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THE MALLOPHAGA OF BIRDS

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INTRODUCTION

The *Mallophaga*, a suborder of the insect order the *Phthiraptera*, are a group of obligate ectoparasites living on birds and mammals. Their complete life-cycle from egg to adult is spent on the host, away from which, under natural conditions they cannot feed nor survive for more than a short time. They feed on the feathers or on both feathers and blood and serum, blood may also be taken by some species from the developing feather; at least one genus (*Ricinus*) probably takes only blood and serum; the lice living inside the calamus of the quills feed on the central pith. The eggs are attached to the feathers or in a few cases laid inside the quills; the nymph which hatches from the egg is similar to the adult in general appearance and after three moults reaches the adult stage. The present distribution of the *Mallophaga* on the class *Aves* suggests that they became parasitic on birds at an early stage in the evolution of that class and that they evolved with their hosts. In a group of related host species, each species may be parasitized by an allopatric species of each of a number of sympatric genera of *Mallophaga* common to the host group, and in addition, sympatric species of one or more of these genera. In many cases, therefore, a single host species may be parasitized by a number of genera and species of *Mallophaga*.

PART I

THE PARASITE

CLASSIFICATION

A brief outline of the classification is necessary to understand the references in the following sections. The order *Phthiraptera* includes the *Mallophaga* or chewing lice and the *Anoplura* or sucking lice and appears to be most nearly related to the *Psocida* or book lice. It is generally assumed that the order is derived from a primitive psocid-like ancestor which probably became parasitic first on birds and later migrated to mammals. The suborder *Mallophaga* is divided into two distinctive superfamilies, the *Amblycera* and *Ischnocera*, perhaps even derived from different psocid ancestors. The *Amblycera* (Pl. I, figs. 1-4) are believed to have retained more of the habits and morphological characters of the primitive louse than have the *Ischnocera* and, in general, are not so closely adapted to the different host groups nor so specialized for the different habitats on the body of the individual host. Thus, the *Amblycera* are contained in about fifty homogeneous genera, while the *Ischnocera* (Pl. II, figs. 1-8) can be divided, even conservatively, into nearly a hundred, many of which are divisible into well marked species groups. The generic and

suprageneric classification of the *Mallophaga* presents great difficulties but some understanding of this is necessary in host-parasite problems.

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 the ancestral stock to the general environmental factors provided by the body of the host. The ancestral avian Ischnoceran stock probably became parasitic on birds at a time when the latter had a more uniform feather covering and before they diverged into the different groups with ensuing modification of feather structure. During the evolution of the *Mallophaga* there seems to have been convergence, parallelism, and changes of ecological niches with ensuing secondary modifications often resulting in the original relationships being 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 (CLAY, 1951 : 173).

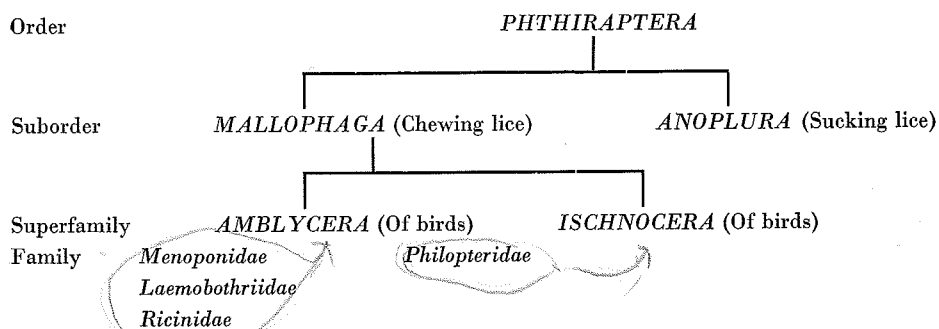
Suprageneric classifications of the Ischnocera have been attempted by various authors but no satisfactory system has yet been evolved. The *Ischnocera* from mammals (with the exception of *Trichophilopterus*) can be distinguished from those on birds and can be included in a separate family the *Trichodectidae*. 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, the *Phlopteridae*.

The small amount of divergence in the basic characters of the genera within this superfamily reflected in the suprageneric classification, is an indication of the similarity of the environment in which the parasite lives and has lived during its history on the birds.

The superfamily *Amblycera* which at the specific and generic levels show less diversity than the *Ischnocera*, can be divided into at least three families and show differences in certain characters, e.g. female antennae, tentorium, some characters of the thorax and abdomen, number of ovarioles, which are constant throughout the *Phlopteridae*.

Table 1

The Suprageneric Classification of the Avian Mallophaga.



ADAPTATION

A. *Occupation of Niches on the Same Host.* — The population of *Philopteridae* on one host is usually 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 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 (Pl. II, fig. 4). This type seems to be adapted to movement on the shorter narrower feathers of the head and neck and being out of reach of the bill does not need to have the rather flattened form found in other types; on any other part of the body it would be easily picked off or crushed by the bill during preening. On the longer broader feathers of the back and wings is found a flattened elongate type (Pl. II, fig. 8) which can slip sideways across the feathers with great rapidity. Examinations of freshly killed birds show that in general these habitat forms are not found outside their own territories except sometimes in cases of abnormally heavy infestations. The eggs of the head louse are found on the head and neck and those of the wing louse on the wings and their axillary feathers, being laid between the barbs to avoid damage during preening. Apart from these two main ecological types (Table 2) there are others, differing in size and body form (Pl. II, figs. 5-6), which either inhabit different parts of the plumage or are perhaps not so closely restricted and specialized for any one habitat. The *Amblycera*, in general, appear to rely more on their greater speed for protection from the bill and are not so diverse in form. Two other specialized niches have been utilized: the inside of the quills of the wing feathers in some birds, for example *Numenius* by a species of *Actornithophilus*, and the throat pouches of pelicans and cormorants by species of *Piagetia*.

Table 2

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

Host group	Genus of head louse	Genus of wing louse
<i>Tinamiformes</i>	<i>Pseudophilopterus</i>	<i>Pseudolipeurus</i>
<i>Procellariiformes</i>	<i>Trabeculus</i>	<i>Naubates</i>
<i>Pelecaniformes</i>	—	<i>Pectinopygus</i>
<i>Ciconioidea</i>	<i>Neophilopterus</i>	<i>Ardeicola</i>
<i>Threskiornithoidea</i>	<i>Ibidoecus</i>	<i>Ardeicola</i>
<i>Anseriformes</i>	<i>Anatoecus</i>	<i>Anaticola</i>
<i>Falconiformes</i>	<i>Craspedorrhynchus</i>	<i>Falcolipeurus</i>
<i>Rallidae</i>	<i>Incidifrons</i>	<i>Fulicoffula</i>

B. *Adjustment to Host.* — The environment of the avian *Mallophaga* is formed by the chemical composition and physical structure of the feathers; the chemical composition of the blood and serum taken by some species and certain physiological characters of the bird such as skin temperature and humidity. Unfortunately little is known about the factors which prevent a louse from living on a strange host but the chemical composition of the feathers may be a limiting factor. It has been shown that chicken lice kept on feathers of the little green heron (*Butorides virescens*)

would eat the feathers but the adults died after 3-16 days and the nymphs did not complete their moults (WILSON, 1934). It seems also probable that the physical structure of the feathers is one of the important factors in the adjustment of the louse to its environment. In the *Ischnocera* the dorsal and ventral region round and anterior to the mandibles shows considerable variation within the group and gives those characters on which much of the classification is based; this region is associated with feeding, and further the mandibles serve an important function in clinging to the feathers to prevent dislodgement. One of the reasons for the greater diversity of external morphology in the *Philopteridae* of birds compared to that of the *Trichodectidae* of mammals may be the greater diversity in the structure of feathers compared to that of hairs; further, the *Philopteridae* feed on parts of feathers whereas it is doubtful whether mammalian hairs are a normal part of the diet of the *Trichodectidae* (WATERHOUSE, 1953). Experiments on the limiting factors in the blood of the hosts have been carried out on sucking lice only: KRYNSKI *et alia*, 1952 found in *Pediculus humanus* fed on guinea pig blood that the blood cells were rapidly haemolyzed and the released haemoglobin crystallized in the form of triangular pyramids which mechanically damaged the intestinal epithelium of the lice. Time of hatching of eggs and development of nymphs is affected by temperature, and BOYD & CHUTTER, 1948 suggest that host specificity of the adult may be dependent to a certain extent on the temperature of the host. However, it would seem that further experimental work is necessary; it is perhaps doubtful whether the differences in temperature between most birds are likely to be significant. /a

Other characters of the *Mallophaga* dependent on feather structure and pigment are most probably the shape and size of the claws, the chaetotaxy, the apparently stronger sclerotization and sculpturing of the exoskeleton of species living on birds with iridescent feathers (CLAY, 1951 : 210) and the occurrence of pigmentless *Mallophaga* on white feathers. This correlation between colour of host and parasite appears to be a protective adaptation as in both the white gulls and the white swans which have white body lice the head lice (out of range of the bill) are the normal dark colour.

It has already been shown that there is a general correlation between the size and shape of the *Mallophaga* and form of the feathers in the specialization of the lice for the ecological niches of the head and wing. It is also found that the typical wing lice genera are absent on those orders containing the smaller birds, for example the *Passeriformes* or on the smaller members of an order. Thus, the wing louse genus *Falcolipeurus* of the *Falconiformes* is not found on the smaller hawks, one exception is *Rostrhamus*, perhaps an indication that this species has become reduced in size relatively recently. One of the most puzzling correlations between host and parasite is that of size (CLAY, 1951 : 207) : in a genus of *Mallophaga* distributed over a number of nearly related birds, the size of the parasites varies with the size of the hosts. In *Degeeriella*, a genus found on hawks, the population on *Buteo buteo* is not taxonomically separable from that of *Buteo lagopus*, but the average size of the individuals found on the smaller *Buteo buteo* is less than that on the large *B. lagopus*. 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 would presumably mean an increase in the size of the individual parts of the feathers such as the barbules. Size of these, as they are eaten by the *Philopteridae*, might directly affect the size of certain structures used in feeding and attachment, the increased or decreased size of which might be reflected in the size of the whole animal. In some genera of *Mallophaga* there are certain characters associated with this increase or

decrease in size which may confuse host-parasite relationships. There is a tendency for the smaller species found on smaller hosts in some genera to have the head pointed or narrowed anteriorly e. g. the subspecies of *Degeeriella rufa* on the small *Falco sparverius*; the species of *Cuclotogaster* on *Coturnix*, *Synoicus* and *Excalfactoria*. In *Degeeriella* there is a tendency for the populations with a larger average size (on the larger hosts) to have broader and more flattened heads and to average a greater number of abdominal setae. Thus, *Falco peregrinus* and *F. biarmicus* belonging to different subgenera according to PETERS (1931), are of similar size and have populations of *Degeeriella* with similar average measurements, similar shape of head and similar number of abdominal setae; while *F. tinnunculus* and *F. sparverius* placed in the same subgenus but differing in size, have populations of *Degeeriella* differing in these characters. The characters correlated with increase of size in the parasites may corroborate the systematic position of the hosts either because the larger species of *Falco*, for instance, may be related or because the birds themselves have been wrongly classified on size and certain correlated characters. The suggestion (TIMMERMANN, 1952 : 1029, 1037) that the species of *Quadriceps* parasitizing the smaller *Rhinoptilus africana* is a more primitive type than that from the larger *R. chalcop-terus* because the latter shows a more robust form, and from this to deduce that the former host is more primitive, is possibly based on a misunderstanding of the relationship between size of host and parasite.

Preening by the host is an important factor in the control of the size of the populations of *Mallophaga* and has probably affected body structure and the area and position on the feathers where the eggs are laid. There are many records of birds with damaged bills having abnormally heavy infestations and a similar increase in parasites was shown in experiments with birds from which the beaks had been removed (ANON., 1948). The comb on the claws of some birds may help in clearing the head of lice as it is found that in certain orders in which some species have a comb the typical head louse is absent on those species (see Table 3). There are some exceptions to this and other factors (see p. 144) restricting the presence of head lice. Dust baths also serve to keep down the number of lice (see p. 144).

Table 3

Examples of birds with (+) and without (—) comb on middle claw and with or without head lice. No exceptions included.

Host Group	Comb	Head lice	Host Group	Comb	Head lice
Caprimulgi			Ciconiiformes		
<i>Caprimulgus</i>	+	—	Ardeae	+	—
<i>Podargus</i>	—	+	Ciconiae	—	+
Pelecaniformes			Gruiformes		
<i>Phaethon</i>	—	+	Rallidae	—	+
<i>Suloidea</i>	+	—	Podica	+	—
Gaviiformes	+	—			

Close adaptation to the host is no disadvantage in those parasites which spend their whole life-cycle on a single host form and where each generation is not faced with the difficulty of finding a new host and where the parasite anyhow has little chance of interspecific transfer between dead or living birds. Thus, once host

specificity has been achieved variability is no longer advantageous to the species and the small number of males in proportion to females, usual in the *Mallophaga*, may be an adaptation to this end.

C. Parallel and Convergent Evolution.

a) *Parallel Evolution.* There is no doubt that there must have been a considerable amount of parallel evolution in the *Mallophaga*, especially in the *Philopteridae*. As shown above these are basically similar in their external and internal anatomy, probably the result of an early and rapid evolution specializing them for life on the birds; these initial modifications might largely predetermine the direction of further evolution so that within certain groups the possible mutations would tend to be the same, 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. This is especially true of the head: SYMMONS (1952) has shown the fundamental similarity of the head of the *Philopteridae* and a study 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 (CLAY, 1951). 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. It is probable that the primitive mallophagan head had the mandibles near the anterior margin, an uninterrupted line of sclerotization round the anterior margin and without well developed lines of thickening passing anteriorly from the mandibular framework. The structure which seems to have affected the primitive head most fundamentally was the development of the pulvinus. This is a lobe of soft cuticle (probably the clypeo-labral suture) lying immediately in front of the oral opening and supported, at least proximally by bars of thickening, the ventral carinae; it has an important function in partly enclosing the piece of feather and directing it towards the mandibles for attachment and feeding. In some forms each carina has a thickened flattened surface lying parallel to that of the other side and to which is attached a lobe of the pulvinus (Pl. I, fig. 6); thus the piece of feather lies in a groove of the pulvinus held in position by the lateral lobes. Specialization seems to have taken place in the *Philopteridae* by the lengthening of the region of the head in front of the mandibles, the interruption of the sclerotization of the anterior margin of the head, the development of various sutures perhaps allowing a limited mobility to the preantennal region of the head, and in the various modifications of the ventral carinae. It is not yet possible to be certain whether the interrupted (Pl. I, fig. 6) or complete (Pl. I, fig. 5) ventral carina represents the primitive condition in the *Philopteridae*; it would seem, however, that the former condition is advantageous to the parasites of the majority of bird orders as there are only four host groups (see below) on which the parasite genera with the complete ventral carina are dominant. The modifications of both the ventral carinae and the preantennal region seem to have developed on parallel lines and may be one of the sources of error in the formulation of a natural classification; the differences in the details of the modifications being caused presumably both by the isolation of the groups and by the differences in the minute feather structure in the different host groups. Superficially both the head and body have also become adapted to the different ecological niches on the body of the bird, these adaptations having taken place on parallel lines in different stocks (see further below).

As an example of parallel evolution the following case may be given. There is a group of genera, the *Degeeriella*-complex, with a wide host distribution (see Table 6); it seems probable that this is an ancient stock which has remained relatively unchanged. Some of the host groups are parasitized by more than one species group of this complex, these having diverged from each other on the host group in question; the species groups are either sympatric and probably restricted to different ecological niches, or are restricted to different taxonomic divisions of the host group. There has been parallel evolution on the different host groups so that there is a superficial resemblance between these species groups. For instance, on the *Galliformes*, *Falconiformes*, and *Cuculi* there are in addition to the usual member of the *Degeeriella*-complex, species (*Lagopoecus* on the *Megapodidae*, *Acutifrons vierai* Guimarães on the *Accipitridae* and *Cuculicola acutus* (Rudow) on the *Cuculi*) in which the abdomen is rounded and the head is enlarged and pointed anteriorly with a dorsal preantennal suture and additional bars of thickening (temple carinae); all these characters are typical of the species found in the head niche (see CLAY, 1951). They also all have those characters common to the *Degeeriella*-complex. These three species, therefore, in some respects resemble each other more closely than they do the more nearly related species on the same host group. However, in this case there is a clue to their origin in the form of the tergal and sternal plates which follow the basic pattern found in the species of the *Degeeriella*-complex confined to the three host groups. Further, some of the host groups have in addition a typical head louse, *Craspedorrhynchus* on the *Falconiformes*, for instance, and *Cuculoecus* on the *Cuculi*; there are indications which suggest that perhaps both these genera may have been derived from members of the *Degeeriella*-complex on their respective host groups. If this proves to be so it would explain a certain similarity between the two genera. Hence, if two host groups are parasitized by members of a primitively wide-spread stock which has remained relatively unchanged, and in addition, given rise to other derived genera which show parallel evolution in their development, the host groups in question will have two or more similar genera in common, and this may give the impression that they are more nearly related than in fact they are. However, perhaps the nearer in time that the separation of the host groups took place the more similar the genera of *Mallophaga* would be: there is more similarity between the members of the *Degeeriella*-complex in the passerine fauna (see p. 166), on the *Cuculidae* and the *Falconiformes* than between these and the species on the *Galliformes*. There are only four host groups on which the parasite genera with complete marginal and ventral carinae (Pl. II, fig. 1) are dominant: these are the *Sphenisciformes*, *Tinamiformes*, *Galli* and *Columbae*; all have other genera in which one or both of these carinae are interrupted. The *Procellariiformes* have one genus (*Episbates*) with the simplified head structure, but all the other genera of this order and all other known genera from the *Aves* have ischnoceran genera in which there is some complication of these bands even if there is only a median interruption of the ventral carina. CHANDLER has shown that the *Tinamiformes*, *Galli* and *Columbae* (parasitized by *Mallophaga* with the simplified heads) all have a similar type of down with a typical structure. Without discussing whether this fact denotes a relationship between the *Tinamiformes*, *Galli* and *Columbae*, it may prove that this type of head is best suited to this feather structure and thus has a selective value which has prevented the dorsal modifications found in genera on other host orders. Thus, if the structure of the feathers favours the retention of the more primitive type of head, the genera concerned 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

166

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feather structure. This may be one of the causes of erroneous deductions of host relationships from those of their parasites.

b) *Convergent Evolution*. It is probable that most of the cases of convergent evolution have by now been recognised, although some of the untenable suprageneric classifications are still based on characters which distinguish the various types found in the different ecological niches and which have presumably been acquired independently in response to the environment of the niche. The genera of the *Heptapsogaster*-complex found on the Tinamidae are believed to be descended from a single ancestral stock on this group which has branched out to fill the different ecological niches on the body of the bird; the species now have a superficial resemblance to the unrelated occupants of similar niches on other orders. *Sturnidoecus* is probably another case of convergent evolution (see p. 149). The fundamental similarity of all the *Philopteridae* make it difficult to recognise whether the external characters common to two groups are due to parallel or convergent evolution or to phylogenetic relationships.

c) *Divergent Evolution*. This could be caused by some members of a host group showing 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. Again three host groups (L, M, N, fig. 1) might be parasitized by species of a genus Y; on one of the host groups (N) there might be a second genus Z derived from Y which because of adaptation to a different niche had become so distinct that its affinities were in doubt. If Y then became extinct on N, the *Mallophaga* of this group would no longer show relationship to those of L and M.

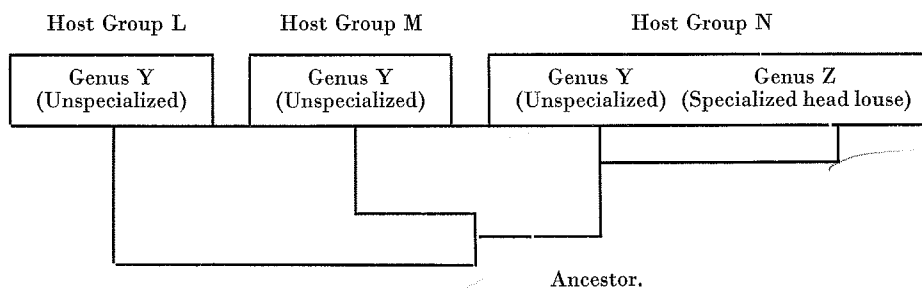


Fig. 1. — Distribution and relationships of a hypothetical ischnoceran genera complex.

DISPERSAL

Transfer to New Hosts Occupying Similar or Distinct Ecological Niches. — Normal intraspecific dispersal can take place during copulation, brooding of the young and during roosting in gregarious species. Interspecific transfer in the Mallophaga must be comparatively rare as normally birds of different species do not come into close enough contact for such transferences to take place. However, this might happen between birds occupying the same ecological niche, such as the colonial nesting place of certain herons. It is probable that the *Mallophaga* never leave the living bird unless in contact with another warm surface such as another bird, nesting materials or eggs: there are some records of species of the genus *Austromenopon* being found on the eggs of waders. Interchange can also take place between nestling and foster

parent in brood parasites ; by the use of common dust baths, HOYLE (1938) has found chicken lice on sparrows which were using the same dust bath as chickens ; and between predator and prey, hawks and owls are sometimes found with parasites which could have come only from a recently eaten victim. Another method which may account for the interspecific transfer of lice is by their attachment to louse-flies (*Hippoboscidae*), the latter often visiting more than one species of bird. There are now many records of these flies being found with *Mallophaga*, sometimes in large numbers : CORBET (1956) found a fly with 22 *Mallophaga* attached to it. The difficulties of a louse establishing itself on one of these new hosts, apart from the actual transfer, are discussed below under speciation (A. 3).

SPECIATION

The development of feathers by the ancestral bird 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 mallophagan stock ; 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 was the evolution caused by each habitat type adapting itself to the changes of its own particular niche, these changes being brought about by the evolution of the birds themselves. Thus, each ecological type, as the result of changes in the characters of their hosts, evolved with their hosts, but in general, at a slower rate (that is after an initial period of rapid evolution) ; this is reflected in the general correlation found between the classification of host and parasite (see Tables 2, 4). The isolating factors which may have been responsible for speciation in the group can now be discussed :

Table 4

Examples of ratios of species of *Mallophaga* to species of host.

Host Group	A	B	C	Genus of <i>Mallophaga</i>
<i>Alectoris</i>	$\frac{4}{4}$	4	1 : 1	<i>Cuclotogaster</i>
<i>Lagopus</i>	$\frac{3}{4}$	1	1 : 3	<i>Goniodes</i>
<i>Tringa</i>	$\frac{9}{9}$	7	1 : 1.29	<i>Quadriceps</i>
<i>Actitis</i>	$\frac{2}{2}$	1	1 : 2	<i>Quadriceps</i>
<i>Numenius</i>	$\frac{8}{8}$	6	1 : 1.34	<i>Luniceps</i>
<i>Limosa</i>	$\frac{4}{4}$	3	1 : 1.34	<i>Luniceps</i>
<i>Limosa</i>	$\frac{3}{4}$	1	1 : 3	<i>Actornithophilus</i>
<i>Pernis</i>	$\frac{2}{3}$	2	1 : 1	<i>Degeeriella</i>

Host Group	A	B	C	Genus of <i>Mallophaga</i>
<i>Pernis</i>	$\frac{2}{3}$	1	1 : 2	<i>Craspedorrhynchus</i>
<i>Buteo</i>	$\frac{17}{26}$	1	1 : 17	<i>Degeeriella</i>
<i>Microhierax</i>	$\frac{3}{5}$	3	1 : 1	<i>Falcolius</i>
<i>Pterocletes</i>	$\frac{11}{16}$	11	1 : 1	<i>Syrrhaptocetus</i>
<i>Cygninae</i>	$\frac{6}{7}$	5	1 : 1.2	<i>Ornithobius</i>

A = $\frac{\text{Number of species of host group from which } Mallophaga \text{ known (= D)}}{\text{Number of species of host group described.}}$

B = Number of allopatric species of *Mallophaga* known from D. Some of these species may comprise one or more populations which are more or less taxonomically separable.

C = ratio of B : D.

A. Host or Host-group as Isolating Factor.

1. *Isolation by Species Formation of the Hosts.* The host distribution of the louse is the equivalent of the geographical distribution of the freelifving animal. If the populations of the 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. SEWALL WRIGHT and others have shown the evolutionary potentialities of small and semi-isolated populations. If one of these isolated populations of the bird gives rise to a new species and even if later becomes sympatric with its parent population there would be no further interchange of lice owing to the discontinuance of interbreeding between the two bird populations, now distinct species. Here, therefore, is 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 B 2). It follows that the same conditions, isolation and semi-isolation of populations, which led to speciation in the hosts would also encourage speciation in the parasites, this perhaps partly accounts for the larger number of mallophagan genera and species groups on those bird orders with many species (see below, p. 147).

2. *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 reproductive isolating mechanism had developed. The reunion of the bird population 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 characters (see CLAY, 1949 : 286) 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.

3. *Isolation by the Development of Host Specificity.* In addition to the difficulty of interspecific transfer the migrant louse must be able to establish itself on the new host. This may be prevented not only by 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. A bird might become more easily infested with lice from another unrelated bird if both had similar feather structure, this perhaps being one of the factors limiting the establishment of host specific species. Individuals of both sexes or a fertilized female must of course be transferred to the new host. If a louse is able to pass to a nearly related host species, then it is possible that the resident louse population would not be more than subspecifically distinct and interbreeding might take place; it has been shown that crosses between the subspecies of *Pediculus humanus* tend to produce an abnormal proportion of males and many gynandromorphs and that a high proportion of female *Pediculus h. humanus* die when crossed with *P. h. capitis* (HOPKINS, 1949 : 419). Such hybrid populations would, therefore, probably not survive and spread throughout the species, although in some cases they might become a source of sympatric species parasitic on the new host species (see below under B 1). 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 transfer and no established population on the new host. The European cuckoo (*Cuculus canorus*) has species of three genera of lice found on many other species of *Cuculidae* and which are distinct from those of its passerine foster-parents. Thus, 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 (see above under Dispersal) has allowed the close adaptation of the parasite to the environment provided by its particular host and led to the development of host specificity. In turn host specificity will make interspecific transfer more difficult and increase the isolation of louse populations.

6 4. *Extinction of Louse Populations.* The potential range of a louse species is that of its host species, but collections of *Mallophaga* from one host species in different parts of its range show that there may be a true geographical distribution superimposed on the host distribution (CLAY, 1949: 285). This type of discontinuous distribution may have had two important effects on speciation: (i) the isolation of populations by an intervening area of absence and (ii) the emptying of a particular ecological niche enabling either another species on the same host or an immigrant louse species from another host species to occupy it.

B. *Ecological Niches as Isolating Factors.*

1. *Sympatric Speciation.* It seems unlikely in the light of modern knowledge of genetics that sympatric speciation has taken place on the body of the 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 areas of back and wings. The presence of sympatric genera and species normally found amongst the *Mallophaga* can be explained by isolation and the later re-union of parts of the louse populations as shown above (under A 1, 2, 4) and probably to a lesser extent by secondary infestations. Host specificity has already been discussed and it was shown that,

in general, the *Mallophaga* are host specific but it is not known to what extent host specificity is carried between related birds. Within the *Galliformes*, for instance, chicken lice can establish themselves on pheasants and partridges and guinea fowl lice and turkey lice have become normal parasites of chickens. This colonization of a new host by the *Mallophaga* is analogous to the transoceanic colonization of oceanic islands by free-living animals, and as in the latter case, may have contributed to the formation of sympatric species and genera. It has been shown (EICHLER, 1942 : 78) that those orders of birds which are represented by a small number of species are those which have only one or two genera of *Mallophaga* while those with many species usually support a number of sympatric genera and species (Table 5). 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

Table 5

Number of species in host group with number of sympatric genera and species groups of Mallophaga.

Host Group	A	B	Host Group	A	B
<i>Opisthocomi</i>	1	5	<i>Pelecaniformes</i>	51	4
<i>Struthioniformes</i>	1	1	<i>Apodi</i>	79	2
<i>Rheiformes</i>	2	2	<i>Alcedinidae</i>	87	2
<i>Dromiceidae</i>	2	1	<i>Procellariiformes</i>	90	15
<i>Apterygiformes</i>	3	1	<i>Caprimulgiformes</i>	92	3
<i>Mesoanatidae</i>	3	1	<i>Ciconiiformes</i>	104	10
<i>Gaviiformes</i>	4	1	<i>Cuculi</i>	128	8
<i>Coliiformes</i>	6	2	<i>Rallidae</i>	132	5
<i>Gruidae</i>	14	4	<i>Strigiformes</i>	134	3
<i>Turnicidae</i>	16	1	<i>Anseriformes</i>	148	8
<i>Pterocletes</i>	16	2	<i>Galliformes</i>	240	20
<i>Sphenisciformes</i>	16	3	<i>Falconiformes</i>	271	10
<i>Musophagi</i>	19	5	<i>Columbae</i>	289	11
<i>Podicipediformes</i>	20	2	<i>Charadriiformes</i>	301	10
<i>Tinamiformes</i>	33	ca 23	<i>Psittaciformes</i>	316	7
<i>Bucerotidae</i>	45	8	<i>Passeriformes</i>	5073	12

Sections of a host group which have a different mallophagan fauna are omitted (see pt. II). Although all the genera and species groups will not be found throughout the host group, an attempt has been made to count only those which could be sympatric and to omit any which appear to be an allopatric replacement of another genus or species group, e. g. in the case of *Halipeurus* and « *Synchautes*, » only the former is included.

A = Number of species in host group (according to MAYR & AMADON, 1951).

B = Number of genera and species groups of Mallophaga.

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 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 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, e. g. *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. It may be significant that the ostriches with few or no feathers on the head and neck have one genus of *Mallophaga*, whereas the rheas with well-feathered heads and necks have two genera. 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. 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 formerly represented by a greater number of species. 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 evolution of this family there must have been many cases of isolation and semi-isolation of parts of the lice populations and in addition 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 on the *Tinamiformes*.

The 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 favourable habitat for the lice, resulting in a greater number of immigrant lice being able to establish themselves. A bird group may also be parasitized by a greater number of genera than would be expected because it does in fact belong to a larger host group e. g. the *Musophagi* and *Galli* (see p. 164). Those orders with a large number of species but with few genera of *Mallophaga* 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. Or there may have been less change of interspecific transfer of *Mallophaga* during the evolution of the bird group. 10

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. Factors such as the preadaptation for a certain niche by the immigrant louse population, 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. 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 may have also been a number of cases of a louse species establishing itself on a host of another bird order. It is also probable 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

159 themselves, less divergent during the earlier stages of their evolution, offered a more uniform environment. This suggestion is supported by those cases where secondary infestation may account for the occurrence of the same genus on two unrelated host groups, since in the majority of cases the species are widespread throughout the two groups and of a distinctive kind, for example the distribution of *Quadriceps* on the *Charadriiformes* and the *Alcedinidae* and the distribution of *Saemundssonina* and *Austromenopon* on the *Charadriiformes* and the *Procellariiformes*; such distributions can be explained only by secondary infestation having taken place at an early stage in the evolution of the groups or by a common ancestor of the groups being parasitized by the genera in question. Examples of more recent secondary infestations are perhaps the presence of *Heptapsogaster* on the *Cariamidae* (see p. 163) and *Ciconiphilus* on the swans and geese (see p. 163).

2. *Intrinsic Changes in Each Ecological Niche.* The changes brought about in each habitat type by adaptation to the changes in its particular ecological niche have probably been mainly responsible for the production of the allopatric genera and species. This is SIMPSON's « phyletic evolution » and consists of changes of populations as a whole, the new species replacing the former species. Once the *Mallophaga* had been able to adapt themselves to life on the body of the bird, the main selecting factors were presumably both interspecific 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 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 such as diving birds; a sparse covering or the complete absence of feathers might also make this niche uninhabitable. In general, it is the head louse which is the most specific to the group of birds, suggesting that it is in this niche that the louse has become most closely adapted to its host. Thus, on the hawks and cuckoos, the head lice are more distinct from each other than are the members of the *Degeeriella*-complex on each host group; the *Ciconiidae* and the *Threskiornithidae* have a wing louse genus common to the two groups, but head lice which belong to distinct genera; the *Momotidae* and *Meropidae* which have the genus *Brüelia* also found on the *Passeriformes*, each have a specialized head louse, generically or subgenerically different from that of the latter order. The dorsal preantennal region of the heads of the nymphs of the head lice genera are often more similar to those of the adults than are those of other genera, suggesting that this specialization is perhaps necessary for the survival of the louse.

3. *Change of Ecological Niche on the Same Host Species.* Although any one host species may have a number of genera and species recorded from it, any individual bird does not necessarily have them all; a louse species, as shown above, may become extinct in parts of its host's range and thus one of the ecological niches would be empty of its specialized louse type. This might be occupied by another species which would become secondarily adapted to its new habitat. This may have happened in the *Sturnidae*; in this family the specialized head genus *Philopterus* (Pl. II, fig. 4), characteristic of the *Passeres* is absent, but it has a genus *Sturnidoecus* (Pl. II, fig. 2) which superficially resembles *Philopterus*, but is in fact more nearly related to another genus (*Brüelia*) found on other *Passeres*.

The chief factor, therefore, influencing the production of the allopatric species and genera of *Mallophaga* seems to have been the successive splitting of the host populations 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 presumably slight and this has led to any one genus of parasite confined to an order of birds having a number of allopatric species, one on each host species or on a group of related species (Table 4). These allopatric species usually differ but little from each other, and are separable mainly on the characters of external sclerotization, chaetotaxy, head shape and size (perhaps all correlated with feather texture and size) and on characters not adapted to the environment such as the male genitalia and secondary sexual characters. It is probably largely due to the uniform environment and to the necessity of being able to move easily through the feathers that the *Mallophaga* tend to have a relatively smooth uniform surface without the development of feathered setae, scales and other modifications of the exoskeleton which provide useful specific characters in many groups of insects.

The sympatric forms are found in every stage of divergence, from those which differ only in the details of the male genitalia (the females being similar or indistinguishable) to those which can be separated generically on well marked characters. It seems possible to account for the occurrence of these forms by isolation and reunion of the host populations and by secondary infestations of lice populations.

PHYLOGENY

A. Correlation between Evolution of Host and Parasite.

It must be emphasized for those not familiar with this group that it is normal for the *Mallophaga* of related hosts to be themselves related and that it is almost always possible to say from the *Mallophaga* to what order, at least, the host belongs. Hence, the evidence from the distribution of the *Mallophaga* should carry considerable weight in those cases where the ornithologist is in doubt about the correct systematic position of a bird. Further, in most cases where there is a difference of opinion about this, the evidence from the mallophagan fauna usually supports one of the ornithological opinions as to the relationships of the bird in question. The evidence of relationship provided by one genus of *Mallophaga* is obviously less convincing than if more genera are involved and comparisons in the second part of this paper have, therefore, been made between the mallophagan faunas, that is the genera of *Mallophaga* found throughout the host group; a genus may be characteristic of a certain fauna and give a clue to the relationships of that fauna, although the genus is also found on other host groups.

B. Clues Presented by Parasites on the Phylogeny of the Hosts.

1. *Relationships between Orders of the Class Aves.* The majority of bird orders were probably established by the Eocene and are now so distinct that in most cases little is known of their relationships. This is reflected in their mallophagan parasites; many orders having a definite and distinctive parasite fauna, the affinities of the genera comprising the faunas often being obscure.

2. *Relationships between Subordinal Groupings.* There are some cases shown below where it is considered that a genus, family or suborder is placed in the wrong host order. Deductions of host relationships within families or genera are likely

to be unreliable until more material has been acquired and detailed and careful revisions of the mallophagan species have been made. However, when the *Mallophaga* are as well known as their hosts there is little doubt that they will form a useful source of evidence on such relationships—HOPKINS and TIMMERMANN (1954) and TIMMERMANN (1954, a-d) have discussed the arrangement of species within certain groups of waders based on the mallophagan parasites. Further, the distribution of the *Mallophaga* may indicate the previous geographical distribution of the host. It has been shown (CLAY, 1953) that *Corvus kubaryi* from Guam Island has an established population of a form of *Rallicola* only subspecifically distinct from the form on *Porphyrio poliocephalus*; according to MAYR, 1945 there is now no species of *Porphyrio* on Guam and Rota in the Marianas where the *Corvus* is found; it must be assumed that at some time the distribution of the two overlapped.

Although it is the general rule that related hosts have related parasites, there have been, as already shown, many factors operating during the evolution of the *Mallophaga* which have obscured the initial relationship between host and parasite. The cases of anomalous distribution (Table 6) of both genera and species, the possible causes of which are discussed below, show that the phylogenetic relationships of the *Mallophaga* cannot be used as infallible evidence of the phylogenetic relationship of their hosts.

Table 6

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

Genera of Mallophaga	Host Groups
<i>Colpocephalum</i> (sens. CLAY, 1947 a)	<i>Pelecaniformes</i> , <i>Ciconiiformes</i> , <i>Phoenicopteriformes</i> , <i>Falconiformes</i> , <i>Galliformes</i> , <i>Cariamae</i> , <i>Columbae</i> , <i>Psittaciformes</i> , <i>Cuculi</i> , <i>Strigiformes</i> , <i>Pici</i> , <i>Passeriformes</i> .
<i>Otidoecus</i> , <i>Rhynonirmus</i> <i>Cuclotogaster</i>	<i>Otides</i> , <i>Chardriiformes</i> , <i>Galliformes</i> , <i>Musophagi</i> .
<i>Degeeriella</i> -complex	<i>Galliformes</i> , <i>Falconiformes</i> , <i>Cuculi</i> , <i>Trogoniformes</i> , <i>Coraciidae</i> , <i>Upupidae</i> , <i>Bucerotidae</i> , <i>Ramphastidae</i> , <i>Pici</i> , <i>Passeriformes</i> .
<i>Rallicola</i>	<i>Apterygiformes</i> , <i>Rallidae</i> , <i>Charadriiformes</i> (<i>Jacaniidae</i>), <i>Cuculi</i> , <i>Passeriformes</i> (<i>Furnariidae</i>).
<i>Saemundssonina</i>	<i>Procellariiformes</i> , <i>Phaethontes</i> , <i>Charadriiformes</i> , <i>Gruidae</i> .

3. Causes of Apparent Anomalous Distribution of Parasite.

a) *Discontinuous Distribution of Genera.* Related species of *Mallophaga* parasitic on unrelated host groups may be the relatively unchanged descendants of a common ancestor which evolved early in the evolution of the birds; the species have become extinct on some host groups or were absent from the stocks giving rise to these groups. The rather similar species of *Colpocephalum* on unrelated host groups may be an example of such a genus. Another example is given on p. 143, fig. 1.

b) *Discontinuous Distribution of Species.* Three related host species, A, B, C may originally have been parasitized by three pairs of sympatric species α^{1-3} and γ^{1-3}

(fig. 2) ; if the x species become extinct (or have never been collected) on some hosts and the y species on others, then those hosts with x may erroneously be considered more nearly related to each other than those with y . This may have happened in the genus *Degeeriella* on *Buteo* and *Milvus* where there are two distinct species, one

Host Species	A	B	C
Parasite Species	x^1 (y^1)	(x^2) y^2	x^3 (y^3)

Fig. 2. — False deduction of host relationships through extinction or ignorance of some of the sympatric species. x^{1-3} and y^{1-3} are respectively closely related allopatric species ; those in brackets are extinct or unknown, x and y belong to the same genus.

D. fulva found on the majority of *Buteo* and the other *D. regalis* found on *Buteo swainsoni*, *B. galapagoensis* and *Milvus* species. It is unlikely that the two latter species of *Buteo* are more closely related to *Milvus* than they are to the rest of *Buteo*. However, specimens of *D. fulva* sympatric with *D. regalis* have been found on one specimen of *B. swainsoni*. This suggests that the two species of *Degeeriella* were originally found on both *Buteo* and *Milvus* or their ancestral stock, that *D. fulva* became extinct on *Milvus* or the stock which gave rise to it, that it became rare on *B. swainsoni* and *B. galapagoensis*, and that *D. regalis* became extinct on the rest of *Buteo*.

c) *Secondary Infestations*. As discussed above it is most probable that this has happened within related groups of birds and also more rarely between hosts belonging to different orders. Errors due to secondary infestation are difficult to recognise, especially if this had taken place early in the evolution of the hosts and the species of the common genus are now widely distributed throughout two orders ; the ancestral stock may also have diverged further and given rise to other genera specialized for each host group.

d) *Parallel and Convergent Evolution*. This has been discussed above and examples given in which confusion of relationships may arise. In the second part of this paper when it is stated that two host groups have parasite species belonging to the same genera or if there is any doubt, species group, then it is almost certain that the apparent relationship of these species cannot be explained either by parallel or convergent evolution—their similarity is too great. If the distribution is not due to relationship between the hosts, then it is probably a case of secondary infestations.

e) *Human Error*. This may always be present in the true evaluation of the systematic position of the parasite and is the cause of the differences of opinion between parasitologists on certain relationships between hosts. The incorrect placing of a bird group by the avian systematist may also explain the apparent anomalous distribution of some of the parasites.

In spite of these reservations workers on *Mallophaga* believe that the distribution and relationships of the *Mallophaga* if cautiously and accurately interpreted provide a reliable source of evidence on the relationships of the birds. As reliable, as that often based on a single fossil bone or fragment of bone or on what one ornithologist calls « the unalterable anatomical evidence » of muscles, pterylosis and other anatomical features, the evidence from which is often contradictory (see p. ■■).

C. Chronology of the Relationships.

HOWARD (1950) has shown that the fossil record of birds is comparatively poor, especially that from the Cretaceous, when presumably the ancestors of the modern orders were evolving; bird bones are fragile and most of the fossil birds are based on separated bones, often single bones, and there are no consecutive series of fossils showing evolutionary trends as are found in the mammals. Thus, the evidence from the fossil record bearing on relationships between bird groups is limited and there is little against which to check the relationships and age of the parasites. Deductions of the age of the avian parasites must be made partly from their present distribution and partly from evidence from the mammal *Mallophaga*, the hosts of which have a better documented past. HOPKINS (1949: 558-561) has discussed this subject fully and much of the following is based on his discussion. By the Eocene most of the modern orders of birds were clearly distinguished as well as several family divisions (HOWARD, 1950), as all birds orders have *Mallophaga* and as the majority of orders have distinctive mallophagan faunas it can be presumed that the *Mallophaga* were parasitic on birds well before this time. HOPKINS has shown that it was likely that the *Trichodectidae* were parasitic on mammals by early Cretaceous. As the *Trichodectidae* and the *Phloptoridae* both belong to the *Ischnocera*, then if the proto-Ischnoceran evolved on birds, these would have been parasitized before that date; if, as is possible, it evolved on mammals then the *Phloptoridae* must have separated from the Trichodectid-stock before the latter had assumed the typical characters of the family as now known. Hence, it can be assumed that the *Phloptoridae* have been parasitic on birds at least by early Cretaceous and if the *Ischnocera* evolved on the birds, perhaps earlier. HOPKINS has also shown that the *Amblycera*, more primitive and probably ancestral to the *Ischnocera*, must have been parasitic on mammals at least during the Jurassic and if the latter acquired these from the birds then this class must have been parasitized by then and perhaps as early as the Upper Triassic. It seems reasonable to deduce from the available evidence that the *Mallophaga* have been parasitic on both birds and mammals from an early time in the evolution of both these classes.

Many factors must have affected the rate and degree of speciation in the *Mallophaga*, and at the present time it is not possible to make reliable deductions of the relative ages of the host groups based on the degree of speciation of their *Mallophaga*. The rates of speciation have obviously been so different in the *Amblycera* and *Ischnocera* that comparisons of these on the same host group are of little value. If a comparison is made between the degree of speciation in two or more genera of *Ischnocera* parasitic on one host group there are sometimes considerable differences, this may be due to the age of the genera or because one has been more stable in the evolutionary sense than the other. For instance, *Fulica atra* and *F. americana* have the same species of *Incidifrons* and *Fulicoffula*, but the populations of *Rallicola* are specifically distinct on the two hosts. Sometimes the species of a genus may show different degrees of speciation on different parts of a host group; *Larus*, for instance, has only one species of *Saemundssonina* on the eighteen species of host from which this genus is known while there are eight species of *Saemundssonina* on the ten species of *Sterna*. In this case the populations of *Quadriceps* are also more distinct on *Sterna* than on *Larus* suggesting a more recent origin for the latter group. In the hawks each genus of host, or in some cases two or more genera, are usually parasitized by a single species of *Degeeriella*, sometimes comprising more or less taxonomically separable populations; but two species of *Pernis*, *apivorus* and *ptilorynchus*, each have a dis-

tinctive species of *Degeeriella*; it is of course possible that these are the relics of a sympatric pair (see p. 151). The four European species of *Corvus* each have a distinct species of *Myrsidea* (*Amblycera*) and *Philopterus* (*Ischnocera*), whereas all the species of *Anas* examined have the same species of *Holomenopon* and *Trinoton* (*Amblycera*) and *Anatoecus* (2 sympatric species) and *Anaticola* (*Ischnocera*). This might be due to the greater age of *Corvus* or to the different evolutionary potentialities of the genera on the two groups or to the different environmental or evolutionary histories of the parasites; possibly there was more interchange of parasites between the species and incipient species of *Anas* preventing speciation in the parasites. The parasite of the ostrich and rhea are close, perhaps not more than subspecifically distinct. In the bird genus *Threskiornis*, PETERS, 1931 considers that *aethiopica*, *melanocephala* and *molucca* are distinct species; each of these is parasitized by two genera of *Mallophaga* (*Ibidoecus* and *Ardeicola*) with distinct species on each. MAYR, 1931 in describing *pygmaeus* considered that *molucca* and *pygmaeus* were subspecies of *aethiopica* whereas the *Mallophaga* (two genera) from *pygmaeus* are the same as those from *molucca* and differ from those of *aethiopica*.

These examples and those in table 4, show some of the difficulties inherent in this problem, but as in many cases (see part II) there is a definite relationship between the distribution of the parasite at the generic, specific or subspecific level and the usually accepted taxonomic divisions of the hosts it seems probable, when the systematics and distribution of the *Mallophaga* are sufficiently well known for a thorough analysis to be made that evidence from this source may assist in assessing the relative ages of host groups and perhaps give some indication of whether an infestation of parasites is primary or secondary.

PART II

A SURVEY OF THE DISTRIBUTION OF THE MALLOPHAGA ON THE CLASS AVES¹

Struthioniformes (Ostriches) and *Rheiformes* (Rheas).

The ostriches are parasitized by one genus (*Struthiolipeurus*) also found on the rheas; the latter order has, in addition, a second related genus (*Meinertzhageniella*). *Struthiolipeurus* is a distinctive genus found on no other orders of birds and the species found on *Struthio* and *Rhea* are very similar. The evidence from the *Mallophaga* is supported by that from other parasitic groups and conforms with CHANDLER's conclusion from feather structure and those of LOWE (1942) from other anatomical features that the two orders are related and not the relics of independent unrelated stocks.

Casuariiformes (Cassowaries and Emus).

Mallophaga have been seen from *Dromiceius novaehollandiae* only: a single species belonging to a distinctive genus (*Dahlehornia*), found on no other group of birds and with no obvious affinities.

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

¹ WETMORE, 1951 has been followed in most cases for the names of orders and for the subordinal classification.

between the three host orders, but *Dahlemhornia*, 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. CHANDLER (1916) on feather structure and LOWE (1918) on other characters believed that this order was related to the two previous orders; there is no obvious relationship between the *Mallophaga*, but too little is known about the fauna of the *Casuariiformes* for any reliable deductions to be made from it.

Apterygiformes (Kiwis).

Only one genus (*Rallicola*) is known from *Apteryx* with a species on each of the three species of host; these species are similar to some of the *Rallicola* found on the *Rallidae*. This supports the belief of FÜRBRINGER that there is a relationship between the kiwis and the rails.

Tinamiformes (Tinamous).

142 /

This order is parasitized by species belonging to the *Heptapsogaster*-complex of which about 25 genera have been described, a number which will probably be reduced to 15 or less. These genera are believed to be the descendants of a stock parasitic on an ancestral tinamou which have diverged within this host group to form the genera now known. These genera resemble those of the *Goniodes*-complex found on the *Galliformes* and *Columbae* in the simplified anterior marginal and ventral carinae of the head. In fact, one genus *Rhopaloceras* is similar to *Goniodes* in not having the modified thorax characteristic of the *Heptapsogaster*-complex, however in the form of the vesicular apparatus and ductus ejaculatorius of the male genitalia *Rhopaloceras* resemble the *Heptapsogaster*-complex and not the *Goniodes*-complex. As suggested above (p. 142) the form of the head found in the parasites of the *Galliformes* and *Tinamiformes* may be a retention or a specialization of the primitive type best suited to the feather structure of these birds which according to CHANDLER (1916: 347) is similar. On the other hand there may be a phylogenetic affinity between the *Heptapsogaster*- and *Goniodes*-complex denoting a relationship between the hosts. Of the other *Ischnocera* found on the *Tinamiformes*, two (*Pseudophilopterus* and *Pseudolipeurus*) have no obvious affinities and one (*Tinamotfecola*) probably belongs to the widely-distributed *Degeeriella*-complex. Of the two genera of *Amblycera* one (*Menacanthus*) is also found on the *Galliformes* but occurs elsewhere, the other *Microtenia* has no obvious affinities. Thus, the mallophagan fauna of the *Tinamiformes* does not rule out a galliform-relationship and does not show affinities to that of any other group of birds. a

Gaviiformes (Divers).

This order is parasitized by a genus of *Ischnocera* (*Craspedonirmus*) the affinities of which are doubtful, but is not obviously related to the genus found on the *Podicipediformes*. A single record of *Pseudomenopon* (see below under the grebes) from this order needs confirmation. In this case the *Mallophaga* throw no light on the relationships of their hosts.

Podicipediformes (Grebes).

The single genus of *Ischnocera*, *Aquanirmus*, parasitising this order has no obvious relationship to any other and throws no light on the relationship of its hosts. The *Amblyceran* genus *Pseudomenopon* is established on some of the members of this order (but see also p. 163).

Sphenisciformes (Penguins).

The penguins are parasitized by two genera (*Austrogoniodes* and *Nesiotinus*) not obviously related to each other nor to any other known genera. Although the head of *Austrogoniodes* has the simplified form and thus a superficial resemblance to that of the *Goniodes*-complex there is no suggestion of relationship in other characters. The *Mallophaga* support the view that the penguins were separated from other birds at an early date (SIMPSON, 1946) and the ancestral lice became adapted to this rather peculiar habitat; the small number of genera are probably a result of the uniform feather covering of the hosts (see above, p. 148).

Procellariiformes (Petrels).

This order is parasitized by three genera belonging to the *Amblycera* and about eleven belonging to the *Ischnocera*. Of the latter, nine (referred to here as the *Philoceanus*-complex) are probably all descendants of a single ancestral stock which diverged after it had become parasitic on the petrels; another (*Docophoroides*) has no obvious affinities but may also be a derivative of the *Philoceanus*-complex. The remaining genera either parasitize other host groups as well or are related to genera found elsewhere. Previously (CLAY, 1950) it was suggested that the presence of genera found both on petrels and other groups of birds might be due to secondary infestation. Since then further material has become available and it seems possible that a review of the mallophagan fauna of the petrels may throw some light on the relationships of the order (Table 7). Considering first the *Philoceanus*-complex comprising nine genera it is found, as pointed out by HARRISON, 1937: 36, that there is some similarity between certain of these genera and the species group of *Pectinopygus* found on the *Fregatidae*, *Pelecaniformes*.

Table 7

Genera *Mallophaga* common to the *Procellariiformes*,
Pelecaniformes and *Charadriiformes*.

	PROCELLARIIFORMES	PELECANIFORMES		CHARADRIIFORMES	
		<i>Phaethontes</i>	<i>Fregatidae</i>		<i>Pelecani</i>
<i>Actornithophilus</i>	} +			+	
<i>Longimenopon</i>					
<i>Austromenopon</i>	+	+	[<i>Eidmaniella</i> ¹]	[<i>Eidmaniella</i>]	+
<i>Philoceanus</i> -complex	+		[<i>Pectinopygus</i> ²]	[<i>Pectinopygus</i>]	+ ³
<i>Saemundssonina</i>	+	+			+

¹ *Eidmaniella* species near *Austromenopon*. ² *Pectinopygus* species near *Philoceanus*-complex. ³ On the *Stercorariidae* only.

Saemundssonina which is well distributed on the *Procellariidae* and *Hydrobatidae* within the order, is also found on various other host groups (Table 6). The *Charadriiformes* also have other genera (*Cummingsiella*, *Quadriceps* and *Luniceps*) related to *Saemundssonina*, suggesting either that *Saemundssonina* evolved on the *Charadriiformes*, or that the other genera have become extinct on the petrels. The species on *Phaëthon* resemble some of those on the petrels in the superficial characters of the anterior part of the head; this may or may not be significant.

Austromenopon (*Amblycera*) is well distributed on the petrels and appears to be generically inseparable from the species on the *Charadriiformes* and *Phaëthon*. On the *Pelecaniformes* there is a related genus, *Eidmaniella*, which differs amongst other characters in the position of the eyes and the form of the antennal fossa. However, one species, that from *Fregata*, has the eyes and the posterior part of the antennal fossa as in *Austromenopon*; the male genitalia of this species differ from the usual type found in both *Eidmaniella* and *Austromenopon*, but are similar to those of *Ancistrana*; this latter genus, confined to the petrels, is most probably related to *Austromenopon*.

Longimenopon (*Amblycera*) was previously thought to be a distinctive genus confined to the petrels, but recently Dr. K. C. EMERSON (in press) has re-discovered *Colpocephalum pediculoides* Mjöberg which occurs on *Arenaria interpres*¹ (*Charadriiformes*). This species is difficult to place generically as it is somewhat intermediate between *Longimenopon* and *Actornithophilus*—a wide-spread genus on the *Charadriiformes*, but should probably be placed in the latter genus.

Thus the *Mallophaga* of the *Procellariiformes* show a relationship to those of the *Pelecaniformes* through the *Fregatidae* by two genera and also perhaps the *Phaëthontidae* by two genera. LATHAM, 1947 has suggested that the *Fregatidae* and *Phaëthontidae* may form a link between the two orders. There is also a relationship (by three genera) between the mallophagan faunas of the *Procellariiformes* and *Charadriiformes*. The skuas (*Stercorariidae*, *Charadriiformes*) have species of *Perineus*, a genus of the *Philoceanus*-complex elsewhere restricted to the petrels; this may be a case of secondary infestation or another link between the two orders. There is no indication of a relationship between the *Mallophaga* of the petrels and penguins.

Within the order the distribution of the genera and species groups of the *Mallophaga* follows fairly closely the usual division of the order into four families; the *Diomedeidae* have two genera (*Episbates* and *Harrisoniella*) not found elsewhere, one genus (*Docophoroides*) found elsewhere only on *Macronectes*, and *Perineus* as the dominant genus and with none of the *Naubates-Halipeurus-Philoceanus* group. The *Procellariidae* are characterised by the *Naubates-Halipeurus* group and by the genera *Pseudonirmus* and *Trabeculus*, not known from other families; *Perineus* is less wide-spread. The *Mallophaga* of the *Hydrobatidae* have a species group of *Halilipeurus* («*Synantes*») and *Philoceanus* (of which *Naubates* may be no more than a species group) restricted to it. The form of some of the *Mallophaga* suggests that the *Hydrobatidae* contain the smaller petrels. The *Pelecanoididae* have one genus (*Halilipeurus*) found on the *Procellariidae* and one other genus (*Pelmatocerandra*) not found elsewhere.

Pelecaniformes (Tropic birds, Pelicans, Cormorants and Frigate birds).

The possible relationships of the *Mallophaga* of this order to those of the *Procellariiformes* have been discussed above. The order is divided into three suborders,

¹ Host record further confirmed by another lot taken from the same host in Ceylon by W. W. A. PHILLIPS.

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the *Phaëthontes*, *Pelecani* and *Fregatae*, a division which is, in general, supported by the distribution of the *Mallophaga*. The *Phaëthontes* have none of the genera found on the rest of the *Pelecaniformes* but have two genera characteristic of the faunas found on the *Procellariiformes* and *Charadriiformes*. On this evidence it was previously suggested (CLAY, 1950: 433) that *Phaëthon* should be included with the *Charadriiformes* and not the *Pelecaniformes*; a possible relationship with the *Procellariiformes* was not discussed because at that time it was thought that the occurrence of *Saemundssonina* and *Austromenopon* on this latter order might be secondary and because various authors (CHANDLER, 1916; MATHEWS and IREDALE, 1921 and Murphy, 1936) have drawn attention to the resemblances between *Phaëthon* and the *Laridae* (see CLAY, 1950 for further discussion and references). The *Fregatae* have a mallophagan fauna which although typical of the *Pelecaniformes* shows some affinities to that of the *Procellariiformes* as discussed above. In the suborder *Pelecani* there is a well marked species group of the genus *Pectinopygus* on the *Pelecanidae*; the species of this genus found on the *Sulidae* and *Phalacrocoracidae* are more similar to each other than to those of the *Pelecanidae*; the species parasitic on the *Anhingidae* are nearer those from the cormorants than the gannets.

Ciconiiformes (Hérons and Storks).

The mallophagan fauna of this order (omitting that from the *Scopidae* and the *Phoenicopterii*) comprises 10 genera and shows no obvious affinities with any other order. The distribution of the genera within the order is given in table 8; this shows that only two of the genera (*Ciconiphilus* and *Ardeicola*) are common to the

Table 8
The *Ciconiiformes* (according to Wetmore, 1951) and their *Mallophaga*.

	<i>Colpocephalum</i>	<i>Ciconiphilus</i>	<i>Ardeiphilus</i>	<i>Plegadiphilus</i>	<i>Eucolpocephalum</i>	<i>Laemobothrion</i>	<i>Ardeicola</i>	<i>Ibidocetus</i>	<i>Neophilopterus</i>	<i>Ardeiphagus</i>
ARDEAE										
<i>Ardeidae</i>	+	+	+				+			?+
<i>Cochleariidae</i>										+
BALAENICIPITES		+								
CICONIAE										
<i>Scopoidea</i>	+									
<i>Ciconioidea</i>	+	+					+		+	
<i>Threskiornithoidea</i>	+			+	+	+	+	+		
PHOENICOPTERI	+									

suborders *Ardeae* and *Ciconiae*. *Ciconiphilus* has not been found on the superfamily *Threskiornithoidea* and is the only genus so far known from the suborder *Balaenicipites*; elsewhere *Ciconiphilus* is known only from *Anser* and the *Cygninae* (see below under *Anseriformes*). The division of the suborder *Ciconiae* into the superfamilies *Ciconioidea* and *Threskiornithoidea* is reflected in the distribution of the two

distinct but related genera, *Neophilopterus* restricted to the former superfamily and *Ibidoecus* to the latter; *Ibidoecus* is also found on *Aramus scolopaceus*. The *Threskiornithinae* have species of the distinctive species group of *Laemobothrion* found elsewhere on various members of the *Rallidae*, *Aramidae*, *Psophiidae* and *Opisthocomus*; the presence of two genera common to the *Threskiornithinae* and *Aramus* may be cases of secondary infestations or may indicate that *Aramus* has affinities both to the rails and the ibises. Only one genus (*Ardeiphagus*) of doubtful affinities, has been seen from *Cochlearius*; a single record of this genus from *Tigrisoma* (*Ardeidae*) needs confirmation.

Scopus sometimes placed in a separate superfamily of the *Ciconiae* has two genera, *Austromenopon* and *Quadriceps* characteristic of the waders and (apart from *Colpocephalum*¹) none of the genera characteristic of the *Ciconiiformes*.

The *Phoenicopteri* often placed as a suborder of this order are parasitized (apart from *Colpocephalum*) by three genera (*Trinoton*, *Anatoecus* and *Anaticola*) found elsewhere only on the *Anseriformes*. CHANDLER (1916 : 320) considers that the details of the minute structure of the feathers of the *Phoenicopteri* agree with the *Anseres* more closely than 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 show less elongation of the legs and have a straighter bill (HOWARD, 1950), and recently a fossil (*Telmabates antiquus*) has been described by HOWARD (1955) which according to this author emphasizes the relationship of flamingoes to the *Anseriformes*. WETMORE (1955) considers the flamingoes related to the *Anseres* and the storks and MAYR and AMADON (1951) placed them in a separate order. It seems possible on the evidence now available that the *Phoenicopteri* should be included in the *Anseriformes*.

Anseriformes (Screamers, Ducks, Geese and Swans).

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The mallophagan fauna of the *Anseriformes* together with that of the *Phoenicopteri* comprises a homogeneous and distinctive group with no obvious affinities to any other. There are three amblyceran genera: *Trinoton* with no obvious affinities; *Holomenopon* perhaps related to *Austromenopon*; *Ciconiphilus* found on *Cygnus* and *Anser* perhaps secondarily acquired from the *Ciconiiformes*, or perhaps merely a broad-headed derivative from *Colpocephalum* independently evolved on the two groups. The ischnoceran genera *Anatoecus*, *Anaticola* and *Acidoproctus* with its three related genera or subgenera have no obvious affinities. From the *Anhimidae* only two genera are recorded, one *Dictesia*, known from no other group of birds and probably a derivative from *Colpocephalum*, the other *Bothriometopus* related to *Acidoproctus* (see above). Thus the *Mallophaga* of the *Anhimidae* suggest that the hosts form a distinctive group within the order.

Falconiformes (Birds of Prey).

The mallophagan fauna of this order shows some affinities with that of the *Strigiformes* and the *Cuculi*: *Kurodaia* is found only on the hawks and the owls; *Cuculiphilus* is found only on the hawks and cuckoos, although some workers consider that the species on the two host groups are generically distinct. *Degeeriella* from

¹ *Colpocephalum* is a primitive genus of the *Amblycera* and is found on many diverse orders; it is perhaps a relic of a stock which occurred on the ancestral birds.

165

the hawks and *Cuculicola* from the cuckoos are obviously related and have undergone parallel evolution on the two host groups (see above, p. 142); both these genera may be relics of a once widespread stock occurring on many host groups, and are apparently nearly related to those belonging to the *Degeeriella*-complex found in the passerine mallophagan fauna (see below p. 142). Certain apparent resemblances between the head lice genera of the hawks and cuckoos, may prove to be significant or explicable by parallel evolution from a degeerielline-ancestor (see above p. 142).

142

142

MAYR and AMADON (1951 : 6) have suggested the possibility that the *Cathartae* and *Sagittarius* may not be related to the rest of the *Falconiformes*. This view is supported by JOLLIE (1953 : 369) who goes even further in suggesting that there are four, possibly five, unrelated groups, the *Cathartidae*, *Sagittarius*, *Accipitridae*, *Falconidae* and *Pandionidae* (if not placed with the *Accipitridae*). CLAY (1951) gave some evidence from the distribution of the *Mallophaga* suggesting that the only reasonable explanation of this was to postulate a common origin for the group as now constituted. This evidence, somewhat enlarged, is given in table 9; from this it is seen that the fauna of the *Falconiformes* comprises nine genera, one of which

Table 9

Mallophaga of the *Falconiformes*.

	CATHARTIDAE	SAGITTARIIDAE	ACCIPITRIDAE	PANDIONIDAE	FALCONIDAE
<i>Colpocephalum</i>	+	+	+		+
<i>Kurodaia</i>			+	+	+
<i>Cuculiphilus</i>	+		+		
<i>Nosopon</i> *			+		+
<i>Laemobothrion</i> *	+	+	+		+
<i>Degeeriella</i> *			+		+
<i>Craspedorrhynchus</i> *			+		
<i>Falcolipeurus</i> *	+	+	+		+
<i>Falcoecus</i> *			+		

* Genus or species group found on no other group of birds.

Degeeriella has a sympatric species group (or genus, *Acutifrons*). Of these genera *Nosopon*, *Craspedorrhynchus* (and the probably related *Aegypocetus*) and *Falcolipeurus* are found on no other group of birds, *Falcolipeurus* is an extremely distinctive genus with no obvious affinities. *Kurodaia* as shown above is also found on the owls; *Cuculiphilus*, also found on the cuckoos, has a well marked species group on the *Carthartae* and another species group nearer that of the cuckoos parasitic on the *Aegyptinae*; *Laemobothrion* and *Degeeriella* are found elsewhere but are represented by well marked species groups on the *Falconiformes*. *Falcolius* from *Microhierax* is not included as it is not relevant to the discussion and seems to be either a case of secondary infestation or indicates that *Microhierax* does not belong to the *Falconiformes* (CLAY, 1955). Thus, the *Cathartae* have four out of the nine genera, two of

them belonging to genera or species groups not found outside the Falconiformes and one which is found amongst the Falconiformes only on the old world vultures ; apparently the fossil record suggests that the old world and new world vultures may have a common ancestry (HOWARD, 1950). *Sagittarius* has three genera (although the occurrence of *Laemobothrion* needs confirmation) including the important *Falcolipeurus*, the *Accipitridae* have all nine genera and the *Falconidae* have four. The Mallophaga throw no light on the position of *Pandion* within the order as it is parasitized by only one species (of *Kurodaia*) of a distinctive type. Some of the evidence presented by the ornithologists on relationships within the order is conflicting (COMPTON, 1938 ; HUDSON, 1948 ; JOLLIE, 1953) and it is here suggested that the mallophagan fauna provides better evidence than that of certain anatomical features of the birds such as the muscles which may have been more affected by habit and environment.

Galliformes (Game birds).

The *Galliformes*, with the exception of *Opisthocomus*, has a large and distinctive mallophagan fauna. This shows affinities with that of the *Musophagi* and with that of the *Columbae* (both discussed below under the respective suborders). A possible relationship between the faunas of the *Tinamiformes* and the *Galli* has been discussed above under the former order.

The fauna comprises some 18 genera some of which (*Chelopistes* and *Lagopoecus*) show a discontinuous distribution within the *Galli* suggesting that they are relics of once more widely distributed stocks. It also seems possible that there has been a certain amount of secondary infestation within the order : this may explain the occurrence of rather similar species of *Chelopistes* on the *Cracidae* and *Odontophorinae* of Central and South America and the presence of *Clayia*, perhaps originally a guinea-fowl (*Numididae*) parasite, on *Francolinus*, *Pternistes* and *Afropavo* of Africa, unless there is a relationship between these genera. Common dust baths might explain the method of transfer.

There is still much work to be done on revisions of the genera, but a brief review of the *Mallophaga* show that the *Megapodiidae* are parasitized by six genera, one (*Kelerimenopon*) not found elsewhere among the *Galli* and the others represented by rather distinct species groups. These *Mallophaga* are in no way closely related to those of the *Cracidae* ; this latter order has a mallophagan fauna nearer to that of the *Phasianidae*. The families included under the *Phasianoidea* each have a fairly characteristic fauna : the *Tetraonidae* have *Goniodes* and *Lagopoecus* as the dominant genera ; *Lipeurus* apparently being absent and *Oxylipeurus* rare. The *Phasianidae* are subdivided into the *Phasianinae* and the *Odontophorinae*, each showing a rather different fauna, suggesting that on the analogy of the other divisions the *Odontophorinae* should be given family rank. The *Phasianinae* have 13 of the 18 genera found on the order : one of these (*Clayia*) elsewhere found on the *Numididae* has been taken only on *Francolinus*, *Pternistes* and *Afropavo*, perhaps due to secondary infestations (see above) ; the widest distribution of *Lipeurus* and *Oxylipeurus* is found on this subfamily, these genera being replaced on some hosts (*Alectoris*, *Ammoperdix*, *Coturnix*, *Excalfactoria* and *Perdix*) by *Cuclotogaster*, related to *Otidoecus* on the *Otididae* and *Rhynonirmus* on the *Scolopacinae*. The *Numididae* have a rather distinct fauna with four genera (the related *Clayia*, *Numidicola* and *Somaphantus* and one of doubtful affinities, *Numidilipeurus*) not found elsewhere except for *Clayia* (see above). The *Meleagridae* differ from the *Phasianinae* only in the reduction of their fauna,

only three genera being known. *Chelopistes*, rare on the *Phasianinae*, appears to have replaced *Goniodes* on the *Meleagridae*.

The *Opisthocomi* usually placed with the *Galliformes* has a distinctive fauna of five genera, none of which is found on the *Galliformes*. There are three amblyceran genera: one, *Carrikeria*, of doubtful affinities; one *Laemobothrion* belonging to the distinctive ~~subspecies~~ found on the *Rallidae* and the *Threskiornithinae*; one *Hoazinus*, apparently related to *Heleonomus* of the *Gruidae*; and two Ischnoceran genera: one (*Wilsoniella*) perhaps related to *Rallicola* of the *Rallidae* and one (*Osculotes*) with no obvious affinities. These *Mallophaga* suggest that *Opisthocomus* would be better placed with the rather heterogeneous *Gruiformes* than with the *Galli*.

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Gruiformes (Cranes, Rails and Others).

The *Mallophaga* of the various suborders included in this order suggest that this is not a homogeneous order analogous with most of the other avian orders.

In WETMORE (1951) the suborder *Grues* is divided into two superfamilies: the *Ralloidea* (rails) and *Gruoidea*. The rails have a mallophagan fauna comprising five genera; two of these genera are also found on the *Psophiidae* and three on the *Aramidae*, both these families are included in the second superfamily, the *Gruoidea*. The suborders *Heliornithidae* and the *Rhynocheti* each have one genus belonging to the ralline fauna; the *Jacanoidea* a group of birds with an obscure systematic position but usually placed with the *Charadriiformes*, have two genera belonging to the ralline fauna. The *Gruidae*, however, have a fauna of four genera none of which belongs to the ralline fauna, one (*Saemundssonina*) characteristic of the *Charadriiformes* is also found elsewhere (see above) and three are of doubtful affinities. The *Mallophaga* of these groups suggest that the *Rallidae*, *Aramidae*, *Psophiidae*, *Heliornithes*, *Rhynocheti* and *Jacanoidea* are more nearly related to each other than to the *Gruidae*. Evidence from ornithological sources on the relationships between these groups is conflicting: CHANDLER (1916: 354) deduces from feather structure a relationship between the *Gruidae*, *Aramidae* and *Rallidae* and considers them offshoots from a primitive stem leading to the *Charadriiformes*; while the *Otididae*, *Psophiidae* (and possibly the *Aramidae*) he considers are more closely related to each other and may be early offshoots from the stem leading to the *Columbae* 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 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 *Jacaniidae*, however, suggests ralline not gruimorphine affinities. LOWE (1931) considers that the *Burhinidae* (Stone-curlews)—placed by WETMORE, 1951 as a superfamily of the *Charadrii*, 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 moved about between the *Gruiformes* and the *Charadriiformes* is *Rostratula*, the painted snipe. It is, therefore, of interest that this bird has two genera (*Quadriceps* and *Actorni-*

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thophilus) belonging to the charadriine fauna and one (*Pseudomenopon*) to the ralline fauna. However, *Pseudomenopon*, which is widely distributed on the *Rallidae* and *Aramidae* is also found on the grebes and has possibly become secondarily established on certain water and marsh birds.

The *Mallophaga* of the other five suborders of the *Gruiformes* are of little assistance in deducing the relationships of their hosts. The *Mesoenatides* are parasitized by one genus belonging to the wide-spread *Degeeriella*-complex and which throws no light on the relationship of the host. The *Turnices* are also parasitized by one genus, *Turnicola*, showing some resemblances to *Penenirmus* on the *Passeres*; both these genera may be derivatives from an ancestral *Degeeriella* stock, their present resemblances being due to parallel evolution or to relationships between the hosts; LOWE (1923 : 277) showed that the *Turnices* possess some passerine characters. The *Otides* have one genus (*Otidoecus*) the nearest relatives of which are found on the *Galli* (*Cuclotogaster*) and on the *Scolopacidae* (*Rhynonirmus*); these genera are perhaps relics of a previously more widely distributed group of genera. The *Cariamae* are parasitized by one genus (apart from *Colpocephalum*), this genus (*Heptapsogaster*) is found elsewhere on the *Tinamiformes* and may be a case of secondary infestation; the occurrence of a second genus (*Tinamotaecola*) on both the *Cariamidae* and *Tinamididae* needs confirmation. A single record of *Quadriceps* from the *Eurypygididae* also needs confirmation.

Charadriiformes (Waders, Gulls, Auks).

This order should perhaps be considered with the *Gruiformes* as there is evidence from the morphology (LOWE, 1931 : 531 and CHANDLER, 1916 : 353) and the fossil record (HOWARD, 1950) suggesting that the two orders have arisen from a common stock. Further, certain families are placed sometimes in one order and sometimes in the other. There is, however, no decisive confirmation of such a common origin from the mallophagan faunas. As shown above the *Mallophaga* of the *Rostratulidae* are partly ralline and partly charadriine, apart from this the *Mallophaga* of the *Jacaniidae* are wholly ralline in affinities, and those of other doubtfully placed families, the *Burhinidae* and the *Thinocoridae* are typical of the *Charadriiformes*. One genus, *Saemundssonina* is also found on the *Gruidae* and may be related to *Incidifrons* on the *Rallidae*, but has a wider distribution (see under *Procellariiformes*). Another, *Rhynonirmus*, found only on the *Scolopacinae* and *Bartramia* is related to genera on the *Otides* and *Galliformes*. Apart from these two genera, which can only doubtfully be used to show affinities between the faunas of the *Gruiformes* and *Charadriiformes*, the latter order has eight genera not found on the *Gruiformes*. The possible affinities between the faunas of the *Charadriiformes* and the *Procellariiformes* have been discussed above under the latter order. In regard to relationships within the order more material and more detailed study is needed before a complete review can be given (but see various papers by TIMMERMANN, 1952 a, 1952 b, 1954 a, 1954 b, 1954 c, 1954 d).

Columbiformes (Sand-grouse, Pigeons, Doves).

This order is divided into two suborders, the *Pterocletes* (sand-grouse) and the *Columbae* (pigeons), the *Mallophaga* of the two suborders showing no affinities. The *Pterocletes* have one amblyceran genus (*Neomenopon*) of doubtful affinities and one ischnoceran (*Syrrhoptoecus*), also of doubtful affinities, but perhaps a derivative from the *Degeeriella*-complex. These *Mallophaga* throw no light on the affinities of the hosts.

The *Columbae* are parasitized by a number of related genera (*Coloceras*, *Campulotes*, *Auricotes*, *Kodocephalon* and *Physconelloides*) which are apparently related to the *Goniodes*-complex parasitic on the *Galli*. This does not seem to be a case of convergence due to similarity of feather structure (see CHANDLER, 1916 : 362) as the resemblance is found in both the external morphology and internal structure of the male genitalia. *Columbicola* and the related *Turturicola* have no obvious affinities, nor do the two amblyceran genera *Hohorstiella* and *Bonomiella*, although *Hohorstiella* may belong to the *Menacanthus* group, rather widely distributed and found on the *Galli* amongst others; *Colpocephalum* is also rarely found. Thus, the only affinities shown by the fauna of the *Columbae* is to that of the *Galli*.

Psittaciformes (Parrots).

a/ This order is parasitized by two genera of the *Amblycera*, one *Psittacomenopon* is probably *Colpocephalum* derivative, the other *Eomenopon* has no obvious affinities. There are four or five genera of *Ischnocera*, some of which at least are closely related and none has any obvious affinities to those of other orders. The parrots may be an example of an order on which the whole of the ischnoceran mallophagan fauna is derived from a single ancestral stock which has evolved on the order itself giving the genera now found; these genera will, therefore, be more closely related to each other than to these on any other order.

Cuculiformes (Plantain-eaters and Cuckoos).

This order is divided into the suborder *Musophagi* (Plantain-eaters) and the *Cuculi* (Cuckoos) but the mallophagan faunas of these two suborders show no affinities.

The fauna of the *Musophagi* comprises five genera, one of which (*Turacoeca*) has no obvious affinities but may be a *Colpocephalum* derivative, the other all belong to the galliform fauna. The possibility of a relationship between the *Galli* and the *Musophagi* suggested by the mallophagan fauna has been discussed elsewhere (CLAY, 1946 : 402, 1950 : 437).

The *Cuculi* have a mallophagan fauna which is difficult to assess. It comprises seven genera : of the three genera of *Amblycera* one, *Colpocephalum* has so far been found only on *Centropus*, another, *Osborniella* probably a *Colpocephalum* derivative, only on *Crotophaga*, and the third, *Cuculiphilus* which is fairly wide-spread is also found on some of the hawks. Of the four ischnoceran genera : one, *Cuculicola*, belongs to the *Degeeriella*-complex and has branched out into various rather distinctive species in a similar way to the *Degeeriella* of the hawks; another, *Cuculoecus*, as tentatively suggested above may be a derivative from *Cuculicola*; *Centropus* has species of *Rallicola* related to those found on the *Rallidae*, and perhaps secondarily acquired. The other ischnoceran genus, *Vernoniella* is at present known only from the *Crotophaginae* and has no obvious affinities. The *Mallophaga* of the *Crotophaginae* as at present known are quite distinct from the rest of the *Cuculi* having two genera not found elsewhere on the suborder.

Strigiformes (Owls).

This order is parasitized by only three genera. Two of them, *Colpocephalum* and *Kurodaia* belong to the *Falconiformes* fauna, *Kurodaia* not being found elsewhere outside these two orders. The third *Strigiphilus* has no obvious affinities. Thus the only apparent relationship of this fauna is to that of the hawks, and perhaps the following order.

Caprimulgiformes (Nightjars and Frogmouths).

Only two genera have been seen from this order, one (*Mulcticola*) has no obvious affinities, the other known only from the *Podargidae* may be related to *Strigiphilus* from the *Strigiformes*.

Coliiformes (Colies).

The isolated position of the mallophagan fauna of this order reflects that of its hosts. The colies are parasitized by two genera, the affinities of which are doubtful; one *Colilipeurus* seems to be related to *Falcolius* from *Microhierax* (*Falconiformes*) (see CLAY, 1955).

Apodiformes (Swifts, Hummingbirds), *Trogoniformes* (Trogons), *Coraciiformes* (Kingfishers, Bee-eaters, Rollers, Hornbills), *Piciformes* (Jacamars, Barbets, Toucans, Woodpeckers), *Passeriformes* (Perching birds).

These orders are considered together as some members of all of them are parasitized by elements of the passerine mallophagan fauna. This fauna comprises ten genera (table 10), seven of which are not found outside the orders listed above and two of which have been found only on the *Passeriformes*. It appears probable that the ancestral stock (or stocks) of these orders was parasitized by a primitive member of the *Degeeriella*-complex which gave rise to *Degeeriella* (species undescribed) on the *Bucerotes*, *Trogononinirmus* on the *Trogoniformes*, *Upupicola* on the *Upupidae* and probably *Hopkinsiella* on the *Phoeniculidae*, *Capraiella* on the *Coraciidae*, *Austrophilopterus* on the *Rhamphastidae* and *Picicola* on the *Picidae* and the *Passeriformes*. These genera are most nearly related to *Degeeriella* on the hawks and *Cuculicola* on the cuckoos. *Colpocephalum* and *Menacanthus* are probably also relics of widespread stocks which now occur on many groups of birds. *Sturnidoecus* and *Machaerilaemus*, unless secondarily absent on other groups, appear to have evolved on the *Passeriformes*: *Bizzarifrons* is probably the allopatric replacement of *Sturnidoecus* on the *Icteridae*. The distribution of this fauna suggests that the *Piciformes* are closely allied to the *Passeriformes* as they have in common with the latter order seven genera including the genus *Penenirmus* unknown elsewhere and the typical passerine *Philopterus*. This relationship of the two orders suggested by the mallophagan faunas is supported by the evidence of CHANDLER (1916) and LOWE (1914) based on the morphology of feathers, skeletons and muscles. The *Trogoniformes* and *Momotoidea* appear to be rather nearer the *Passeriformes* than are some of the other groups; CHANDLER (1916: 378) considered on the basis of feather structure that the *Trogoniformes* and *Passeriformes* were related.

The *Bucerotes* have a distinctive fauna comprising seven genera, which apart from a member of the *Degeeriella*-complex and perhaps some other genera derived from this, has no apparent affinities with the passerine fauna; it suggests a rather more isolated position for the *Bucerotes* than is generally allotted to them. Some of the groups have in addition one or more other genera not belonging to the passerine fauna. The *Meropes* (bee-eaters) have in addition to *Brüelia*, a distinctive head louse, *Meropoecus* and a distinctive amblyceran genus, *Meromenopon*, the latter is also found on the *Coraciidae* (rollers). The *Brachypteraciidae* have a distinctive species, *Brüelia longiceps* (Piaget), apparently a derivative of *Brüelia*, but probably not congeneric. In the *Passeriformes* the *Furnarioides* have species which are apparently not generically separable from the species of *Rallicola* found on the rails; this seems to be a case either of secondary infestation or perhaps an extreme case of parallel evolution from a common stock giving rise to *Rallicola* and *Brüelia* (CLAY,

1953 : 582). The *Tyrannoidea* have one genus *Pseudodocophorus* of no obvious affinities, but perhaps derived from an ancestral *Brüelia* stock.

Parts of some of the host groups listed above have no elements of the passerine fauna : the *Apodiformes* are usually divided into the *Apodi* (swifts) and the *Trochili* (hummingbirds). The former suborder has two genera of *Amblycera* (*Eureum* and *Dennyus*) probably related to each other and possibly related to *Myrsidea* of the *Passeriformes*. The *Trochili*, on the other hand are parasitized by two genera, *Ricinus* and *Trochiloecetes*, doubtfully distinct (CLAY, 1949), *Ricinus* is found elsewhere only on the *Passeriformes*. CHANDLER (1916 : 379) states that the structure of the feathers of the *Trochili* shows a striking likeness to that of the *Passeriformes* and LOWE (1939) considered that the *Trochili* should be placed as a suborder of the latter order.

Table 10
Bird groups with elements of the passerine mallophagan fauna.

	<i>Colpocephalum</i>	<i>Menacanthus</i>	<i>Myrsidea</i>	<i>Machaerilaemus</i>	<i>Ricinus</i>	<i>Degeeriella-complex</i>	<i>Penenirmus</i>	<i>Brüelia</i>	<i>Sturnidoecus</i>	<i>Philopterus</i>	No. of Passerine-fauna genera	No. of non-Passerine-fauna genera	Total no. of genera
APODIFORMES													
<i>Apodi</i>												2	2
<i>Trochili</i>					+						1		1
TROGONIFORMES													
			+			+		+			3		3
CORACIFORMES													
<i>Alcedinidae</i>											0	2	2
[<i>Todidae</i>]													
<i>Momotidae</i>								+		+	2		2
<i>Meropidae</i>								+			1	2	3
<i>Coraciidae</i>						+					1	1	2
<i>Brachypteraciidae</i>								?	+		?1		1
[<i>Leptosomatidae</i>]													
<i>Upupidae</i>			+			+					2		2
<i>Phoeniculidae</i>						?	+				?1	1	2
<i>Bucerotidae</i>						+					1	6	7
PICIFORMES													
[<i>Galbulidae</i>]													
[<i>Bucconidae</i>]													
<i>Capitonidae</i>			+					+	+		3		3
<i>Indicatoridae</i>								+			1		1
<i>Ramphastidae</i>			+	+		+		+			4		4
<i>Picidae</i>	+	+				+	+	+		+	6		6
PASSERIFORMES													
	+	+	+	+	+	+	+	+	+	+	10	2 ¹	12

No *Mallophaga* have been seen from those groups in square brackets and only little from the *Brachypteraciidae*. ¹ *Rallicola* (= *Furnaricola*) from the *Furnarioidea* and *Pseudodocophorus* from the *Tyrannoidea* have been omitted from the passerine fauna. Other explanations in text.

The *Alcedinoidea* (kingfishers) are parasitized by two genera of *Ischnocera*, one *Alcedoffula* is probably congeneric with *Quadriceps* found elsewhere only on the *Charadriiformes* and perhaps a case of secondary infestations, but if so this must have taken place early in the evolution of the kingfishers as the species are now wide-spread throughout the group and distinctive in form. The affinities of the second genus *Alcedoecus* are obscure. CHANDLER (1916) shows that in feather structure the *Alcedinoidea* and the *Bucerotes* (see above) both included in the order *Coraciiformes*, are somewhat different from the rest of the order, a fact supported by the mallophagan faunas. The *Phoeniculidae* have a rather distinctive fauna, one genus *Hopkinsiella*, probably derived from the *Degeeriella*-complex and one *Odorophila* of uncertain affinities but perhaps derived from *Colpocephalum*.

This evidence is summarised in the last three columns of table 10 and shows that the mallophagan faunas of the *Trochili* a suborder of the *Apodi*, *Piciformes* and *Trogoniformes* can be placed near that of the *Passeriformes*. It also suggests that the order *Coraciiformes*, as now constituted, is not a homogeneous order and may include a collection of not very closely related groups the affinities of some of which are obscure.

ed/ The suggestion~~s~~ affinities between the mallophagan faunas of the birds discussed above are shown in figure 3; this tentative arrangement will no doubt have to be modified as more material becomes available from some of the groups and when more is known about the relationships between the genera of *Mallophaga*.

NOTE

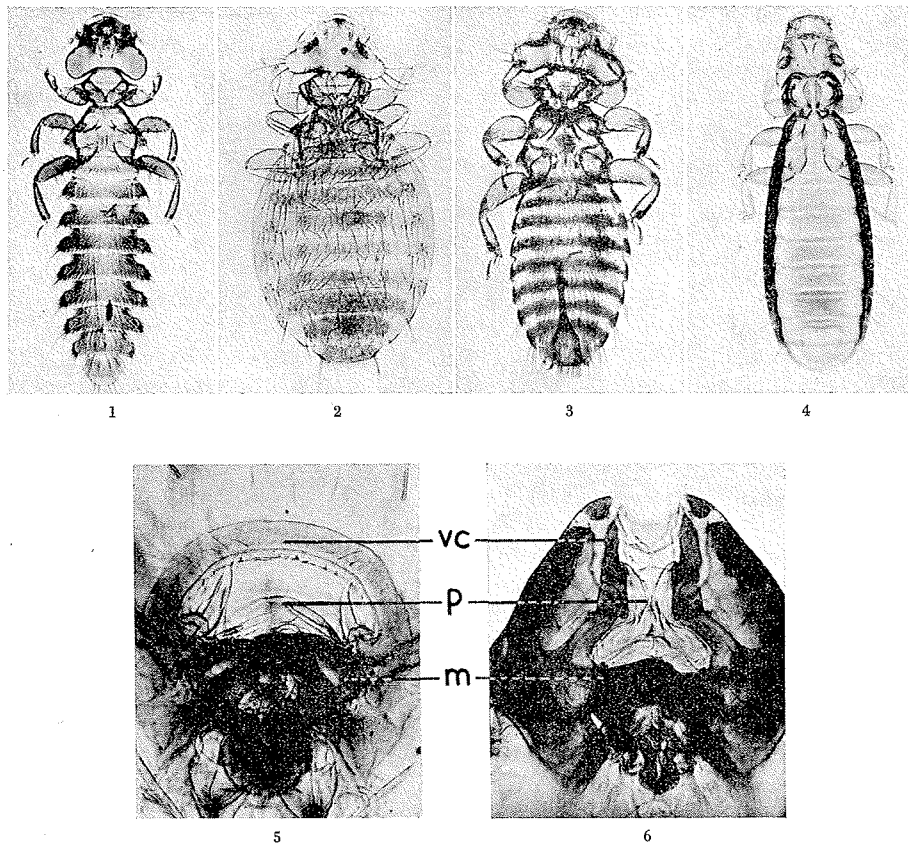
It is obvious that much of the above is highly speculative and any discussion on the origin and relationships of the *Mallophaga* is at the present time necessarily so. However, as the knowledge of the biology, relationships and distribution of the *Mallophaga* increases, together with the evolutionary history of their hosts it will be possible to correct and expand this tentative outline of the evolution and relationships of the *Mallophaga*. As this is mainly a summary of already published material, extracts have been made from papers published by the present writer, and ideas, the origins of which are now forgotten, may be included without acknowledgment to the author who first published them.

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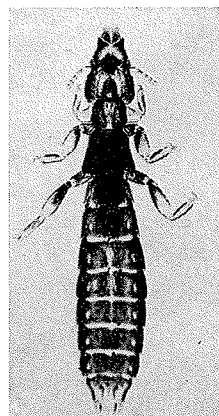
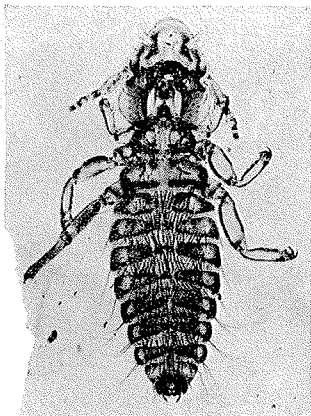
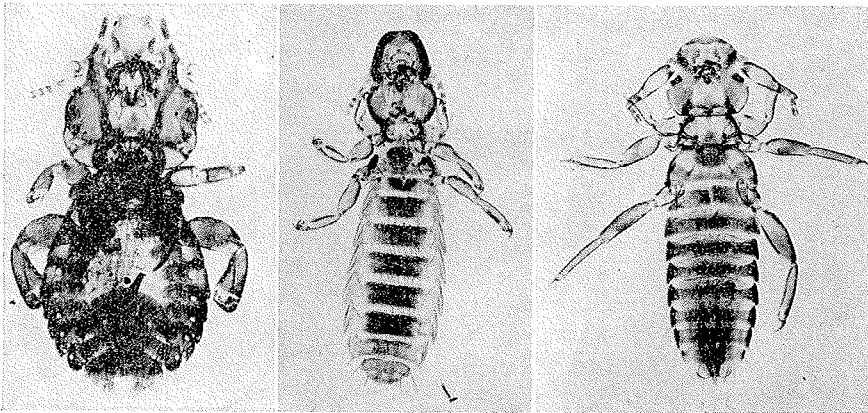
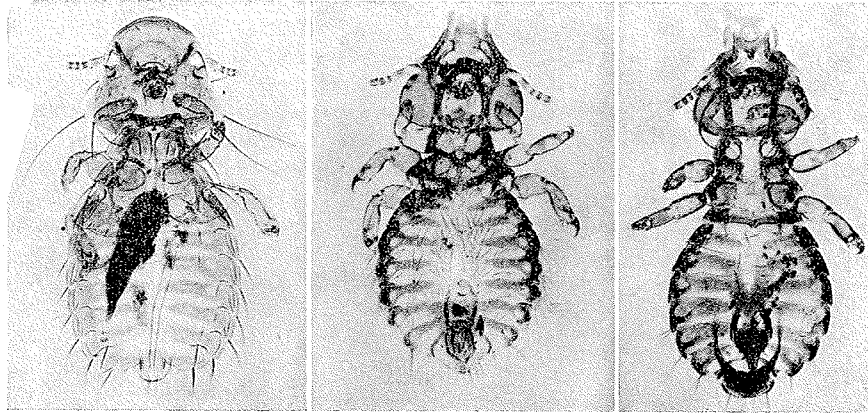
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Plate I



Figs. 1-4. — Examples of genera of *Amblycera* (magnifications various).
1. *Colpocephalum*. 2. *Menacanthus*. 3. *Myrsidea*. 4. *Ricinus*.
Figs. 5-6. — Oral regions of *Ischnocera*.
5. *Coloceras*. 6. *Brüelia*. vc. ventral carina ; p. pulvinus ; m. mandible.

Plate II



Examples of genera of *Ischnocera* (magnifications various).
1. *Campanulotes*. 2. *Sturnidoecus*. 3. *Anatoecus*.
4. *Philopterus*. 5. *Degeeriella*. 6. *Falcolius*. 7. *Buncorvellus*. 8. *Fulicoffula*.