

SOME PROBLEMS IN THE EVOLUTION OF A GROUP OF ECTOPARASITES

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

I. THE PRESENT DISTRIBUTION AND HOST RELATIONSHIPS OF THE MALLOPHAGA

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

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

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

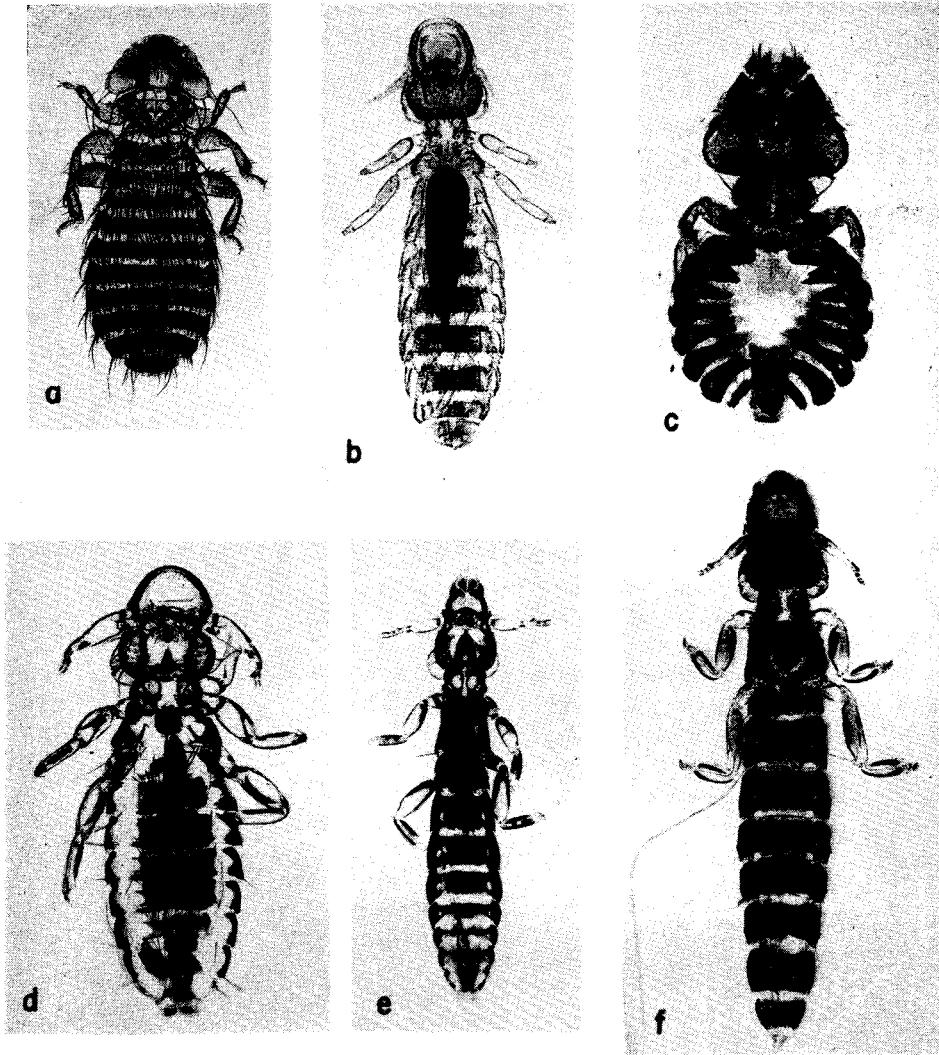


FIG. 1. a. Species of the superfamily Amblycera from the Anseriformes. b-f. Species of the Superfamily Ischnocera. b. *Degeeriella* species from the Falconiformes. c. *Craspedorhynchus* species from the Falconiformes. d. *Cuclotogaster* species from the Galliformes. e. *Fulicoffula* species from the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

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

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

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

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

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

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

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

Position on the bird of starred genera not recorded.

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

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

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

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

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

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

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

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

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

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

II. ISOLATING FACTORS IN MALLOPHAGA SPECIATION

1. Isolation by species formation in the hosts

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

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

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

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

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

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

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

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

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

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

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

2. *Isolation by the development of host specificity*

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

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

3. *Isolation and reunion of host populations*

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

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

4. Extinction of louse populations

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

III. ECOLOGICAL FACTORS IN MALLOPHAGA SPECIATION

1. *Intrinsic changes in each ecological niche*

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

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

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

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

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

2. Change of ecological niche on the same host species

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

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

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

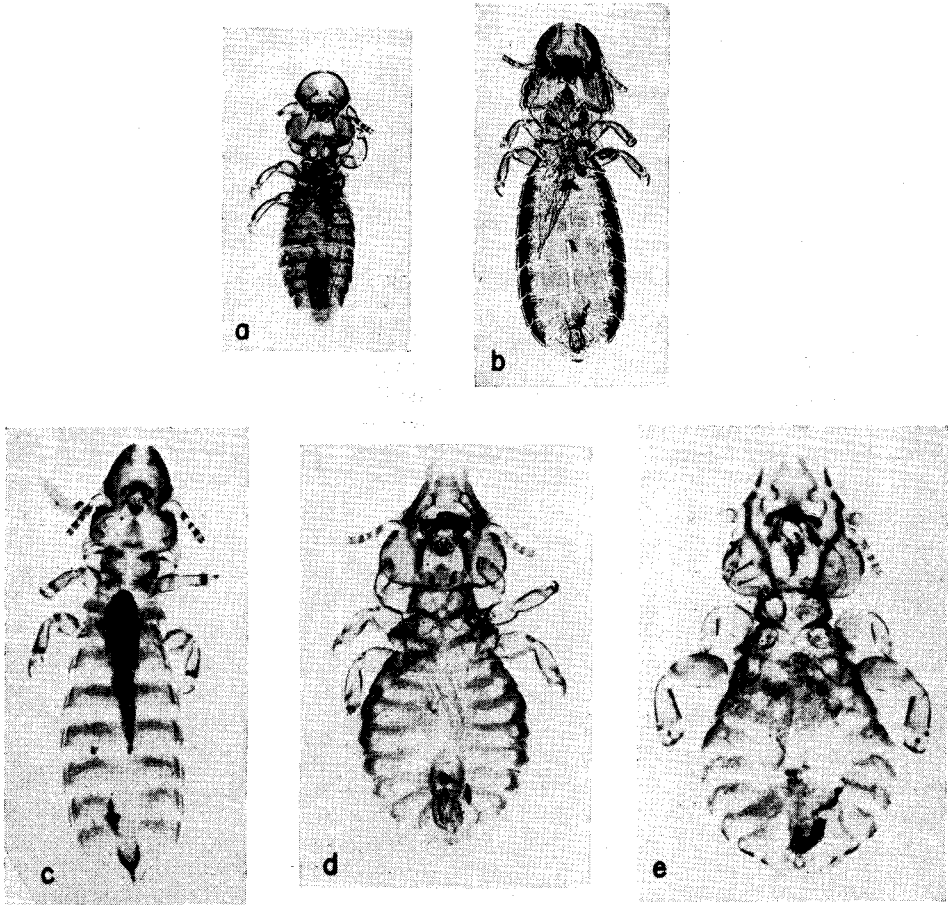


FIG. 2. Mallophaga of the Passeriformes. a. *Bruelia biguttata*. $\times 35$. b. *B. daumae*. $\times 35$. c. *B. nebulosa*. $\times 65$. d. *Sturnidoecus sturni*. $\times 56.5$. e. *Philoaterus* sp. $\times 60$.

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

IV. THE ORIGIN OF SYMPATRIC SPECIES

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

V. CAUSES OF ANOMALOUS DISTRIBUTION

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

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

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

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

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

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

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

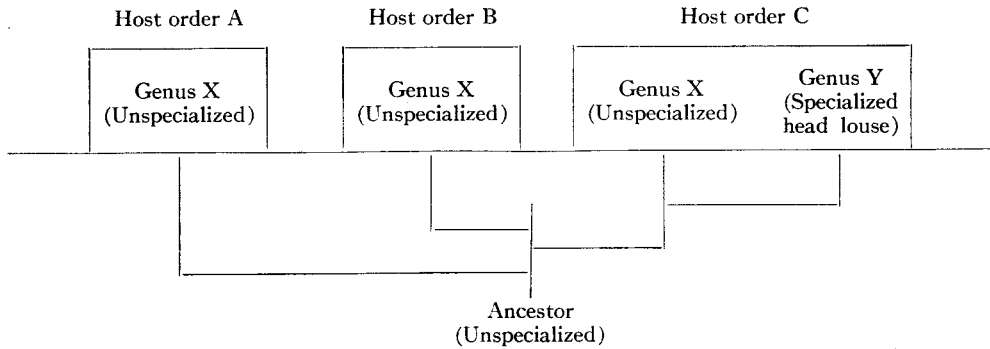


FIG. 3. Distribution and relationships of a hypothetical Ischnoceran genera complex.

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

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

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

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

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

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

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

concerned. In the genus *Philopterus* parasitic on the Passeriformes, for instance, a certain type of thickening of the anterior margin of the head and framework supporting the mouth parts has been developed in species from hosts belonging to different families; the available evidence suggests that this is a modification in response to feathers showing iridescence and hence a different physical structure. *Sympatric pairs*. Three related host species, x, y, z, may have been parasitized by three pairs of sympatric species, a¹ and b¹ on host x, a² and b² on y,

Host species	x	y	z
Parasite species	a ¹ (b ¹)	(a ²) b ²	a ³ (b ³)

FIG. 4. False deduction of host relationships through the extinction or ignorance of some of the sympatric species. All the parasite species belong to the same genus. Those in brackets are now extinct or unknown. a¹⁻³ and b¹⁻³ are, respectively, closely related allopatric species.

and a³ and b³ on z (fig. 4); species a¹⁻³ and species b¹⁻³ are, respectively, closely related allopatric species. If some of these species become extinct (or have not been collected) so that host species x appears to have only parasite species a¹, and y to have only b² and z only a³ (fig. 4); then, from a consideration of the parasites, host species x and z will appear to be more closely related to each other than either is to y because the parasite species a¹ and a³ are in fact more closely related to each other than to b². *Secondary infestations*. This has already been discussed above, and it was shown that the occurrence of a species of *Saemundssonina* common to the two terns, *Sterna hirundo* and *Gelochelidon nilotica*, did not necessarily mean close relationship between the two hosts, but could be explained as a case of secondary infestation.

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

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

CONCLUSIONS

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

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

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

NOTE ON TABLES

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

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

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

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SUMMARY

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

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

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

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

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

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

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

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

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

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