

Preliminary Observations on the Origin of Some Nearctic Bird Lice (Mallophaga)

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ABSTRACT

A study of the host-parasite distribution of the biting lice parasitizing the Nearctic gallinaceous birds indicates that the distribution patterns of the lice are related to the geographical area in which the host group evolved. The site of origin of the parasite group is still discernible despite the penetration of the host group into a new area. Some widespread aquatic birds as the skimmers present special problems and their site of origin is not apparent by this approach.

INTRODUCTION

The distribution of Mallophaga has been traditionally interpreted along strict host-parasite lines. In some instances geographic factors have played a role in producing present-day distributional patterns. Despite the lack of a fossil record, the distribution of Mallophaga genera may often be used as means of faunal analysis. Vanzolini and Guimarães (1955) have made an admirable study of the zoogeographic relations of South American mammals and their lice. Jellison (1942) has made a similar analysis for the Nearctic rodents. As yet, no comparable study has been made of the entire North American mammal fauna. The purpose of the present paper is to present some of the results of investigations by the author on avian Mallophaga which may serve to demonstrate the utility of these ectoparasites in a study of this nature. Vanzolini and Guimarães emphasize, "No phylogenetic or zoogeographical discussions should be based on isolated cases, but rather on patterns of infestation." This practice has been followed and it is hoped that future investigators will assume the same approach.

The zoogeographic scheme proposed by Schmidt (1954) will be used throughout this paper to designate the faunal realms and regions.

LICE OF GALLINACEOUS BIRDS

The order Galliformes (megapodes, curassows, pheasants and hoatzin) is world-wide in occurrence. Two suborders are recognized (Wetmore, 1951); a single aberrant Neotropical species, the hoatzin, comprises the Opisthocomi and the remaining form the Galli. The Cracoidea contain two living groups, the Megapodidae of the Australian and Oceanian regions and the Oriental subregion, and the Cracidae of the Neotropical region and Central American province of the Caribbean subregion. Most of the well-known forms are members of the Phasianoidae. The Tetraonidae or grouse are typical of the Holarctic. The Phasianidae contain three subfamilies; the Phasianinae (pheasants and peacocks) and the Perdicinae (partridges) are endemic to the Old World while the Odontophorinae (quail) are only present in the New World. The Meleagridae (turkeys) are confined to the Nearctic and Caribbean transitional. The Numididae (guinea fowl) are present in the Ethiopian and Malagasy subregions.

Table I serves to summarize the distribution of Mallophaga genera on the Galli.¹ *Colpocephalum* is not included because of the paucity of authentic records. In examining this chart it may be observed that certain parasite genera as *Goniodes*, *Oxylipurus* and *Menacanthus* have a fairly wide host distribution; others as *Cuclotogaster*, *Chelopistes* and *Clayia* have a more restricted host distribution. *Passonomedia*, *Labicotes*, *Pachyskelotes*, *Numidicola* and *Somaphantus* are each known from a single host. If the two dubious records are not considered, only a single genus, *Oxylipurus*, of the eight found on the Cracoidea is common to both constituent families. A comparison among the families of the Phasianoidae shows that no single genus is common to all four families. Only *Goniodes* and *Menacanthus* occur on 3/4 of the families. If one compares genera which are common to two families it is seen that excluding the dubious record, 5/16 (31%) of the genera parasitizing

¹The hoatzin is parasitized by *Hoazineus*, *Osculotes*, *Rallicola* (*Wilsoniella*) and *Laemobothrion* (*Eulaemobothrion*). The first three groups are only found on this host.

the Phasianidae and Numididae are common to both families, 3/14 (21%) are shared between the Phasianidae and Tetraonidae, and Phasianidae and Meleagridae, 1/10 (10%) between Tetraonidae and Numididae, 1/9 (11%) between Numididae and Meleagridae and none are common among the Meleagridae and Tetraonidae. It is worth noting that the above relationships between families as indicated by the distribution of bird lice are quite close to those expressed by ornithologists.

TABLE I. Distribution of Mallophaga Genera on the Galli.

MALLOPHAGA GENERA	HOSTS							
	Cracoidea		Phasianoidea					
	Megapodidae	Cracidae	Phasianidae					Numididae
			Tetraonidae	Phasianinae	Perdicinae	Odontophorinae	Meleagridae	
<i>Ischnocera</i>								
<i>Lipeurus</i>	X	0	0	X	X	0	0	X
<i>Cuclotogaster</i>	0	0	X ¹	X	X	0	0	0
<i>Lagopoecus</i>	0	0	X	X	X	X	0	0
<i>Oxylipaurus</i>	X	X	0	X	X	X	X	0
<i>Goniocotes</i>	0	0	X ²	X	X	0	0	X
<i>Goniodes</i>	X	0	X	X	X	X	0	X
<i>Chelopistes</i>	0	X	0	X ³	0	X	X	0
<i>Passonomedia</i>	0	0	0	0	0	M	0	0
<i>Labicotes</i>	0	M	0	0	0	0	0	0
<i>Pachyskelotes</i>	0	0	0	M	0	0	0	0
<i>Amblycera</i>								
<i>Kelerimenopon</i>	X	0	0	0	0	0	0	0
<i>Cracimenopon</i>	0	X	0	0	0	0	0	0
<i>Desumenopon</i>	0	0	0	0	0	X	0	0
<i>Menopon</i>	0	0	0	X	X	0	0	0
<i>Clayia</i>	0	0	0	X	0	0	0	X
<i>Amyrsidea</i>	X ⁴	0	X	X	X	0	0	0
<i>Menacanthus</i>	0	X	0	X	X	X	X	X
<i>Numidicola</i> and <i>Somaphantus</i>	0	0	0	0	0	0	0	M

X = Widely distributed throughout host group.

0 = Absent on host group.

M = Monotypic genus present on a single species in the host group.

X¹ *C. cameratus* (de Haan) on *Lyrurus tetrix* is the only known species on this family.

X² A dubious record, see footnote number 2.

X³ *C. leucicola* (Clay) on *Lerwa lerwa* is the only known species on this subfamily.

X⁴ *A. latiusculata* (Pugnet) is the only known species of this genus on a member of the family. It has not been encountered since its description from a single female and is probably a dubious host record.

In the Galli, only the Phasianidae are divided into subfamilies. A comparison of the Phasianinae and Perdicinae shows a majority of the genera are common to both groups (9/11 or 81%). Approximately 1/3 of the genera present on the Odontophorinae also occur on the Phasianinae and Perdicinae. An interesting feature of the quail subfamily is that its Mallophaga fauna is closely allied to that of the Meleagridae, a related family. The Cracidae, which are ornithologically remote from the Odontophorinae, share three of the nine genera on these two groups. This type of distribution can best be interpreted in terms of the sites of geographical origin of the host groups.

Lipeurus, *Cuclotogaster*, *Goniocotes*, *Kelerimenopon*, *Menopon* and *Clayia* are restricted to Galliform groups which evolved in the Old World. These six genera are all absent from birds of New World origin and in part are represented by ecological equivalents, such as *Chelopistes*, *Cracimenopon* and *Desumenopon*. The wide distribution of *Lagopoecus* in the New World and its limited occurrence in the Old World points to a New World origin for the genus. Genera such as *Oxylipaurus*, *Goniodes*, *Amyrsidea* and *Menacanthus* are found on both New and Old World hosts and appear to be rather old forms.

A detailed consideration of the native Nearctic Galliformes and their lice will serve to substantiate these statements. There are four families, fourteen genera and twenty-one

species of this order in this subregion (Hellmayr and Conover, 1942). Two species of Cracidae, both in the genus *Ortalis* (chacalacas), penetrate the lower limits of the Nearctic. Their fauna is characterized by *Chelopistes* and *Cracimenopon*. With the exception of these species, *Chelopistes meleagridis* (Linnaeus) and possibly *Chelopistes leucicola* (Clay), these two genera are exclusively Neotropical and Caribbean Transitional in distribution.

The seven genera of Tetraonidae in the Nearctic subregion (*Dendragapus*—grouse, *Lagopus*—ptarmigan, *Canachites*—spruce grouse, *Tympanachus*—prairie hen, *Bonasa*—ruffed grouse, *Pedioecetes*—sharp-tailed grouse and *Centrocercus*—sage grouse) are all parasitized by species of *Lagopoecus* and *Goniodes*. The three remaining Tetraonids, *Lyrurus*, *Tetrastes* and *Tetrao*, are restricted to the Palearctic, while the previously mentioned genera as their Nearctic relatives. The conspicuous absence of *Lipeurus*, *Goniocotes* and *Cuclotogaster* (with two exceptions²) points to the Nearctic origin of the lice of this group.

All the Nearctic Phasianidae are in the subfamily Odontophorinae. This includes *Oreortyx* (plumed and mountain quail), *Callipepla* (scaled quail), *Lophortyx* (valley quail), *Colinus* (Bob white) and *Cyrtonyx* (Mearns' quail). *Lagopoecus* and *Goniodes* infest all the above genera. *Oxylipaurus* probably occurs on all members, but presently has been recorded only from *Callipepla*, *Colinus* and *Cyrtonyx*. Like the grouse, *Lipeurus*, *Goniocotes* and *Cuclotogaster* do not occur on the New World quail. *Chelopistes* replaces *Goniodes* on the genera of this family (*Odontophorus*, *Dendroortyx* and probably others) which are exclusively Caribbean Transitional and Neotropical in distribution. *Lagopoecus* is absent on these groups. The only deep Neotropical extensions of *Goniodes* and *Lagopoecus* are shown by the species present on *Colinus cristatus* which ranges between Salvador and Brazil. It is likely that *Chelopistes* evolved in North America during the Tertiary and after reunion with South America in the Pliocene pushed southward to Central and South America via genera such as *Odontophorus*. The absence of *Lagopoecus* cannot be attributed to competition as there is no other genus occupying its niche on the host.

Meleagris gallipavo, the turkey, is the sole Nearctic representative of the Meleagridae. Its fauna consists of only a *Chelopistes*, two species of *Oxylipaurus* and *Menacanthus stramineus* (Nitzsch). The first two genera point to a Nearctic origin for these lice. The *Menacanthus*, which is almost cosmopolitan in host and geographic distribution, is neutral insofar as indicating affinities.

Due to the extensive taxonomic investigations of M. A. Carriker, Jr., Theresa Clay and K. C. Emerson we have a better knowledge of the Ischnocera of Nearctic Galliformes than those of virtually any other order in this region. Because of this background it is possible to postulate the possible zoogeographical history of these genera.

Goniodes and *Oxylipaurus* arrived fairly early in the Tertiary in the New World by means of the Bering land bridge. During the Miocene in North America the *Goniodes* stock evolved into *Chelopistes* and allied forms while *Oxylipaurus* diverged only at the species level. About the same time *Lagopoecus* evolved from the generalized *Degeeriella* stock in North America. Some species of *Lagopoecus* were able to enter the Old World via the Bering land bridge,³ but were prevented from entering South America because of its isolation. *Oxylipaurus* never parasitized the Tetraonidae or became extinct on this group during this period. With the reunion of North and South America in the upper Pliocene, *Goniodes* and *Lagopoecus* were able to enter northern South America by means of the species on *Colinus cristatus*. They were unable to parasitize additional hosts because of the extensive speciation of *Chelopistes* and *Oxylipaurus* species groups on the Cracidae and their subsequent rapid speciation and radiation to the Odontophorinae and Meleagridae. *Chelopistes* on the whole has not been successful in the Nearctic subregion. It has only been able to reach the Nearctic-Caribbean Transition boundary in northern Mexico on the

²*Cuclotogaster cameratus* (de Haan) has been described from *Lyrurus tetrix*. This is probably a case of a successful host transference and subsequent speciation.

³*Goniodes megaloccephalus* Uchida was described from a single female from a skin of *Tetrastes bonasia* from Sukhain. No subsequent records of this species have been reported and there is the possibility that this specimen was a stray from some species of Phasianidae.

⁴Five species are known from the Phasianidae including three Palearctic species (*L. colchicus* Emerson ex *Phasianus colchicus*, *L. meimertzhageni* Clay ex *Lerwa lerwa* and *L. ovatus* (Uchida) ex *Syrmatiscus mikado*), one Oriental (*L. heterotypus* (Megnin) ex *Lophophorus impejanus*) and a single Ethiopian species (*L. waterstoni* (Bedford) ex *Francolinus gariepinus*).

Three are represented on the Tetraonidae; two are Palearctic (*L. lyrurus* Clay ex *Lyrurus tetrix* and *L. pallidiventris* (Grube) ex *Tetrao urogallus*) and one is Holarctic (*L. affinis* (Children) ex *Lagopus lagopus*).

Odontophorinae. Of the 35 described species, only a single one, *C. lervicola* (Clay) on *Lerwa lerwa* (Phasianinae), is known from the Palaearctic. The generic assignment of this species (Hopkins and Clay, 1952) deserves further consideration in view of its distribution.

The absence of *Goniocotes*, *Cuclotogaster* and *Lipeurus* from the New World could be interpreted in three ways. 1). These genera arose after the initial New World invasion of the primitive Galliform stock. 2). They did not reach the New World because of the filtering effect of the Bering land bridge which permitted *Goniodes* and *Oxylipeurus* access while excluding others. 3). These genera did enter but all became extinct because of the superiority of the forms which evolved in North America. The second interpretation appears to be the most probable one. *Lipeurus* and *Lagopoecus* both occur on several species of Old World pheasants and apparently coexist on the same host by inhabiting different feather tracts.

LICE OF THE SKIMMERS

Not all birds possess a fauna which is capable of analysis like the preceding order. Such a group is the Charadriiformes (gulls, terns, waders, skimmers, etc.) which contains many widespread shore and oceanic birds. One family will serve as an illustration. The Rhynchopidae (skimmers) has a single genus, *Rhynchops*, with three closely related species. *R. nigra* is present in the New World ranging between New Jersey and the Gulf coastal area in the United States southward to encompass most of the coastal and inland waters of South America. Other species are encountered in Africa and southern Asia. They are never found very far out at sea and the species on the different continents are completely isolated from one another. The Mallophaga fauna of the skimmers is remarkable because of its uniformity. *Quadriceps elongatus* (Piaget), 1885 and *Saemundssonina ansorhamphos* Timmermann, 1951 have been described from *R. flavirostris*, the African species. In 1952, specimens of *Quadriceps* were obtained from the American *R. nigra* and just this year K. C. Emerson provided *Saemundssonina* specimens from this host. A detailed comparison of this material with African specimens, including some of Timmermann's type series, showed no means of differentiating between populations of lice separated by several thousand miles of ocean. Despite a long temporal separation, there has been no visible speciation of these two species. In terms of our modern species concept, the Ethiopian and American populations of these Mallophaga deserve separate species names. This is the first known situation of this kind for this order of insects.

Mayr (1946) states that the present relationships among the skimmers indicates an extremely slow evolutionary rate or an enormous capacity for transoceanic dispersal. The habits of these birds would tend to negate the latter suggestion.

SUMMARY

It has been possible to adequately treat only a small portion of the Nearctic bird lice—less than 10%. The choice of groups has been limited to those having a sound taxonomy and good distributional data. But it is believed that the general patterns present in the Galliformes should be perceived in other orders.

Unlike the dispersal patterns of many insect groups such as the termites (Emerson, 1955), saturniid moths and the mosquito genus *Culex* (Ross, 1953), which can be traced back to the Mesozoic, the Mallophaga have a later period of initial dispersal. This is based on the fact that modern bird orders did not appear until the early Tertiary (Romer, 1945). The availability of a new niche provided the basis for the rapid evolution of a new insect order, the Mallophaga, in a relatively short time.

The contemporary Nearctic Mallophaga fauna may be resolved into several faunal elements. The oldest consists of an Old World element, which entered via the Bering land bridge. Certain components of this have persisted today while others have evolved into new genera and species groups in North America during its separation from South America during the Tertiary. The largest portion of the Nearctic Mallophaga fauna appears to have evolved in America north of Mexico with a few members later joining the Central and South American fauna. None of the ancient Neotropical groups which evolved in South America during the long Tertiary isolation have made contributions to the Nearctic Mallophaga fauna. The filter bridge effect has been very apparent. After the initial dissemination through the Bering land bridge, little movement from the New World to the Old World has occurred. The lice of oceanic and aquatic birds of world-wide distribution present special problems and at present remain an unanalyzed component.

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