginal seta lying each side of the midline, either on the marginal carina or just below it—the dorsal submarginal seta (*d.sm.s.*). In the specialized forms this is usually found on the premarginal carina (fig. 16, *d.sm.s.*). Posterior to this seta is a single seta—the anterior dorsal seta (*a.d.s.*), which is commonly associated with the dorsal preantennal suture when this is present. In the great majority of species with modified heads this seta arises either in the suture or on its posterior margin. However, in some genera (e.g., *Haliperus*) it may arise some distance posterior to the suture, or its position in relation to the suture may vary in different species of one genus (e.g., *Ardeicola*). In *Columbicola* the anterior dorsal setae are never associated with the suture (which in any case may not be homologous with the dorsal suture of other genera), and there is a second pair of setae posterior to these, about the level of the conus.

The margins of the temple always have a number of setae, some arising dorsally and some ventrally, but for the purposes of terminology they are all called the marginal temporal setae (*m.t.s.* 1, 2, 3 . . .). The first seta on the temple (*m.t.s.* 1) usually arises on the ventral surface just behind the eye; in a few genera (e.g., *Saemundssonina*) it is actually on the ventral surface of the lens, and in others (e.g., species of *Goniodes*) it may arise some considerable distance behind the eye. Its position on the eye is apparently of generic value in *Saemundssonina*. Specimens of this genus have been examined from 52 species belonging to 24 genera of the Charadrii, 39 species belonging to 11 genera of the Lari, 8 species of 5 genera of Alcae, 8 species of 8 genera of Procellariformes and 1 species of GRUIDAE. In all these the first marginal temporal seta is on the lens. In *Quadriceps*, probably a related genus, this seta may be either on the lens or just below it, and where it is close to the lens it arises on it in some specimens of a species and below it in others. The remaining temporal setae usually comprise a small ventral seta (*m.t.s.* 2), two dorsal macrochaetae, and two smaller setae on the occipital margin (fig. 16). But there is considerable variation in the number and size of the temporal setae even within one genus: in *Goniodes* many of the species have the number as shown in fig. 15, but *G. wilsoni* and *G. perlatus* have eight or more elongated setae each side.

Near the midline on each side there is a single seta above the occipital margin, the post-temporal seta (*pt.s.*).

All or any of the head setae may become greatly elongate (e.g., *Meinertzhageniella*) or reduced to stout spines (e.g., *Austrophilopterus*, *Anatoecus*), or reduced to microchaeta so that they are often difficult to find. Some species may have additional setae on the dorsal surface of the head (e.g., *Austrogoniodes*), arranged in such a way that it is no longer possible to identify the primitive ones to which names have been given. Abnormally any of the setae may be duplicated in a specimen, often on one side of the head only.

#### *The Phylogenetic Importance of the Characters of the Head.*

In the superfamily Amblycera (which is the more primitive) the mandibles are near the anterior margin of the head; in the Ischnocera the region of the

head in front of the mandibles has become elongated, sometimes to a considerable extent in the more specialized genera such as *Craspedorrhynchus* and *Echinophlopterus*. With the elongation of the preantennal region is found the tendency for the breakdown of its rigidity by the formation of sutures and by the interruptions of the endocarinae. The most important line of evolution seems to have been that which increased the efficiency of the pulvinus as a holding groove for pieces of feathers. This was achieved by the interruption of the primitive semicircular ventral carina, thus increasing the mobility of the pulvinus and giving better attachment for its lateral lobes. This interruption of the ventral carina has certainly taken place more than once—the HEPTAPSOGASTRIDAE have genera both with and without the complete carina. The prolongation of the ventral carina each side and its fusion with the interrupted marginal carinae gives additional support to the pulvinus, and strengthens that form of head in which the presence of both dorsal and ventral membranous areas allows a limited mobility. Although the interruption of the endocarinae and the formation of sutures have probably taken place on the same general lines in unrelated stocks, their present arrangement differs in detail to a greater or less extent. These differences may have been caused by the differences in the minute feather structure of the host. There are only four host groups—the Sphenisciformes, Tinamiformes, the Galli and the COLUMBAE on which the parasite genera with unmodified heads are dominant; the last three groups also have parasite genera with modified heads. On the Tinamiformes are found *Pseudolipeurus*, *Pseudophlopterus*, and *Tinamotaecola*, all with modified heads, and even within the family HEPTAPSOGASTRIDAE the ventral carina is interrupted in some genera (e.g., *Megapeostus*) and the marginal carina modified (e.g., *Discocorpus*). In the genera from the Galli, apart from *Lagopoecus* and *Cuclotogaster* in which the ventral carina is interrupted, *Oxylipeurus* shows a tendency towards the formation of anterior sutures and the modifications of the marginal carina. In *Columbicola* from the COLUMBAE the ventral carina is interrupted and the anterior region of the head shows considerable modification. One genus (*Episbates*) on the Procellariiformes has the head unmodified, but all the other genera from this Order and the rest of the Aves have the head modified in some way even if it is only the median interruption of the ventral carina. It would seem, therefore, that the modifications of the preantennal region of the head are advantageous to the parasites on the majority of bird orders. Elsewhere (Clay, *in press*) tentative suggestions have been made on the possible role played by the minute structure of the feathers in the retention of the primitive features of the head.

*Briëlia*, a genus which parasitizes the Passeriformes and some related orders, comprises a large number of species, amongst which can be traced a series from those with an entire marginal carina and no anterior plate, to those with the marginal carina interrupted medianly and laterally, and with the anterior plate well developed. Thus, the species from *Podoces* (fig. 17) shows the complete marginal carina although medianly less heavily sclerotized, that from *Nucifraga* (fig. 18) shows a greater median modification, that from *Bombycilla* (fig. 19), the types species of *Briëlia*, has the marginal carina indented medianly and the anterior margin of the head at this point hyaline. In this and other species there is a triangular-shaped area of sclerotization in the indented part of the marginal carina. In the species (fig. 20) from *Harpactes erythrocephalus* (Trogoniformes) the marginal carina is entire, but

there is a dorsal suture which cuts off a simple anterior plate. In that from *Turdus pilaris* (fig. 21) the marginal carina is interrupted medianly and there is an incomplete interruption laterally; the dorsal suture does not pass across the head, and leaves the posterior part of the anterior plate continuous with the dorsal sclerotization of the head. In the species from *Turdus merula*, *Brüelia merulensis* (fig. 22), the marginal carina is interrupted medianly and laterally and there is a well-marked dorsal suture and anterior plate. The nymph of this latter species (fig. 23) has the marginal carina entire, and similar to that of the adults of other species of *Brüelia*.

Ventrally all species of *Brüelia* have the ventral carina interrupted. In some the ventral carina may be sclerotized only proximally each side (species from *Podoces*, fig. 24), giving a situation similar to that in *Degeeriella* (fig. 13). In those species in which the marginal carina is complete (but indented) dorsally and interrupted ventrally, the sclerotization of the inner edge of the ventral carina is carried forward each side to fuse with the interrupted marginal carina; in *Brüelia merulensis*, where the marginal carina is divided laterally into a pre- and postmarginal portion, this sclerotization is fused to the distal ends of the premarginal carinae (fig. 25). *Sturnidoecus*, obviously nearly related to *Brüelia*, owes its distinctive appearance to the elongation of this ventral thickening beyond the dorsal marginal carina, and to its broader head, which has those characters associated with increased size (see below). Thus, the species of *Brüelia*, which by the characters of the abdomen form a compact group, show considerable diversity in the characters of the head. Any attempt to separate them into genera on these head characters would mean the erection of five or six genera, which would not only grade into each other but completely obscure their relationships, and in some cases would mean the association of a number of species not forming a natural group. The characters on which *Guimaraesiella* Eichler, 1949, for instance, was separated from *Brüelia* are found not only in the type-species, *Docophorus subalbicans* from the PARADISEIDAE, but in species from the TURDIDAE, GEOSPIZIDAE and others. There seems no reason, therefore, to recognize the following genera: *Corvonirmus* Eichler, *Guimaraesiella* Eichler, *Xobugirado* Eichler, *Meropsiella* Conci, *Painjunirmus* Ansari and *Traihoriella* Ansari. The genera *Sturnidoecus* and *Bizarrifrons* and species from the CORACIIDAE ("*Docophorus*" *longipes* Piaget) are also closely related to *Brüelia*, as shown by the characters of the abdomen, but have probably diverged far enough from their original *Brüelia*-like ancestor to be recognized generically.

The most specialized species of *Brüelia* (for example, *B. merulensis* or *B. galapagensis*) have a form of head which, with various minor modifications, is found in a great number of related or not closely related forms. The characters of this head are as follows:

Part of the median anterior margin of the head hyaline.

Marginal carina interrupted anteriorly and laterally.

Dorsal preantennal suture and dorsal and ventral anterior plate present.

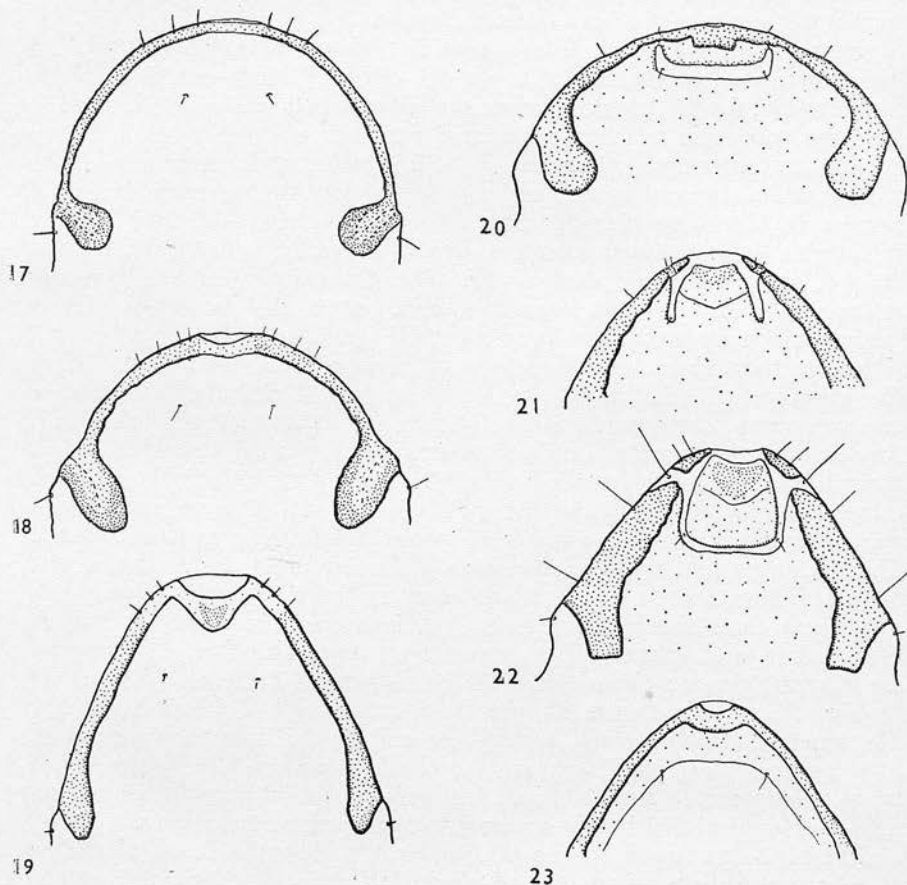
Ventral carina interrupted and fused to the ends of the premarginal carina.

Pulvinus with lobes attached to the flattened parallel surfaces of the ventral carina.

In those species with heads modified on the above lines some show the complete marginal carina (at least dorsally) in the nymph, for example



*Brüelia merulensis* (fig. 23), *Strigiphilus oculatus* (fig. 26), *Aptericola novae-zealandiae*; in others such as *Philopterus* even the first stage nymphs are little different from the adult. This may mean that either the latter have been established for a longer period of time, or (which is more likely) they have assumed a mode of life which necessitates the modification of the head and without which the nymphs could not survive. It is probable that this type of head has been evolved more than once in both related and unrelated

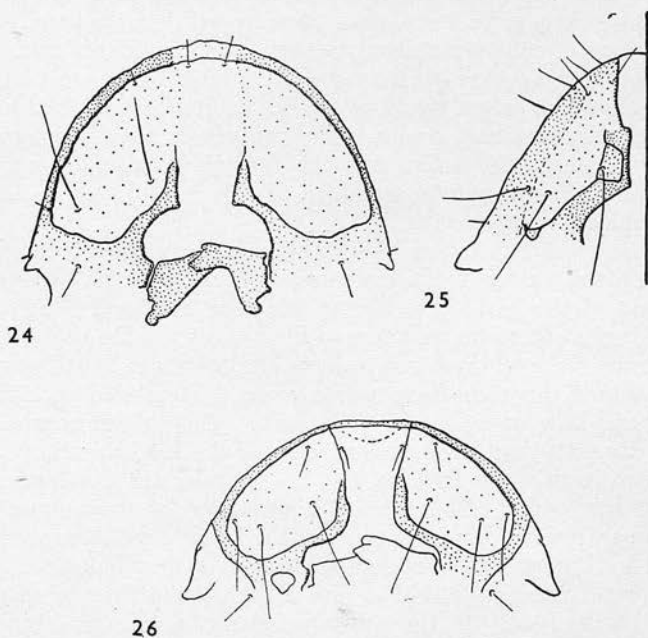


FIGS. 17-23.—Preantennal region of the head, dorsal. (17) *Brüelia koslovae*. (18) *B. multipunctata*. (19) *B. brachythorax*. (20) *Brüelia* species from *Harpactes erythrocephalus*. (21) *B. marginata*. (22) *B. merulensis*. (23) *B. merulensis*, nymph.

forms, due no doubt to the similarity of the basic Ischnoceran type in which specialization would be forced to take place on similar lines (see Clay, 1949, for fuller discussion). Thus, *Philopterus*, *Quadriceps*, *Wilsoniella*, *Mulcticola*, *Penenirmus* and *Pectinopygus* all have this general type of head, but are in no way closely related. It is not supposed that all the genera with this similar type of head evolved on the same lines, nor that the development from nymph to adult is always the same—an examination of the nymphs of *Ibidoecus*, for instance, suggests that the anterior plate has been formed rather differently

from that of *Brüelia*. It is possible that the method of formation of the dorsal suture and anterior plate may give an indication of relationships between the genera, but a study of the embryology and nymphal development will have to be made before a supra-generic classification based on mode of development can be formulated.

Although this form of modification of the head (discussed above) appears to be the most widespread, examples being found on the majority of bird orders, there are cases where specialization has been achieved on other lines. The genera of *Ischnocera* found on the Galli have the primitive type of head with a complete marginal carina and uninterrupted ventral carina (fig. 10), or if interrupted the sclerotization is not carried forward. One genus, *Oxylipeurus*, however, shows a tendency for the anterior region of the head to become



FIGS. 24-26.—Preantennal region of the head, ventral. (24) *Brüelia koslovae*. (25) *B. merulensis*. (26) *Strigiphilus oculatus*, nymph.

modified in various ways. The unmodified species (e.g., *O. mesopelios*) have a complete marginal carina with the dorsal preantennal suture not interrupting the marginal carina laterally; the dorsal suture may be indistinct (species from *Oreortyx*, *Epicolinus* Carriker), or absent (*O. himalayensis* from *Tragopan* and a species from *Crax*). In other species (e.g., *O. repandus*) the preantennal suture may partially interrupt the marginal carina laterally; in *O. inaequalis* the postero-lateral margin of the suture is sclerotized each side, giving short dorsal carinae. In *O. megalops* there is considerable modification of the anterior part of the head in a way which cannot be homologized with that discussed under *Brüelia*, and which is unlikely to lead to a form of head found in the most specialized species of that genus, although it is a type which could have led to the modifications found in *Columbicola*. The

temporal carinae are never fully developed, and may be absent. The pulvinus is either of the primitive lobe-like type, or has lateral lobes as in *Coloceras*, or internal sclerotization (*O. ischnocephalus*). The ventral carina usually merges each side with the ventral sclerotization of the head, and does not join with that of the other side to form a definite semicircular band as in *Goniodes* (fig. 10). The sclerotization may be interrupted by a ventral suture which runs anteriorly (as in *Degeeriella*), reaching nearly to the marginal carina (*O. megalops*); in *O. aepyodius* there is a thickening along the edges of part of this suture forming distally short ventral carinae similar to those found in *Pseudonirmus*.

Thus *Oxylipeurus*, parasitizing a single host order, comprises a related group of species (as shown by the characters of the abdomen) which show a tendency towards the modification of the anterior region of the head. This has probably taken place more than once, sometimes on parallel lines, in different groups of species restricted to particular families of birds. It seems unsatisfactory to use these head characters as criteria for the erection of genera—at least six of such genera would be needed, and in some cases would include species from unrelated host groups. The two genera already separated from *Oxylipeurus*, namely *Eiconolipeurus* and *Epicolinus*, should, therefore, not be recognized; *Splendoroffula*, found on the MUSOPHAGIDAE, is also doubtfully separable from *Oxylipeurus*.

Structural modifications in the Ischnocera have been caused by the adaptation of the parasite to the environment of the different ecological niches on the body of the bird. This factor has been discussed elsewhere (Clay, 1949), but in relation to the structure of the head it was the occupation of the head and neck niche which seems to have had the most important influence. The occupants of this niche have a broader head, correlated with the general shortening and broadening of the whole body. This enlargement of the head is usually associated with the prolongation of the head anteriorly and with the enlargement of the mandibles and the concomitant development of the mandibular framework. This type of head shows the greatest development of endocarinae, presumably for support of the larger mandibles and the larger size of the head in general. It also has the greatest development of sutures in the preantennal region, possibly to give a limited mobility to this flattened expansion of the head. In the postantennal region support is given to the mandibular framework by the prolongation of the occipital carinae to the occipital margin; and further support to this region is given by the development of the temporal carinae. Although well developed temporal carinae are found in narrow-headed forms, these lines of thickening are, in general, characteristic of the broad-headed forms, and are found in such unrelated genera as *Megaginus*, *Docophoroides*, *Trabeculus*, *Anatoecus*, *Philopterus* and *Sturnidoecus*. Moreover, where there are two related genera or species groups which differ mainly in shape, these endocarinae are usually present in the broad-headed forms and absent in the narrow-headed ones: thus *Sturnidoecus* has these carinae well developed, unlike *Brüelia*, in which the species have narrower heads; *Acutifrons* contains broad-headed species, which differ only from *Degeeriella* by the well-developed temporal carinae; *Cuculicola cheluria*, a broad-headed species, has well-developed temporal carinae, which are absent in the narrow-headed *Cuculicola latirostris*.

Thus, the apparent similarity between different genera is often caused by linked characters dependent on the environment in which the parasite lives;

this has resulted in many of the round-bodied, large-headed forms (head lice) being placed in one family and many of the long-bodied narrow forms (wing lice) in another. On the other hand, it has also led to the erection of genera for groups of species which, because they have changed their habitat or possibly because their host has a broader type of feather with the resulting broadening of the parasite, differ only in those superficial characters of the head (and sometimes abdomen) correlated with increased size. It is doubtful, for instance, whether *Acutifrons* is more than a species group of *Degeeriella*. Hopkins (1943), in a most instructive paper, has shown how the TRICHO-DECTIDAE from the antelopes have been separated into genera on adaptive, not phylogenetic characters, the environmental factor probably responsible being the texture of the coat of the host.

The value of the characters of the head in showing phylogenetic relationships can now be summarized. The variation is discussed in relation to characters of the abdomen which are constant throughout any group in question.

*Marginal carina.*—In many groups the form of this carina is a good generic character, but there are a number of exceptions: *Brüelia* and *Oxylipeurus* have already been discussed; in *Philopterus* the marginal carina may have the well-marked lateral interruption characteristic of most of the genus, or there may be no interruption but a deep indentation (species from *Megarhynchus*, TYRANNIDAE), or the marginal carinae may be complete laterally (species from the PITTIDAE). Although the form of the marginal carina may sometimes be a generic character, there seems little doubt that it will not form a supra-generic character except in those cases where it is unmodified (GONIODIDAE); the majority of families will probably prove to have genera with the carinae both entire and specialized to a greater or less extent.

*Hyaline margin.*—This region is only appreciably developed in those forms with modified heads, although it seems to be homologous with the narrow hyaline rim of the head in *Goniodes* (fig. 10) called the "limbus" by Kéler (1939: 14). Its form is largely dependent on that of the marginal carina and, therefore, in a genus (e.g., *Brüelia*) where there is considerable variation of this carina there is also variation of the hyaline margin. In *Rallicola*, where it is always present, it may be extremely narrow (*R. fulicae*) or broad (*R. ortygometae*). In those species with modified heads its point of origin each side gives a characteristic appearance. In *Anatoecus*, *Craspedonirmus* and *Carduiceps* it arises each side at the point of the lateral interruption of the marginal carina, and this point of origin appears to be constant and characteristic throughout these genera. In other genera its point of origin varies: in *Philopterus*, for instance, it may arise at the anterior ends of the marginal carinae (*P. cincli*), or some little way proximal to this (species from *Graucobus*); its breadth at the lateral sides of the head also varies in this genus: it may run forward as a narrow strip (*P. fringillae*), or be enlarged laterally (species from *Dicrurus*, MOMOTIDAE and others), giving a characteristic appearance to the head. The anterior edge of the hyaline margin may be medianly indented as a generic character (*Incidifrons*), or as a specific character (*Philopterus*); the anterior edge may be more heavily sclerotized and pigmented, a character found in some species of *Philopterus* (those from the MOMOTIDAE, TYRANNIDAE, NECTARINIDAE and others) and in the species of *Penenirmus* parasitizing the CAPITONIDAE (Barbets).

*Dorsal carina.*—The form of this carina (bordering the posterior edge of the preantennal suture) may be of generic value (*Pseudonirmus*), or vary

considerably in closely related forms: in the *Saemundssonina* species from *Alle alle* it is strongly developed and passes round the posterior end of the preantennal suture, while in the species from another of the ALCIDAE (*Fratercula arctica*) it is scarcely developed.

*Transverse carina.*—Where this is present as a complete band across the head it seems to be constant throughout the genus (e.g., *Columbicola*), but it is not of supra-generic importance, as in *Turturicola*, apparently related to *Columbicola*, it is absent.

*Temporal carina.*—These carinae may be absent, partially developed or fully developed within one genus, but their distal point of termination when fully developed seems to be constant throughout a genus; in *Philopterus*, for instance, they pass to the preantennal nodus, and in *Saemundssonina* to the preocular nodus.

*Anterior plate.*—In those genera containing species in which the dorsal anterior plate is a superficial area marked off from the rest of the preantennal surface of the head by the dorsal suture, there may also be species where it is absent altogether (e.g., *Brüelia*). Where the anterior plate is a thickened discrete structure its form is usually of generic value (e.g., *Ibidocetus*). There are, however, exceptions: in the *Philopterus* species from the PITTIDAE the posterior prolongation of the anterior plate is lightly sclerotized, and is not the heavily thickened point characteristic of most species of *Philopterus*; in one species of *Quadriceps* (from *Limnodromas griseus*) the posterior part of the plate is prolonged into a thickened point, and is similar to that found in *Saemundssonina*.

*Dorsal suture.*—Where the marginal carina is complete the presence or absence of a dorsal suture (e.g., *Goniodes*, *Lagopoecus*) is rarely a generic character. Again in the same genus it may or may not be continued to the margin and interrupt the marginal carina (*Oxylipeurus*, *Brüelia*). In the forms with specialized heads where it is present throughout the genus, its point of origin is usually constant: in *Rallicola* (species examined from 23 genera of RALLIDAE) the marginal carina is never interrupted laterally, and the dorsal suture always arises at the anterior end of the marginal carina each side; and in *Philopterus*, even in those species where the marginal carinae is not interrupted, the dorsal suture always arises near the middle of the preantennal region. In the species with modified heads the form of the dorsal suture also seems to be generically constant: either passing straight across the head (*Luniceps*), passing posteriorly to a point (*Quadriceps*) or as two points (*Sturnidoecus*).

*Ventral carina.*—This endocarina shows great diversity throughout the Ischnocera, and its form is rarely (perhaps in the GONIODIDAE) a supra-generic character. It may be entire or interrupted in the same genus (*Heptapso-gaster*), but its general form tends to be constant throughout a group of related species. In *Brüelia*, for instance, in which there is much diversity of head form, the ventral carina is always interrupted and the sclerotization carried forward as a flattened surface each side (fig. 24); in *Degeeriella* (fig. 13), in which the general form of the head resembles that of the simplest species of *Brüelia*, the ventral carina is always interrupted, but the sclerotization is not carried forward in the form found in *Brüelia*. The ventral carinae may or may not be fused with the marginal band within one genus (*Brüelia*). The area between the proximal part of the ventral and marginal carinae may show generic characters in the specialized forms (e.g., *Saemundssonina*). The form

of the pulvinus is closely linked with that of the ventral carina, and its character seems to be constant through groups of related species.

*Occipital carina.*—These may or may not reach the occiput in the same genus (e.g., *Oxylipeurus*).

*Gular plate.*—A true gular plate seems to be absent in all the GONIODIDAE, *Austrogoniodes*, *Chelopistes*, some of the genera of the HEPTAPSOGASTRIDAE and in some of the genera parasitizing the Procellariformes. In *Oxylipeurus* it may or may not be present. In *Colilipeurus* and *Turnicola* it is apparently absent, but may only lack pigmentation. It is also absent in *Hopkinsiella*, although in related genera it is present. The presence of a gular plate may, therefore, be a supra-generic, generic, or only a specific character.

*Antennae and conus.*—These structures have already been discussed (Clay, 1946 : 355) and it was suggested that the form of the conus was often correlated with the size of the antennae, and that sexual dimorphism in either of these structures was of little phylogenetic interest, the presence or absence of sexual dimorphism being found in closely related species. In *Philopterus* the conus may be well developed (species from CAMPEPHAGIDAE), reduced (species from TYRANNIDAE), or absent (species from PITTIDAE).

*Chaetotaxy.*—As already shown, the setae are, in general, constant throughout the Ischnocera and do not show supra-generic characters. The form of the setae may be of generic value: the spine-like dorsal setae of *Anatoecus*, the peculiar flattened third anterior setae of *Columbicola*, and the stout second anterior setae of *Anaticola*. Some large groups of species (*Goniodes*) show variation in number, size and position of the setae so that the chaetotaxy may give specific differences.

*Mouthparts.*—The form of the mouthparts may be constant throughout groups of unrelated genera, or may vary considerably in related species where the differences are merely of specific value. Cummings (1916 : 670) has shown, for instance, that the hypopharynx in *Ibidoecus* may be normally developed or greatly reduced.

In conclusion it can be said that the head is basically similar throughout the superfamily Ischnocera.<sup>3</sup> Superimposed on this basically similar structure are found many variations in the superficial characters of the head—this part of the body apparently being the most closely adapted to the environment. Much of this adaptation seems to have taken place on parallel lines. This has resulted in groups of species obviously closely related by the more stable characters of the abdomen showing very different head characters, and others probably not related having similar characters of the head. This, together with the fact that in most groups of related genera there are some which have retained the primitive head characters, makes it difficult to base a supra-generic classification on the characters of the head, although it may prove that the manner by which the specialization of the head is brought about during development will indicate relationships between some of the genera. Further, the many genera which have developed modifications of the head on similar lines (as discussed under *Brüelia*) may be descendants of a common ancestor in which this was the only modification of the head possible, whereas those in which specialization has taken place on different lines (e.g., *Anaticola*, *Columbicola*, *Oxylipeurus*) are not related to the genera with the "*Brüelia*"-like heads.

<sup>3</sup> Dr. S. Symmons (*in press*) has shown that the tentorium of the Ischnocera, unlike that of the Amblycera, is uniform in structure throughout the group; species from a number of unrelated genera were examined.

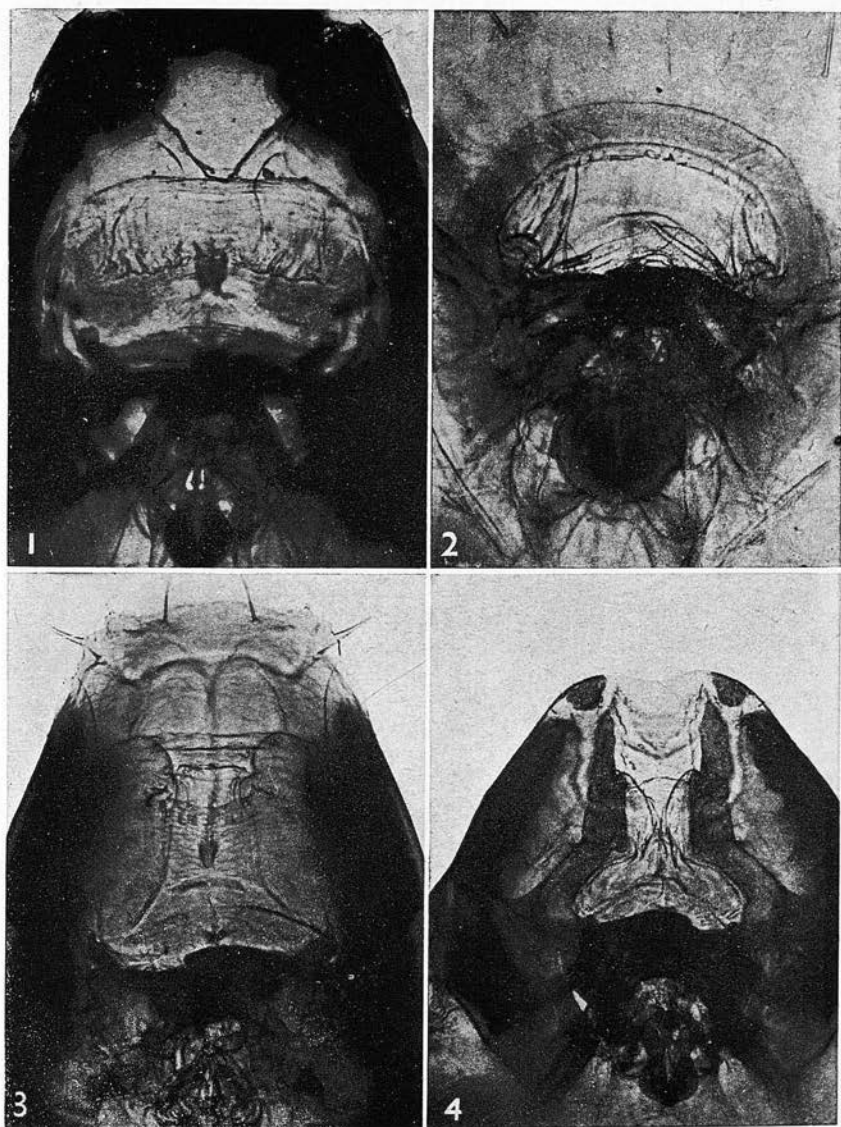
At the present time groups of species inseparable on the characters of the abdomen should probably not be separated generically on small differences in head structure, especially where they do not parasitize a related group of hosts, and hence, where the characters they have in common may be adaptive not phylogenetic.

## SUMMARY

This paper is the first of a series dealing with a reassessment of the characters used in the generic separation of the Ischnocera. The generic concept as applied to the Mallophaga is discussed. The primitive head and its specializations are described and a terminology of the structures useful in classification given. The phylogenetic significance of the variation in the characters of the head is discussed.

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Heads of Mallophaga species to show pulvinus. Fig. 1.—*Perineus* sp. Fig. 2.—*Coloceras* sp. Fig. 3.—*Anaticola* sp. Fig. 4.—*Brüelia* sp.

(Specimens mounted in polyvinyl lactophenol and photographed by H. M. Malies.)



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## SPECIES OF THE GENUS *SAEMUNDSSONIA* (MALLOPHAGA) FROM THE STERNINAE

BY THERESA CLAY

The species of *Saemundssonina* from the Sterninae, owing to their general uniformity of appearance, have been regarded by many authors as belonging to one species; Harrison, 1916, placed all the species from the European terns as synonyms of *S. melanocephalus* (Burmeister). However, an examination of the male genitalia shows that there are a number of distinct and easily recognizable species, making it necessary to reestablish the earlier names. The descriptions of the early authors did not include the characters of the male genitalia, and in general their species are only referable to the genus. It is reasonably certain that the material on which Linné's species was based is no longer in existence. Dr. Kéler informs me that there is no doubt that the Halle collection which contained the greater part of the type material of the Nitzsch, Giebel, Taschenberg, Burmeister, and some of the Rudow species was, with the exception of the Gonioididae, *sensu lato*, and Trichodectidae, *sensu lato*, totally destroyed during the late war. Through the kindness of Dr. Eichler and Signor Conci I understand that the material on which Olfers and Picaglia based their descriptions is unlikely to be found; the Piaget material is virtually complete. This inadequacy of the descriptions and loss of the type material mean that the only satisfactory method of fixing the earlier names is to select a species from the original host, the characters of which do not conflict with the original description, and to erect neotypes. It is important that the neotypes should be selected from a subspecies of the host that could have been the original one, and for this reason no erection of neotypes for *brevicornis* Giebel (see below) has been made. At the present

time it is impossible to give a name to a specimen of *Saemundssonina* from any tern which makes it generally recognizable, and thus all previous records of *Saemundssonina* are valueless. *S. melanocephalus* (Burmeister), as restricted below, is a distinctive species known only from *Sterna albifrons*, but it has been recorded from nearly all the European, South African, and New World terns in addition to many of the gulls. For this reason references to the species in the early literature are discussed only where these are relevant to the fixing of the name. An exception is made in the case of Piaget, for the reason that this author has been and still is taken as an authority on the synonymy of the Nitzsch-Burmeister-Giebel names. In fact, in the majority of cases Piaget merely made his deductions from the published descriptions, often redescribed and figured species from the wrong host, and in some cases the fact that he mentions the correct host does not necessarily mean that he had seen material from it. His interpretations are often incorrect and cannot be accepted. A glance through the specimens in the Piaget collection listed below under the species shows many cases of straggling and misdetermination; his host records should not, therefore, be accepted without further confirmation.

Paratypes and examples of all the species available have been deposited in the American Museum of Natural History.

VARIATION: The *Saemundssonina* species here considered are heavily sclerotized forms, and such species are liable to show considerable variation in the extent and shape of the sclerites from specimen to specimen, and from side to side of the same specimen. In these species, in addition to and surrounding the definite sclerites of the thorax and abdomen, there are further sclerotized areas. The extent and pigmentation of these secondary areas appear variable, and in some specimens examined the true sclerites may have their outline obscured, resulting in the apparent fusion of sclerites which are actually distinct. For this reason the exact outlines of the sclerites cannot be used as diagnostic characters.

An indication of the range of variation found throughout one species is shown under *sternae*, of which a good series has been examined; it is probable that other species show a comparable range of variation.

HOST DISTRIBUTION: The distribution of the species of *Saemundssonina* found on the Sterninae will be discussed elsewhere.<sup>1</sup>

<sup>1</sup> Paper in press.

Here attention can be drawn to the anomalous occurrence of *S. sterna* (Linné) on *Gelochelidon nilotica*, which cannot be explained by either contamination or misidentification of hosts (three different hosts from three localities), and the close relationship of the species from *Sterna aurantia* and *Chlidonias* sp. Specimens from all species of *Thalasseus* examined (with the exception of those from *T. maximus* and *T. eurygnatha*) appear to be conspecific, and similarly with those from all the species of *Chlidonias*. It is possible that when large series of specimens are available, it will be found that each host species has a distinct subspecies of *Saemundssonina*. For this reason the measurements of the head breadth (tables 6 and 7) of specimens from the different host species are given separately.

There is an interesting correlation between size of parasite and size of host. Harrison (1915, p. 96) was the first author to draw attention to the principle which appears to have a wide application. If the three related species of *Saemundssonina* (*sterna*, *melanocephalus*, and *laticaudata*) are considered (tables 6 and 7), it is seen that the smallest parasite, *melanocephalus*, is found on the smallest host, *Sterna albifrons*; and the largest, *laticaudata*, on the largest host, *Thalasseus sandvicensis*; the parasite of intermediate size, *sterna*, being found on *Sterna hirundo*, which is intermediate in size between the two former hosts.

Owing to the great similarity between some of the species of *Sterna* (e.g., *hirundo*, *paradisaea*, and *vittata*) considerable caution must be used in accepting host identifications; only those specimens about the host of which there is no doubt have been used for types or neotypes. The host name as given in the original description is used for the first mention of the parasite followed by its present equivalent and author according to Peters (1934, p. 327).

**MEASUREMENTS:** It has been found that the breadth of the head at the temples in *Saemundssonina* species remains fairly constant under different treatments in mounting. This measurement is relatively constant for the species and in one case forms the most satisfactory character by which two species can be separated in the females. It is a more useful criterion of specific differences than the cephalic index, as (except in the case of male *hopkinsi*, new species) the proportions of head breadth to length are relatively constant. The measurements for the main divisions of the body are given only for the type specimens as a

general indication of size and should not be used as a basis for erecting new subspecies. Length measurements are taken along the midline for the head (including the hyaline margin), and from the most anterior lateral dorsal point to the most posterior point for the thorax and abdomen; the cephalic index (C.I.) is breadth:length.

KEY TO SPECIES<sup>1</sup>

## MALES

1. Basal plate with distal sclerotized cross bar (figs. 20, 21)..... 2  
    Basal plate without distal cross bar..... 3
2. C.I. > 1.03; length of paramere > 0.24 mm..... *lobaticeps*  
    C.I. < 1.05; length of paramere < 0.28 mm..... *hopkinsi*
3. Endomere with terminal, strongly sclerotized, tooth-like process (fig. 29)  
    ..... *melanocephalus*  
    Endomere without above process..... 4
4. Linear arrangement of mesosomal setae (fig. 26)..... *laticaudata*  
    Clustered arrangement of mesosomal setae (fig. 22)..... 5
5. Details of endomere and paramere head as in figures 16, 22, 23..... *sternae*  
    Details of endomere and paramere head as in figures 17, 24, 25..... *lockleyi*

## FEMALES

1. Hyaline anterior margin of head medianly emarginate..... 2  
    Hyaline anterior margin of head not emarginate..... 3
2. Breadth at temples usually > 0.72; setae lateral to last abdominal sternite  
    5-7 in number; shape of signature as in figure 14..... *lobaticeps*  
    Breadth at temples usually < 0.73; setae lateral to last abdominal sternite  
    3, occasionally 4, in number; shape of signature as in figure 15. *hopkinsi*
3. Sternite VII with posterolateral angles free or partially fused to subgenital  
    plate..... *sternae, vittata*  
    Sternite VII with posterolateral angles fused to subgenital plate..... 4
4. Breadth at temples > 0.60 mm..... *melanocephalus*  
    Breadth at temples < 0.63 mm..... *laticaudatus*

***Saemundssonina sternae* (Linné), 1758**

Figures 1-6, 16, 22, 23

*Pediculus sternae* LINNÉ, 1758, p. 612. Hosts: "Habitat in Sternis, Laris."

*Nirmus fornicatus* OLFERS, 1816, p. 89. Hosts: "Hab. in laris et sternis."

*Docophorus 5-maculatus* PIAGET, 1885, p. 9. Host: *Hirundo urbica* = *Chelidon u. urbica* (Linné).

*Pediculus sternae* Linné (1758, p. 612) has no description but a reference to "Fauna Suecica" (1746, p. 339) and to Redi (1668), plate 9, figure 2. The description in "Fauna Suecica" mentions a

<sup>1</sup> *Saemundssonina peristicus* and *S. snyderi* omitted.

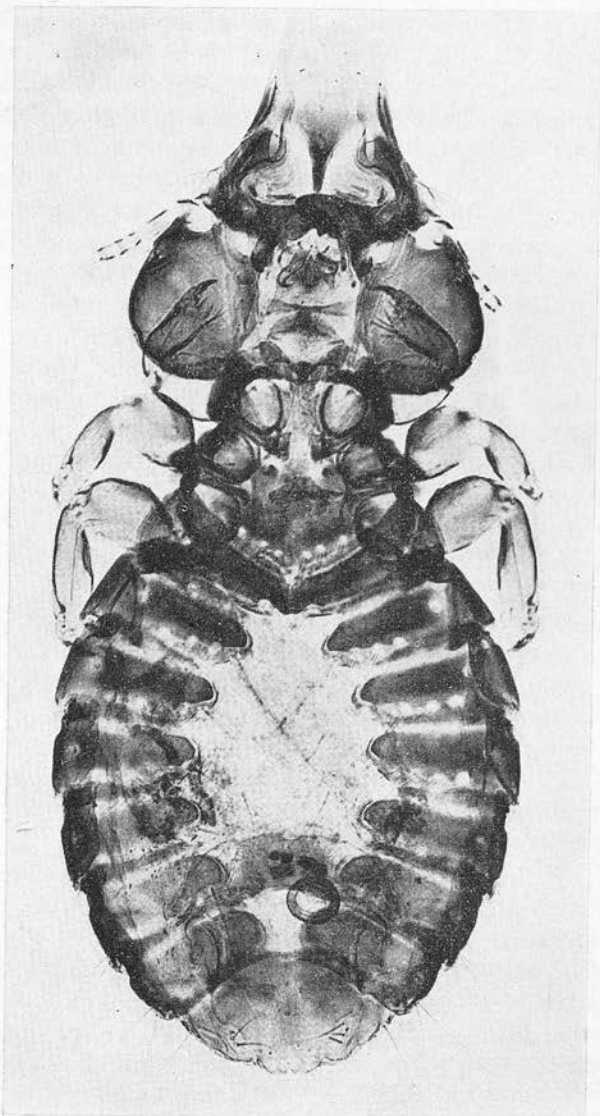


FIG. 1. *Saemundssonina sterna*, female.

triangular head which is only applicable to *Saemundssonina* or *Quadriceps* among the species found on *Sterna*. The description suggests the former, an interpretation confirmed by Redi's

figure, which although poor must be taken to represent a *Saemundssonina*. The host record in 1758 is "habitat in Sternis, Laris." Linné always gave a secondary appellation to his species, derived from a specific name of a host, before he gave the host record, such as "habitat in Sternis." This secondary appellation is taken to be a definite restriction of type host. In the case of *sternae*, the secondary appellation is *P. sternae hirundinis*; the only host given in "Fauna Suecica" is "*Sterna secunda* 128" (= *Sterna h. hirundo* Linné). *Pediculus sternae* Linné is therefore considered to be the earliest name for the *Saemundssonina* species described below, with *Sterna h. hirundo* as type host.

*Nirmus fornicatus* Olfers is a composite species; the description undoubtedly refers to a *Saemundssonina*. The host record is "Hab. in laris et sternis," and there are references to *P. sternae* Linné, the left-hand figure of Redi's plate 9, and to *Ricinus lari* De Geer, excluding the figure. As there is no restriction of type host in the original description, the name *fornicatus* Olfers is here restricted in such a way as to make it a synonym of *Saemundssonina sternae* (Linné).

*Docophorus 5-maculatus* Piaget was described from specimens alleged to have come from *Hirundo urbica* [= *Chelidon u. urbica* (Linné)]. These specimens are in the Piaget collections (one male, one female in the British Museum, one male, one female in the Rijksmuseum, Leiden) and prove to be *Saemundssonina sternae* (Linné). The specimens must have come from *Sterna hirundo*, and the explanation of the error is probably confusion between the names *Hirundo urbica* and *Sterna hirundo*.

MALE: Head (fig. 2) with general arrangement of sclerotized bands typical for the genus. Anterior hyaline margin flattened; clypeal signature with anterior margin flattened or slightly concave, and projecting beyond point of fusion of internal and marginal bands. The median dorsal pre-antennal suture varies in the extent of its posterior prolongation. In some specimens it may reach to the level of the posterior margin of the conic. The chaetotaxy shows no individual variation except in the number and position of the minute setae on the dorsal postantennal region. The number and arrangement of the larger setae are constant for all the species described below.

Thorax as shown in figure 2. There is variation in the extent of the sclerotization, and hence in the shape, of the sternal plates. The number of elongate setae on the dorsal posterior margin of



the pterothorax varies from seven to 10 each side in the specimens examined, and the number is not necessarily symmetrical each side of the same specimen.

Abdomen as shown in figure 2. Segment II with tergal plates

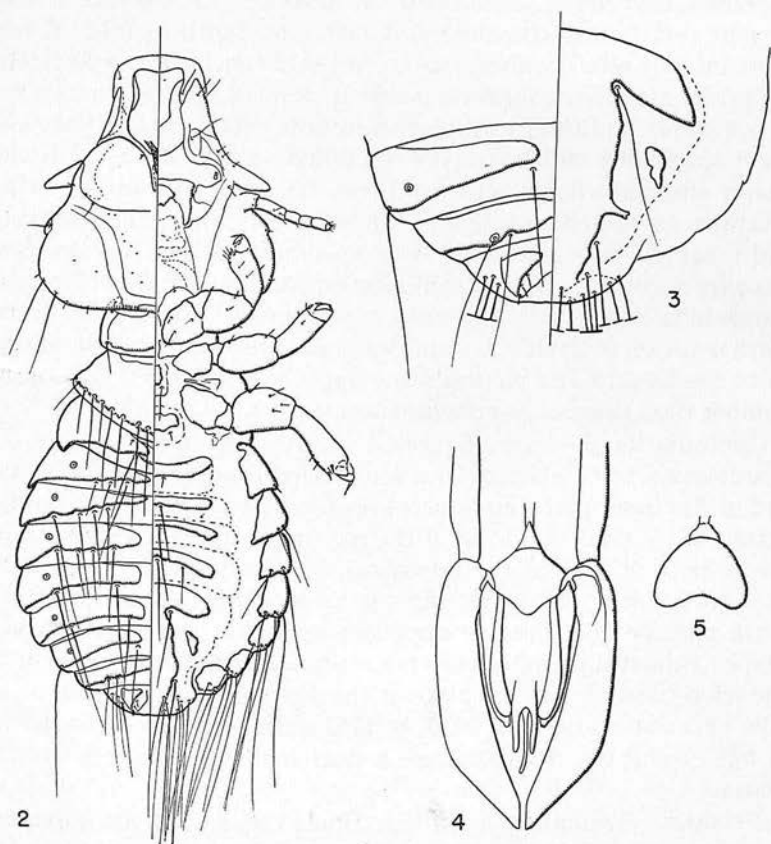


FIG. 2. *Saemundssonina sterna*, male.  
 FIG. 3. Terminal segments of abdomen, male.  
 FIG. 4. Male genitalia.  
 FIG. 5. Uncus.

approximate or in contact medianly, and joined together by well-marked secondary sclerotization. As mentioned above, there is considerable variation in the area and thickness of the primary sclerites and of the surrounding secondary sclerotization. This, together with a varying amount of overlapping of the segments,

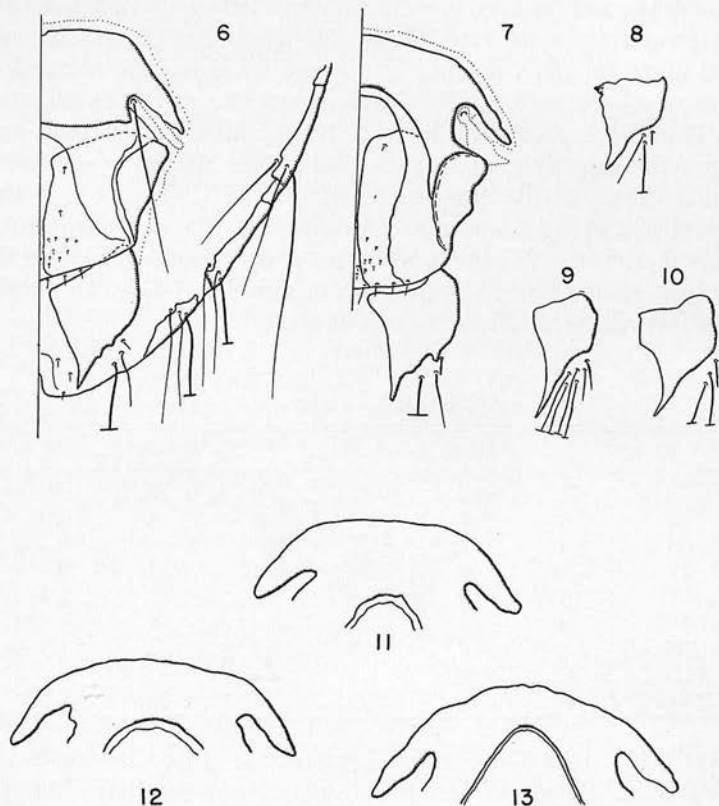
probably owing to different methods of treatment, results in a certain amount of variation in the general appearance of the abdomen. The subgenital plate has an irregular and variable outline (cf. figs. 2 and 3). The ventral posterior margin of the abdomen may have a rounded or flattened appearance. The normal variation of the abdominal setae is shown in table 1, but there may be plus or minus one to two setae each side; specimens are rarely symmetrical on each side in respect to the chaetotaxy. There are, in addition, a number of minute setae on the dorsum of some specimens which are not included in the table. On the venter there are fewer setae and less variation in number. One specimen examined had the minute setae on segment III elongate and reaching to segment V. One specimen lacked the elongate setae on segment VII. In some specimens the minute setae (not shown in table), usually present on segments III-V, lateral to the normal one on each side, become enlarged and elongated on one or more segments. The pleural setae appear to be more constant in number than those of the dorsum and venter.

Genitalia as shown in figures 4, 5, 16, 22, and 23. Specific characters are the absence of a sclerotized cross bar at the distal end of the basal plate, endomeral projections not fused medianly, details of the proximal head of the paramere, and the extension of the penis well beyond the telomeres. There appears to be little true variation in the parts, but owing to distortion in mounting there may be considerable apparent variation, especially in the shape of the distal end of the endomeres. The anterior margin of the sclerotized mesosomal plate at the distal end of the basal plate (the *uncus* of Waterston, 1915, p. 172) varies in outline (as shown in figs. 4 and 5). It may have a flattened or concave posterior margin.

FEMALE: Head and thorax (fig. 1) as in male, but the measurements are greater (tables 4, 5, and 7).

Abdomen is longer and broader than in the male (fig. 1). Segment II with tergal plates as in male. Segments III-VIII with tergal plates separated widely medianly; IX and X with fused transverse plate; XI with distinct tergal plate each side. Segment II with median sternal plate, irregular in outline and varying in area; in some specimens it is not apparent. Segments III-VI with small, well-marked lateral plates and narrow median plates showing variation in extent, and not apparent in all specimens. The unpigmented parts of the venter of the abdomen show the

ornamented appearance as figured by Ferris (1932, fig. 20c) for the species he calls *snyderi*. Pleurites as in male. As in the male there is variation in the thickness and extent of the sclerites and



- FIG. 6. *Saemundssonina sterna*, subgenital plates, female.  
 FIG. 7. *Saemundssonina laticaudata*, subgenital plates, female.  
 FIG. 8. *Saemundssonina melanocephalus*, last abdominal sternite, female.  
 FIG. 9. *Saemundssonina lobaticeps*, last abdominal sternite, female.  
 FIG. 10. *Saemundssonina hopkinsi*, last abdominal sternite, female.  
 FIG. 11. *Saemundssonina melanocephalus*, sternite VII, female.  
 FIG. 12. *Saemundssonina lobaticeps*, sternite VII, female.  
 FIG. 13. *Saemundssonina hopkinsi*, sternite VII, female.

the areas of secondary sclerotization. This fact is especially important in comparing the subgenital plates of the different species. The following characters of the subgenital plate appear to be rel-

atively constant for *sternae*: anterior and posterior margin of sternite VIII flattened, not curved into an arch-like effect; however, in the series of *S. lockleyi*, new species, there are some specimens with sternite VII flattened and some with it arch-like. This may therefore not be a reliable character in *sternae*. In *sternae* the posterior margin of sternite VII is not fused laterally to the subgenital plate (cf. figs. 6 and 7). There is, however, a band of secondary sclerotization which runs across the gap between sternite VII and the plate, and in heavily pigmented specimens this may give the superficial appearance of fusion. In one specimen on one side, the posterior margin of sternite VII is drawn out as a narrow strip and fused to the subgenital plate, and in one specimen of *lockleyi*, sternite VII has a narrow strip each side fused to the plate, thus resembling the condition in figure 7. The chaetotaxy and its normal variation are shown in table 1.

TABLE 1  
ABDOMINAL CHAETOTAXY

	Male			Female		
	T	S	P	T	S	P
II	2-6	2	0,0	2-6	2	0,0
III	6-10	2	1,1	6-12	2	1,1
IV	8-12	2	2,2	8-12	2	2,2
V	10-12	2	2,2	8-12	2	2,2
VI	8-10	4	3,3	8-12	4	3,3
VII	4-6	2	3,3	4-10	2	3,3
VIII	4	fig.	3,3	4-6	fig.	3,3
IX-X	4	fig.	3,3	4	fig.	3,3

MATERIAL FROM TYPE HOST EXAMINED: Fifty-six males, 50 females from *Sterna h. hirundo* Linné, from Sweden, Estonia, Great Britain, Eire, Syria, and South Africa.

OTHER MATERIAL EXAMINED: Eight males, nine females from *Gelochelidon n. nilotica* (Gmelin) from Sudan, Ceylon, and Rajputana, India.

TYPE MATERIAL: Neotype (male) and neallotype (female) of *Saemundssonina sternae* (Linné), slide No. 16151 in the Meinertzhagen collection, from skin of *Sterna h. hirundo* Linné, Sweden. Neoparatypes: Fifty-four males and 48 females from the same host species, localities as listed above.

Neotype (male) and neallotype (female) (agreeing with description and figures of *sternae*) of *Saemundssonina fornicatus* (Olfers),

slide No. 1340 in the Meinertzhagen collection, from *Sterna h. hirundo*, Estonia.

Lectotype of *Saemundssonina 5-maculatus* (Piaget), male, slide No. 597 in the British Museum Piaget collection, from *Hirundo urbica* (in error).

### ***Saemundssonina lockleyi*, new species**

Figures 17, 24, 25

This species is close to *S. sterna*, from which it can be distinguished only by the male genitalia.

MALE: Head, thorax, and abdomen as in *sterna*. Male genitalia (figs. 17, 24, 25) with following characters distinguishing *lockleyi* from *sterna*: details of proximal head of parameres, shape of endomeres and telomeres, and details of mesosome.

FEMALE: No reliable character can be found on which to separate the females of this species from those of *sterna*.

Described from two males and six females from *Sterna vittata georgiae* Reichenow from Wiencke Island, Palmer Archipelago.

OTHER MATERIAL EXAMINED: Fourteen males, 25 females from *Sterna vittata bethunei* Buller from Campell Island; 10 males, 12 females from *Sterna paradisaea* Pontopiddan from East Greenland, Spitzbergen, Scotland, and the Antarctic.

TYPE MATERIAL: Holotype (male) and allotype (female), slides Nos. 314 and 315 in the British Museum collection, from *Sterna vittata georgiae* Reichenow, locality as above. Paratypes: One male and five females from the same host species and locality.

The type material was presented to the British Museum by the Falkland Islands Dependencies Survey Committee. The species is named in honor of Mr. G. J. Lockley who collected the specimens. The material from *S. v. bethunei* was seen through the kindness of Dr. Falla, Canterbury Museum, Christchurch, New Zealand.

### ***Saemundssonina melanocephalus* (Burmeister), 1838**

Figures 8, 11, 19, 28, 29

(*Docophorus melanocephalus* NITZSCH, 1818, p. 290, *nomen nudum*.)

*Docophorus melanocephalus* BURMEISTER, 1838, p. 426. Hosts: "Auf mehreren *Sterna* und *Larus* Arten."

*Nirmus melanocephalus* GIBBEL, 1861, p. 315. Host: *Sterna minuta* = *Sterna a. albifrons* Pallas.

The first appearance of this name (Nitzsch, 1818, p. 290) is as a *nomen nudum*. Burmeister (1838, p. 426) gives a description

which can be taken to apply to a *Saemundssonina*, but without exact host. As he was the first to describe the species he is the author of the name. Giebel (1861, p. 315) lists the name under *Nirmus*, without a description but with the host *Sterna minuta* (= *Sterna a. albifrons*). He refers to Nitzsch, 1818, Burmeister and Nitzsch MS. These references undoubtedly mean that the species he mentions is the one previously described by Burmeister, and the placing of the species in *Nirmus* must have been an error. Giebel (1874, p. 110) described and figured *D. melanocephalus*, giving as hosts *Larus ridibundus*, *Sterna caspia*, and *S. canthiaca*, with the remark "auf letzen beiden mit besonderen, wenn auch nur geringfügigen Eigenthümlichkeiten." This would seem to be a clear restriction of host to *Larus ridibundus*, but it is considered, as further discussed below, that the 1861 reference must take precedence and that *Sterna a. albifrons* is the type host of *melanocephalus*. Mr. G. H. E. Hopkins, in a private communication, has pointed out that this name cannot be discussed apart from *Docophorus karicola* and states "this latter name makes its first appearance in 1861 [Giebel, 1861, p. 315] as a *nomen nudum*, the hosts mentioned being *Sterna leucoparia* and *Larus ridibundus*; in 1866 [p. 363] Giebel again mentions it, the hosts being '*Sterna canthiaca*, *leucoparia*, *Larus ridibundus*.' His treatment of the name in 1874 (p. 110) is most extraordinary. He first sinks it to *melanocephalus* Burmeister, then immediately afterwards describes it as a good species from *Sterna leucoparia*. As this is the first valid appearance of the name, there is no doubt that (whatever may have been Nitzsch's original intentions) *Saemundssonina laricola* must have *Sterna leucoparia* [= *Chlidonias h. hybrida* (Pallas)] as its type host. Reverting to *melanocephalus*, it is perfectly clear that Giebel's 1874 list of hosts is complicated by the addition of two hosts (*Larus ridibundus* and *Sterna "canthiaca"*) which had been attributed to *laricola*, while it remained a *nomen nudum*, and the apparent restriction to the *Larus* therefore cannot be accepted. The third host mentioned, *S. caspia*, is the type host of Giebel's own *nomen nudum*, *Docophorus caspicus* (1866, p. 362). But can we accept the fact that in 1861 Giebel mentioned *Sterna minuta* as the sole host as a legitimate restriction of *melanocephalus*? It seems to me that we can and must. A most important fact in this connection is that Nitzsch, Burmeister, and Giebel all worked on the same material, though additions were made to the collection after Nitzsch's death. Giebel's 1861 paper

is a list of the material then in the Nitzschian collection, and it seems clear that the only specimens of *melanocephalus* which were labeled with this name were those from *Sterna minuta*. These specimens must, therefore, be regarded as Burmeister's type series."

**MALE:** General characters of head, thorax, and abdomen as in *sternae*. The breadth of the head tends to be smaller (table 6), but the proportions are the same (table 5). The genitalia (figs. 19, 28, 29) are distinguished from all other species mentioned here by the characters of the paramere head, endomeres, and mesosome.

**FEMALE:** General characters as in *sternae*, but measurements tend to be smaller (tables 4, 5, 7). Sternite VII is fused to the subgenital plate as in *laticaudata*; the inner anterior angle of the last sternal plate each side is pointed and more heavily sclerotized (fig. 8). The females can also be distinguished from *laticaudata* by the considerably smaller measurements of the head and by the greater length of sternite VII in the midline, usually actually, and always proportionally to length of abdomen (fig. 11).

**MATERIAL FROM TYPE HOST EXAMINED:** Twenty-two males and 18 females from *Sterna a. albifrons* Pallas from Egypt and Scotland.

**TYPE MATERIAL:** Neotype (male) and neallotype (female) of *S. melanocephalus* (Burmeister), slide No. 4674 in the Meinertzhagen collection, from *Sterna a. albifrons*, Egypt. Neoparatypes: Twenty-two males and 17 females from the same host species, localities as listed above.

Piaget (1880, p. 109, pl. 9, fig. 5) described and figured a *Saemundssonina* under the name *Docophorus melanocephalus* Nitzsch from *Sterna cantiaca* (= *Thalasseus s. sandvicensis*) and recorded it also from *Larus cirrhocephalus*. The Piaget collection at Leiden contains one female *Saemundssonina* (not examined critically) from *Sterna cantiaca*. The British Museum Piaget collection contains two males and four females of *Saemundssonina laticaudata* (Rudow) (slides Nos. 900, 901) from *Sterna cantiaca*, one male and one female of *S. sternae* (Linné) (slide No. 902) from *Sterna cantiaca* (presumably stragglers from *Sterna hirundo*), and one male of a *Saemundssonina* not dealt with in this paper (slide No. 903) and presumably a straggler. The specimen from *Larus cirrhocephalus* is missing.

**Saemundssonina laticaudata** (Rudow), 1869

Figures 7, 18, 26, 27

*Docophorus laticaudatus* RUDOW, 1869, p. 12. Host: *Sterna cantiaca* = *Thalasseus s. sandvicensis* (Latham).

?*Docophorus brevicornis* GIEBEL, 1874, p. 112. Host: *Sterna acutifluida* = *Thalasseus sandvicensis acutifluidus* (Cabot).

There is nothing in Rudow's original description which prevents this name's being used for the *Saemundssonina* species on *Thalasseus s. sandvicensis* (Latham). No specimens have been seen from the type host of *brevicornis* = *Thalasseus sandvicensis acutifluidus* (Cabot), but it is probable that the two subspecies of *sandvicensis* have the same subspecies of *Saemundssonina*. As the type of *brevicornis* is no longer in existence, the name is placed provisionally as a synonym of *laticaudata* but remains available for the species from the type host if this should prove to be distinct from that on *T. s. sandvicensis*.

MALE: General characters of head, thorax, and abdomen as in *sternae*. All measurements tend to be larger, especially of the head, but the proportions are the same (tables 4-6). The genitalia are distinguished from *sternae* by the characters of the paramere head, endomeres, and mesosome (figs. 18, 26, 27).

FEMALE: General characters of head, thorax, and abdomen as in *sternae*, but, as in the male, all measurements tend to be greater. Sternite VII is fused to the subgenital plate (fig. 7).

MATERIAL FROM TYPE HOST EXAMINED: Four males and eight females from *Thalasseus s. sandvicensis* (Latham) from England and Mauretania.

OTHER MATERIAL EXAMINED: Six males and three females from *Thalasseus benghalensis par* (Mathews and Iredale), Aden and Port Sudan; 12 males and 10 females from *Thalasseus bergi velox* (Cretzschmar), Red Sea; and two males and two females from *Thalasseus b. bergi* (Lichtenstein), southwest Africa.

TYPE MATERIAL: Neotype (male) and neallotype (female) of *S. laticaudata* (Rudow), slide No. 313 in the British Museum collection (presented by G. H. E. Hopkins) from *Thalasseus s. sandvicensis*, Norfolk, England. Neoparatype: Three males and eight females from the same host species, localities as listed above.

Specimens from two South American species of *Thalasseus*, *T. m. maximus* (Boddaert) and *T. eurygnatha* (Saunders), do not appear to be quite typical of the above and may prove to be new subspecies.



### **Saemundssonina peristica** (Kellogg and Kuwana), 1902

*Docophorus peristicus* KELLOGG AND KUWANA, 1902, p. 462. Host: *Sterna fuliginosa* = *Sterna fuscata crissalis* (Lawrence).

This species was described from material taken from *Sterna fuscata crissalis* (Lawrence), and allegedly from *Dendroica aureata* = *D. petechia aureola* Gould and *Nesomimus carringtoni* = *N. barringtoni* Rothschild. The figure is undoubtedly that of a *Saemundssonina*, and the occurrence of this species on the two passerine hosts must have been due to contamination. This species is discussed below under *S. snyderi*.

### **Saemundssonina snyderi** (Kellogg and Paine), 1910

*Docophorus snyderi* KELLOGG AND PAINE, 1910, p. 124. Host: *Sterna lunata* Peale.

No information is available on the types of *S. peristica* or *S. snyderi*, nor have specimens been seen from the type hosts. It is not, therefore, possible to resolve the present confusion which has arisen over these two names, resulting from the redescription of alleged *snyderi* from the type host of *peristica* (see Ferris, 1932, p. 71). In this redescription no mention is made of *peristica* or whether or not the types of *snyderi* were examined. *S. snyderi* (*sensu* Ferris, 1932) appears from the figures to be near *laticaudata*.

### **Saemundssonina lobaticeps** (Giebel), 1874

Figures 9, 12, 14, 20, 30, 31

*Docophorus lobaticeps* GIEBEL, 1874, p. 109. Hosts: *Sterna hirundo* and *Sterna fessipes* = *Chlidonias n. nigra* (Linné).

?*Docophorus pustuliferus* PICAGLIA, 1885, p. 3. Host: *Hydrochelidon surinamensis* = *Chlidonias nigra surinamensis* (Gmelin).

(*Docophorus laticola* Nitzsch, GIEBEL, 1861, p. 315, *nomen nudum*.)

(*Docophorus laticola* Nitzsch, GIEBEL, 1866, p. 363, *nomen nudum*.)

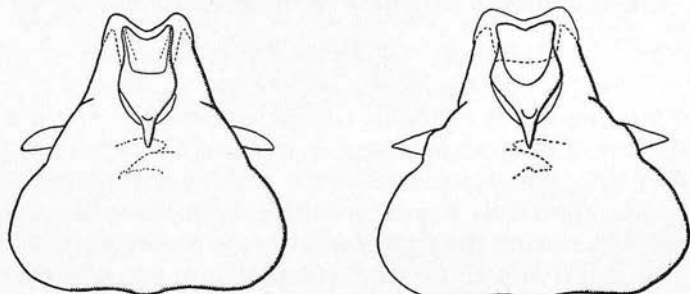
*Docophorus laticola* Nitzsch, GIEBEL, 1874, p. 110. Host: *Sterna leucoparia* = *Chlidonias h. hybrida* (Pallas).

*Docophorus lobaticeps* was described from specimens alleged to have come from *Sterna hirundo* and *Chlidonias nigra*. However, there seems little doubt that the original description must have been made from a specimen from *Chlidonias nigra*. The characters separating *Saemundssonina sterna* (from *Sterna hirundo*) from the *Saemundssonina* of *Chlidonias nigra* are the emarginated hyaline

margin of the head in the latter species, and (in the male) the usually greater width of the head proportional to its length. As attention is drawn to both these characters in the original description of *lobaticeps*, this name must be used for the *Saemundssonina* from *Chlidonias nigra*.

No specimens have been seen from the type host of *pustuliferus*, but it is probable that the *Saemundssonina* from this host would be conspecific with that from *C. n. nigra*. *S. pustulifera* is therefore placed provisionally as a synonym of *lobaticeps*.

The history of the name *laricola* has been discussed above, and it is accepted as the name for the species of *Saemundssonina* from *Chlidonias h. hybrida*. Specimens from this host appear to be



14

FIG. 14. *Saemundssonina lobaticeps*, head, male.

15

FIG. 15. *Saemundssonina hopkinsi*, head, male.

conspecific with *lobaticeps*; *laricola* is therefore placed as a synonym of this latter name.

MALE: Head (fig. 14) with general characters as in *sternae*, but distinguished from all preceding species by the emarginated hyaline margin of the head and by the clypeal signature which is deeply emarginated anteriorly and scarcely projects beyond the anterior point of the marginal bands.

Thorax as in *sternae*.

Abdomen with general characters as in *sternae*, but is distinguished by having both the tergal plates and secondary sclerotization of segment II separated medianly. Segments II-IV tend to have a greater number of dorsal setae (see table 2).

Genitalia (figs. 20, 30, 31) are distinguished from those of the preceding species by the presence of a sclerotized cross bar at the distal end of the basal plate and by the median fusion of the endomeral projections.

FEMALE: Head and thorax with characters as in male but larger.

Abdomen with general characters as in *sternae*; tergites and secondary sclerotization of segment II separated medianly. Sternite VII and subgenital plate as in *laticaudatus* (fig. 12); last sternites more elongate (fig. 9). Chaetotaxy as in *sternae*, but dorsal setae are more numerous (table 2), and there are five to seven setae instead of three each side of the last sternite.

TABLE 2  
DORSAL ABDOMINAL CHAETOTAXY<sup>a</sup>

	Male	Female
II	8-10	8-10
III	9-14	12-18
IV	13-15	16-18
V	11-13	14
VI	6-8	14-16
VII	5-6	10-14
VIII	4	4
IX-X	4	4

<sup>a</sup> Specimens from *Chlidonias h. hybrida* included.

MATERIAL FROM TYPE HOST EXAMINED: Three males and two females from *Chlidonias n. nigra* (Linné) from Wales, north Greece, and no locality (Piaget collection).

OTHER MATERIAL EXAMINED: Four males and three females from *Chlidonias h. hybrida* (Pallas), Khartoum, Sudan; one male and one female from *Chlidonias hybrida indica* (Stephens), Afghanistan; 16 males and 22 females from *Chlidonias leucoptera* Temminck, Egypt, Sudan, Uganda, and Kenya.

TYPE MATERIAL: Neotype (male) of *S. lobaticeps* (Giebel), slide No. 14035 in the Meinertzhagen collection, from *Chlidonias n. nigra*, south Wales. Neoparatypes: Two males and two females from the same host species, localities as listed above.

Neotype (male) and neallotype (female) (agreeing with descriptions and figures of *lobaticeps*) of *S. laricola* (Nitzsch), slides No. 311 and 312 in the British Museum collection, from *Chlidonias h. hybrida* (Pallas), Khartoum, Sudan.

There are four slides labeled *Docophorus lobaticeps* (see Piaget, 1880, p. 110). In the Leiden portion of the Piaget collection there is one male *Saemundssonina* (not examined critically) from *Sterna*

*hirundo*. In the British Museum Piaget collection are one male, one female, and one nymph of *S. laticaudata* (Rudow) (slide No. 965) from *Sterna gracilis* = *S. dougallii gracilis* Gould (host record not reliable); one male and one nymph of *S. sterna* (slide No. 964) from *Sterna hirundo*; and one male and one female of *S. sterna* (slide No. 966) from *Sterna* sp. Piaget described and figured (1880, p. 110, pl. 9, fig. 6) *Docophorus laricola* Nitzsch, giving as hosts: *Sterna minuta* = *Sterna albifrons*, *Sterna nigra* = *Chlidonias n. nigra*, and *Sterna hirundo*. The figure shows the emarginated hyaline margin of the head characteristic of this species. The Leiden collection contains three slides labeled *D. laricola* (not examined critically): one male, one female, and one nymph (slide No. 66) and one male and two nymphs (slide No. 67) of *Saemundssonina* from *Sterna minuta*; and one male of *Saemundssonina* (slide No. 68) from *Sterna nigra*. In the British Museum collection there are four slides labeled *D. laricola*: three females of *Saemundssonina* sp.? (slides Nos. 904, 905) from *Sterna minuta*; one male and one female of *S. lobaticeps* from *Sterna nigra* (slide No. 906); one male *S. lobaticeps* from *S. hirundo* (slide No. 908); and one male and one female of *S. sterna* from *S. hirundo* (slide No. 907).

### *Saemundssonina hopkinsi*, new species

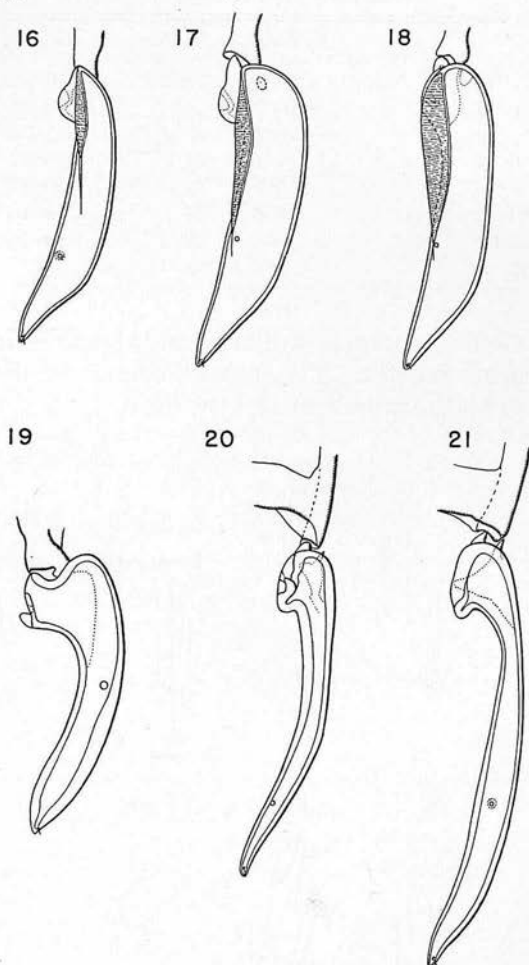
Figures 10, 13, 15, 21

This species is nearest *lobaticeps*, from which it is distinguished in both sexes by the clypeal signature; in the male by the characters of the head of the paramere, and in the female by the breadth at the temples (specimens of *lobaticeps* and *hopkinsi* will probably be found showing an overlap in this measurement), the characters of the genital plate, and by the smaller number of setae lateral to the last sternite.

MALE: Head (fig. 15) resembles that of *lobaticeps* in the characters of the emarginated anterior hyaline margin and in the position of the anterior margin of the clypeal signature. It is distinguished by the shape of the signature and by the greater breadth at temples, both actually and proportionally to length of head (tables 4-6).

Thorax as in *lobaticeps* but tends to have more marginal pterothoracic setae (10-12 each side).

Abdomen as in *lobaticeps* but the dorsal setae are more numerous (see table 3).



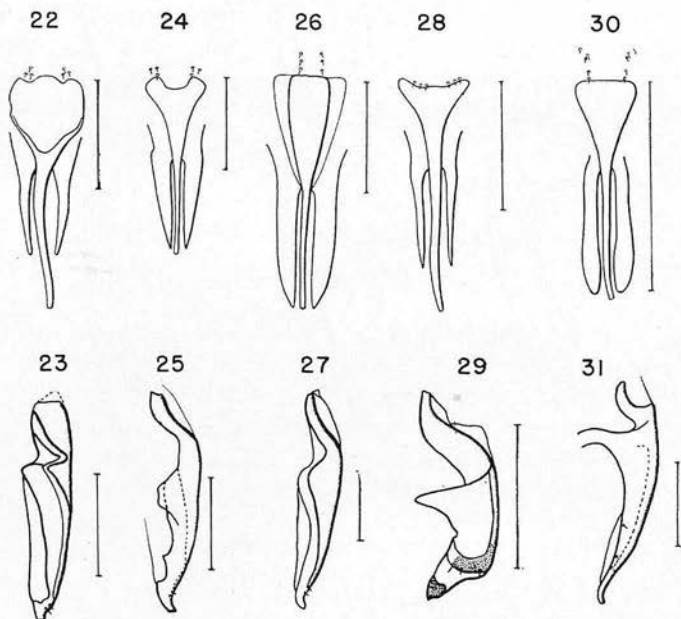
- FIG. 16. *Saemundssonina sterna*, parameres.  
 FIG. 17. *Saemundssonina lockleyi*, parameres.  
 FIG. 18. *Saemundssonina laticaudata*, parameres.  
 FIG. 19. *Saemundssonina melanocephalus*, parameres.  
 FIG. 20. *Saemundssonina lobaticeps*, parameres.  
 FIG. 21. *Saemundssonina hopkinsi*, parameres.

Genitalia of the same type as *lobaticeps* but the parameres are longer and the details of the head different (fig. 21); endomeres and mesosome as in *lobaticeps* but stouter in form.

TABLE 3  
DORSAL ABDOMINAL CHAETOTAXY

	Male	Female
II	10-14	10-16
III	16-20	18-22
IV	18-20	18-26
V	14-16	18-22
VI	10-12	20-22
VII	6-8	14-18
VIII	4	6-8
IX-X	2-4	4

FEMALE: General characters of head and thorax as in male, but all measurements greater. The females cannot be distinguished from *lobaticeps* by the proportions of the head.



FIGS. 22, 23. *Saemundssonina sterna*, mesosomal parts of male genitalia.  
 FIGS. 24, 25. *Saemundssonina lockleyi*, mesosomal parts of male genitalia.  
 FIGS. 26, 27. *Saemundssonina laticaudata*, mesosomal parts of male genitalia.  
 FIGS. 28, 29. *Saemundssonina melanocephalus*, mesosomal parts of male genitalia.  
 FIGS. 30, 31. *Saemundssonina lobaticeps*, mesosomal parts of male genitalia.  
 Lines represent 0.05 mm.

TABLE 4  
MEASUREMENTS OF TYPES

	Male									
	Length					Breadth				
	A	B	C	D	E	A	B	C	D	E
Head	0.57	0.55	0.67	0.58	0.60	0.53	0.52	0.63	0.59	0.65
Prothorax	0.14	0.12	0.19	0.14	0.16	0.28	0.28	0.35	0.31	0.33
Pterothorax	0.19	0.18	0.21	0.17	0.21	0.40	0.38	0.48	0.43	0.46
Abdomen	0.67	0.75	1.02	0.62	0.77	0.62	0.61	0.86	0.67	0.73
Total	1.40	1.47	1.88	1.45	1.59					
Paramere <sup>a</sup>	0.25	0.18	0.29	0.23	0.29					

	Female									
	Length					Breadth				
	A	B	C <sup>b</sup>	D	E	A	B	C <sup>b</sup>	D	E
Head	0.64	0.58	0.71	0.62	0.63	0.65	0.58	0.70	0.67	0.72
Prothorax	0.17	0.15	0.20	0.19	0.16	0.35	0.32	0.37	0.35	0.36
Pterothorax	0.25	0.24	0.23	0.26	0.24	0.50	0.45	0.56	0.50	0.51
Abdomen	1.12	1.03	1.24	0.99	0.89	0.90	0.80	1.01	0.84	0.87
Total	2.00	1.81	2.18	1.86	1.76					
St. VII (mid-line)	0.09	0.11	0.08	0.09	0.07					

A, *sternae*; B, *melanocephalus*; C, *laticaudata*; D, *lobaticeps* (female is not the type); E, *hopkinsi* (female is not the type).

<sup>a</sup> Length from dorsal view.

<sup>b</sup> Specimen slightly distorted.

TABLE 5  
CEPHALIC INDEX

Species	No. of Specimens		C.I. Range	
	Male	Female	Male	Female
<i>sternae</i>	12	20	0.90-0.94	0.97-1.05
<i>lockleyi</i>				
(a)	2	6	0.92-0.95	0.92-0.98
(b)	5	14	0.92-0.95	0.93-0.99
<i>melanocephalus</i>	18	18	0.88-0.96	0.94-1.00
<i>laticaudata</i>				
(c)	3	5	0.93-0.95	0.92-0.96
(f)	3	8	0.91-0.95	0.93-1.00
<i>lobaticeps</i>				
(i)	3	2	0.97-1.02	1.08-1.11
(j)	4	3	0.99-1.03	1.08-1.10
(l)	4	11	0.96-1.00	1.05-1.12
<i>hopkinsi</i>	15	15	1.06-1.11	1.10-1.17

See table 6 for list of hosts.

TABLE 6  
BREADTH (IN MILLIMETERS) OF HEAD AT TEMPLES OF MALES, IN NUMBERS OF SPECIMENS

	.49	.50	.51	.52	.53	.54	.55	.56	.57	.58	.59	.60	.61	.62	.63	.64	.65	.66	.67	.68	.69
<i>sternae</i>	1			2	1	4	6	5	1												
<i>lockleyi</i>																					
(a)								1	1												
(b)				1	3	4	1														
Totals				1	3	4	4	2													
<i>melanoceph-</i>																					
<i>alus</i>	4	5	2	11																	
<i>laticaudata</i>																					
(c)							1					1									1
(d)									1	1	3	1			1						
(e)									1		1										
(f)										2	1	4	3	1							
(g) <sup>a</sup>										2	1	1	1	1							
(h) <sup>a</sup>										1											
Totals							1		2	4	8	2	6	3	3						
<i>lobaticeps</i>																					
(i)								1	1	1	1										
(j)									1	2			1								
(k)											1										
(l)								4	3	3	4	1									
Totals								5	5	6	5	1	1								5
<i>hopkinsi</i>																					
(a) <i>S. vittata georgiae</i>										(c) <i>T. b. bergi</i>											(i) <i>Chidonias n. nigra</i>
(b) <i>S. v. belhunei</i>										(f) <i>T. b. velox</i>											(j) <i>C. h. hybrida</i>
(c) <i>Thalasseus s. sandvicensis</i>										(g) <i>T. m. maximus</i>											(k) <i>C. h. indica</i>
(d) <i>T. benghalensis par</i>										(h) <i>T. eurygnatha</i>											(l) <i>C. leucoptera</i>

<sup>a</sup> Not *laticaudata*, *sensu stricto*.



TABLE 7  
 BREADTH (IN MILLIMETERS) OF HEAD AT TEMPLES OF FEMALES, IN NUMBERS OF SPECIMENS

	.55	.56	.57	.58	.59	.60	.61	.62	.63	.64	.65	.66	.67	.68	.69	.70	.71	.72	.73	.74	.75	.76
<i>sternae</i>							2	2	2	3	3	4	5									
<i>lockleyi</i>																						
(a)				1		1			2	1	1											
(b)					2	1	4	2	2	3	2											
Totals				1	3	1	4	4	4	4	3											
<i>melanocephalus</i>	5	2	7	1																		
<i>laticaudata</i>																						
(c)									2	2			1									
(d)																						
(f)										1			2	3		1	1					
(g) <sup>a</sup>													2		2	1						
Totals									2	3			5	4	2	2						
<i>lobaticeps</i>																						
(i)													1									
(j)																						
(k)													1				1					
(l)																						
Totals												1	5	3	1	2						
<i>hopkinsi</i>														1	6	4	1	5				
																		1	2	1	4	3

See table 6 for list of hosts.

<sup>a</sup> Not *laticaudata*, *sensu stricto*.

Abdomen as in *lobaticeps*. General characters of sternite VII and subgenital plate as in *lobaticeps*, but sternite VII is narrower medianly and strongly arched (fig. 13). Last sternal plate may prove to be diagnostic in general form (fig. 10); setae lateral to this plate three to four each side. Setae tend to be more numerous than in male (table 3).

Described from 15 males, and 17 females from *Sterna aurantia* J. E. Gray from Deccan and Nepal, India, and Myitkyina, Burma.

Holotype (male), slide No. 8730 in the Meinertzhagen collection, from *Sterna aurantia* Gray, Deccan, India. Paratypes: Fourteen males and 17 females from the same host species, localities as listed above. No allotype has been designated, as the only female in good condition from the Indian specimens is deformed, tergite V and VI on one side being partially fused. The Burmese material was examined shortly before going to press after the figures and measurements had been made. This latter material was seen through the kindness of Dr. Henry S. Fuller of the Bowman Gray School of Medicine, Winston-Salem, North Carolina.

The species is named in honor of Mr. G. H. E. Hopkins, to whom I am greatly indebted for the loan of some notes on the nomenclature of these species and for further advice on the same subject.

### *Saemundssonina atlantica* (Kellogg), 1914

*Docophorus atlanticus* KELLOGG, 1914, p. 81. Hosts: *Stercorarius crepidatus* = *S. parasiticus* (Linné) and *Sterna paradisea* Pontoppidan.

This species must be mentioned, as it was described from material alleged to have been collected from *Stercorarius parasiticus* and *Sterna paradisea*, and as Harrison (1916, p. 88) gives only the second host. The species of *Saemundssonina* on these two hosts are quite distinct, and there is no doubt that the figure represents the type of *Saemundssonina* found on *Stercorarius* and not that on *Sterna*. The record on the latter host must therefore be due to some error.

### SUMMARY

All the known species of *Saemundssonina* from the Sterninae are discussed, and two new species are described. The species of previous authors described from more than one host, and therefore

usually composite, are restricted to one type host and redescribed and figured. Neotypes have been erected for species of which the original type material is presumed to be lost and where material from the type host is available.

LIST OF SPECIES DISCUSSED, WITH TYPE HOSTS  
(Synonyms in brackets)

*Saemundssonina*

<i>atlantica</i> (Kellogg), 1914.....	<i>Stercorarius parasiticus</i> (Linné)
<i>hopkinsi</i> , new species.....	<i>Sterna aurantia</i> J. E. Gray
<i>laticaudata</i> (Rudow), 1869.....	<i>Thalasseus s. sandvicensis</i> (Latham)
[ <i>brevicornis</i> (Giebel), 1874.....	<i>Thalasseus s. acustlavidus</i> (Cabot)]
<i>lobaticeps</i> (Giebel), 1874.....	<i>Chlidonias n. nigra</i> (Linné)
[ <i>pustuliferus</i> (Picaglia), 1885....	<i>Chlidonias nigra surinamensis</i> (Gmelin)]
[ <i>laricola</i> (Giebel), 1874.....	<i>Chlidonias h. hybrida</i> (Pallas)]
<i>lockleyi</i> , new species.....	<i>Sierna vittata georgiae</i> Reichenow
<i>melanocephalus</i> (Burmeister), 1838.	<i>Sterna a. albifrons</i> Pallas
<i>peristica</i> (Kellogg and Kuwana),	
1902.....	<i>Sterna fuscata crissalis</i> (Lawrence)
<i>snyderi</i> (Kellogg and Paine), 1910..	<i>Sterna lunata</i> Peale
<i>sternae</i> (Linné), 1758.....	<i>Sterna h. hirundo</i> Linné
[ <i>fornicatus</i> (Olfers), 1816.....	<i>Sterna h. hirundo</i> Linné]
[ <i>5-maculatus</i> (Piaget), 1885.....	( <i>Chelidon u. urbica</i> (Linné)]. In error

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Only those references not included in Kéler's bibliography (1938, p. 487) are listed.

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### Piercing Mouth-Parts in the Biting Lice (Mallophaga)

THE Mallophaga, ectoparasites of birds and mammals, are distinguished within the order Phthiraptera (containing also the Anoplura and *Hæmatomyzus*) chiefly by their relatively unspecialized mouth-parts, especially in having heavily sclerotized chewing mandibles. It has recently been found that in the genus *Trochilæcetes*, parasitic on the Trochili (hummingbirds), the species have a piercing type of mouth-parts (Fig. 1) instead of the mandibulate mouth-parts typical of the Mallophaga. Although four species of this genus have been described in the last fifty years, no previous reference to their mouth-parts is known.

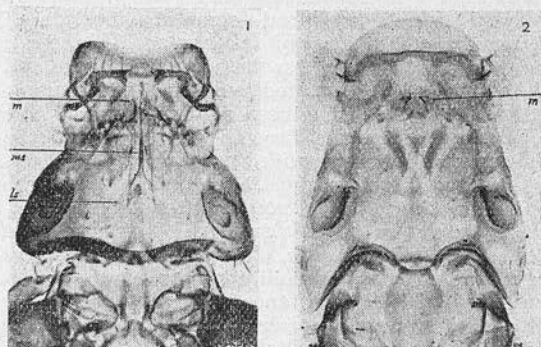


Fig. 1. *Trochilæcetes* sp.  $\times 55$  from a hummingbird. *m*, Mandible; *ms*, median structure; *ls*, lateral structure. (Photo. by H. M. Malles)

Fig. 2. *Ricinus* sp.  $\times 47$  from a passerine. (Photo. by H. M. Malles)

These structures, which will be fully described and discussed elsewhere, comprise a number of elongated extrusible parts and the modified mandibles. There are three closely associated stylet-like structures, almost certainly of hypopharyngeal origin, which are joined by a common membrane, only the distal tips being free. The median structure (Fig. 1, *ms*) which originates from a sclerotized plate (probably the sitophore sclerite) is heavily sclerotized, and gives rise on each side to a flattened lobe, apparently homologous with the hypopharyngeal lobes characteristic of other Mallophaga. A pair of lightly sclerotized lateral structures have their proximal

ends (*ls*) lying lateral and ventral to the sitophore sclerite and seem to represent the modified lingual sclerites. Two flattened elongated outgrowths from the dorsal wall of the distal end of the pre-oral cavity may act as a groove to hold and guide the hypopharyngeal parts. The sclerotized outgrowth of the clypeal wall of the pre-oral cavity (the 'pestle' of the Psocoidea), found in the majority of the Mallophaga, is present in these species. The lacinia are of the typical form found in the Mallophaga, but are distally more elongated and lightly sclerotized. The mandibles (*m*) are lightly sclerotized and the piercing blades lie parallel to the median structure; the end of the left mandible has a minute tooth, the right is sharply pointed. In a related genus *Ricinus* (found on the Trochili and the Passeriformes) the species on the Trochili have also lost the typical Mallophagan mouth-parts, but the modifications both of the mandibles and the hypopharynx are not so extensive. However, in normal *Ricinus* species—which probably also feed entirely on blood—some modification of the mandibles has already taken place (Fig. 2, *m*), these structures being less heavily sclerotized and toothed, and more elongated and pointed than those of other Amblycera which feed on feather parts. The *Ricinus* species on the Trochili are typical of the genus apart from the modified mouth-parts, and this modification, therefore, must have taken place in the *Ricinus* species of the Trochili after the morphological characters of the genus *Ricinus* had been established; *Trochilæcetes*, closely related to *Ricinus* and restricted to the Trochili, must be a later derivative from a *Ricinus*-like ancestor.

Modification from chewing to piercing mouth-parts is now known to have taken place twice in the Phthiraptera, once in the stock which gave rise to the Anoplura or sucking lice of mammals, and, as here described, in the superfamily Amblycera of the Mallophaga. A recent classification<sup>1</sup> divides the Phthiraptera into three suborders: the Mallophaga with chewing mouth parts; the Rhynchophthirina containing only the genus *Hæmatomyzus*, with mandibulate mouth-parts borne at the end of an elongated proboscis; and the Anoplura with highly modified piercing mouth-parts. Recent authors (Webb<sup>2</sup> and Hopkins<sup>3</sup>) have suggested that the Anoplura—in spite of considerable morphological differences, especially those of the mouth-parts—are closely related to the Mallophaga; possibly being derived from an ancestral Ischnoceran stock on a mammal after the mammal-Ischnocera had separated from the bird-Ischnocera. The position of the highly modified elephant louse is still uncertain: it has been placed near the Mallophaga<sup>4</sup> mainly on the possession

of mandibulate mouth-parts, and also near the Anoplura<sup>2</sup>. The present description of chewing and piercing mouth-parts within a group of closely related species in the Mallophaga suggests that these structures tend to be plastic, and are not important characters in showing the phylogenetic relationships of the higher categories within the order.

THERESA CLAY

Department of Entomology,  
British Museum (Natural History),  
London, S.W.7.

April 27.

<sup>1</sup> Weber, H., *Biol. Zbl.*, **59**, 409 (1939).

<sup>2</sup> Webb, J. E., *Proc. Zool. Soc. Lond.*, **116**, 49 (1946).

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<sup>4</sup> Ferris, G. F., *Parasitol.*, **23**, 112 (1931).

## AMERICAN MUSEUM NOVITATES

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NEW SPECIES OF MALLOPHAGA FROM *AFROPAVO*  
*CONGENSIS* CHAPIN

BY THERESA CLAY

Through the kindness of The American Museum of Natural History and of Dr. Schouteden of the Belgian Congo Museum, Tervueren, the author has been able to examine specimens of Mallophaga collected from *Afropavo congensis*, the remarkable gallinaceous bird recently discovered and described by Dr. Chapin. There are eight species represented in the material examined, four belonging to the superfamily Ischnocera and four to the superfamily Amblycera. In the present paper only the ischnoceran species are considered since species of amblyceran Mallophaga from gallinaceous birds cannot be described satisfactorily without a complete revision of the existing genera and species. The author hopes to undertake this revision shortly and will then be in a position to describe the remaining species from *Afropavo congensis*.

The species described below are assignable to two genera, *Lipeurus* and *Goniodes*, and as would be expected from the host these species are not closely related to any of the known species from gallinaceous birds. In a paper shortly to be published the author has shown that the *Lipeurus* species from gallinaceous birds fall into three genera (excluding *Lagopoecus*), examples of which may be found on one host. Within the genus true *Lipeurus* [genotype *L. caponis* (Linné)] there are a number of groups of closely related species, among which is one containing species from the following genera of Phasianidae: *Gennaesus*, *Gallus*, *Phasianus*, *Chrysolophus*, *Rheinardia* and *Rhizothera*; the species from *Pavo cristatus* (description in the press) although resembling this group differs in certain important characters; species from *Numida*, *Acryllium*, *Phasidus* and *Agelastes* form another and quite distinct group. The *Lipeurus* from *Afropavo* is typical of the first-mentioned group containing species from *Gennaesus* and *Gallus*.

The larger *Goniodes* from *Afropavo*, *G. wilsoni*, has no close affinities with the *Goniodes* from such Phasianidae as *Gallus*, *Phasianus* and *Gennaesus*, nor with the typical and distinct species, *G. pavonis* (Linné) from *Pavo cristatus*. A distinct species from *G. pavonis* also from *Pavo*

*cristatus* (to be described shortly) has the terminal segment of the male abdomen similar to that of *G. wilsoni*. However, it is apparent from a comparison of this species from *Afropavo* with all other known species from gallinaceous birds that it resembles most nearly an unnamed species of *Goniodes* from *Guttera plumifera* (correct identity of host doubtful). *G. wilsoni* has the following characters in common with this unnamed species: the general shape of the head; large thickened trabeculae overhanging the antennae; antennae without greatly enlarged first segment; a large number of hairs on the head and thorax; general characters of the abdomen especially in the presence of dorsal clumps of hairs each side of the mid-line of certain segments and the form of the terminal segment; paramera of male genitalia unequal in length. The females of these two species also resemble each other in the form of the head, trabeculae, chaetotaxy of head, thorax and abdomen. In both the male and the female, *G. wilsoni* differs from the other species in the form of the pleurites and in the absence of intertergital thickening.

The remaining two species, *Goniodes chapini* and *G. afropavo*, which are almost certainly closely related to each other, have apparently no near affinities with any of the known *Goniodes*. Superficially these two species recall *G. curvicornis* Giebel from *Argusianus argus* and an unnamed species from *Rheinardia o. ocellata*, but at the present state of our knowledge of the genus *Goniodes* it cannot accurately be said that their true affinities lie with the latter species. These two species, *G. chapini* and *G. afropavo*, are also of interest as an example of the occurrence of two closely related species on the same host in which the females differ but slightly from each other while the two males exhibit a greater degree of difference. In the present case it has not been possible to settle with complete certainty to which males the respective females belong as all the specimens were collected from one host and the differential characters of the males of the two species are the presence of secondary sexual characters in *G. chapini*, i.e., modified antennae, trabeculae and shape of head, and the form of the male genitalia; these characters cannot therefore be used to separate the two females. The differential characters which have been used in the case of the females are the shape of the trabeculae and the size and shape of the abdomen.

It is unwise in the present state of our knowledge of Mallophaga, with so many problematic unknown species, to draw any conclusions from the mallophagan species as to the relationships of the avian host species and genera within a family, but it is of interest to note that the



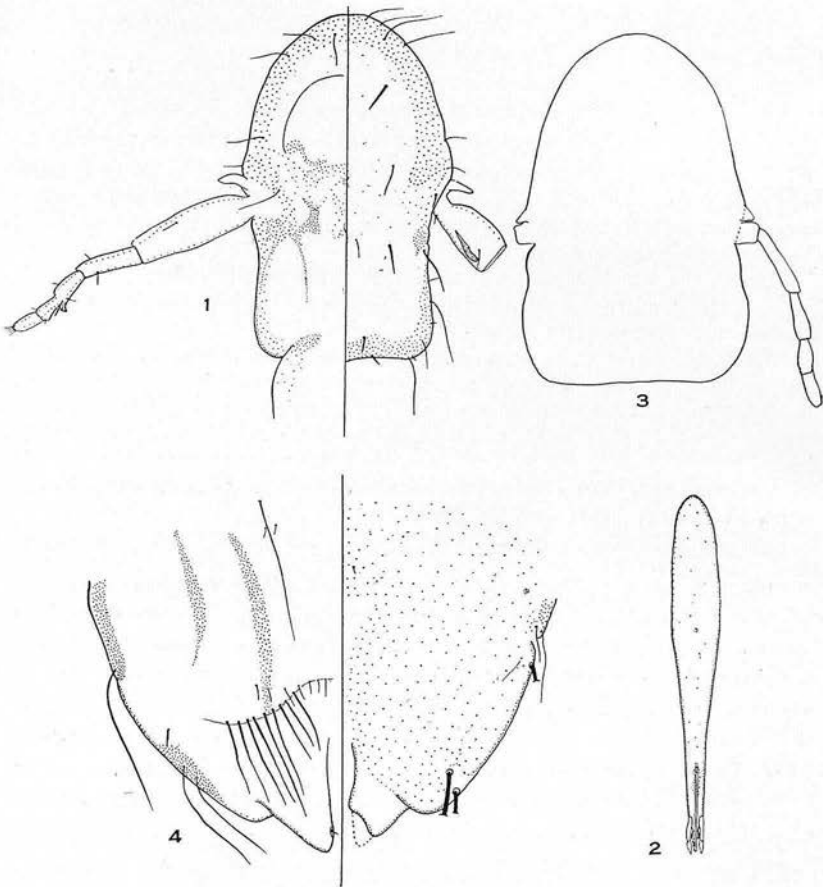


Fig. 1. *Lipeurus schoutedeni*, head of ♂.  
 Fig. 2. *Lipeurus schoutedeni*, genitalia of ♂.  
 Fig. 3. *Lipeurus schoutedeni*, head of ♀.  
 Fig. 4. *Lipeurus schoutedeni*, terminal segments of ♀ abdomen.

Mallophaga parasitic on *Afropavo* are not closely related to any of the known species and that their affinities are found both with species from the Phasianinae and the Numididae. Thus *Lipeurus schoutedeni* has its affinities with species from the *Gennaeus*, *Gallus*, *Phasianus* group; while the affinities of *Goniodes wilsoni* lie with species from *Guttera*; *G. chapini* and *G. afropavo* on the other hand seem to have no close affinities with any known species. It is possible to suggest, therefore, from

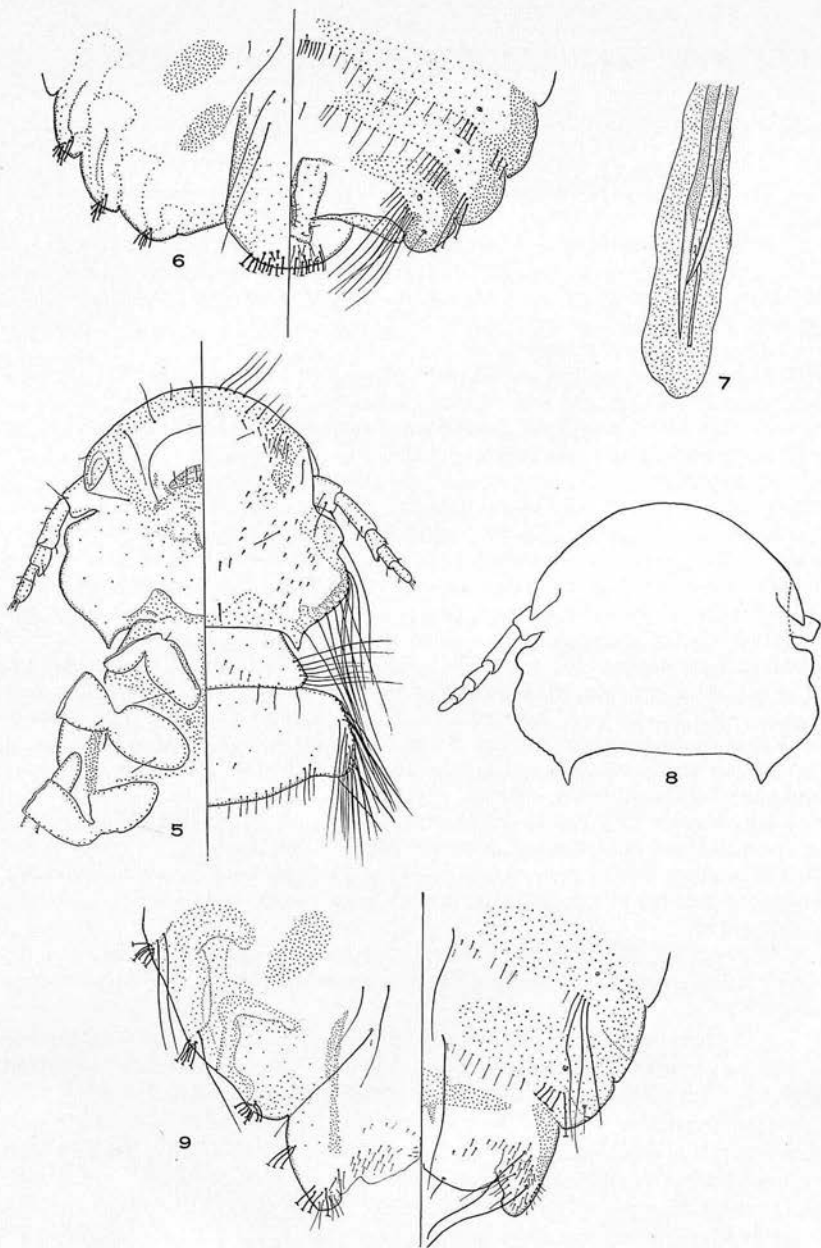


Fig. 5. *Goniodes wilsoni*, head and thorax of ♂.  
 Fig. 6. *Goniodes wilsoni*, terminal segments of ♂ abdomen.  
 Fig. 7. *Goniodes wilsoni*, distal end of ♂ genitalia.  
 Fig. 8. *Goniodes wilsoni*, head of ♀.  
 Fig. 9. *Goniodes wilsoni*, terminal segments of ♀ abdomen.

	Measurements			
	MALE		FEMALE	
	Length	Breadth	Length	Breadth
Head	0.92 mm. <sup>1</sup>	1.13 mm.	1.09 mm.	1.28 mm.
Prothorax	0.35	0.78	0.36	0.89
Pterothorax	0.46	1.16	0.49	1.32
Abdomen	1.69	1.70	2.96	2.04
Total	3.12		4.66	

MATERIAL EXAMINED.—12♂, 16♀, from *Afropavo congensis*, from the E. Congo Forest, collected July, 1937.

HOLOTYPE.—♂ in the Belgian Congo Museum, Tervueren.

Named in honor of Rev. T. H. Wilson of Inkongo, Sonkuru District, who collected the specimens.

### *Goniodes chapini*, new species

Figures 10 to 13

This species is unlike any hitherto recorded and resembles most nearly *G. afropavo* from the same host. It is distinguished from this latter species in the male by the shape of the head and by the form of the trabeculae, antennae and genitalia and in the female by the shape of the trabeculae and chaetotaxy of the terminal segments of the abdomen.

DESCRIPTION OF MALE.—Head (Fig. 10) with short blunt-ended trabeculae; antennae of unusual form with all segments enlarged and with segments I-III differing but little in length and width, and segment V rounded and somewhat globular distally.

Thorax as shown in figure 10.

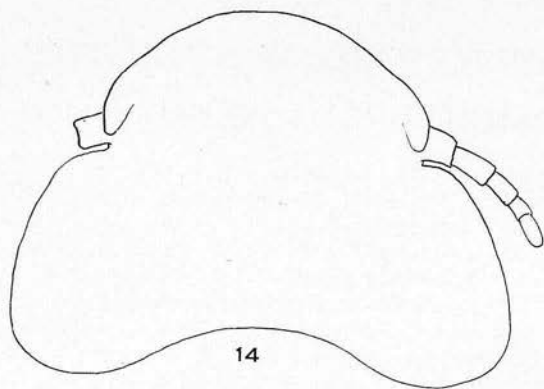
Abdomen short and rounded, broadest at the third segment and with segment I large; segment VIII greatly reduced and segment IX narrow and rounded posteriorly. Tergal plates I-VIII separated medianly; sternal thickening in the form of small lateral segmental plates each side of mid-line. Segments I-VI showing lateral internal circular structures not found elsewhere among the *Goniodes*.

CHAETOTAXY OF THE ABDOMEN.—On the dorsal surface segments I-II have 3 central hairs and 1 post-spiracular hair each side (those on segment I being in an equivalent position to the post-spiracular hairs of the other segments); segments III-V have 2 central hairs and a post-spiracular hair each side; segments VI-IX as shown in figure 11. On the ventral surface segments I-II have a central hair each side of the mid-line; segments III-IV have a central and a stout lateral hair each side; segments V-IX as shown in figure 11. Segment I has no postero-lateral hairs; segments II-VI have 1 postero-lateral hair each side.

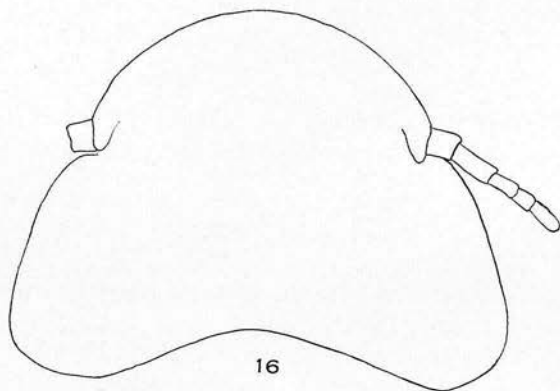
Genitalia with general characters as shown in figure 11 (material inadequate for detailed figure).

DESCRIPTION OF FEMALE.—Shape of head as shown in figure 12, with chaetotaxy as in the male but with the anterior marginal hairs shorter.

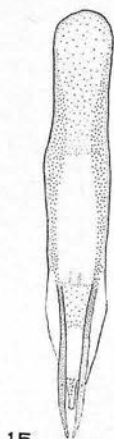
<sup>1</sup> Length measurement of heads taken along the median line; i.e., backward projections of temples are not included.



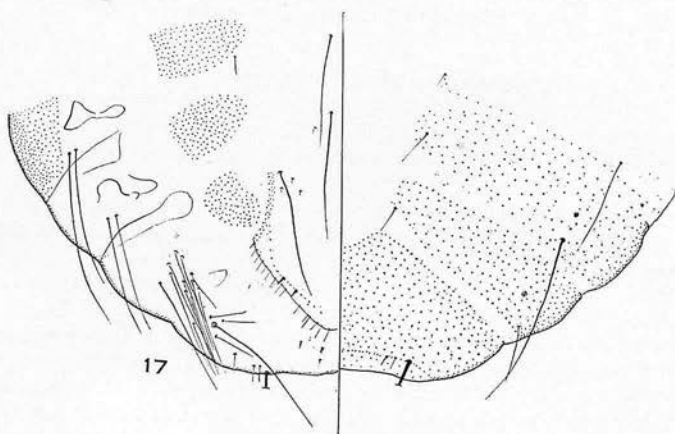
14



16



15



17

- Fig. 14. *Goniodes afropavo*, head of ♂.  
 Fig. 15. *Goniodes afropavo*, genitalia of ♂.  
 Fig. 16. *Goniodes afropavo*, head of ♀.  
 Fig. 17. *Goniodes afropavo*, terminal segments of ♀ abdomen.

DESCRIPTION OF FEMALE.—Shape of head as shown in figure 16, with chaetotaxy as in *G. chapini*.

Thorax as in the male.

Abdomen more elongated than in *G. chapini* but otherwise similar except for the chaetotaxy of the terminal segments (Fig. 17).

#### Measurements

	MALE		FEMALE	
	Length	Breadth	Length	Breadth
Head	0.41 mm.	0.67 mm.	0.42 mm.	0.67 mm.
Prothorax	0.15	0.37	0.16	0.37
Pterothorax	0.21	0.67	0.22	0.67
Abdomen	0.76	0.86	0.91	0.85
Total	1.40		1.57	

MATERIAL EXAMINED.—4♂, 7♀, from *Afropavo congensis* from E. Congo Forest collected in July, 1937.

HOLOTYPE.—♂ in The American Museum of Natural History.

### The Mallophagan Parasites of the Passeriformes.

By THERESA CLAY, B.Sc.

Received 10 April, 1946.

Dr. P. R. Lowe, in 'The Ibis', 1946, p. 103, refers to some remarks by G. H. E. Hopkins, see Ibis, 1942, p. 104, on the Mallophaga of the Passeriformes; it might be of interest to expand these, and to see how far it is possible to use the classification of the Mallophaga to support the classification of their host families in such cases.

The genera listed below are among those which parasitize the Passeres; these genera are also found on certain non-Passerine families as shown:—

Mallophagan Genus.	Host.	
<i>Philopterus</i> Nitsch.....	Passeres.	Momotidæ.
<i>Penenirmus</i> C. & M. ....	Passeres.	Capitonidæ.
	Picidæ.	Indicatoridæ.
<i>Bruelia</i> Kéler .....	Passeres.	Capitonidæ.
	Picidæ.	Rhamphastidæ.
	Momotidæ.	Meropidæ.
<i>Picicola</i> C. & M. ....	Passeres.	Picidæ.
<i>Myrsidea</i> Waterston .....	Passeres.	Rhamphastidæ.

The fact that the families Picidæ, Indicatoridæ, Capitonidæ and Rhamphastidæ, placed by Lowe in the suborder Pici, of the order Passeriformes, are parasitized by species of genera also occurring on the Passeres, suggests some basic relationship between these families and the Passeres; it also suggests a similar relationship between the Passeres and the Momotidæ and Meropidæ.

The genera found on the Upupidæ, Cuculidæ, Coraciidæ and Trogonidæ need further study, but it seems likely that when more material is available, and the relationships between the Mallophagan genera better understood, that some of the genera on these four families will be found to be close, if not inseparable, from the genera listed above.

It is now well accepted that in general the classification of the Mallophaga can be correlated with that of their hosts, but there are a number of factors which may obscure the relationships and give rise to various anomalies. These factors may include ignorance of the true relationship between certain Mallophagan genera, convergence, rare cases of ancient straggling, incompleteness of distribution\*, and different rates of evolution.

Factors causing different rates of evolution include changes in the environment and the inherent stability of the species. Inter-relationships between Avian groups is based largely on muscles and skeletal structures, the characters of which do not in themselves affect the parasite. The environment of the parasite is formed in general by the external characters of the host, such as skin-texture and feather-structure. Such characters, which may be of little importance in showing host relationships, are liable to cause considerable modifications in the parasite, and this has led to the erection of genera in such a way as to obscure the fundamental relationships. Some groups of Mallophaga appear to have been more stable than others, and this is reflected in the extent of their distribution. A genus may be restricted to a host family, host order, or it may be possible that some will be found throughout the Aves, except in those orders and families where they have become extinct, having remained relatively unchanged in comparison with the evolution of their hosts.

The present distribution of a Mallophagan genus is due, therefore, to one or more factors which have affected its evolution, and which are now unidentifiable; these include the variability of the species, shown both in adaptive and non-adaptive † characters, and of the degree of change in the environment caused by the superficial characters of the host, which may or may not reflect relationships between the hosts.

\* See Hopkins, *Ibis*, 1942, p. 104, for discussion of some of these factors.

† The Sewall Wright effect may have been an important factor in the evolution of these small isolated populations.

1946.

*Short Note.*

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For these reasons the Mallophaga do not reflect any constant degree of relationships between the hosts, and are of assistance in indicating only the broadest relationships.



### The Systematic Position of the Musophagi as indicated by their Mallophagan Parasites.

By THERESA CLAY, B.Sc.

Received on 10 February 1947.

In a previous note ("Ibis", 88 (1946): 403) it was emphasized that, owing to certain factors, the basing of deductions of host relationships on those of their parasites might lead to misleading conclusions. The following discussion should therefore be considered in the light of those limiting factors. The Musophagi are usually placed as one of the suborders of the Cuculiformes, the other being the Cuculi. The Cuculi are parasitized by four genera of Mallophaga none of which shows any close relationship to the genera found on the Musophagi. Five genera of Mallophaga are known from the Musophagi, i.e., *Turacæca* Thompson, *Menacanthus* Neumann, *Clayia* Hopkins, *Splendoroffula* C. & M. and *Cuclogaster* Carriker. *Turacæca* is a distinctive genus not closely related to any other known genus: *Menacanthus* is found on the Galli and Passeriformes (*sens.* Lowe, "Ibis", 88 (1946): 127) and probably represents a genus which was once distributed throughout the Aves and is now extinct on most orders. *Clayia* is at present known only on the Galli and on *Crinifer africanus zonurus* (Rüppell), Musophagi; *Cuclogaster* is at present known to occur on the Galli and on two species of the Musophagi. In the original description of *Splendoroffula* it was shown that this genus, represented by species from six genera of the Musophagi, appeared to be closely related to *Oxylipeurus* Mjöberg, known only from the Galli.

The presence of two genera common to the Musophagi and Galli and one genus on the Musophagi closely related to one on the Galli may be explained in one of four ways:—

(1) *Ancient straggling.* At some period there was a transference of Galli parasites to the Musophagi, where they became established and evolved into distinct species; such transference could have taken place through the use of common dust-baths. The Mallophaga are strongly host-specific and usually die when transferred to another host species. There is, however, one genus of Mallophaga the host distribution of which can only be explained by ancient straggling. The fact that in this case there are three genera involved would suggest that this is an unlikely explanation.

(2) *Convergence.* If the Musophagi and Galli had a number of superficial characters in common, this might have led to a resemblance between the external characters of the Mallophaga. However, it is unlikely that response to a similar environment could have resulted in so many common characters in the Mallophagan species, belonging to three genera, from the two host orders.

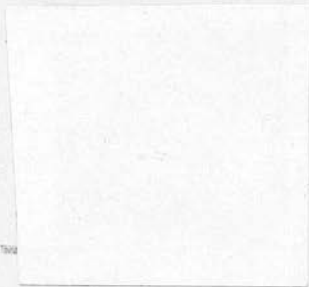
(3) *Discontinuous distribution.* The three genera were once found throughout the Aves and have become extinct except in the Galli and Musophagi. There is evidence that *Cuclotogaster* belongs to an ancient group of genera which shows discontinuous distribution and in which little divergence has taken place, resulting in the presence of apparently closely related genera on hosts which are not considered to be closely related. There is no evidence suggesting that this is also the case in *Splendoroffula* or *Clayia*.

(4) *Relationship between the two host suborders.* This suggestion, which would seem to be the most probable, has been put to Dr. Stresemann of the Zoologisches Museum, Berlin, to whom I am greatly indebted for the following information privately communicated (September and October 1946). Dr. Stresemann sends me an extract from Max Fürbringer (1888 : 1318) as follows: "Yet I do not deny the possibility that the lines of evolution of the ancestors of these two or three divisions (Gallidæ, Opisthocomidæ and Musophagidæ) have been in very remote phylogenetical times not so very far apart; in other words, I believe it possible that the great divergence which now exists between the Gallidæ and Musophagidæ is a more secondary one". Dr. Stresemann himself suggests that a common ancestor might have given rise to two branches, one the Galli and the other which subsequently gave rise to the Musophagi and Opisthocomidæ, but states that the whole question needs to be reconsidered in the light of present-day knowledge, including biology and behaviour.

If this theory is correct it would be expected that the Mallophaga found on the Opisthocomi would be related to those of the Musophagi; this, however, is not the case. It is not possible to discuss here the five genera

found on *Opisthocomus* except to say that these show no obvious relationship to the genera found on the Musophagi or Galli, but suggest that either (a) *Opisthocomi* has no close relationship with the Musophagi-Galli group or (b) that *Opisthocomi* was separated very early from the ancestral stock giving rise to the other two suborders, or (c) that the Mallophaga from this suborder have for some reason diverged more rapidly than those of the other two suborders. Either of the last two causes might result in the relationships of the Mallophaga being largely obscured.

The above note has been shown to Mr. R. E. Moreau, who suggests that there are certain biological resemblances between the Galli and Musophagi: the young are born clothed with dense down and are active from an early age. The harsh crowing or barking quality of the voices of the Musophagi also reminds one of the Galli. It is unfortunate that very little has been recorded of the breeding behaviour of any of the Musophagi, but Hoesch ("Vögel ferner Länder", 6 (1932): 115-120) had some reason to think that *Corythaeoides concolor* A. Smith might at any rate be bigamous.



RELATIONSHIPS WITHIN THE STERNINÆ AS INDICATED  
BY THEIR MALLOPHAGAN PARASITES.

By THERESA CLAY, B.Sc.

Received on 25 August 1947.

During a recent revision of the species of the genus *Sæmundsson* (Mallophaga) occurring on the Sterninæ it was found that the host distribution illustrated both the close classificatory relationships between

host and parasite, as well as the occasional completely anomalous distribution of parasite; and emphasizes further (Clay, 'Ibis', 1946: 403) that in the present state of knowledge the relationships between parasites cannot be used as an invariable clue to the relationships of the hosts. The distribution of these species raises some questions of interest to the ornithologist.

Specimens of *Sæmundssonina* have been examined from five of the seven species grouped by some authors in the genus *Thalasseus* Boie, and found to be conspecific and distinct from any other species examined; this supports the view that the host species form a group more closely related to each other than to the rest of *Sterna*. A distinct species common to the three known species of *Chlidonias* Rafinesque again suggests that the host species form a distinct and nearly related group. Mallophaga from only four of the twenty species of *Sterna* have been examined. The presence of a species of *Sæmundssonina* common to *Sterna vittata* and *Sterna paradisæa* suggests a close relationship between these two hosts and supports the supposition of Kullenberg, 'Arkiv. Zool.' 38 A (17), (1946): 77) that *S. vittata* is a relatively recent derivation from *S. paradisæa*. *Sterna hirundo* has a species distinct from, but nearly related to, the species found on the two former hosts. One point of interest is that the Mallophaga species from *S. hirundo* and *S. paradisæa* are apparently more easily distinguished than are their respective hosts. *Sterna aurantia* Gray has a species of a different type from any found on *Sterna*, but which is closely related to that on *Chlidonias*; this would suggest a relationship between the host species. The opinion of ornithologists on this point would be of interest.

A case of an inexplicable distribution is that of a species common to *Sterna hirundo* and *Gelochelidon n. nilotica*—records from Sudan, Ceylon and Rajputana. This apparent relationship between the hosts is not confirmed by species of another Mallophagan genus found on the two hosts and some other explanation seems to be needed; it is possible that the species on *Sterna hirundo* was in some way transferred to *Gelochelidon*, where it became secondarily established.

THE MALLOPHAGA AND RELATIONSHIPS WITHIN THE FALCONIFORMES.

Drs. Mayr and Amadon have recently published a paper ('Amer. Mus. Novit.' No. 1496, 1951) on the classification of the class Aves in which they show the difficulties of the classification of the higher categories and discuss some of the controversial cases. The evidence on the relationships of the Aves deduced from the distribution of their Mallophagan parasites has recently been summarized (Clay, 'Journ. Bombay Nat. Hist. Soc. 49: 430-443), but it may be of interest to discuss more fully the distribution of the Mallophaga on the Falconiformes as Mayr and Amadon raise some queries on the correct classification of this order. They discuss the possibility of a polyphyletic origin for the Falconiformes, suggesting that the Cathartae and Sagittarius (the Secretary Bird) may not be related to the rest of the order. This order is parasitized by nine genera or species groups of Mallophaga, three of which are relevant to this discussion: Falcolipeurus is a specialized genus not closely related to any other known genus and is found only on the Falconiformes; the other two, Cuculiphilus and Laemobothrion, although found elsewhere on the Aves, are represented by species groups (considered as genera by some authors) on the Falconiformes. Table 1 gives the distribution of these three genera on the two suborders, Cathartae and Falcones, of the Falconiformes. This distribution does not suggest a polyphyletic origin for the Falconiformes, and is difficult to explain except by postulating a common origin for the order as now constituted.

TABLE 1.—Distribution of three Mallophagan genera on the Falconiformes.

Parasite.	Host.	
	FALCONES	CATHARTAE
<i>Falcolipeurus</i>	<i>Sagittarius</i> Larger members of Falconoidea	<i>Cathartes</i> <i>Coragyps</i> <i>Vultur</i>
<i>Laemobothrion</i>	<i>Sagittarius</i> Widespread on Falconoidea	<i>Cathartes</i> <i>Coragyps</i> <i>Sarcoramphus</i>
<i>Cuculiphilus</i>	<i>Pseudogyps</i> <i>Gyps</i>	All genera of Cathartae

4 June 1951.

THERESA CLAY,  
British Museum (Nat. Hist.).

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A PRELIMINARY SURVEY OF THE DISTRIBUTION OF THE MALLOPHAGA ('FEATHER LICE') ON THE CLASS AVES (BIRDS). By THERESA CLAY. (*With 2 plates and 3 text figures*).

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

BY

THERESA CLAY

*British Museum (Natural History)*

*(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 parasitizing 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 parasitized 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 redshank (suborder Charadrii) both belong to the same genus (*Saemundssonina*).

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, 1949 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 *Colpocephalum* seems to be an example of such a genus; it has not been included in the mallophagan faunas shown in the distribution charts, as its presence or absence seems to be of little significance.

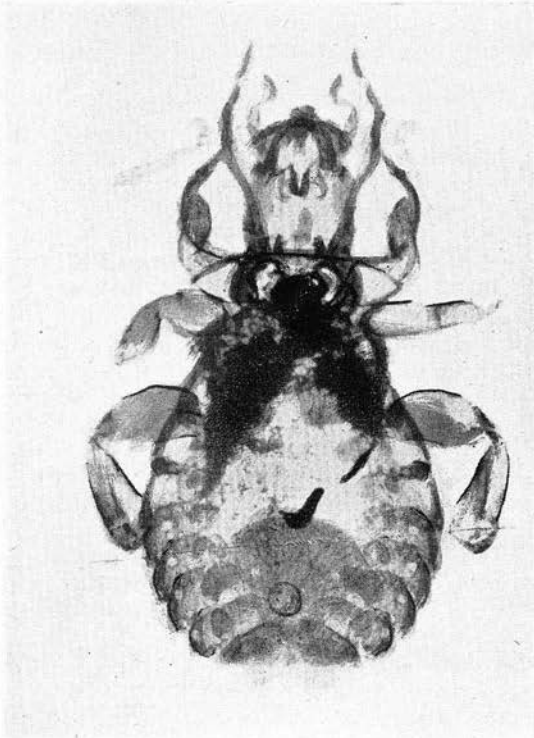
*Secondary Infestations.* Although it is probably rare for the lice of one host order to be able to establish themselves on the host of another order, there is little doubt that such secondary infestation is the explanation of some of the cases of anomalous distributions of genera. The occurrence of the same genus (*Saemundssonina*) on the Charadriiformes (waders, gulls and auks), Procellariiformes (petrels) and the Gruidae (cranes) is probably an example. Among the factors limiting the establishment of a louse 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 (1916) 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.

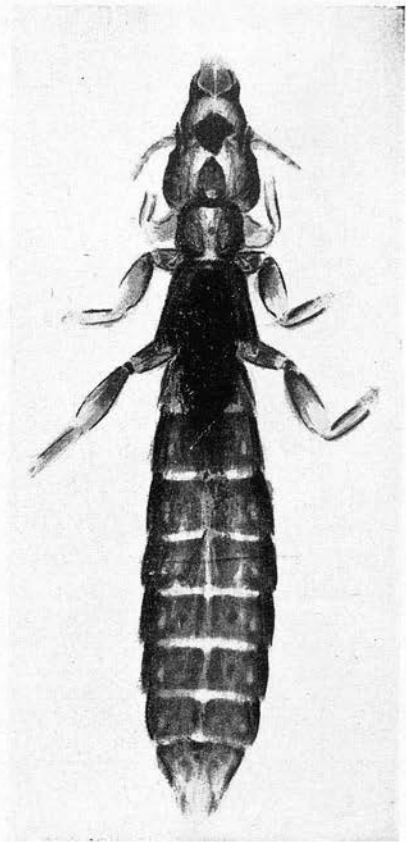
In spite of the limiting factors briefly summarised above there is no doubt that the distribution of the Mallophaga is a source of evidence which, with careful evaluation, should be utilised by the ornithologist in considering the position of birds of doubtful affinities. It is important to note, as will be made clear below, that in those cases where a bird has an anomalous mallophagan 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 (*Struthiolipeurus*) of Mallophaga found on no other order of birds, and also by the same two species of mites (*Paralges pachycnemis*



1. Occupant of head niche  
(*Philopterus* sp.)



2. Occupant of wing niche  
(*Fulicoffula* sp.)

and *Pterolichus bicaudatus*) and subspecies of the same cestode (*Houttuynia struthiocameli*) (Eichler, 1948). Lowe (1928, 1935, 1942) from studies not only of the structure of the feathers, but of many other anatomical features concluded that the Struthioniformes (= Struthioniformes, Rheiformes, Casuariiformes and Apterygiformes) 'represent a perfectly natural group descended from some common ancestor' (1928:244). The relationship between the Struthioniformes and Rheiformes is amply 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 (*Dahlehornia*) is known, which has no obvious relationship to any other. The fact that both this genus and that from the Struthioniformes and Rheiformes show asymmetry of the head has encouraged some authors to deduce a relationship between the three host orders, but *Dahlehornia*, as shown by its general morphology, is not closely related to *Struthiolipeurus*, and asymmetry of the head is found in another unrelated genus (*Bizarrifrons*) 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.

**Apterygiformes** (Kiwis). Chandler on account of the feather structure and Lowe on other anatomical features placed this order near the three orders already discussed. Although only one genus *Rallicola* (*Aptericola*) is known from this order and little, therefore, can be deduced from its presence, it is of some interest that *Rallicola* is found also on the Rallidae. This distribution supports the belief of Fürbringer (1888) that there is a relationship between apteryx 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 (:347): '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.' Fürbringer (1888), Beddard (1898), 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 Palaeognathae, together with the four orders already considered. Evidence from the Mallophaga is here of little assi-

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<sup>1</sup> 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 faunas 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 (Heptapsogastridae) found on no other orders of birds<sup>1</sup> and which are presumably the descendants of a common ancestor parasitic 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 Columbæ; and also bear a superficial resemblance to these species in some other characters. The species on the Galli and Columbæ 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, Columbæ, 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 descendents 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 (*Tinamotaecola*) which belongs to a sub-family (Degeeriellinae) 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) [*Colymbiformes* of European authors] and *Colymbiformes* (Grebes) [*Podicipidiformes* 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 (15) of genera, the majority of which are peculiar to the order, and probably developed from a common ancestor on the order. One genus (*Saemundssonina*) is also found on the Charadriiformes, and a second genus (*Procellariiphaga*) either superficially resembles or is related to one (*Austromenopon*) 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 Phaëthontes (Tropic-birds), the Pelecani (Pelicans, Gannets, Cormorants) and the Fregatae (Frigate-birds). Figure 1 shows that

<sup>1</sup> The occurrence of one species of this family on the Cariamidae is probably due to secondary infestation.

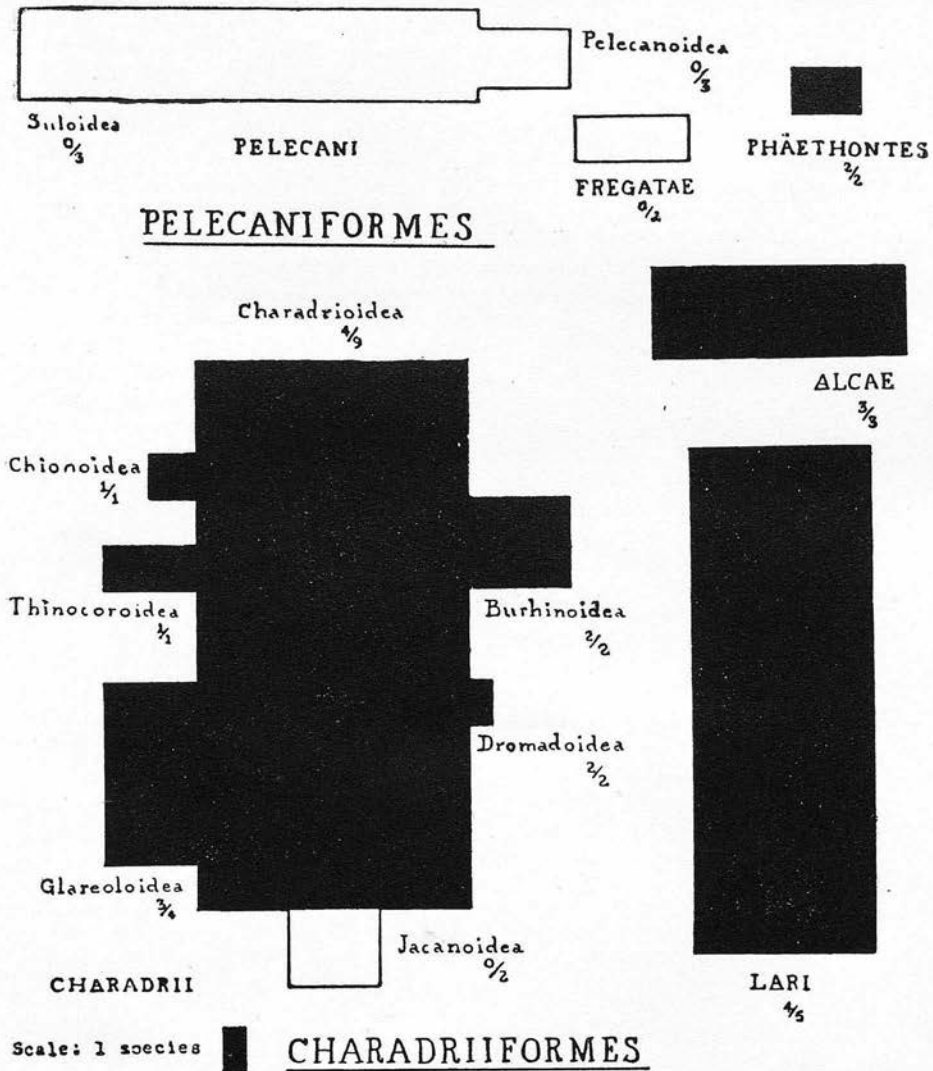


Fig. 1. Pelecaniformes and Charadriiformes (Mallophagan fauna: 4, black).

(See footnote on p. 438).

(For explanation of chart see p. 442).

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 Iredale (1921) basing their conclusions on the anatomy of the Phaethontes placed them as a family of the Lari. Lowe (1926) 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 (1936:796) 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 habitus from all their existing relatives, and share many superficial characters with the terns. 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, 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 the lice in question (*Saemundssonina*) 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 *Saemundssonina*, 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** (Hérons, Storks, Ibises and allies). This order is usually divided into four suborders: the Ardeae, Balaenicipites, Ciconiae and Phoenicopterii. Of the eight genera of Mallophaga (omitting *Colpocephalum*) found on the Ciconiiformes only two (*Ciconiphilus* and *Ardeicola*) are common to the Ardeae (Hérons, Bitterns) and Ciconiae (Storks, Ibises, Spoonbills); only one of these (*Ciconiphilus*) is known from the Balaenicipites (Whale-headed Stork), but little collecting has been done from this last suborder; the Phoenicopterii (Flamingoes) have none of the genera found on the rest of the Ciconiiformes. The Scopioidea (Hammerhead), usually regarded as a superfamily of the Ciconiae has (apart from a somewhat aberrant species of *Colpocephalum*) two genera (*Quadriceps* and

*Austromenopon*) found elsewhere throughout the Charadriiformes, a distribution which may or may not be of significance (see Hopkins, 1942:103). One genus (*Ciconiphilus*) found on the Ciconiiformes is also found on *Cygnus* (Swans: Anseriformes) and another (*Ibidoecus*) characteristic of the Threskiornithoidea (Ibises) is also found on *Aramus scolopaceus* (Limpkin: Gruiformes); a third genus (*Laemobothrion*) found on some of the Threskiornithoidea is again found on *Aramus*, but this genus has a wide distribution with species on the Rallidae (Rails), Psophiidae (Trumpeters), *Opisthocomus* (Hoatzin) and less closely related species on the Falconiformes (Birds of Prey). The distribution of these genera suggests that *Ciconiphilus* may be a straggler on the swans from the Ciconiiformes, *Ibidoecus* a straggler on *Aramus* from the Threskiornithoidea and *Laemobothrion* a straggler on this latter superfamily from the Rallidae. Although Eichler (1949) suggests that the mallophagan fauna of *Aramus* (fig. 1) may indicate a position for this family between the Rallidae and Threskiornithidae.

The Phoenicopterii (fig. 2) are parasitized by three genera found elsewhere only on the Anseres (Ducks, Geese, Swans). Chandler (1916:320) states: 'that in the details of the minute structure of the feathers the Phoenicopterii agree with the Anseres more closely than

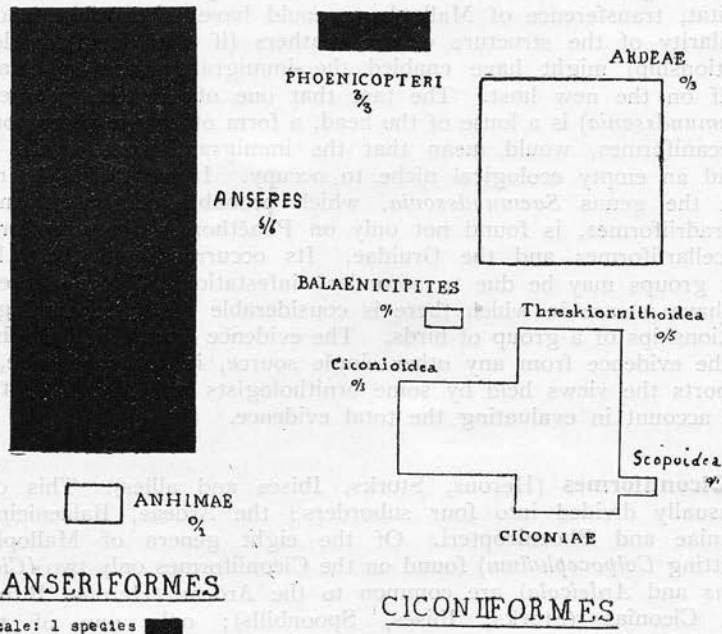


Fig. 2. Anseriformes (Mallophagan fauna: 5, black. Genera of Acidoproctidae counted as one) and Ciconiiformes.

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

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 straighter bill (Howard, 1950). On the other hand, the similarity of feather structure (if this does not denote relationship) might have allowed immigrant lice 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 mallophagan 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 (Screamers). The former have five genera of Mallophaga, two of which (*Holomenopon* and *Ornithobius* and its closely related genera or subgenera) are found only on the Anseres and three others (*Anaticola*, *Anatoecus* and *Trinoton*) found elsewhere only on the Phoenicopteriformes. The Mallophaga 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 mallophaga parasitizing this order is that a species of a genus found elsewhere in the Falconiformes only on the Cathartae (New World vultures) has been taken from *Pseudogyps africanus*<sup>1</sup>, 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, 1950). The Falconiformes have other genera which show a somewhat inexplicable distribution and which are mentioned here without further comment. One genus (*Kurodia*) is also found elsewhere only on the owls (Strigiformes) and another (*Cuculiphilus*) is found elsewhere only on the cuckoos (Cuculiformes).

**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 mallophagan fauna of the Galli (Game Birds) suggests affinities between the Galli and the Columbae (Pigeons, Doves) and the Galli and the Musophagi (Plantain-eaters). The Opisthocomi (Hoatzin) 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, *Laemobothrion*, 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

<sup>1</sup> Also from *Gyps fulvus*, see Eichler, 1944. *Dtsch. ent. Z.*, 1943:57.



other (*Syrrhaptes*) belongs to the widespread *Degeeriellinae*. The *Columbae* have a number of genera a group of which (*Coloceras*, *Campanulotes* and related genera) have obvious affinities with two (*Goniodes* and *Goniocotes*) found on the Galli. Chandler states that in feather structure the *Columbiformes* 'show more similarities to the gallinaceous birds than to any other group', and as the mallophagan 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 *Musophagi*, with four out of five mallophagan genera either the same or closely related to those found on the Galli, seem to show a definite relationship to the Galli and none to the Cuculi. 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 Cuculi and *Musophagi* cannot be placed in the same order. Chandler states that: 'the *Musophagidae* do not differ in any important ways from the *Cuculidae* in the structure of their feathers', but he continues 'the Cuculi (= *Cuculiformes*) especially the *Musophagidae* come nearer the gallinaceous and columbid birds.'

**Gruiformes** (Cranes, Rails and allies) and **Charadriiformes** (Waders, Gulls and Auks). These two orders are taken together as both the anatomical evidence (Lowe, 1931:531, Chandler:353) and the fossil record (Howard, 1950) 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 a 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 re-arrangement based on the mallophagan faunas of the suborders.

The suborder *Grues* is usually divided into two superfamilies: the *Ralloidea* (Rails) and *Gruoidea*. The former has a mallophagan fauna comprising five genera; two of these genera are found also on the *Psophiidae* (Trumpeters) and three of them on the *Aramidae* (Limpkins), both these families usually being included in the second superfamily, the *Gruoidea*. The *Gruidae* (Cranes), the third family of the *Gruoidea*, has a mallophagan fauna of four genera, none of which is found on the other families of the suborder *Grues*, nor the *Ralloidea*. From the *Heliornithes* (Sun-grebes) and the *Rhynocheti* (Kagus)—two other suborders of the *Gruiformes*—genera of the ralline mallophagan fauna have been recorded. The *Jacanoidea* (Jacanas), a group of birds with an obscure systematic position but usually placed with the *Charadriiformes*, have two genera belonging to the

ralline fauna<sup>1</sup>. These facts suggest that the Ralloidea, Aramidæ, Psophiidae, Heliornithes, Rhynocheti and Jacanoidea are more nearly related to each other than to the Gruidae. Evidence on the relationships between these groups from ornithological sources is conflicting. Chandler (:354) deduces from the feather structure a relationship

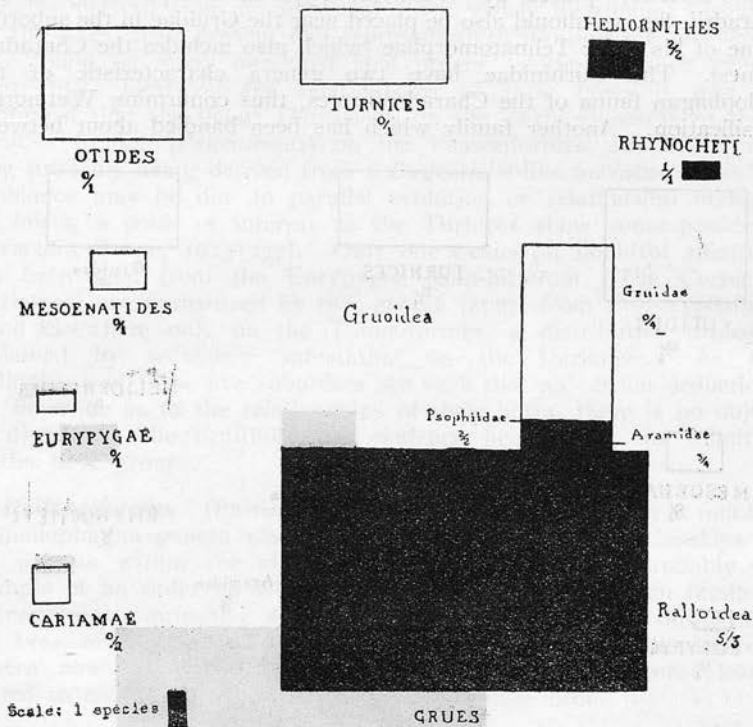


Fig. 3. Gruiformes arranged according to Wetmore, 1940 (Mallophagan fauna of Ralloidea: 5, black).

between the Gruidae, Aramidæ and Rallidae and considers them offshoots from a primitive stem leading to the Charadriiformes; while the Otididae, Psophiidae (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 Galli. This, as shown above, is in conflict with the evidence from the mallophagan faunas. Lowe (1931:496), however, considers that the Rallidae and the Heliornithidae are an isolated group and should be removed from the Gruiformes to form a separate order, the Ralliformes. This view is partly supported by the distribution of the Mallophaga, but the Ralliformes would have to include some of the families which were retained in the Gruiformes by Lowe. This latter author (1925) considers that

<sup>1</sup> Evidence has recently become available (Timmermann, in press and Tandan, in press) that the Jacanoidea also have three genera (*Quadriceps*, *Saemundsonia* and *Actornithophilus*) characteristic of the Charadriiformes.

the affinities of the Jacanoidea are not with the Charadriiformes, but with the Gruiformes; later (1931) he places them with the Gruidae not with the Rallidae in his new order the Ralliformes. Evidence from the Mallophaga of the Jacanidae, however, suggests ralline not gruimorphine 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

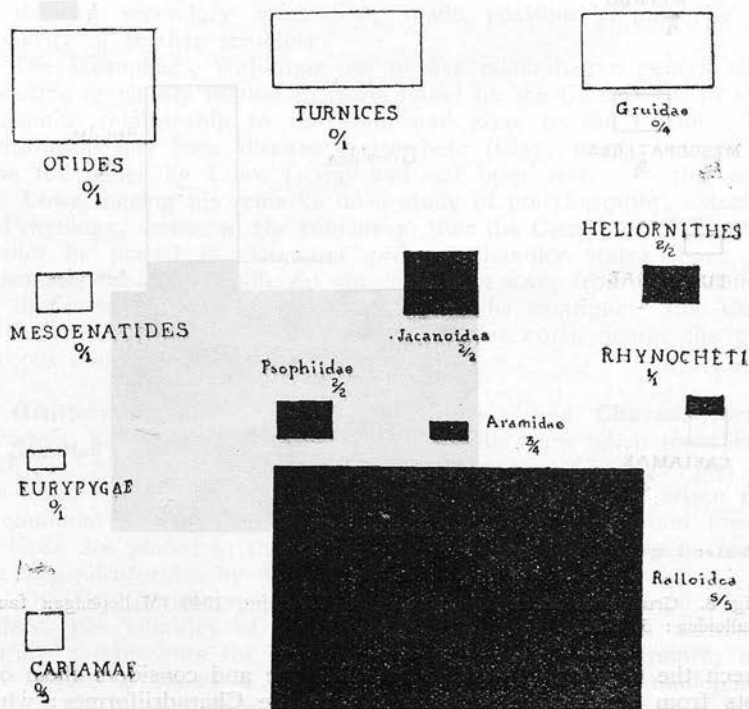


Fig. 4. Gruiformes re-arranged according to the Mallophagan fauna. Scale as in fig. 3.

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 Rallidae. 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 Otides (Bustards)

have one genus (*Otidocetus*), the nearest relatives of which are found on the Galli (*Cuclotogaster*) and on the Scolopacidae—the snipe and woodcock—(*Rhynonirmus*). These genera are perhaps relics of a previously more widely distributed group of genera. The Mesoentatides (Monias) and the Turnices (Bustard-quails, Hemipodes) 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 Degeeriellinae 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 Turnices seems to show affinities to one (*Penenirmus*) on the Passeriformes, the latter also most probably being derived from a *Degeeriella*-like ancestor. This resemblance may be due to parallel evolution or relationship between the hosts, a point of interest as the Turnices show some passerine characters (Lowe, 1923:277). Only one genus (of doubtful affinities) has been seen from the Eurypygae (Sun-bitterns). The Cariamae (Cariamias) are parasitized by two genera (apart from *Colpocephalum*) found elsewhere only on the Tinamiformes, a distribution probably explained by secondary infestation on the Cariamae. 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.

**Psittaciformes** (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 Ischnoceran 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 (*Cuculicola*) belonging to the widespread Degeeriellinae, two of which the affinities are obscure, and one other (*Cuculiphilus*), 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 (*Kurodia*) 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 Apodi (Swifts), the Mallophaga of which give no evidence as to relationship, and the Trochili (Humming-birds). The latter suborder is parasitized by one genus (or two closely related genera, *Ricinus* and *Trochiloecetes*) found also on the Passeriformes (Perching Birds). Chandler (:379) states that the structure of the feathers shows a striking likeness to those of the latter order. Lowe (1939) 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 (Trogons) are parasitized by two genera (*Myrsidea* and *Brüelia*) characteristic of the Passeriformes. Again, Chandler (:378) 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 Alcedines the superfamily Alcedinoidea (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 (*Brüelia* and *Philopterus*) have been taken from the Momotoidea (Motmots) both of which belong to the passerine fauna. In the suborder Meropes (Bee-eaters) one (*Brüelia*) of the three mallophagan genera belongs to the passerine fauna. In the suborder Coracii, the family Coraciidae (Rollers) is parasitized by two genera, one (*Meromenopon*) which is found elsewhere only on the Meropidae, and the other (*Capraiella*) is closely related to one on the Passeriformes (*Picicola*), but is of a generalized type (the Degeeriellinae) found elsewhere in the class Aves. No Mallophaga have been seen from the Leptosomatidae (Cuckoo-rollers). The Upupidae (Hoopoes) have two genera (*Upupicola* and *Menacanthus*) belonging to the passerine fauna, but both belong to groups of genera found elsewhere. The Phoeniculidae (Wood-hoopoes) have two genera, one (*Hophsiella*) probably related to *Upupicola* on the Upupidae and the other (*Odoriphila*) the affinities of which are not known. The Bucerotidae (Hornbills) have six genera, none of which belong to the passerine fauna, but the Ischnoceran genera are all probably derived from a single ancestral stock which belonged to the Degeeriellinae, a genus of which is found on the Passeriformes. Chandler shows that in feather structure the Alcedinoidea and the Bucerotes 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 Galbuloidea from which nothing has been seen) have an entirely passerine mallophagan fauna which supports the evidence put forward by Chandler and Lowe (1946) 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 Pici, Trogoniformes

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<sup>1</sup> *Austrophilopterus* from the toucans is not found on the Passeriformes, but like *Picicola* of the latter order is probably derived from a Degeerielline ancestor.

and Momotidae, and a less close passerine connection for the Trochili, 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 Alcedinoidea 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,<sup>1</sup> 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, 1946) 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 subspecific rank. The names of orders are given in large capitals underlined, suborders in smaller capitals, superfamilies in large 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. *Colpocephalum*, 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: *Bizarrifrons* and *Sturnidoecus*, 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 *Sturnidoecus* on the Icteridae (Troupials).

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<sup>1</sup> No attempt has been made to show the relationship between superfamilies within a suborder.

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REVISIONS OF THE GENERA OF MALLOPHAGA.  
I. THE *RALLICOLA*-COMPLEX.

BY

THERESA CLAY,  
British Museum (Natural History).

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Revisions of the genera of Mallophaga.—I. The *Rallicola*-complex.

By  
 THERESA CLAY,  
*British Museum (Natural History).*

[Received 23rd July 1952.]

(With Plate I and 57 figures in the text.)

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INTRODUCTION.

There are a number of species belonging to the superfamily Ischnocera in which the females have one to three stout setae borne on a ventral tubercle each side of segment IX of the abdomen. Seven genera or subgenera have been erected to include the known species as follows :—

Genus	Type species	Host distribution*
<i>Rallicola</i> Johnston & Harrison, 1911.	<i>R.</i> " <i>attenuatus</i> (Nitzsch)". = <i>R. ortygometrae</i> (Schrank). (Figs. 1-4.)	Rallidae. (GRUIFORMES.)
<i>Parricola</i> Harrison, 1915	<i>P. sulcata</i> (Piaget). (Figs. 5-8.)	Jacaniidae. (CHARADRIIFORMES.)
<i>Aptericola</i> Harrison, 1915.	<i>A. gadowi</i> Harrison. (Figs. 9-11, 45.)	APTERYGIFORMES.
<i>Wilsoniella</i> Eichler, 1940.	<i>W. absitus</i> (Kellogg). (See Guimarães, 1940, 307, figs. 17-24.)	Opisthocomidae. (GALLIFORMES.)
<i>Furnaricola</i> Carriker, 1944.	<i>F. acutifrons</i> Carriker. (Figs. 12-13.)	Furnarioidea. (PASSERIFORMES.)
<i>Corvicola</i> Carriker, 1949.	<i>C. insulanus</i> Carriker.	Corvidae. (PASSERIFORMES.)
<i>Epipicus</i> Carriker, 1949.	<i>E. scapanoides</i> Carriker.	Picidae. (PICIFORMES.)

Apart from species parasitizing the above hosts, specimens have been seen from the following hosts and host groups :—

*Aramus*, *Psophia*, *Rhynochetos* (GRUIFORMES).

*Centropus* species (CUCULIFORMES).

*Macgregoria pulchra* (PASSERIFORMES).

*Eurylaimus ochromelas* (PASSERIFORMES). These are the types of *Rallicola unguiculatus* (Piaget) 1880 collected from a skin; it is possible that *Eurylaimus* is not the true host.

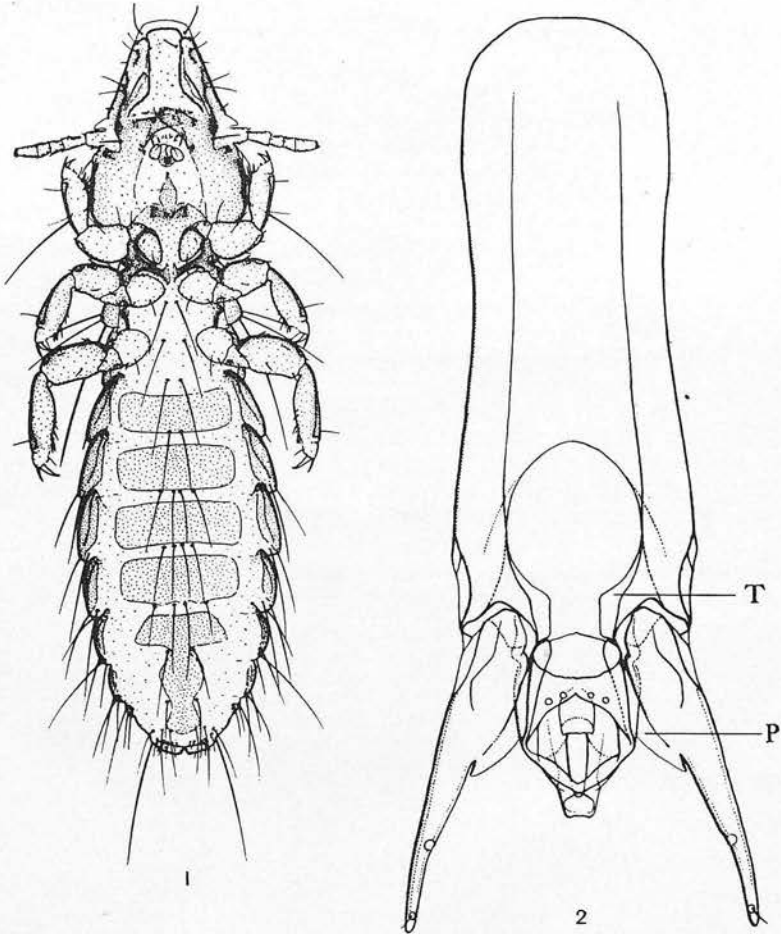
The single species in *Wilsoniella* differs from all the other species in the form of the marginal carina which is interrupted laterally each side, the absence of

\* Classification of hosts according to Wetmore, 1940.

the post-spiracular setae on segment VII, and in the position of the setae-bearing tubercles. *Wilsoniella* can be considered as a distinct genus and will not be further discussed. The other species have the following characters in common:

*Head\**.—Marginal carina always interrupted medially, that is, there is never a complete carina round the anterior margin of head; marginal carinae never interrupted laterally (with the possible exception of *Furnaricola cephalosa*, but only figure seen); dorsal preantennal suture, when present, originates at

Figures 1 and 2.



*Rallicola ortygometrae* (Schrank).

1. Male. 2. Male genitalia.

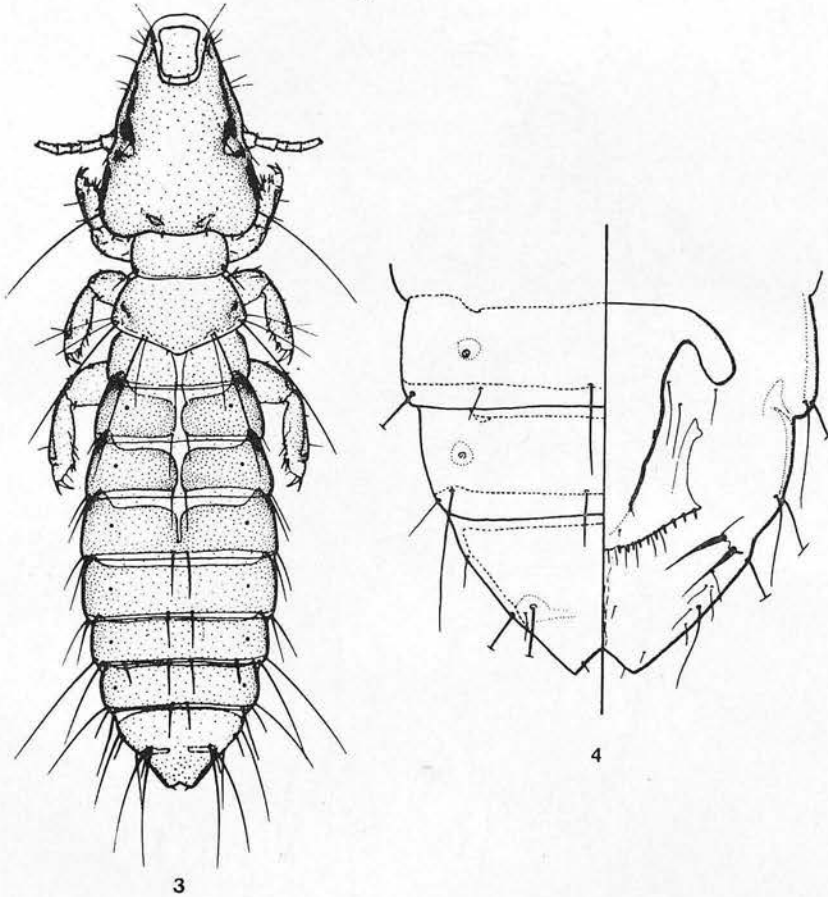
distal end of marginal carinae; dorsal anterior plate usually present with rounded, flattened or pointed posterior margin, never prolonged into a thickened posterior point. Ventral carina always interrupted medianly, and carried forward and fused to distal end of marginal carina each side; pulvinus with lobes attached to the flattened parallel edges of the ventral carinae. Gular plate developed. First marginal temporal seta may or may not be on lens; never

\* For terminology of head see Clay, 1951.

more than one elongated marginal temporal seta (the 4th) each side (as in *Brüelia* and *Sturnidoecus*; the *Degeeriella*-complex, *Penenirmus* and *Philopterus* always have at least two elongated marginal temporal setae each side).

*Abdomen\**.—In the male, segments IX–X are fused and never separated from XI by a definite suture, although in at least one species (that from *Porphyrio madagascariensis*, fig. 23) tergal plates IX–X are separated from

Figures 3 and 4.



3. Female. 4. Terminal segments of female abdomen.

*Rallicola ortygometae* (Schrank).

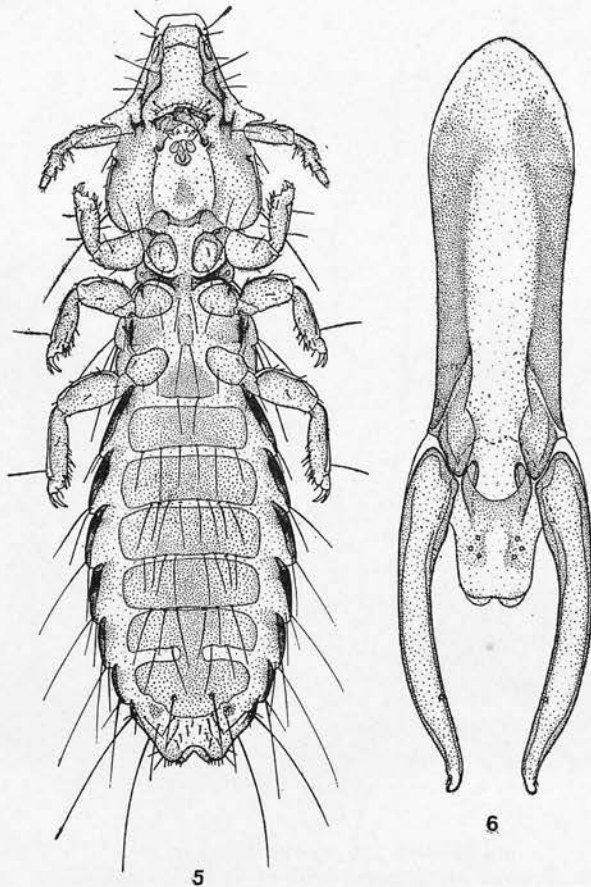
tergal plate XI. Tergal plates IX–X always continuous across the segment and not greatly narrowed medianly as in *Brüelia* (fig. 22). Male genital opening terminal or dorso- or ventro-terminal, rarely on the dorsal surface. If the opening is dorsal then the distance between marginal setae of X and edge of opening always considerably greater than between latter and terminal margin of abdomen (cf. figs. 21 and 22). In the female the fused segments IX–X are never fully separated by a suture from XI and the tergal plates IX–XI are always continuous across the segment. Female with edge of vulva set with fine setae and small spine-like setae and with tubercle on ventro-lateral edge of

\* For the purposes of this paper the apparent first segment of the abdomen is referred to as abdominal segment II and the apparent eighth as the fused abdominal segments IX–X.

segment IX bearing one to three long, stout setae. Post-spiracular setae usually present on segments VII and VIII only,

The above characters distinguish this group of species from all other known Ischnocera. Apart from these there are other characters which show variation throughout the group and it is the object of this paper to discuss the variation and to decide whether it can be used as a basis for generic differentiation. It is natural that the species of Mallophaga from host groups containing a small number of closely related species should form a compact and homogeneous group.

Figures 5 and 6.



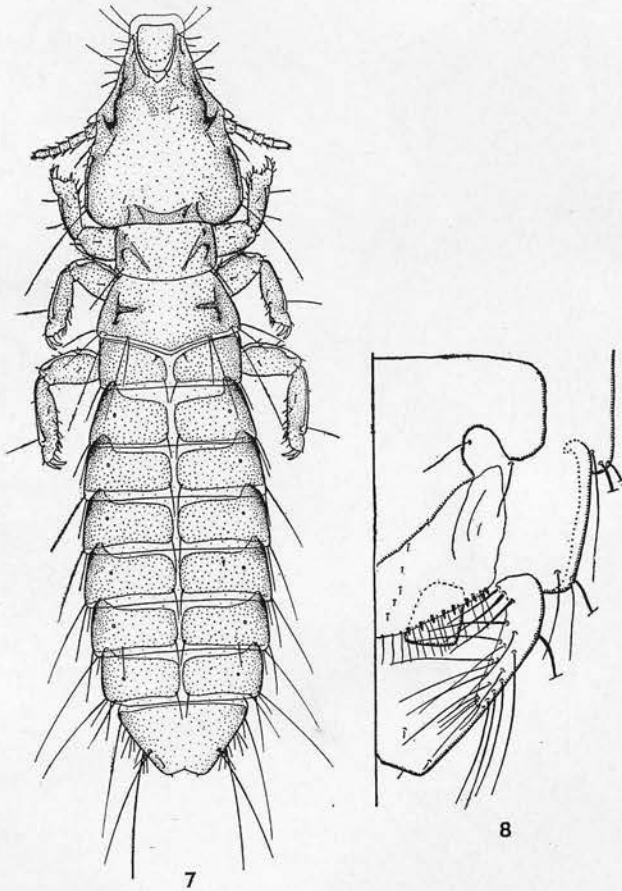
5. *Rallicola sulcatus* (Piaget).  
5. Male. 6. Male genitalia.

Fortunately, in the case of the *Rallicola*-complex, it is possible to consider the variation in the species parasitizing a family of hosts—the Rallidae—containing a large number of somewhat diverse members. This host family (according to Peters, 1934) contains 132 species belonging to 52 genera; specimens of *Rallicola* have been examined from forty-seven of these species belonging to twenty-five genera. Thus, an analysis of the characters found in this group of species parasitic on related hosts will give some idea of the range of variation within one of the genera of the *Rallicola*-complex, namely *Rallicola*, sens. str.

VARIATION IN THE *RALLICOLA* SPECIES PARASITIZING THE RALLIDAE

*Head.*—The characters of the dorsal preantennal region vary considerably in this group: the dorsal preantennal suture may be absent (fig. 14), or visible only at the lateral edges and not forming a complete suture across the head (fig. 15), or it may be well defined, cutting off a distinct dorsal anterior plate (fig. 16). Thus, there is a series showing increased specialization of the head rather similar to that in *Brüelia* (see Clay, 1951, 186), but in *Rallicola* there is

Figures 7 and 8.

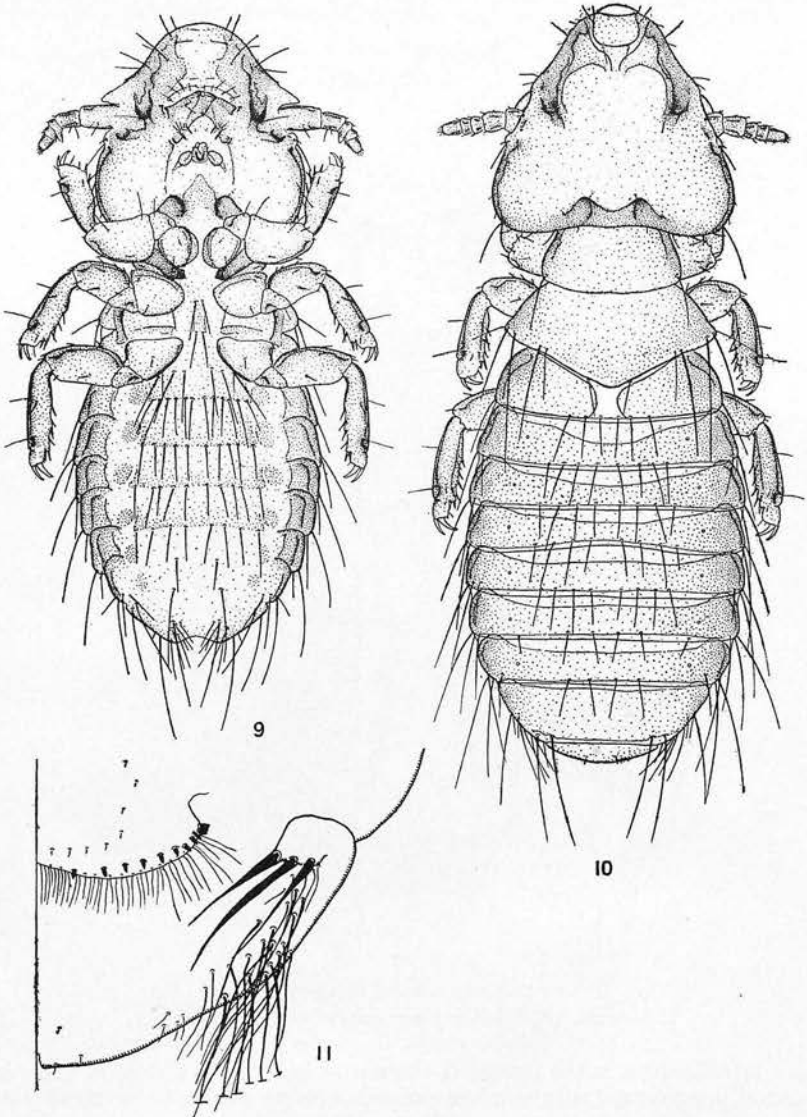
*Rallicola sulcatus* (Piaget).

7. Female. 8. Terminal segments of female abdomen.

never a lateral break in the marginal carinae (as in some species of *Brüelia*) and the dorsal preantennal suture, when present, always arises at the distal end of the laterally unbroken marginal carinae. The hyaline margin may be absent (fig. 15), small (fig. 14), or broadly extended (fig. 16); it may arise at the distal end of the marginal carinae (fig. 14) or some way posteriorly on the lateral margin (fig. 31) and is often continued some considerable distance posteriorly as a thin covering (fig. 16). The dorsal anterior plate may be well defined (fig. 16) or not defined (fig. 14). In the species from *Gymnocrex plumbeiventris* the anterior part of the anterior plate is striated; in some species which are

otherwise well pigmented the anterior plate is only slightly so. The anterior dorsal setae may be on the posterior margin of the anterior plate (fig. 16) or within the dorsal suture (*R. flavescens*). The characters of the ventral carinae are basically similar throughout the group, but the position of the point of

Figures 9-11.



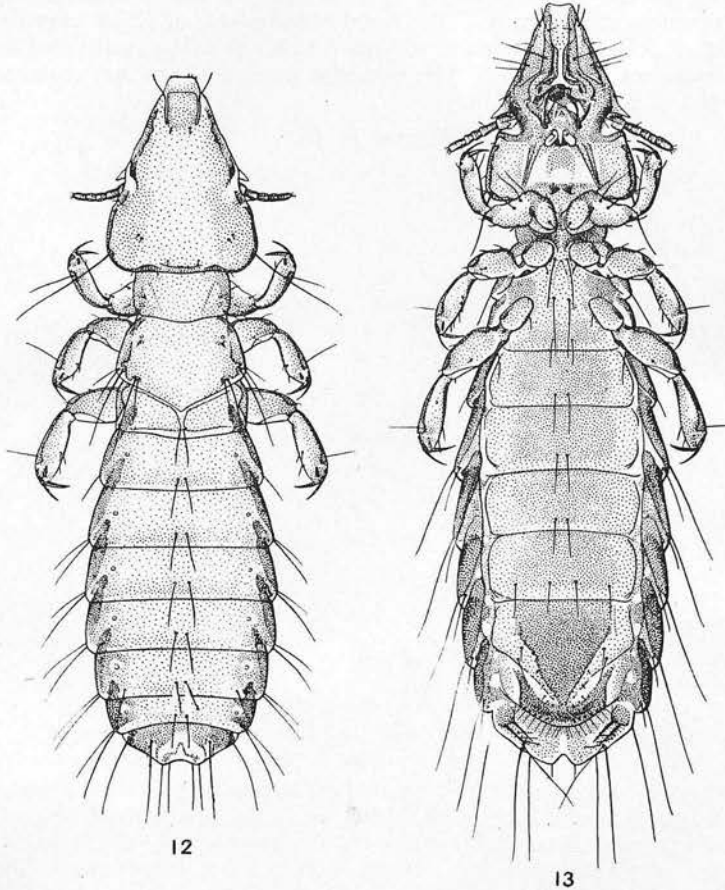
*Rallicola gadowi* Harrison.

9. Male. 10. Female. 11. Genital region of female.

fusion between the ventral and marginal carinae varies: it may be at the level of the origin of the dorsal preantennal suture (fig. 16) or some way anterior to this (fig. 31). In many species there is a small more heavily pigmented area between the ventral and marginal carinae near their distal points of fusion

(fig. 16, S); in others it is not apparent. There may be a slight indication of dorsal carinae (*R. cuspidatus*), and also various thickenings arising from the marginal carinae in the preantennal region. Temporal carinae may be present (species from *Sarothura lineata* (fig. 31)), but are usually absent.

Figures 12 and 13.



*Rallicola subsimilis* (Carriker).

12. Male. 13. Female.

The two anterior tergal setae usually present on abdominal segment II cannot be seen in either of the two available specimens (in poor condition) of this species.

It should be unnecessary to discuss the sexual dimorphism of the antennae except that it is still used by some authors as a generic character. The species parasitizing the Rallidae show all grades of sexual dimorphism of the antennae: it may be absent (figs. 1, 17), the male may have segment I slightly enlarged (*R. bisetosus*), or considerably enlarged with the distal post-axial angle of segment III slightly (fig. 18) or markedly prolonged (fig. 19); segment I may have a stout seta borne on a hyaline (fig. 19) or a sclerotized, distally bilobed process (fig. 20).

*Thorax*.—This shows no special features and is similar throughout the group.

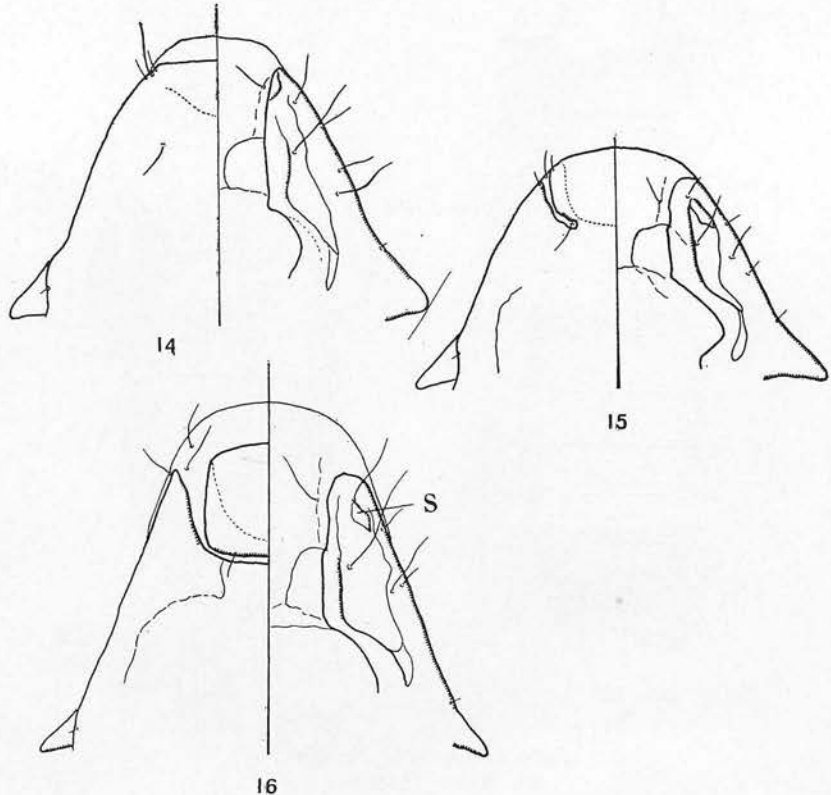
*Abdomen*.—*Tergites*: In both sexes these plates show variation. In the male, tergite II seems to be always at least partially divided medianly. In *R. lugens*



the remaining tergites form continuous plates across the segments, in other species, II, III, or IV may be interrupted medianly. The fused tergal plates of IX-X may be partially or completely (fig. 23) divided from that of XI.

In the female tergites II and III seem to be always medianly interrupted; the remaining tergites may be in the form of continuous plates (*R. lugens*), or II-V may be completely or partially (*R. ortygometae*) interrupted, or II-VII (*R. fulicae*) or II-VIII (one of the species from *Porphyrio madagascariensis*) may be interrupted medianly. The fused tergal plates of IX-X may be fused with that of XI (species from *Sarothura lineata*) or partially divided (species from *Limnocorax flavirostris*). The posterior margin of the last segment may be flattened or bifid.

Figures 14-16.



Heads of *Rallicola* spp.

14. *Rallicola lugens* (Giebel). 15. *R. minutus* (Nitzsch). 16. Species from *Rallus elegans levipes* Bangs.

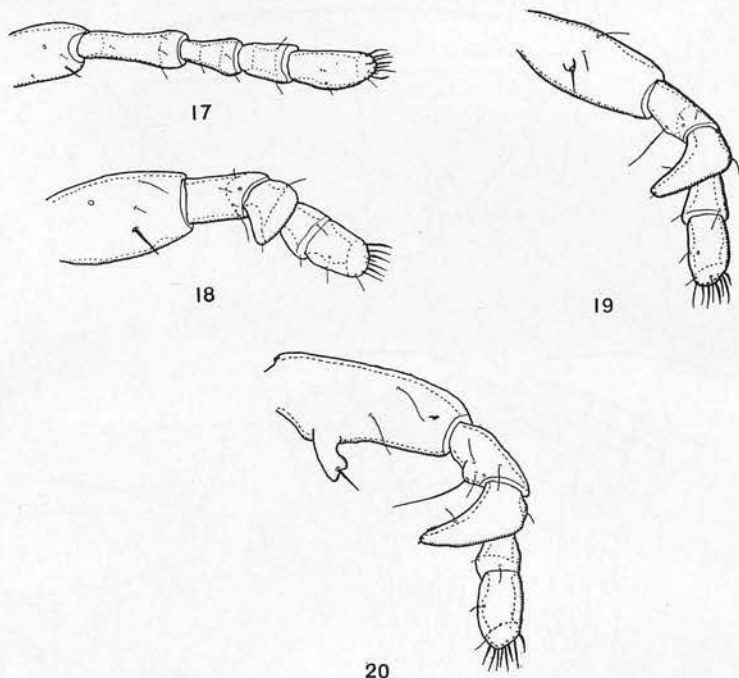
*Sternites*.—In the male the sternal thickening is in the form of median plates, with those of the posterior segments fused to form an irregular-shaped genital plate (fig. 1); in some species this plate is not apparent.

In the female the sternal thickening of some species is in the form of median plates which are lobed laterally; in others the lobe is detached and the sternal thickening is in the form of a median plate with a small rounded lateral plate each side (species from *Megacrex*), in others the median plate is apparently absent and segments II-VI show only the small lateral plate (*R. minutus*).

*Female Genital Region*.—In its characteristic form the genital plate has two lateral lobes anteriorly (fig. 35), but in some species the lobes are separated from

the plate and appear as irregular-shaped sclerites each side. The stout setae borne on lateral tubercles, which are characteristic of the genus, vary in number from two to three each side; in some species the number cannot be used as a specific character as it varies from specimen to specimen and from side to side of the specimen.

Figures 17-20.



Male antennae of *Rallicola* spp.

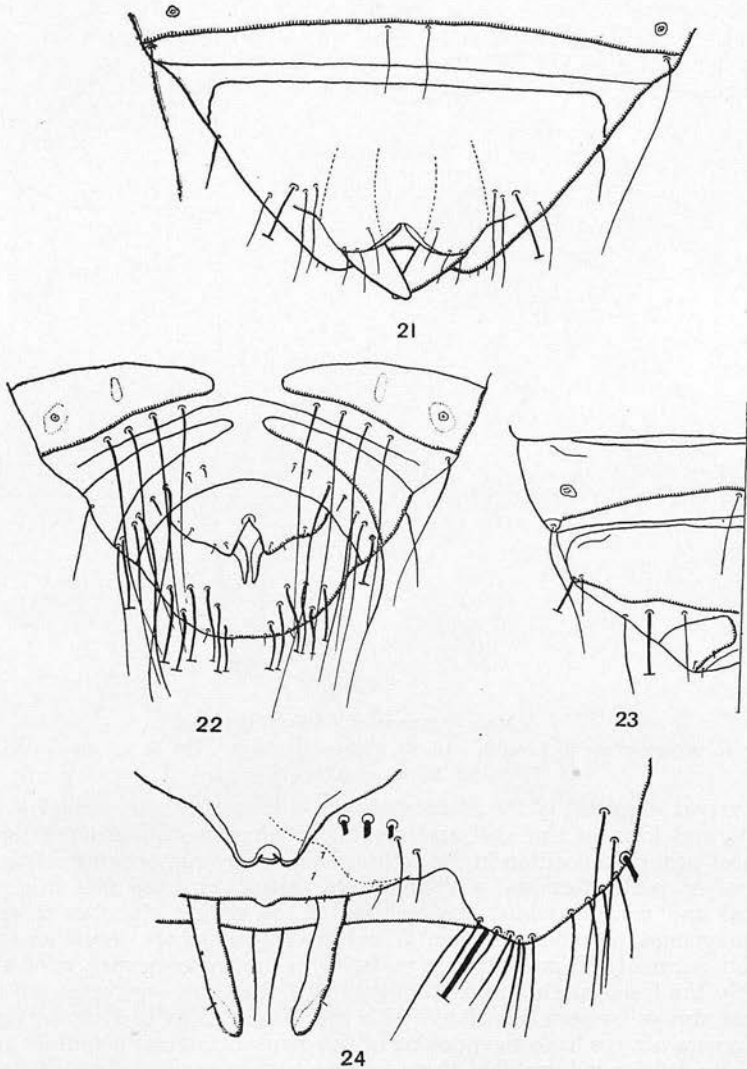
17. *R. ortygometae* (Schrank). 18. *R. fulicae* (Denny). 19. *R. sarothurae* sp. n.  
20. *R. lugens* (Giebel).

*Terminal Segments of the Male Abdomen.*—There is some variation in the position and form of the anal and genital openings in this group of species. The most primitive position in the Ischnocera for the anal opening seems to be terminal or ventro-terminal with the three associated setae (the anal setae) terminal and ventral, whilst the opening of the genital chamber is ventral. In some genera, however, the genital and anal openings are dorsal on what is probably segment XI, immediately posterior to the posterior margin of what is probably the fused ninth and tenth segments; the three anal setae are dorsal and can always be seen associated with the openings (as in *Brüelia*, fig. 22). Some genera always have the opening of the genital chamber definitely ventral and others definitely dorsal, but there are a number of genera, of which *Rallicola* is one, in which the species may have the opening terminal, dorso- or ventro-terminal or even dorsal; the condition apparently depending on the relative development of the dorsal and ventral abdominal sclerites with which the openings are associated. In *Rallicola* the usual position of the anus is dorso-terminal with the anal setae dorsal and the opening of the genital chamber terminal (fig. 33), but in some species (fig. 21) the openings are dorsal and approach the condition found in *Brüelia* (fig. 22). Again, in some species (fig. 24)\*, the tergum (? epiproct) is prolonged so that one or more of the anal setae are internal.

\*In the reproduction of fig. 24 the anal setae have been lost; they should lie on the dotted line.

The end of the male abdomen may be modified in various ways: in the species from *Amawornis akool* the dorsal margin of the last segment has a median point; in those from *Gallinula chloropus*, *Limnocorax flavirostris*, *Rallina tricolor* and *Sarothura lineata* (fig. 33) the ventral margin of the last

Figures 21-24.



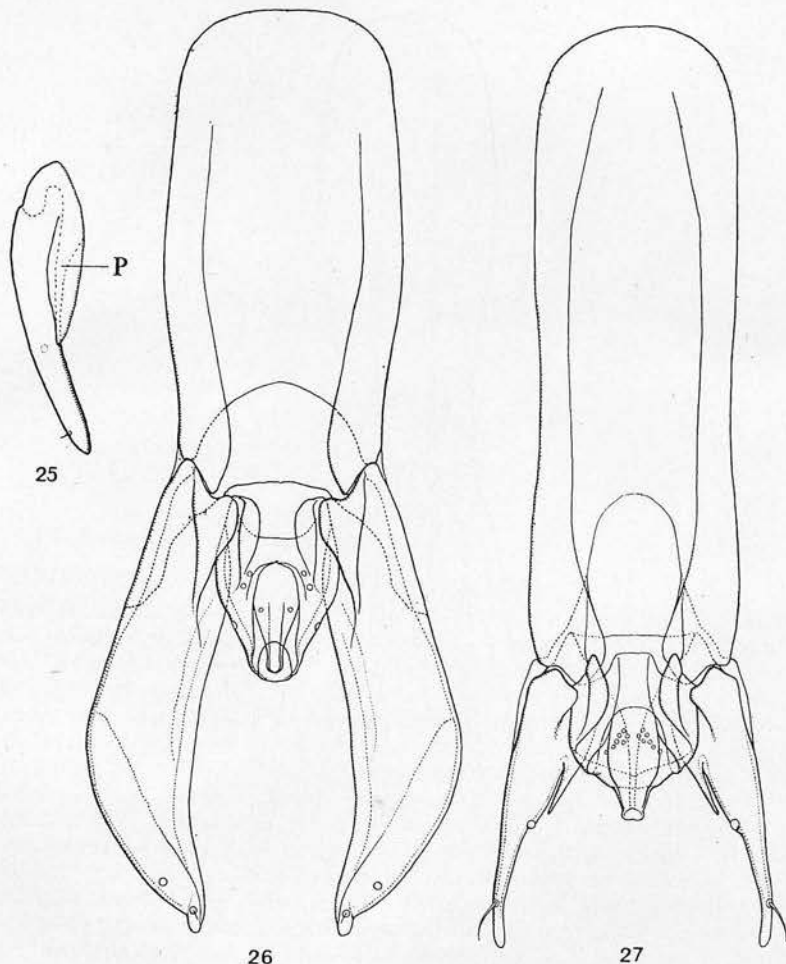
Terminal segments of abdomen.

21. *Rallicola cuspidatus* (Scopoli), dorsal. 22. *Brüelia* species from *Corvus corax* Linn., dorsal. 23. *Rallicola* sp. from *Porphyrio madagascariensis* (Latham), dorsal. 24. *R. andinus* Carriker, ventral.

segment has a small median point and in that from *Porzana tabuensis* it is longer and heavily pigmented. In the species from *Fulica americana* (fig. 54), *Gymnocorax plumbeiventris* and *Tribonyx mortieri* segment VIII (or IX) has a well-developed ventral median lobe; in other species (that from *Gallinula*, for instance) there may be only a small median point.

*The Male Genitalia.*—Although these structures are mainly similar throughout the group there is considerable variation in details. In many species there is a sclerotized part of the basal plate inside the normal lateral sclerotization which articulates with the head of the paramere (fig. 2, T). This thickening is part of the outer sclerotized bar, but may appear free to a greater or less

Figures 25-27.



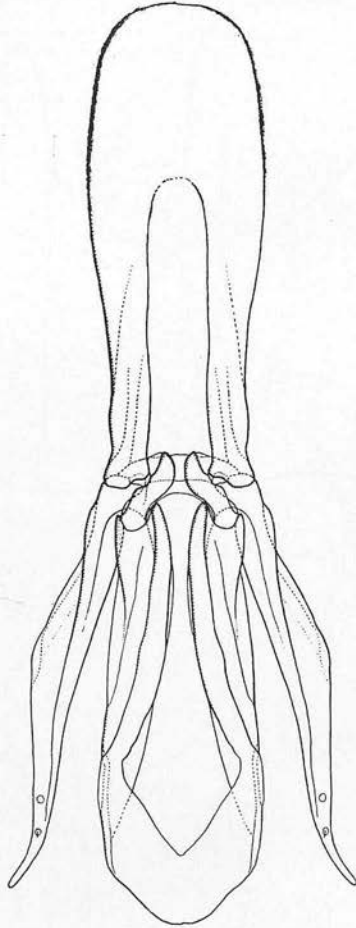
Male genitalia of *Rallicola* spp.

25. *R. fulicae* (Denny), paramere only. 26. *R. cuspidatus* (Scopoli). 27. *R. minutus* (Nitzsch).

extent forming the so-called "tubercle" (Carriker, 1944, 85); in some species it appears merely as the bifid end of the outer sclerotized bar. The parameres are always elongated, but vary in shape (figs. 25-28). Arising from the head of each paramere there may be a process, either well sclerotized and easily seen (fig. 25, P) or hyaline and liable to distortion in mounted specimens (fig. 2, P; figs. 43, 45, 47). It may be small (*R. ortyometrae*, fig. 2) and does seem to be absent in some species; in *R. fulicae* (fig. 25) these processes are large and appear as two structures each side of the mesosome, reaching over half the length of the parameres,

The mesosome is usually shorter than the parameres and may have a well-sclerotized penis (fig. 2), but in some species (*R. mystax*, fig. 28) it is greatly elongated and prolonged beyond the end of the parameres. In the species from *Himantornis* the mesosome is asymmetrical and the penis is elongated and curled back on itself (fig. 36).

Figure 28.



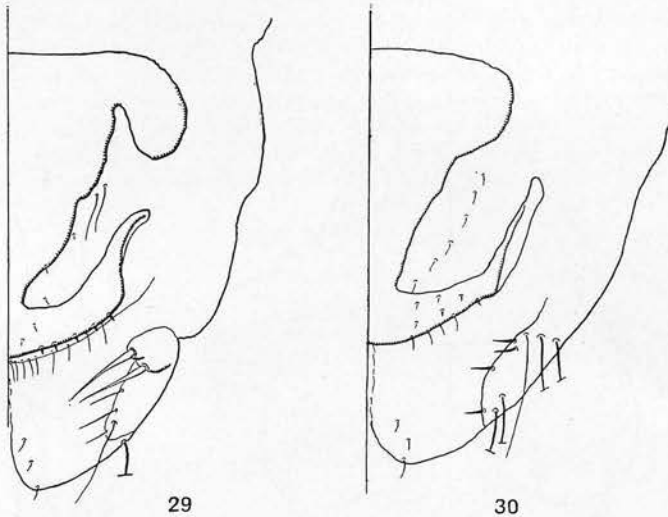
*Rallicola mystax* (Giebel), male genitalia.

Thus, in a group of species from one family of hosts are found all the characters listed by Carriker (1944, 85) for the separation of *Rallicola*, *Parricola* and *Furnaricola*, namely, the presence or absence of sexual dimorphism of the antennae; the median separation or not of the tergites; presence or absence of "tubercles" in the male genitalia; and the length of the parameres. *Parricola* is said (*ibid.*) to lack the tubercle on which the female spine-like setae are borne and to have divided sternites in both sexes; these characters have not been found in the species examined from six members of the Jacanidae. In the original descriptions of *Corvicola* and *Epipicus* no attempt was made to give any characters distinguishing these supposed genera from *Rallicola*, *Parricola* and *Furnaricola*.

SPECIES OF THE *RALLICOLA*-COMPLEX FROM OTHER HOST GROUPS.

Having discussed the variation within a group of species from related hosts, those from less closely related or unrelated hosts can now be considered.

Figures 29 and 30.



Female genital regions.

29. *Rallicola subsimilis* (Carriker). 30. *Brüelia* sp. from *Corvus corax* Linn.

## GRUIFORMES.

The Rallidae is the only family in the Ralloidea, the latter usually considered as a superfamily within the order Gruiformes. This order contains a number of rather diverse suborders of which the following (in addition to the Ralloidea) are parasitized by species of the *Rallicola*-complex: the Rhynocheti and the families Aramidae and Psophiidae usually included in the superfamily Gruoidea of the suborder Grues.

**RHYNOCHETI.** This contains a single species, *Rhynochetos jubatus*, which is parasitized by a typical *Rallicola* belonging to the group found on the Rallidae.

**ARAMIDAE.** This again contains a single species, *Aramus scolopaceus*, which is parasitized by a distinctive species of *Rallicola* (*R. funebris*). It has the dorsal anterior plate modified centrally (fig. 40), the mesosome of the male genitalia elongated (fig. 39) and the female genital plate greatly reduced. Tergal plates II-VIII are divided medianly in both sexes and the female has a ventral sclerite each side of abdominal segments IX-X; similar sclerites are found also in some of the species from the Jacanidae.

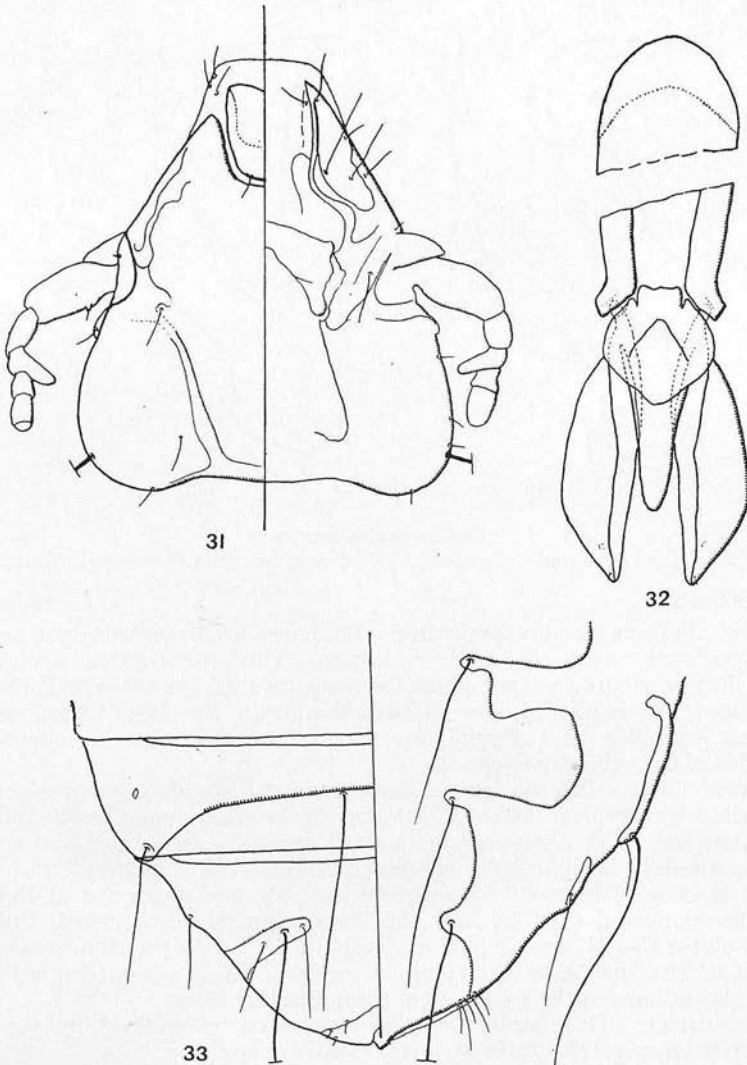
**PSOPHIIDAE.** This family contains one genus parasitized by the most distinctive species (*R. foedus*) of the *Rallicola*-complex. Its characteristic appearance is mainly due to the elongated abdomen with entire tergal plates and absence of well-marked pleurites (Pl. 1, figs. 1-2). The head has a narrow hyaline margin, no definite anterior dorsal plate nor anterior dorsal suture; in these characters it resembles somewhat the species found on *Porphyrio porphyrio*. The female genital plate lacks the lateral lobes or the discrete lateral sclerites found in species from other members of the Gruiformes.

## CHARADRIIFORMES.

**JACANIDAE.** This is the only family of the Jacanoidea, usually placed as a superfamily of the suborder Charadrii of the Charadriiformes; some authors

consider that the affinities of this superfamily lie with the Gruiformes (see Clay, 1950). The species from the Jacanidae were separated by Harrison as a subgenus, *Parricola* (figs. 5-8). Specimens have been examined from the six genera of the Jacanidae and these show characters and a similar range of

Figures 31-33.



*Rallicola sarothurae* sp. n., male.

31. Head (for details of antenna see fig. 19). 32. Genitalia. 33. Terminal segments of abdomen.

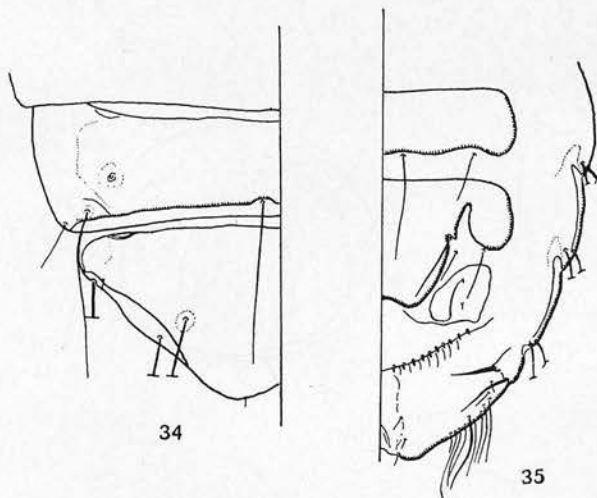
variation as in the species from the Rallidae. The species from *Hydrophasianus* and *Actophilornis* have small ventral sclerites on abdominal segments IX-X in the female as in species from *Aramus*. In the male genitalia the "tubercle" may (species from *Jacana*) or may not (species from *Irideparra*) be delineated; the paramere may be narrow (species from *Jacana*) or broadened (species from *Actophilornis*); the form of the mesosome is variable. There are, therefore,

no characters which make it possible to separate the species parasitizing the Jacanidae from those found on the Rallidae either generically or subgenerically, in fact, the species on *Jacana spinosa* (*R. exiguifrons*) is apparently nearer to that on *Crex crex* than is the species from *Porphyrio porphyrio*.

#### APTERYGIFORMES.

The single genus *Apteryx* is parasitized by species which Harrison (1915) separated from *Rallicola* as a subgenus *Aptericola* (figs. 9–11). These species form a distinctive group mainly due to their stouter habitus and the well-developed dorsal carinae of the head. This last character may be directly correlated with the broader head (see Clay, 1951, 190); the *Rallicola* species from *Macgregoria pulchra* (Passeres), with a similar stout habitus, also has dorsal carinae although these are less well developed than those of the species from *Apteryx*.

Figures 34 and 35.



*Rallicola sarothrae* sp. n., female abdomen.

34. Dorsal. 35. Ventral.

#### PASSERIFORMES.

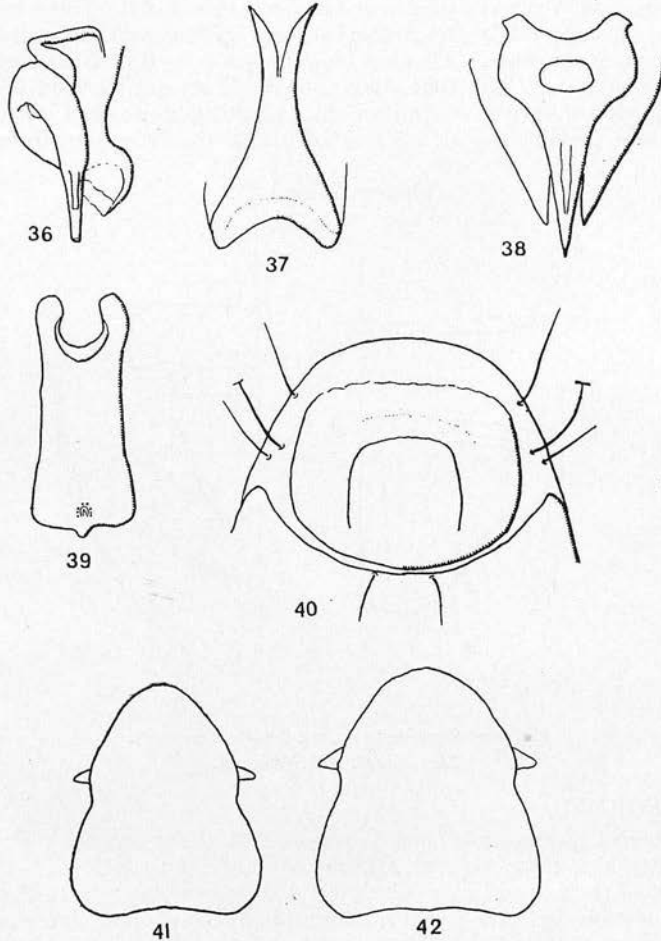
A number of species have been described from the superfamily Furnaroidea and separated as a distinct genus, *Furnaricola* (Carriker, 1944). The characters of the head of these species are somewhat diverse, but fall within the *Rallicola* range of variation (with the possible exception of *F. cephalosa*, figure only seen). There also seem to be no characters of the abdomen which make it possible to separate the *Furnaricola* group of species from *Rallicola*: in some species (*F. acutifrons*) the sclerotization of the female genital plate is continuous with that round the edge of the vulva, giving an anchor-shaped mark like that characteristic of *Brüelia* species (figs. 29–30), but other species have the form of the female genital plate typical of *Rallicola*. The male genitalia show some variation: *F. laticephala* and *F. heterocephala* have the process from the head of the paramere as in some species of *Rallicola* from the Rallidae. The group of species from the Furnaroidea, therefore, show considerable variation amongst themselves and have no constant characters on which a generic separation could be made.

*Corvicola* Carriker was erected for a single species, *insulana* taken from *Corvus kubaryi*. However, *insulana* appears to be identical with specimens found on *Porphyrio poliocephalus melanotus* and close to a second species,



*Rallicola lugens* (Giebel) from the same host; it cannot, therefore, be separated generically from *Rallicola*. According to Carriker (1949, 4) the type series of *insulana* comprises fourteen males and thirteen females taken from four different individuals of *Corvus kubaryi* collected by Rollin H. Baker on Guam Island (Marianas); Mr. Rollin H. Baker (*in litt.*) shows that there is no reason

Figures 36-42.



Figs. 36-39. Parts of mesosome of male genitalia of *Rallicola* spp.

36. *R. flavescens* (Piaget). 37. *R. unguiculatus* (Piaget), 1880. 38. *R. foedus* (Nitzsch).  
39. *R. funebris* (Nitzsch).

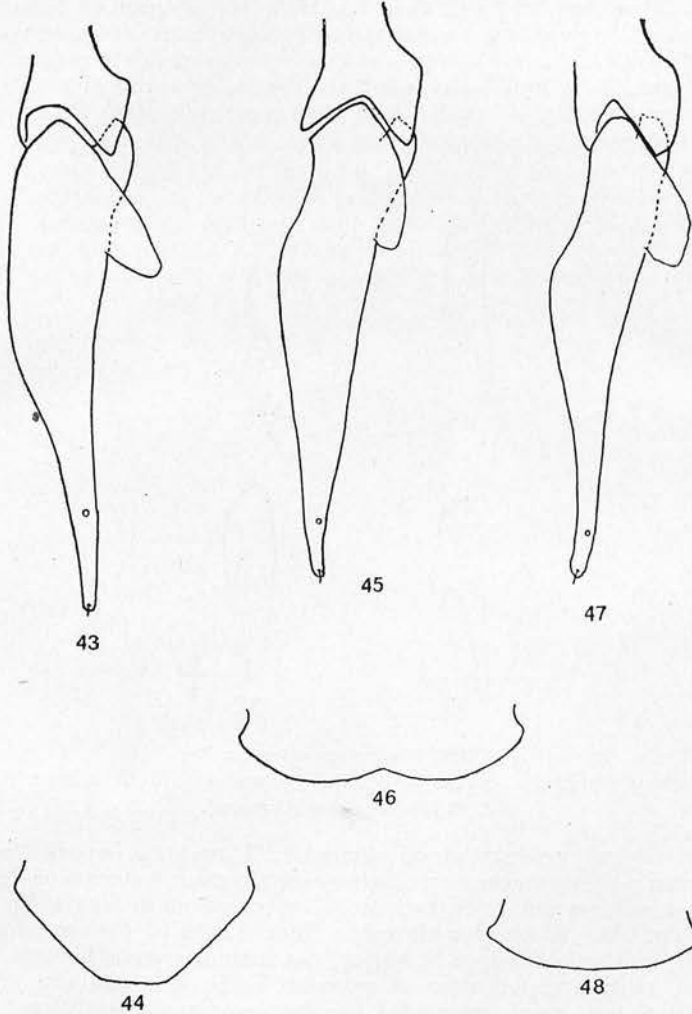
Figs. 40-42. Heads of *Rallicola* spp.

40. *R. funebris* (Nitzsch), anterior plate. 41. *R. lugens* (Giebel), outline. 42. *R. insulamus* (Carriker), outline.

to doubt the authenticity of the host record. It seems reasonably certain, therefore, that this species of *Rallicola* has become established on *Corvus kubaryi*. According to Mayr (1945, 298) *Corvus kubaryi* is restricted to Guam and Rota in the Marianas, while *Porphyrio poliocephalus* is found, in this region, only in the Palau group, the subspecies being *pelewensis*. Neither of the closely related species of *Rallicola* occurring on *Porphyrio poliocephalus* has

been seen from this subspecies, but it is unlikely that they differ from those of *P. p. melanotus*. It seems likely that at some time the distribution of *Corvus kubaryi* and *Porphyrio poliocephalus* overlapped and that the *Corvus* acquired the *Rallicola* species, possibly by feeding on the dead bodies of the rail. The

Figures 43-48.



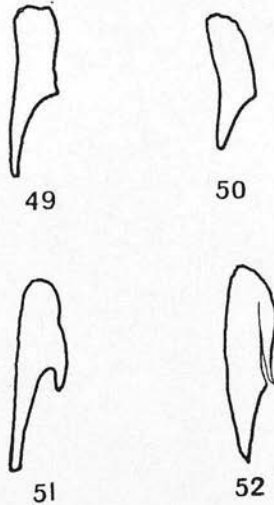
- Rallicola gracilentus* nom. nov.  
 43. Paramere. 44. Vulva.
- Rallicola gadowi* Harrison.  
 45. Paramere. 46. Vulva.
- Rallicola novaezealandiae* Harrison.  
 47. Paramere. 48. Vulva.

other explanation is that the specimens of the *Rallicola* were temporary stragglers on the *Corvus* from one of the species of Rallidae occurring on Guam. According to Mayr (1945) the following are found on Guam: *Rallus owstoni*, *Poliolimnas cinereus* and *Gallinula chloropus*. From none of these genera have

species of *Rallicola* resembling those on *Porphyrio* been seen, and it is most unlikely that they would have a second species the same as that on *Porphyrio poliocephalus*. This case is an example of the dangers of erecting new genera based on the phylogenetic position of the host and not on the morphological characters of the parasite.

A further species from one of the Passeriformes (*Macgregoria pulchra*, family Paradisaeidae) has been seen. As these specimens were taken from a skin there must be some doubt about the host record, but twenty-one specimens of males, females and nymphs were collected and the species in general habitus and male genitalia is unlike any seen from the Rallidae. It shows, however, no characters on which it can be separated generically from *Rallicola*. The dorsal and temporal carinae are slightly developed and the male has a strongly

Figures 49-52.



Parameres of *Rallicola* species (after Carriker, 1944)

49. *R. acutifrons* (Carriker). 50. *R. parvigenitalis* (Carriker). 51. *R. titicacae* (Carriker).  
52. *R. heterocephalus* (Carriker).

sclerotized ventral prolongation of segment VIII, reaching beyond the end of the abdomen; the mesosome is unlike any seen in other members of the group, but these structures tend to be variable (cf. species from *Gallinula*, fig. 27, and *Porzana*, fig. 28). A single male taken from a skin of *Urocissa flavirostris* (Corvidae), and quite likely a straggler, has a similar stout habitus, but no sclerotized ventral prolongation of segment VIII; the genitalia, relatively much larger than in any other species, has the mesosome quite different, but the process on the inner edge of the paramere is well developed as in some of the species from the Furnaroidea and Rallidae.

#### PICIFORMES.

*Epipicus* Carriker was erected for a single species taken from a woodpecker; although this is a distinctive species there seems to be no characters as given in the description and figures which warrants its separation from *Rallicola*.

#### CUCULIFORMES.

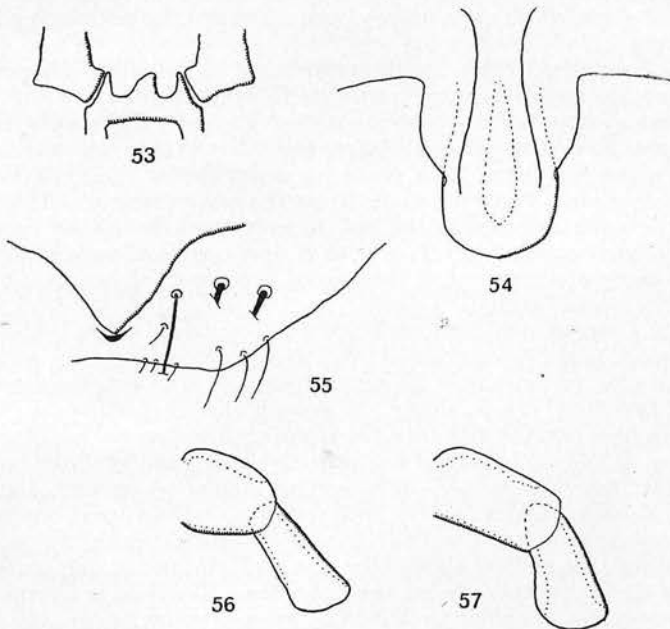
A species of *Rallicola* has been taken from *Centropus sinensis* (fifty-two specimens from three localities), from *C. rufipennis* (three specimens from a skin)

and from *C. bengalensis* (one specimen from a skin). The characters of this species fall within the range of variation found in *Rallicola* from the Rallidae. Possibly conspecific with the species from *Centropus* is *Rallicola unguiculatus* (Piaget) alleged to have come from *Eurylaimus ochromelas*, but as many of Piaget's specimens have been found to be stragglers the host record must be considered as quite unreliable. Also close to the species from *Centropus*, probably only subspecifically distinct, are five specimens taken from a skin of *Gallirex cinerea*, Canton, a host record which also needs confirmation.

#### THE PHYLOGENETIC ORIGIN OF *RALLICOLA*.

The facts discussed above show that on morphological grounds all these species should be included in one genus. With the exception of *Aptericola* (possibly a good subgenus) and *Epipicus* (containing only one species) all the genera which have been described contain species which would be generically unplaceable if their hosts were unknown. Before deciding to relegate the genera listed on the first page (with the exception of *Wilsoniella*) as synonyms of *Rallicola* it is necessary to consider whether the species from some of the host

Figures 53-57.



53. *R. subsimilis* (Carriker), proximal part of mesosome. 54. *R. advenus* (Kellogg), lobe-like process on sternite VIII (or ? IX) of male. 55. *R. exiguifrons* (Carriker), last abdominal sternite of male. 56. *R. ortygetrae* (Schrank), 1st two male antennal segments. 57. *R. clayae* Tandan, 1st two male antennal segments.

groups may have a different phylogenetic origin or are more closely related to other genera than to the rest of the *Rallicola*-complex. The following are possible explanations of the present distribution of *Rallicola*:

*Relationship between the host groups.* This would mean that the host orders on which *Rallicola* occurs are more closely related to one another than to any other orders. This is of course not supported by any other evidence and cannot be put forward as a serious explanation. However, some of these host groups

may have a comparatively recent common ancestor which was parasitized by *Rallicola*. The Apterygiformes are considered to be related to the Rallidae by some authors, and Harrison (1915, 100) suggested that the presence of *Rallicola* on both host groups denoted such a relationship. Further, some ornithologists place the Jacanoidea in the Gruiformes near the Rallidae. Thus, it is possible that *Rallicola* was present on an ancestral stock which gave rise to the Apterygiformes, Rallidae, Jacanidae, Aramidae, Psophiidae and Rhynchotidae. Its occurrence on other host groups could be explained by one of the theories discussed below.

*Discontinuous distribution.* This would mean that a *Rallicola* ancestor similar to the present-day species was parasitic on the ancestral stock which gave rise to modern birds before the divergence of the Apterygiformes, and that *Rallicola* has become extinct on those groups on which it is now absent. This theory would have to postulate that there had been little change in the species of the genus in spite of the time involved and the diversity of environments. *Rallicola* species found on the Gruiformes, which if this theory were true would be more closely related to one another than those on the Passeriformes, do in fact show considerable diversity. Hence, it would be expected that the species found on the different host orders would have diverged to a greater extent.

However, if this theory is the correct interpretation of the present distribution of the species, there is no phylogenetic reason for not placing them in a single genus.

*Parallel evolution.* This would mean that a primitive ancestral stock parasitic on a common ancestor continued to evolve on parallel lines after the parasites were separated on the different host groups. *Wilsoniella* on *Opisthocomus* might have belonged to the same stock but evolved on rather different lines. The present distribution could be explained by the extinction of the genus on other host orders descended from the same ancestor. This theory is open to the same criticism as the last, namely, that during the time and the diversity of environments involved such a close degree of parallel evolution is difficult to accept. However, if this theory is correct the species can again be contained in a single genus.

*Parallel evolution and divergence on the different host orders.* The ancestral *Rallicola* stock might have retained primitive characters until the separation of the present-day host groups. On some orders the primitive stock might have split into two lines, one retaining the general characters of the ancestor and evolving on lines parallel with those on the other host groups, the other perhaps losing some of the characters of the primitive stock and evolving on different lines. This idea is suggested by a certain similarity between some of the species of *Furnaricola* and *Brüelia*, both parasitic on the Passeriformes. In the female the abdomen is similar, including the diagnostic genital region. A comparison of figs. 29 and 30 shows that the *Brüelia* species differs only in the absence of the lateral tubercle-borne stout setae. The head in nymphs of some of *Rallicola* species is similar to that of nymphs of many *Brüelia* species and of the more primitive type of *Brüelia* adult. It could be presumed that a primitive type of Ischnocera with a circumfasciate head, male genital opening terminal, and the female genital region of the *Rallicola*-type branched into two lines on the Passeriformes. One of these lost the stout tubercle-borne setae of the female and the male opening became dorsal, thus developing into the genus *Brüelia*, the species of which may have the head modified to a greater or less extent (see Clay, 1951). The other branch changed little except for the median interruption of the marginal carina, a character which was also developed independently in the *Rallicola* stock on the other host orders. If this was the case, then *Furnaricola*, the species on *Macgregoria pulchra* and *Brüelia*, would be more closely related to each other than *Furnaricola* is to *Rallicola*, and it would be phylogenetically incorrect to amalgamate the two latter genera. Similar problems have been discussed elsewhere (Clay, 1949, 294; 1951, 174) where

it has been suggested that in the present incomplete state of knowledge of the group, genera should be based on morphological criteria only. It seems possible, however, that *Brüelia* and *Rallicola* have been derived from a common ancestor.

*Convergence.* This would postulate unrelated stocks developing the *Rallicola*-type of head carinae and sutures, the genital region of the female abdomen, and male genitalia on the same general lines in the different environments found on the diverse host groups on which these species occur. This seems unlikely and need not be further considered. It is possible, however, that the presence of the tubercle-borne setae in the female *Wilsoniella* may be a case of convergence and does not denote any phylogenetical relationship.

*Secondary infestations.* The genus may have evolved on a ralline ancestor, it being most widely spread on the family Rallidae, or possibly on an ancestral stock which gave rise to the Apterygiformes, Rallidae and some of the related families included in the Gruiformes; its sporadic occurrence on other orders being due to secondary infestations. This would explain the similarity of the species on the different host groups and the fact that *Rallicola* has been recorded from three (possibly four) families of the Passeriformes, one genus of the Cuculi and one family (Jacanidae) of the Charadriiformes, although this last case may be explained by relationship between the Jacanidae and Rallidae. The occurrence of a ralline-infesting species (*R. insulana*) established on a member of the Passeres, *Corvus kubaryi*, suggests that this is a recent case of secondary infestation and that the species of *Rallicola* may not be strongly host-specific. This theory, suggesting that the present distribution of *Rallicola* has been brought about partly by relationship between the hosts and partly by secondary infestations, seems to explain the facts most simply and means that there is no phylogenetic objection to placing all the species in one genus. This is also the most convenient classification.

#### A NEW SPECIES OF *RALLICOLA*.

##### *Rallicola sarothurae* sp. n.

This species is distinguished from other described species by the anterior prolongation of the ventral carinae beyond the dorsal sclerotization of the marginal carinae and by the male genitalia. It is difficult to say where the affinities of this species lie, but *sarothurae* seems to be nearest to *R. cuspidatus*, from which it can be distinguished by the shape of the head and male genitalia.

*Male.*—Head as shown in figs. 19 and 31. Thorax similar to that of *R. ortygometae* (fig. 1). Abdomen with only tergite II definitely divided; sternites in the form of single median plates. Posterior segments as shown in fig. 33. Genitalia with broad parameres and somewhat elongate mesosome (fig. 32).

*Female.*—Head and thorax similar to that of male, without modified antennae. Abdomen with only tergite II definitely divided medianly. Sternites in the form of median plates slightly lobed laterally. Posterior segments as shown in figs. 34–35.

Measurements (in mm.) of types (in canada balsam)

	Male		Female	
	Length	Breadth	Length	Breadth
Head	0.45	0.40	0.47	0.43
Prothorax		0.25		0.25
Pterothorax		0.35		0.37
Abdomen	0.83	0.47	1.00	0.58
Total	1.48		1.70	
Genitalia	0.37			

*Abdominal chaetotaxy* (male and female).—Dorsal, II : 2 anterior (elongated) and 2 posterior ; III–VI : 4 ; VII : 1 post-spiracular each side and 2–4 central ; VIII–XI : see figs. 33–34. Ventral, II–VI : 4 ; VII–XI : see figs. 33, 35.

Holotype (male) and allotype (female) slide 6530 in the Meinertzhagen collection, British Museum (Natural History) from *Sarothura antoni* Madarasz & Neumann from Kenya. Paratypes : 8 ♀♀, 9 ♀♀ from the same host species, Kenya.

#### KEY TO THE SPECIES OF *RALLICOLA*.

A key to the species is given below although there are still many undescribed from the Rallidae alone ; for this reason additional characters are given in brackets after some of the species to distinguish them from known but undescribed species. The key is based almost entirely on the males as the characters on which the females are separated, such as the form of the tergal and sternal plates, are not always given in descriptions and where the material is inadequate are difficult to make out correctly\*. In some cases two forms are not separated in the key ; this means that either they are closely related subspecies, or that the original description or the available material is inadequate for separation. An asterisk denotes that no specimens of a species have been seen. The following species are omitted from the key for the reasons given :—

- R. acuminatus* (Piaget) = *R. sulcatus* (Piaget).  
*R. attenuatus* (Burmeister) = *R. ortyometrae* (Schränk).  
*R. bipustulatus* (Piaget). There are no specimens in the Piaget collection, the host is wrong and the description and figure inadequate for recognition.  
*R. bisetosus* (Piaget). A specimen from *Rallina tricolor* will be selected as lectotype.  
*R. bresslaui* Pessôa & Guimarães = *R. fumebris* (Nitzsch).  
*R. californicus* (Kellogg & Chapman). No specimens seen from the type hosts ; figure and description inadequate for recognition.  
*R. chunchotambo* (Carriker). Known only from the female.  
*R. dubius* (Piaget) = *R. gracilis* (Piaget).  
*R. fallax* (Piaget) = *R. lugens* (Giebel).  
*R. gracilis* (Piaget). Female only.  
*R. intermedius* (Giebel) = *R. mystax* (Giebel).  
*R. microcephalus* Uchida, 1948. No figure and unrecognizable from description. No holotype nor type host designated, but as the only male was taken from *Gallimila chloropus indica*, this specimen will presumably subsequently be designated as lectotype.  
*R. minhaensis* (Kellogg & Chapman). Generic position doubtful, but may prove to be a *Rallicola*.  
*R. minutotrabeulatus* (Osborn) = *R. advenus* (Kellogg).  
*R. parvulus* (Piaget) = *R. minutus* (Nitzsch).  
*R. porzanae* (Piaget). Female only seen.  
*R. subfallax* (Piaget) = *R. lugens* (Giebel).  
*R. unguiculatus* (Piaget), 1890 nec *R. unguiculatus* (Piaget), 1880. This species is represented in the Piaget collection by a single male, the true host of which is unknown. It is, however, apparently conspecific with the male specimen which will be designated as the lectotype of *Oncophorus major* Piaget, 1888. *O. major* Piaget, 1888 is invalidated by *O. major* Piaget, 1885, and as the former is a good species it is here re-named.  
*Rallicola piagetii* nom. nov. for *Oncophorus major* Piaget, 1888.  
As *Rallicola gracilis* Harrison, 1915 is pre-occupied by *R. gracilis* (Piaget), 1871 it is here re-named :  
*Rallicola gracilentus* nom. nov. for *Rallicola gracilis* Harrison.

A complete list to 1950 of species, authors, references and type hosts is given in Hopkins & Clay, 1952, 318.

#### KEY.

- |  |                                     |
|--|-------------------------------------|
| 1. Penis elongated and recurved (fig. 36) .....                                | <i>flavescens</i> .                 |
| — Penis not as above .....   | 2.                                  |
| 2. Mesosome funnel-shaped (fig. 37) .....                                      | <i>unguiculatus</i> (Piaget), 1880. |
| — Mesosome not funnel-shaped ; reaching beyond the ends of the parameres ..... | 3.                                  |

\* It is possible that the size of the two anterior tergal setae on abdominal segment II (whether minute or elongated) might be useful characters in both sexes for a key, but these are seldom shown in figures.

- Mesosome not funnel-shaped and not reaching beyond the ends of the parameres..... 4.
- 3. Tergite III with more than 10 setae; shape of mesosome characteristic (fig. 38) ..... *foedus* (1) †. (Pl. 1, figs. 1-2.)
- Tergite III with less than 4 setae; shape of mesosome characteristic (fig. 28) ..... *mystax* (2).  
*zumpti*.
- 4. Segment I of ♂ antenna with stout seta on well-developed terminally bilobed process (fig. 20).... 5.
- Segment I of ♂ antenna without process or process not terminally bilobed (figs. 17-19) ..... 7.
- 5. Tergal plates II-VIII divided in mid-line in both sexes, dorsal anterior plate (fig. 40) and mesosome (fig. 39) characteristic ..... *funebris* (3).
- Without above combination of characters. (Terminal margins of abdomen without median processes)... 6.
- 6. Preantennal margin broadly rounded anteriorly (fig. 42) ..... *insulanus*.
- Preantennal margin pointed anteriorly (fig. 41).... *lugens*. (Fig. 20.)
- 7. Ocular seta elongated, 1st marginal temporal seta on lens, dorsal carinae well developed, 1st segment of ♂ antenna without process, more than 6 central dorsal setae on abdominal segment III. Mesosome narrowing distally. (♂ without ventral prolongation of abdominal segment VIII.)..... 8.
- Without above combination of characters ..... 10.
- 8. Normally 2 stout setae each side of ♀ genital region, shape of vulva and paramere characteristic (figs. 43-44)..... *gracilentus* nom. nov.
- Normally 3 stout setae each side of ♀ genital region, shape of vulva and parameres not as above (figs. 45-48)..... 9.
- 9. Vulva with median emargination (fig. 46), shape of paramere characteristic (fig. 45) ..... *gadowi*. (Figs. 9-11.)
- Vulva without median emargination (fig. 48), shape of paramere characteristic (fig. 47) ..... *novaezealandiae*.
- 10. Abdominal segment III with more than 10 dorsal setae. (Mesosome broadening distally.) ..... *scapanoides*\*.
- Abdominal segment III with less than 6 dorsal setae 11.
- 11. Proximal part of mesosome with central process in addition to lateral processes (fig. 53)..... 12.
- Proximal part of mesosome with lateral processes only (fig. 32) ..... 13.
- 12. Paramere narrows abruptly about midway (fig. 49) *acutifrons*\*.  
*subsimilis*. (Figs. 12-13, 29, 53.)
- Paramere narrows abruptly near distal end (fig. 50) *parvigenitalis*\*.
- 13. No definite hyaline margin to head (fig. 15) ..... 14.
- Definite hyaline margin to head (fig. 16) ..... 16.
- 14. Distal post-axial angle of 3rd segment of ♂ antenna prolonged as definite process (fig. 18). (1st segment without well-developed unilobed seta-bearing process.)..... 15.
- Distal post-axial angle of 3rd segment of ♂ antenna not prolonged as above ..... *minutus*. (Fig. 27.)
- 15. ♂ sternite VIII (or ? IX) with lobe-like process reaching to or beyond end of abdomen (fig. 54)... *adventus*.
- Without such process ..... *fulicae*. (Figs. 18, 25.)
- 16. ♂ sternite VIII (or ? IX) with bilobed process, terminal segments of abdomen diagnostic (fig. 24) *andinus*.
- Without above characters ..... 17.
- 17. Paramere narrow, outer edge convex (fig. 6). (Paramere tip rounded, not flattened, and seta subapical. 1st segment of ♂ antenna longer than 2nd, distal post-axial angle of 3rd prolonged; last ♂ abdominal sternite without lobe-like process.)..... *sulcatus*. (Figs. 5-8.)
- Paramere broad, outer edge convex (fig. 26) ..... 18.
- Paramere with straight outer edge, inner with median lobe (fig. 51) ..... *titicacae*\*.

† Number in brackets after a name refers to notes on p. 586.



- Paramere with straight outer edge, no inner median lobe, inner edge narrowing abruptly (fig. 52) . . . . . 19.
- Paramere not as above . . . . . 21.
18. Ventral posterior margin of last ♂ abdominal segment without median point (fig. 21). (Mesosome characteristic, fig. 26.) . . . . . *cuspidatus* (4).
- Ventral posterior margin of last ♂ abdominal segment with median point (fig. 33). (Last ♂ abdominal sternite without lobe-like process.) . . . . . [(Figs. 19, 31–35.)  
*sarothuræ* sp. n. 20.
19. Head of paramere with process . . . . . 20.
- Head of paramere without process (according to original fig.) . . . . . *cephalosus*\*.
20. Ventral carinae of head projecting beyond sclerotized part of marginal carinae . . . . . *laticephalus*\*.  
*heterocephalus*\*†.
- Ventral carinae not as above. (Paramere, fig. 52.) . . . . .
21. 1st segment of ♂ antenna always definitely longer than 2nd; distal post-axial angle of 3rd distinctly prolonged (5). (Ventral posterior margin of last ♂ abdominal segment straight, last ♂ abdominal sternite without posterior lobe-like process; paramere tip rounded not flattened and seta sub-apical.) . . . . . *piageti* nom. nov.
- 1st segment of ♂ antenna equal to, or less or slightly longer than 2nd; distal post-axial angle of 3rd not distinctly prolonged (fig. 17) . . . . . 22. (*guami*\*) (6).
22. Ventral posterior margin of last ♂ abdominal segment with thickened median point . . . . . *bisetosus*. 23.
- Without such point . . . . . 23.
23. ♂ with tergal plate IV divided in the midline; last sternal plate of abdomen pointed with discrete semi-circular sclerotization distal to point (fig. 55) . . . . . *exiguifrons*.
- Without above combination of characters . . . . . 24. (*affinis*) (7).
24. Segment I of ♂ antenna proportionally shorter (in relation to II) (fig. 56). (♀ abdominal tergites II–V divided or partly divided medianly) . . . . . *ortygometrae*. (Figs. 1–4, 17.)
- Segment I of ♂ antenna proportionally longer (in relation to II) (fig. 57). (♀ abdominal tergites II–VII divided medianly.) . . . . . *clayae*.

## NOTES TO KEY.

(1) A figure of *R. foedus* in the Nitzsch manuscript shows that this is the correct interpretation of the species.

(2) The close relationship between *R. zumpti* (Kéler) from *Atlantisia rogersi* and *R. mystax* (Giebel) from *Porzana porzana*, together with the fact that they are unlike any other known species, suggests a close relationship between the hosts.

(3) A figure of *R. funebris* in the Nitzsch manuscript shows that this is the correct interpretation of the species.

(4) See Clay & Hopkins, 1951, 25 for a redescription of this species.

(5) One undescribed species has the first segment definitely longer than the second, but the third has no distinct prolongation.

(6) No specimens of *R. guami* Carriker have been seen and the description and figures are not sufficiently detailed to enable this species to be taken further in the key.

(7) The single ♂ type of *affinis* is in too poor condition to take it further in the key‡.

† Through the kindness of Mr. M. A. Carriker it has been possible to examine paratypes of this species which show that it also has the head character as given under *laticephalus*: the two species cannot therefore be distinguished by this character.

‡ Since going to press the British Museum (Natural History) has acquired a further part of the Piaget collection which is almost certainly the unmounted residue of the specimens on which Piaget based his original descriptions. This contains specimens of *affinis* and *ortygometrae*. *R. ortygometrae*: —2–3 setae on sternite V; *affinis* and *clayae*: —5–6 such setae. *R. affinis*: —♂, tergal plates II–III completely divided. ♀, II–VI completely divided. *R. clayae*: —♂, tergal plates II only completely divided; ♀, II–VII.

## ACKNOWLEDGMENTS.

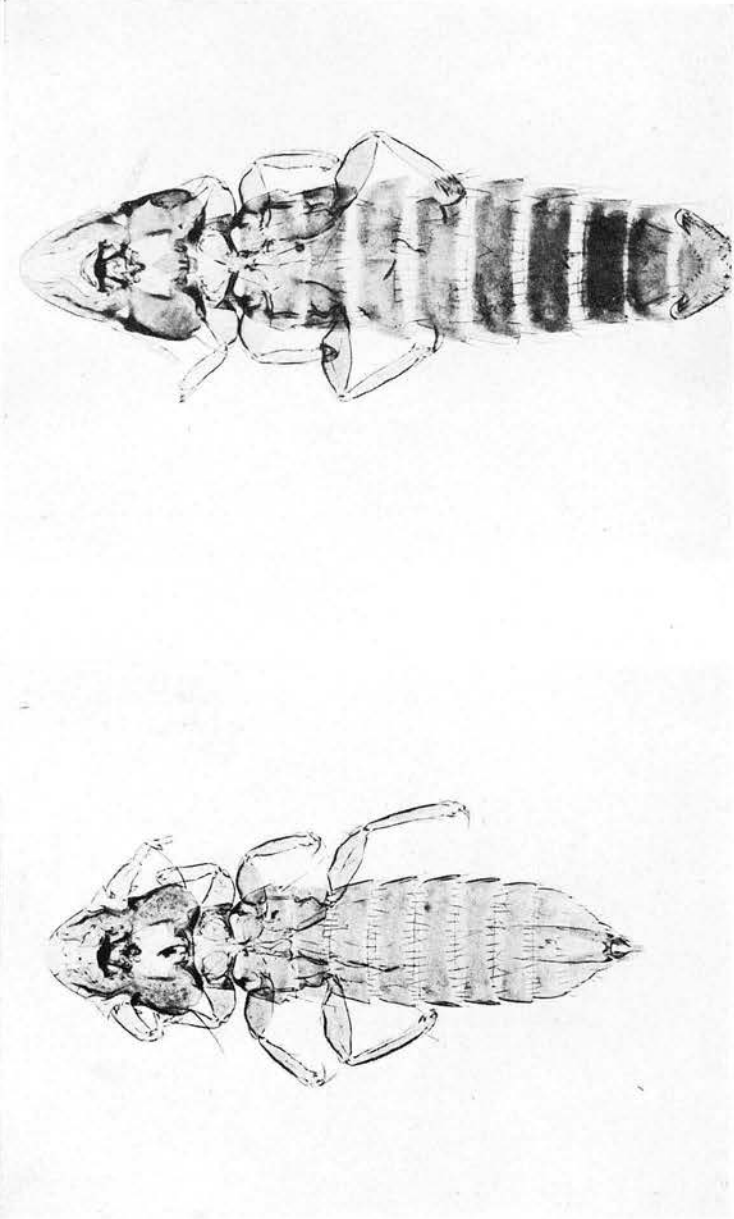
I am indebted to the Trustees of the British Museum for permission to publish figs 2, 26 to 28 drawn by Mr. A. J. E. Terzi and to publish fig. 26 which appeared in the *Bulletin of the British Museum (Nat. Hist.)*, *Entomology*, **2**, 26, f.34, and to Colonel R. Meinertzhagen for figs. 1, 3, 5, 6, 7, 9, 10, 12, 13 drawn by Mr. R. S. Pitcher. I am also indebted to Dr. S. Symmons and Mr. G. H. E. Hopkins for advice on various points.

## SUMMARY.

The various genera included in the *Rallicola*-complex are listed. The variation within a group of related species parasitizing one host family (the Rallidae) is discussed, and the characters and range of variation in the species from other host groups are compared. The phylogenetic origin and possible explanation for the present distribution of the *Rallicola*-complex are considered. In conclusion it is suggested that all the groups under discussion should be contained in the single genus *Rallicola*. A new species of *Rallicola* is described and two species re-named. A key to the known species of *Rallicola* is given.

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*Rallicola foedus* (Nitzsch)

Male  $\times$  40

Female  $\times$  40