

# Geographical distribution of the avian lice (Phthiraptera): a review<sup>1</sup>

THERESA CLAY

*British Museum (Natural History)*

The avian lice are obligate parasites, spending their whole life-history from egg to adult on the body of their host without a free-living stage as in the fleas or intermediate hosts as in some of the endoparasites. It might therefore be thought that they would be independent of external conditions such as climate and other ecological aspects of the host's environment. However, the great diversity of structure found amongst the eggs of the lice laid in comparable situations on the body of the bird, some of the differences apparently being related to the host's environment (Balzer, in preparation), suggests that the external environment may affect the louse and its distribution. The kangaroo louse *Heterodoxus spiniger* which has become established on the domestic dog in many parts of the world is found almost entirely between lat. 40°N and 40°S (Thompson 1940) and is perhaps limited by some climatic circumstances. Thus, the louse population may be subject to both a micro- and macro-environment, the latter perhaps sometimes influencing distribution (Table III).

The distribution of the lice of birds is mainly a host one and in many cases a genus of louse will be restricted to an order or family of birds with each species restricted to a host species or a group of related host species. It is interesting however, that some orders of birds are parasitized by species with a wide host and geographical distribution (Table I). Published work on the Phthiraptera has concentrated on the host distribution and since Jardine, 1841 first suggested that ornithologists might use the distribution of the Mallophaga to trace relationships between their hosts (see Hopkins 1951), this aspect of the distribution of the Phthiraptera has been developed by Kellogg, Harrison, Hopkins, Clay, Eichler, Timmermann, Kéler and others. Deductions of host relationships from those of their parasites have been made with enthusiasm not always tempered by judgement. In Clay (1957) an assessment was made of the value of this source of evidence for host relationships and the factors which might influence and modify the original relationships. It was

---

<sup>1</sup> Received August 1972.

shown that, in general, the relationships of the lice do reflect those of their hosts and that anomalous distributions are the exception. In some examples of anomalous distribution a species appears to exhibit a geographical not a host distribution, but until recently discussion on this subject hardly appeared in the literature. Hopkins (1949) and Clay (1949) gave some instances and since then it has been mentioned in various papers; these together with unpublished examples are reviewed here. Apologies are made to those authors who have written on this subject but whose papers have been overlooked.

TABLE I

PHTHIRAPTERAN SPECIES WITH WIDE HOST AND GEOGRAPHICAL DISTRIBUTIONS

PHTHIRAPTERA	S.	G.	N.	P.	E.	O.	A.
<i>Colpocephalum turbinatum</i>	36	20 (Falconiformes)	+	+	+	+	+
<i>Colpocephalum fregeli</i>	15	3 (Corvidae)	+	+	+	+	+
<i>Ciconiphilus decimfasciatus</i>	22	16 (Ardeidae)	+	+	+	+	+
<i>Cuculiphilus snodgrassi</i>	14	9 (Cuculidae)	+	+	+	+	?
<i>Laemobothrion maximum</i>	32	18 (Falconiformes)	+	+	+	+	+
<i>Eidmanniella pellucida</i>	10	1 ( <i>Phalacrocorax</i> )	+	+	+	?	+
<i>Holomenopon leucoxanthum</i>	29	12 (Anseriformes)	+	+	+	+	+
<i>Degeeriella regalis</i>	9	4 (Falconiformes)	+	+	+	+	—
<i>Saemundssonina africana</i>							
Timmermann, <i>sens. lat.</i>	11	10 (Vanellinae)	—	—	+	+	+
<i>Columbicola theresae</i> Ansari	5	2 (Columbidae)	—	+	+	+	—

S. species, and G. genera of the host parasitized. N = New World (Nearctic & Neotropical); P. Palearctic; E. Ethiopian; O. Oriental; A. Australasian (including New Zealand). ? None recorded, possible hosts present.

Authors and dates of all Phthirapteran species up to 1951 as in Hopkins & Clay 1952.

The Amblyceran examples are taken from the revisionary work of Price *et al.* and the *Columbicola* from Tendeiro, 1952.

Geographical distribution in the Phthiraptera may be due to various causes which for convenience can be considered under the following headings: Absence, Primary and Secondary; Secondary Infestations; Geographical Isolation of Host; Unexplained Distributions. These divisions are not entirely satisfactory as some of the examples could be considered under more than one of the headings and there is always the dual role of host distribution and geographical distribution making much of the evidence difficult to evaluate.

#### ABSENCE

a. *Primary.* The most obvious example of this is the absence of lice from certain geographical areas owing to the absence of the host, the distribution of the lice being fundamentally a host one. Thus, none of

the 20 or so genera specific to the Tinamidae are found in Africa because there are no tinamous in Africa.

Another reason for the primary absence of a louse genus in a geographical area could be the absence of the genus on the ancestral stock which gave rise to the avian group in that area. Ward (1958) has made an interesting analysis of the louse fauna of the Galliformes and shows that two Ischnoceran genera : *Cuclotogaster* and *Lipeurus*, now represented by many species on the Old World Galliformes, are not found in the New World and suggests that they were not present on the Avian stock which crossed the Behring land bridge. The absence of one of the starling lice in North America could be a modern example of this : Boyd (1951) examined 300 starlings (*Sturnus vulgaris*) from six states in the U.S.A. and found only three of the four species which parasitize this bird in Europe ; *Sturnidoecus sturni* common on the European starling being absent on the introduced bird. The *Coloceras*-complex on the Columbidae may show another case of primary absence, *Campanulotes* being absent in the Ethiopian region and *Coloceras* perhaps absent in the New World ; although both are possibly replaced by related genera. In the Palearctic, Oriental and Australasian regions species of both genera are present, sometimes on the same host individual, showing that the absence in certain regions is not due to competition between the species of the two genera.

The absence of *Quadraceps ridgwayi* in part of the range of its host, *Haematopus ostralegus* (Table III, 3) is probably primary, the parasite having perhaps been acquired from another member of the Charadriiformes by the host stock which gave rise to the southern populations of *Haematopus*.

b. *Secondary Absence*. A species of louse may be found in part only of the range of its host or a genus found only on members of an avian order in certain areas, having become extinct elsewhere. Clay (1949) gave examples of the absence of a host-specific species even within quite small areas, local populations apparently lacking certain species ; presumably in such cases the missing species will be acquired again from neighbouring inter-breeding host populations. However, where the population is isolated then that species may be completely lost from the population. The example given above under Primary Absence of the missing species on North American starlings could equally well be explained as a case of secondary absence by extinction. Another example which could be primary or secondary is shown in the distribution of *Piagetiella* (Amblycera) : the species of this genus are confined to the Pelecaniformes, living in the throat pouches ; they are represented by five species on pelicans and three species parasitic on six species of cormorants (Price 1970). These three species belong to a distinctive species group easily separable from those on the pelicans, indicating that they

have not recently been acquired by the cormorants. There is no evidence suggesting that the hosts form a group of closely related species. Table II shows that with the exception of *Phalacrocorax auritus* and *penicillatus*, all the records are found within an area bounded by latitude 0° and 70°S and longitude 80°W and 20°E. It is possible that *Piagetiella* was once found throughout the genus *Phalacrocorax* but has become extinct in other parts of the world. Alternatively, this genus was parasitic on the stock which gave rise to some of the southern cormorants, being secondarily acquired by other unrelated cormorants and carried further north in the New World by *Phalacrocorax olivaceus* and *auritus*. The fact that *Phalacrocorax neglectus* from South Africa is parasitized by the same species of *Piagetiella* (*P. incomposita*) as the two American cormorants (*auritus* and *penicillatus*) suggests, if not a relationship between the hosts, at least a common distribution at one time. It is probable that *Piagetiella* will be found on other cormorants but it can be predicted that these will be cormorants from the subantarctic and adjacent regions; it is unlikely that it occurs on the European *Phalacrocorax carbo* and *aristotelis*, many of these birds having been examined without result. This distribution may therefore be an example partly of host isolation (see below) and partly of secondary infestation (see below).

TABLE II  
DISTRIBUTION OF *Piagetiella* ON *Phalacrocorax*

<i>Piagetiella</i>	<i>Phalacrocorax</i>	Locality
<i>caputincisa</i> Eichler	<i>a. atriceps</i>	S. Georgia ; S. Orkney Is. ; Graham Land
<i>vigua</i> (Eichler) (unrecognizable)	<i>a. albiventer</i> <i>o. olivaceus</i>	Falkland Is. No locality
<i>transitans</i> (Ewing)	<i>bougainvillii</i>	Peru
<i>incomposita</i> (Kellogg & Chapman)	<i>penicillatus</i> <i>auritus</i> <i>neglectus</i>	California Florida, Georgia, Louisiana, Illinois, Minnesota, Quebec. Dassen Is., South Africa.

Secondary absence may occur where a host species is parasitized by sympatric species belonging to the same genus or by species of a number of related sympatric genera. Such genera are presumably the result of divergence of an ancestral stock on a host group so that the resulting genera are more closely related to each other than to genera found on other host groups. Examples are the *Philoceanus*-complex on the Procellariiformes (comprising about 10 genera), the *Coloceras*-complex of the Columbidae; the *Goniodes*-complex of the Galliformes and the *Ischnocera* of the Psittaciformes and of the Bucerotidae. Thus, if one

of a pair of sympatric species becomes extinct in part of the host's range and the other in another part (Clay 1949, fig. 4), the two species will show a geographical distribution; the *Falcolipeurus* species on *Gyps ruppellii* (Table III, 6) may be an example. The same would apply if some of the genera belonging to a generic complex became extinct in part of the host's range; the North American game-bird fauna and the African and New World pigeon fauna, if not explicable by primary absence, may be examples of this.

TABLE III

PHTHIRAPTERAN TAXA FOUND IN PART OF THE HOST'S RANGE

Host	Phthirapteran Taxa	Locality
1. <i>Phalacrocorax</i>	<i>Piagetiella</i>	See Table II.
2. Vanellinae	<i>Saemundssonina africana</i> Timmermann	Ethiopian; Oriental; Australasian (Timmermann 1971).
3. <i>Haematopus ostralegus</i>	<i>Quadriceps ridgwayi</i>	Neotropical; Australasian (Timmermann 1971).
4. <i>Sula leucogaster</i> <i>Sula sula</i> <i>Sula leucogaster</i> <i>Sula sula</i>	<i>Pectinopygus garbei</i> <i>Pectinopygus garbei</i> <i>Pectinopygus sulae</i> <i>Pectinopygus sulae</i>	Atlantic Atlantic Indian Ocean Indian Ocean; Coral Sea (Clay 1964)
5. <i>Tyto alba</i>  <i>Tyto alba</i>	<i>Strigiphilus aitkeni</i> Clay  <i>Strigiphilus rostratus</i>	New World; Australasian; Oriental. Palearctic; Ethiopian (Clay 1966).
6. <i>Gyps ruppellii</i>  <i>Gyps ruppellii</i>	<i>Falcolipeurus</i> <i>quadripustulatus</i> <i>Falcolipeurus lineatus</i>	Egypt, Arabia. Somaliland, Tanzania, Nigeria (B. K. Tandan).
7. <i>Corvus orru</i>  <i>Corvus orru</i>	<i>Myrsidea schizotergum</i> Klockenhoff <i>Myrsidea arafura</i> Klockenhoff	Queensland, Australia. Northern Territory, Australia.
8. <i>Podiceps</i>	<i>Aquanirmus</i>	See Table IV.

## SECONDARY INFESTATIONS

The establishment of a louse population on a new host may have taken place at any time during the evolution of louse species and host species. It seems probable that establishment is more likely to take place on a new host of the same family or order than on one belonging to a totally unrelated group. That this is so is supported by the cases of geographical

distribution discussed below and which may be explained by such intra-group transfers. Little is known about what prevents a louse establishing itself on a new host, but it seems possible that much of the isolation of the Phthiraptera is due more to birds of different species not normally coming into close enough contact for the transfer of lice, than to the louse being unable to establish itself on the new host. Possible methods of inter-specific transfer were given in Clay, 1957.

There are a number of examples of two or more hosts in one geographical area having the same or similar species of parasite whereas this would not be expected from their relationships. An example is the occurrence of a species of *Rhynonirmus* on *Bartramia* (subfamily Tringinae) related to one on *Philohela* (subfamily Scolopacinae); the genus *Rhynonirmus* elsewhere being known only from the latter subfamily. If the placing of *Bartramia* in the Tringinae is correct then this may be a straightforward case of secondary infestation (Clay 1961). Another distribution, perhaps explicable by secondary infestation, is that of the species of *Anatoecus* on the flamingoes: *Phoenicopterus antiquorum* and *Phoeniconaias minor*, sympatric in Africa, have the same species of *Anatoecus*, while *Phoenicopterus ruber* and *P. chilensis* in the New World each have a distinct species. It would be expected that *P. minor*, considered generically distinct, would have the different parasite. Alternatively, this distribution could be explained by divergent evolution of the New World lice or a mistaken assessment of flamingo relationships. However, that secondary infestation may have taken place between the two African species of flamingoes is supported by the distribution of the species of another genus parasitic on this host family. Tandan & Brelih (1971) have shown that the three species of *Phoenicopterus* (*antiquorum*, *ruber* and *chilensis*) are parasitized by one species [*Anaticola phoenicopteri* (Coinde)], whereas *Phoeniconaias minor* has this species and also a distinct species of the same genus (*Anaticola dissonus*), the two never having been found together on the same host individual. It is suggested that *phoenicopteri* evolved on *Phoenicopterus* and *dissonus* on *Phoeniconaias* and that subsequently the former species became secondarily established on *P. minor*. The wide distribution of *Saemundsonia africana* (Table III, 2) on the southern populations of the Vanellinae may be due to secondary infestations on some of the hosts.

Tendeiro (1962) has analysed the distribution of the louse genus *Columbicola* parasitic on the Columbidae and shown that the distribution of some species is more a geographical one than a host one and that these can be attributed to secondary infestations.

There are other examples, probably due to secondary infestation, but in which the transfer of lice must have taken place at a time when the distribution of the host was different. Thus, *Corvus kubaryi* (Corvidae) on Guam Island (Marianas) has an established population

of a louse species belonging to a genus normally parasitic on the Rallidae, the species *Rallicola insulana* (Carriker) also being found on a *Porphyrio* (Rallidae); at the present time there is no overlap in distribution of the possible hosts (Clay 1953). Another example is the unexpected occurrence of *Actornithophilus hoplopteri*, a parasite characteristic of the Vanellinae, on *Charadrius vociferus* (see Clay 1962). The absence of members of the Vanellinae in North America at the present time suggests extinction or changes in distribution of hosts from which this louse might have been acquired by *Charadrius vociferus*. The same may apply to the Coliiformes in Africa which are parasitized by a genus *Colilipeurus* apparently most nearly related to *Falcolius* on *Microhierax* (Falconiformes) found in the Oriental region (Clay 1955). Relationship between the hosts is unlikely but if the distribution is due to secondary infestation then it must be postulated that the two host groups have at some time been sympatric. As both parasite genera now comprise a number of host-specific species, it must be presumed that the transfer preceded the divergence of the hosts.

#### GEOGRAPHICAL ISOLATION OF HOST

The present distribution of *Chelopistes* can be explained by the isolation of the host group on which it evolved. Ward (1958) suggests that this genus, now widely distributed on the Cracidae, Odontophorinae and the Meleagrididae, evolved from a *Goniodes* stock in N. America during the Tertiary and after the re-union of North and South America in the Pliocene, moved southwards to Central and South America on such genera as *Odontophorus*. However, a study of the morphology of *Chelopistes* suggests that it (as well as *Labicotes*) is a derivative of *Oxylipeurus*, although it occupies the *Goniodes*-niche. Therefore, it seems possible that only the ancestral *Oxylipeurus* (among the Ischnocera) reached S. America, perhaps on an early Cracidae stock, which either crossed before the severance of connections between North and South America in the Paleocene or as one of Simpson's 'Old Island Hoppers' (Simpson 1950). During this isolation *Chelopistes* evolved from an *Oxylipeurus* stock to occupy the niche used by *Goniodes* in many of the Nearctic and Palaearctic birds. With the re-uniting of the Americas during the late Pliocene and the movement south of other families of birds, *Chelopistes* became established on the Odontophorinae and Meleagrididae. This would explain its absence on members of the Odontophorinae north of Mexico and the absence of *Goniodes* on the Cracidae. Thus, the present distribution may be the result of divergence on an isolated host group, with some subsequent secondary establishment in other host groups, all taking place during the early evolution of the hosts. This shows the difficulty of using host-parasite relationships to

elucidate the phylogeny of the higher categories of birds. However, such cases if correctly interpreted may throw some light on the origins and migrations of avian groups.

Another unusual type of distribution perhaps explicable by host isolation is that of *Aquanirmus* on the grebes (*Podicipitiformes*). Edwards (1965) has shown that two of the grebe species common to Europe and North America are parasitized by species of *Aquanirmus* belonging to different species groups on the two sides of the Atlantic (Table IV). In addition, *Podiceps cristatus* is parasitized in Europe by *A. podicipis* (Denny) belonging to the *colymbinus* species group and

TABLE IV  
THE SPECIES OF *Aquanirmus* ON *Podiceps*

<i>Podiceps</i>	Locality	<i>Aquanirmus</i>	Species Group
<i>auritus</i>	Europe .. .. N. World .. ..	<i>colymbinus</i> <i>bucomfishi</i> Edwards	<i>colymbinus</i> <i>bahli</i>
<i>nigricollis</i>	Europe .. .. N. World .. ..	<i>colymbinus</i> <i>americanus</i> (Kell. & Chap.)	<i>colymbinus</i> <i>bahli</i>
<i>ruficollis</i>	Europe .. .. S. Africa, India	<i>podicipitis</i> <i>bahli</i> Tandan	<i>colymbinus</i> <i>bahli</i>
<i>cristatus</i>	Europe .. ..	<i>podicipis</i>	<i>colymbinus</i>
<i>griseigena</i>	Europe .. .. N. World	<i>emersoni</i> Edwards	<i>emersoni</i>
<i>dominicus</i>	N. World .. ..	<i>chamberlini</i> Edwards	<i>bahli</i>

*Podiceps griseigena* on both sides of the Atlantic has the same species of *Aquanirmus*, belonging to a species group otherwise found on North American grebes. If, as has been suggested, the grebes originated in North America, it is possible as Edwards says that only one of the grebes arriving in Europe had the *colymbinus* stock and that the others acquired it by secondary infestation. However, another perhaps more likely explanation is that the *colymbinus* stock was the original stock on all the grebes and on the European grebes it diverged little, perhaps now representing only a polytypic species, whereas on the North American stock greater divergence took place; it should be noted that the differences between the species groups of *Aquanirmus* are small. If this is a correct hypothesis, the following deductions can be made: a. *Podiceps griseigena* became established in Europe at a later date than the other species of *Podiceps*. b. The possibility of a New World *ruficollis* stock, now extinct, which gave rise first to the Northern European



*ruficollis* parasitized by the *colymbinus* species group and at a later date to the African and Oriental *ruficollis* populations after it had acquired *bahli* from a New World grebe. Specimens from *ruficollis* in other parts of its range might throw further light on its distribution routes. Isolation of host may be responsible for the two species of *Strigiphilus* parasitic on the widely distributed *Tyto alba* (Example 5, Table III) and may indicate the distribution routes from the centre of origin of this bird.

Some apparent cases of geographical distribution of lice are probably host distributions due to the hosts in one region being closely related to each other, having evolved from a common stock in that area. *Trinoton aculeatum*, for instance, is parasitic on *Dendrocygna viduata* in South America and South Africa and on *D. bicolor* and *D. autumnalis* in the New World, while each of the species *D. javanica* (Oriental), *D. arcuata* (Australia, Papua) and *D. eytoni* (Australia) are parasitized by a separate species (Clay 1963). This is probably a host distribution, the divergence of the lice being dependent on the time and divergence of the hosts.

Other cases which may be either host or geographical distribution are those in which two subspecies of host are each parasitized by a species of louse, as for example, the occurrence of *Heleonomus semiluctus* on *Balearica p. pavonina* in west Africa and *H. cornutus* on *Balearica pavonina gibbericeps* in east Africa (Price 1970). The specific differences may have arisen during the geographical isolation of the louse populations or as an adaptation to some difference in the host's external characters, arising during the isolation of the hosts themselves. The distribution of *Myrsidea* on the subspecies of *Corvus macrorhynchos* may be partly a geographical and partly a host one (Klockenhoff 1969). In the case of *Corvus orru ceciliae* in Australia (Table III), the same subspecies is parasitized by one species of *Myrsidea* in the Townsville area, Queensland and by another species (or a distinct subspecies) at Port Essington, Northern Territory (Klockenhoff 1972).

#### UNEXPLAINED DISTRIBUTIONS

The explanation of the distributions discussed above are highly conjectural; in the following examples any conjecture at all may be unwise: a. Example 4 in Table III in which *Sula sula* and *Sula leucogaster* (Pelecaniformes) share the same parasite in the Atlantic and share a different one in the rest of their range. Some possible explanations for this were given in Clay, 1964. b. The distribution of *Degeeriella regalis sens. lat.* on the *Milvinae*; *Buteo jamaicensis*, *B. swainsoni* and *B. galapagoensis*; *Haliaeetus vocifer*, *H. leucoryphus* and *Gypohierax angolensis* (see Table I for geographical range). This may be an example

of secondary absence by extinction of one of a sympatric pair, the *fulva* group taxa having become extinct on these hosts, and the *regalis* group taxa on others of the Falconiformes. c. Two similar species of *Struthiolipeurus*, one on the ostrich (*Struthio*) in Africa, the other on the *Rhea* in South America, the genus *Struthiolipeurus* being found only on these two host genera. This could be explained either by relationship between the hosts or by overlap of distribution at some time. d. The occurrence of *Chelopistes* on *Lerwa lerwa*. As shown above *Chelopistes* is found on the New World families Cracidae, Odontophorinae and the Meleagrididae and this distribution suggests that its origin and divergence took place in the New World. Why therefore does a typical member of the genus turn up on *Lerwa* (subfamily Phasianinae) now restricted to Afghanistan and the Himalaya east to the mountains of Szechuan? *Chelopistes* is a distinctive genus and the species on *Lerwa* resembles the other species too closely to suggest that it could have arisen by parallel evolution. It must be presumed that *Chelopistes* was found on hosts with a continuous distribution from the New World to the Oriental region, of which only that on *Lerwa* in a small part of Asia remains. It may be relevant that also parasitic on *Lerwa* is a species of *Lagopoecus* which does not resemble the species-group typical of the Tetraonidae and found on some members of the Phasianinae, but is more similar to the species found on the Odontophorinae, especially to *Lagopoecus numidianus* (Denny) from *Colinus virginianus*. This group of species of *Lagopoecus* parasitic on the Odontophorinae shows rather diverse characters especially in the form of the male genitalia, so that the fact that those of the *Lerwa*-infesting species are distinct would not rule out a relationship.

#### CONCLUSIONS

The present distribution of the avian Phthiraptera is the result of a complex of circumstances and factors operating at all stages of the evolution of the host and parasite and involving host specificity, geographical isolation, extinction, secondary infestations and the various changing ecological factors in the environment of the louse provided by the body of the bird. The ornithologist may benefit from a knowledge of the distribution of the Phthirapteran parasites, not only from the light this may throw on bird phylogeny, the phylogenetic relationship being the basic one, but the evidence provided of early migrations, dispersal routes (Table V) and of former distributions. More extensive collecting and closer study of the genera, based on detailed revisions, are revealing and will reveal further examples of geographical distribution and perhaps help to elucidate some of the present inexplicable cases.

TABLE V  
SPECIES AND GENERA OF PHTHIRAPTERA SHOWING  
DISCONTINUOUS GEOGRAPHICAL DISTRIBUTION

Louse & Host Group		New World	Austra- lasian	Ethiopian	Oriental	Palearc- tic
<i>Physconella</i> Columbidae	..	+	+	—	—	—
<i>Quadriceps ridgwayi</i> <i>Haematopus ostralegus</i>	..	+	+	—	—	—
<i>Strigiphilus aitkeni</i> <i>Tyto alba</i>	..	+	+	—	+	—
<i>Aquanirmus bahli</i> <i>Podiceps</i>	..	+	?	+	?	—
<i>Struthiolipeurus</i> <i>Struthio, Rhea</i>	..	+	—	+	—	—
<i>Saemundssonina africana</i> Vanellinae	..	—	+	+	+	—
<i>Piagetiella incomposita</i> Phalacrocoracidae	..	+	—	+	—	—
<i>Trinoton aculeatum</i> <i>Dendrocygna</i>	..	+	—	+	—	—
<i>Chelopistes</i> Galliformes	..	+	—	—	+	—
<i>Strigiphilus rostratus</i> <i>Tyto alba</i>	..	—	—	+	—	+

? No records, possible host present.

#### REFERENCES

- BOYD, E. M. (1951): A survey of parasitism of the starling *Sturnus vulgaris* in North America. *J. Parasit.* 37: 56-84.
- CLAY, T. (1949): Some problems in the evolution of a group of ectoparasites. *Evolution* 3: 279-299.
- (1953): Revisions of the genera of Mallophaga. 1. The *Rallicola*-complex. *Proc. Zool. Soc. Lond.* 123: 563-587.
- (1955): Revisions of the Genera of Mallophaga. *Colilipeurus* and a new genus. *Trans. R. ent. Soc. Lond.* 107: 169-186.
- CLAY, T. (1957): The Mallophaga of Birds in *Premier Symposium sur la spécificité parasitaire des parasites de Vertébrés*. Neuchatel.
- (1961): Three new species of Mallophaga (Insecta). *Bull. Brit. Mus. (Nat. Hist.)*.
- (1962): A key to the species of *Actornithophilus* with notes and descriptions of new species. *Bull. Br. Mus. Nat. Hist. (Ent.)* 11: 189-244.
- (1963): New species of *Trinoton* (Mallophaga, Insecta). *Mem. Queensland Mus.* 14: 87-93.
- (1964): Geographical distri-

bution of the Mallophaga (Insecta). *Bull. B.O.C.* 84: 14-16.

CLAY, T. (1966): The species of *Strigiphilus* (Mallophaga) parasitic on the barn owls (*Tyto*). *J. Ent. Soc.* 5: 10-17.

EDWARDS, R. L. (1965): Revision of the genus *Aquanirmus* (Mallophaga) parasitic on Grebes (Podicipidae). *Can. Ent.* 97: 920-935.

HOPKINS, G. H. E. (1943): The host-associations of the lice of mammals. *Proc. Zool. Soc. Lond.* 119: 387-604.

——— (1951): Stray notes on Mallophaga, XI. *Ann. Mag. nat. Hist.* 4: 371-377.

HOPKINS, G. H. E. & CLAY, T. (1952): A check list of the genera and species of Mallophaga. British Museum (N.H.) London.

KLOCKENHOFF, H. (1969): Zur Verbreitung der Mallophagen der Gattung *Myrsidea* auf der Dschungelkrähe *Corvus macrorhynchos*. *Z. Zool. Syst. Evol. Forsch.* 7: 53-58.

——— (1972): Zur Taxonomie der auf der Salvadori Krähe *Corvus orru* lebenden Mallophaga-Gattung *Myrsidea* Waterston. *Bonn. zool. Beitr.* 23: in press.

PRICE, R. D. (1970): The *Piagetiella* (Mallophaga: Menoponidae) of the Pelecaniformes. *Can. Ent.* 102: 389-404.

——— (1970): A review of the genus *Heleonomus* (Mallophaga: Menoponidae) from the Cranes. *Ann. ent. Soc. Am.* 63: 1162-1174.

SIMPSON, G. G. (1950): History of the fauna of Latin America. *Am. Scient.* 38: 361-389.

TANDAN, B. K. & BRELIH, S. (1971): A new species of *Anaticola* (Phthiraptera: Ischnocera). *Entomologist* 104: 268-276.

TENDEIRO, J. (1962): Revisao monografica do genero *Columbicola* (Ischnocera, Philopteridae). *Mems. Jta. lav. Ultramar.* 32: 1-460.

THOMPSON, G. B. (1940): The distribution of *Heterodoxus spiniger*. *Pcp. Proc. R. Soc. Tasm.* (1939): 27-31.

TIMMERMANN, G. (1971): 'Regelwidrigkeiten' im Ausbreitungsbild bei Vogelmallophagen. *Mitt. Hamb. Zool. Mus. Inst.* 67: 135-174.

WARD, R. A. (1958): Preliminary observations on the origin of some Nearctic Bird Lice (Mallophaga). *Proc. 10th Intern. Congress Entom., Montreal 1956*, 1: 745-749.