

A STUDY OF THE HOST DISTRIBUTION AND SOME RELATIONSHIPS OF MALLOPHAGA PARASITIC ON BIRDS OF THE ORDER TINAMIFORMES PART 1¹

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INTRODUCTION

Data derived from comparative anatomy and embryology are often inadequate for expressing the relationships between groups of animals. In some groups of animals, particularly the birds and mammals, the use of ectoparasites has become a supplementary tool. The students of ectoparasites, especially the Mallophaga, Anoplura, Siphonaptera and Analgesid feather mites, can often provide exact data on hitherto obscured relationships. The basic assumptions in an analysis of this type have been summarized by Rothschild and Clay (1952) as follows:

- (1) At an early stage of its evolution, a host group became parasitized by a group of parasites.
- (2) With the speciation and divergence of the host into different environments, changes occurred in the form, physiology and integument of the host.
- (3) The parasite because of its intimate relation to the host had to adapt itself to the above changes, which became reflected in its structure.
- (4) The evolution of the parasite is slower and less drastic because environmental changes are of less magnitude for the parasite than for the host.

An investigation was undertaken to determine the correspondence between host and parasite both at the generic and higher levels, and the lower categories, particularly the species. Some host-parasite relations have been analyzed with the aid of statistical techniques, and these will be treated in Part II of this study. The Mallophaga parasitic on the bird order Tinamiformes were utilized in this investigation. Certain advantages were achieved by the use of these two groups. The host order is ideal because of the relatively small number of species grouped into nine genera. A workable classification of the tinamous was available (von Boettischer, 1934) as a check with the observations on the Mallophaga. An excellent collection of tinamou skins was available which could be examined for Mallophaga. Contrary to the situation for many

avian Mallophaga, virtually all the species living on tinamous could be identified from the literature. Much of the descriptive work had been completed by Carriker (1936, 1944, 1946, 1953a, 1953b, 1954, 1955a, and 1955b), Clay (1937 and 1943), Guimarães (1936, 1942a, 1942b, 1942c, 1943, 1944a, 1944b, 1946, 1947a, 1947b, 1948, 1950a, 1950b, and 1953), Guimarães and Lane (1937), and von Kéler (1938, 1939a, and 1939b). Species described prior to 1900 have all been redescribed.

MATERIALS AND METHODS

When a bird is killed, the Mallophaga fauna living in the feathers dies within a few hours. Observations of many workers show that the Ischnoceran population usually remains on the skin after death of the host while the Amblycera have a tendency to wander. Some lice are lost during preparation of the bird skin but a sufficient number remain to make it profitable to examine the study skin for specimens. As many as 12 species of Ischnocera have been observed from a single subspecies of tinamou although a maximum of only nine species have been recovered from a single bird skin. In contrast, only two Amblycerans ever occur on these birds and are apparently scarce.

Each skin of a tinamou in the collection of the Chicago Natural History Museum was thoroughly examined three times for Mallophaga. A total of 1500 skins were examined. The technique involved a careful ruffling of the feathers of the study skin over a large sheet of paper. Individual feathers were spread apart and lice were removed with a camel's hair brush and forceps. All specimens from a single skin were placed in a vial of 70% alcohol, with the host catalogue number. The paper was shaken to remove any lice that might possibly be clinging to it.

The adults were later cleaned and cleared in potassium hydroxide, washed in distilled water, dehydrated by successive strengths of alcohol (30%, 70%, and 100%), placed in xylene, and mounted on slides in Canada balsam. A record of the species of Mallophaga present on each bird was kept, with the numbers of males, females, and immatures noted. These basic data were utilized in a study of the relation between the number of birds infested with Mallophaga and the number of louse species present, and will appear in Part II of this work (Ward, 1957).

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The host nomenclature used here is that of Hellmayr and Conover (1942), brought up to date by the revisions of Conover (1949, 1950a, 1950b) and Wetmore and Phelps (1951).

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CLASSIFICATION OF TINAMOU HOSTS

The Tinamiformes are an order of terrestrial birds of partridge-like form endemic to the Neotropical region between northern Tamaulipas, Mexico, and Patagonia. Romer (1945) considers the tinamous to be a comparatively ancient relic form of an early tertiary group of weak flying birds with a primitive palate, complete wings and a keeled sternum. Only one extinct genus is recorded. *Tinamisornis* is known from two species from the Monte Hermoso deposits of the Middle Pliocene of Patagonia. An extinct species, *Nothura paludosa* Mercerat, has been described from the Pampean bed of Argentina from the Pleistocene. Extant species of other genera appear from Pleistocene deposits at Luján, Argentina and in cave deposits in Minas Gerais, Brazil (Lambrecht, 1933).

In a study of the structure of the feathers of birds, Chandler (1916) considers the tinamous as an offshoot of the Galliformes. Glenny (1946), reporting on the arterial systems of four genera, believes that the tinamous are more closely related to the Galliformes than to any other groups and that this is not due to convergence. McDowell (1948), in a study of the palate of birds, concludes that the paleognathous palate is an undefinable adaptive feature and not primitive. Wetmore (1951) and Mayr and Amadon (1951) accept McDowell's interpretation of the palate and discard the Paleognathae in their classification of the birds. Mayr and Amadon agree with McDowell that the tinamous and rheas are closely related but doubt that they should be placed in a single order. They believe

it highly unlikely that the Galliformes are related to the Tinamiformes. The current opinion of McDowell (unpublished, *vide* Mayr and Amadon, 1951) is that several or all of the Anhimidae, Cracidae and Tinamidae are representatives of some ancient American radiation.

Von Boettischer (1934) discusses the relationships of the extant genera and bases his classification upon color pattern, characters of the bill, nostrils, tarsi, toes, tail, and ecological distribution. He separates the family into three subfamilies as follows:

- (1) Subfamily Tinaminae: *Crypturellus*, *Tinamus*, and *Nothocercus*.
- (2) Subfamily Rhynchotinae: *Rhynchotus*, *Nothura*, *Nothroprocta*, and *Taoniscus*.
- (3) Subfamily Eudromiinae: *Tinamotis* and *Eudromia*.

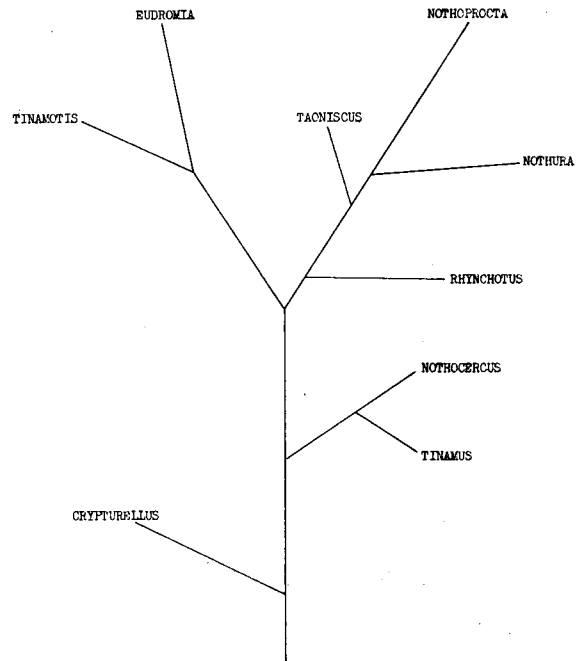


FIGURE 1. Dendrogram of the Tinamidae.

Figure 1 represents a dendrogram of the family Tinamidae as depicted by von Boettischer (1934).

In a review of the Brazilian tinamous, Miranda-Ribeiro (1938) divides them into two subfamilies, the Tinaminae being equivalent to the grouping by von Boettischer and the Nothurinae equivalent to his Rhynchotinae and Eudromiinae. *Crypturellus* is split into three genera, *Orthocrypturellus*, *Crypturornis* and *Crypturellus*. The balance of the genera remain the same.

Todd (1942) gives Miranda-Ribeiro's three groups of *Crypturellus* subgeneric status. Hellmayr and Conover (1942) follow von Boettischer's classification with no mention of suborders and consider *Orthocrypturellus* and *Crypturornis* as synonyms of *Crypturellus*.

The genera *Crypturellus* and *Tinamus* are found in lowland rain forests and low mountains of tropical Central and South America. *Nothocercus* occurs in the subtropical forests and temperate zones of the higher mountains between Costa Rica, Venezuela and southern Peru. The remaining genera are inhabitants of the grasslands in southern South America with certain members of *Rhynchotus*, *Nothura*, *Nothoprocta* and *Tinamotis* attaining the high altitudes of the Andes. On the basis of the biome distribution, the forest-dwellers, *Crypturellus*, *Tinamus*, and *Nothocercus*, would be expected to be more primitive than the genera of the grasslands.

Recent estimates as to the number of species in the family are as follows:

No. of Species	Authority and Date
51	Peters, 1931
73	Miranda-Ribeiro, 1938.
45	Hellmayr and Conover, 1942; Conover, 1949, 1950a and 1950b.
33	Mayr and Amadon, 1951.

This dissimilarity is largely one of differences in assigning the borderline cases to the status of species or subspecies. This may often be attributed to various interpretations of the species definition by different workers in different periods of time.

GENERIC CLASSIFICATION AND HOST DISTRIBUTION OF MALLOPHAGA

The Mallophaga of the Tinamiformes belong to three main groups. The first of these, the Menoponidae, contains two genera found on these birds. *Menacanthus* is a genus of wide host range, found on both tinamous and a wide variety of passerine, piciform and galliform hosts. *Microctenia* is restricted to the tinamous. The second family, the Philopteridae (*sensu* Hopkins and Clay, 1952), contains the greatest number of genera of Mallophaga. Three of these genera, *Pseudolipeurus*, *Pseudophilopterus* and *Tinamotaecola*, are restricted to this host group. The third section constitutes the majority of the tinamou lice. It is restricted to this order except for two species on the Cariamidae (Order Gruiformes). This group of 15 genera (24 as defined by Carriker, 1944, and 18 by Hopkins and Clay, 1952) has been assigned to the Heptapsogastridae.

Carriker (1936) established the Heptapsogastridae on the basis of the unique seven-segmented abdomen and the presence of spiracles on the first visible abdominal segment. The structure of the thorax was also considered to be distinctive, with conditions of complete separation to fusion of the meso- and metathorax.

Due to the almost impossible task of dividing the Ischnoceran Mallophaga into families, it is hard to judge the validity of the Heptapsogastridae. It seems to be a natural group allied to the *Goniodes-Goniocotes* complex of the Galliformes,

but it does not deserve separate family rank. I think it is preferable to include the "Heptapsogastridae" as a part of the Philopteridae. Theresa Clay (*in litt.*) is in agreement with me on this point.

The prothorax of the Ischnocera is free from the remaining thoracic segments. The meso- and metathorax are fused dorsally to form a rigid pterothorax which is usually entirely free of the first visible abdominal segment. Indirect evidence (Wilson, 1936) points to the fusion of the true first and second abdominal segments in late embryological development. Therefore the first visible abdominal segment is actually the true second segment. Spiracles occur on the true third to eighth segments. There is a fusion between the apparent eighth and ninth segments which has been observed in *Cuculogaster heterographus* (Nitzsch) during the third instar (Wilson, 1936). The final result is as follows:

Apparent segment	True segment
1	I and II
2 to 7	III to VIII
8	IX and X
9	XI

For the balance of this paper, the true abdominal segments will be designated by Roman numerals.

The classification of Carriker is founded on a misinterpretation of the thorax and abdomen. He interpreted the pterothorax as composed of two separated to completely fused segments and he considered the first spiracle-bearing abdominal segment as a fusion of the first and second segments. Von Kéler (1938) presented a true interpretation of these relationships but it appears to have been overlooked by Carriker in his later papers.

The chaetotaxy of the Ischnoceran pterothorax is so constant that it provides adequate evidence for the delimitation of this structure. In many examined genera there is always a fine ventrolateral hair arising from a pit in the integument (Clay, 1940). There is also a shorter spine anterior or posterior to the above hair. Several long setae are on the dorso-lateral and posterior margins.

Post-spiracular setae are generally associated with the abdominal spiracles. A post-spiracular sensillum is in contact with the alveolus of each of these setae on segments III to V (Clay, 1954). This sensillum may occur on segment II where spiracles are absent. The true position of a segment may be ascertained by these landmarks.

These structures were studied in all available "heptapsogastrine" species. A pterothorax is present in every species examined and no evidence was found of a partial fusion of the meso- and metathorax. In all of the genera except three the pterothorax shows more or less fusion with the second abdominal segment. Segment II may remain fairly large in proportion to the

other segments or it may be reduced so that it lies embedded in segment III. Spiracles are always lacking on segment II as in other avian Ischnocera but are present on segments III to VIII. A post-spiracular sensillus is usually present and visible on segment II. This segment may be free from III or partially fused with it on the posterior edge of the tergite.

These thoracic features are among the most conservative characters of this group of Mallophaga and a generic classification can be made with these criteria.

- I. Abdominal segment II little changed in size when compared with segment III; pterothorax partially joined to segment II medially; segment II free from III.
 - Rhopaloceras* Taschenberg. (Figure 2).
- II. Abdominal segment II considerably reduced in size when compared with III.
 - A. Pterothorax free from segment II.
 - Kelloggia* Carriker. (Figure 3).
 - Strongylocotes* Taschenberg. (Figure 4).
 - Ornicholax* Carriker. (Figure 5).
 - B. Pterothorax partially united with abdominal segment II; lateral edges of pterothorax and segment II form a sinuous line.
 1. Second abdominal segment separate from the third.
 - Lamprocorpus* Carriker. (Figure 6).
 - Heptapsogaster* Carriker. (Figures 7-11).
 - Petenosoma* Ewing. (Figure 12).
 - Trichodopeosius* Carriker. (Figure 13).
 - Megaginus* Carriker. (Figure 14).
 - Discocorpus* Carriker. (Figure 15).
 2. Posterior margin of tergum II joined to anterior margin of tergum III medially.
 - Megapeostus* Carriker. (Figure 16).
 - Pterocotes* Ewing. (Figure 17).
 - Physconella* Paine. (Figure 18).
 - C. Pterothorax completely fused with tergite II; lateral edges of pterothorax and abdominal segment II form a straight line.
 1. Second abdominal segment separate from the third.
 - Cuclotocephalus* Carriker. (Figure 19).
 2. Posterior margin of tergite II joined to segment III.
 - Nothocotus* Carriker. (Figure 20).

Other structures, especially of the head and abdomen, are useful in segregating these genera but give little or no indication of relationship in a phylogenetic sequence. For instance, *Rhopaloceras* is the only known Mallophagan genus with ctenidia on the paratergites yet this feature alone does not help to classify it. Similarly, only *Pectenosoma* possesses rows of raised papillae on the dorsal surface of the integument of the thorax and various abdominal segments.

Changes made in the recognition of genera other than those mentioned by Hopkins and Clay (1952) are as follows:

(1) *Kelloggia* Carriker = *Kelloggia* Carriker + *Austrokelloggia* Carriker. These have been segregated on the absence of coni and the division of abdominal tergite II into two lobes in *Kelloggia* and the presence of coni and undivided second tergite in *Austrokelloggia*. The presence or lack

of coni has been shown by Clay (1946) to be a very variable feature—"although of prime importance in the separation of species, [they] are not necessarily of generic importance." Some species of *Kelloggia* from *Tinamus* show very reduced membranous clavi. The condition of the second abdominal tergite is intermediate in the species parasitizing *Nothocercus*. Two lobes are discernible but are connected by a membranous, less sclerotized area. For these reasons it seems best to consider *Austrokelloggia* Carriker, 1936, a synonym of *Kelloggia* Carriker, 1903. At most *Austrokelloggia* might deserve subgeneric status.

(2) *Megapeostus* Carriker = *Megapeostus* Carriker + *Heterogoniodes* Carriker. Carriker has separated *Megapeostus* from *Heterogoniodes* mainly on the basis of the male genitalia and the structure of the marginal carina. He characterizes the former genus with asymmetrical male genitalia and internal projections of the marginal carina. The latter genus has symmetrical male genitalia and lacks the numerous internal projections of the marginal carina. *Heptapsogaster soui* Carriker and *Heptapsogaster petersi* Carriker are actually members of *Megapeostus*. They have marginal carinae similar to those of *Heterogoniodes*

EXPLANATION OF FIGURES

Dorsal aspect of the pterothorax and abdominal segments II and III. Chaetotaxy is only indicated on the right side.

FIG. 2. *Rhopaloceras brevitemporalis* Carriker, ♂, ex *Crypturellus obsoletus punensis*.

FIG. 3. *Kelloggia latithorax* Carriker, ♀, ex *Tinamus major peruvianus*.

FIG. 4. *Strongylocotes interruptus* Carriker, ♀, ex *Crypturellus noctivagus garleppi*.

FIG. 5. *Ornicholax olfersi* Guimarães, ♂, ex *Tinamus major latifrons*.

FIG. 6. *Lamprocorpus hirsutus* Carriker, ♂, ex *Nothoprocta o. ornata*.

FIG. 7. *Heptapsogaster grandis* (Carriker), ♀, ex *Tinamus major peruvianus*.

FIG. 8. *H. temporalis* Carriker, ♀, ex *Crypturellus undulatus adpersus*.

FIG. 9. *H. rotundatus* (Rudow), ♂, ex *Rhynchotus rufescens rufescens*.

FIG. 10. *H. testudo* Clay, ♀, ex *Nothoprocta p. perdicaria*.

FIG. 11. *Heptapsogaster* sp., ♀, ex *Eudromia elegans albida*.

FIG. 12. *Petenosoma yapuræ* Carriker, ♀, ex *Crypturellus undulatus yapura*.

FIG. 13. *Trichodopeosius aculeatus* (Piaget), ♀, ex *Nothocercus j. julius*.

FIG. 14. *Megaginus emarginatus* Carriker, ♂, ex *Crypturellus obsoletus punensis*.

FIG. 15. *Discocorpus mexicanus* Carriker, ♀, ex *Crypturellus cinnamomeus soconuscensis*.

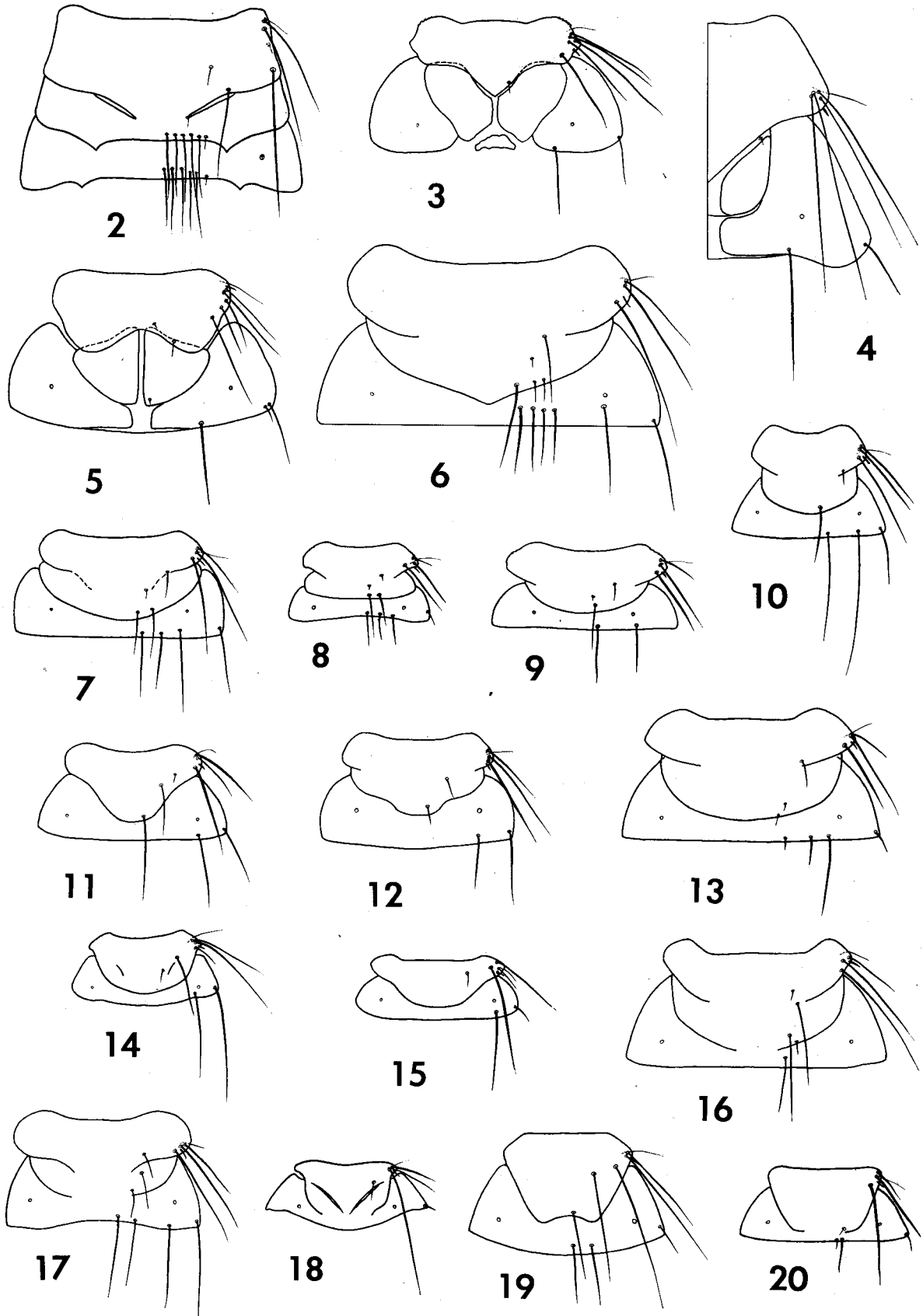
FIG. 16. *Megapeostus clypeiceps* (Giebel), ♂, ex *Crypturellus cinereus*.

FIG. 17. *Pterocotes aberrans* (Carriker), ♂, ex *Tinamus major robustus*.

FIG. 18. *Physconella* sp., ♀, ex *Crypturellus strigulosus*.

FIG. 19. *Cuclotocephalus extraneus* Carriker, ♀, ex *Nothoprocta c. curvirostris*.

FIG. 20. *Nothocotus genitalis* Carriker, ♀, ex *Nothocercus j. julius*.



and male genitalia that only exhibit a slight degree of asymmetry. All the species now included in *Megapeostus* may be characterized by the unique structure of the ventral carina. Apparently only in this genus is it interrupted medially with a flattened spatulate tip extending ventromedially on each side. This modification may increase the efficiency of the pulvinus in feeding. *Megapeostus* Carriker, 1936 has page priority over *Heterogniodes* Carriker, 1936.

(3) *Pterocotes* Ewing = *Pterocotes* Ewing + *Heptapsus* Carriker. *Heptapsus* was separated from *Pterocotes* on the basis of a lessened degree of the extraordinary sexual dimorphism of the head and antennae exhibited by the males of *Pterocotes*. The females are indistinguishable except for slight genitalic differences. The presence of abdominal "scent glands" and the unusual ability of the abdominal segments partly to telescope within one another in both groups serves to unite these into a single genus *Pterocotes* Ewing, 1929, described prior to *Heptapsus* Carriker, 1936.

Table I shows the distribution of Mallophaga genera on the Tinamiformes. The correspondence between the two groups is clearly evident. Of the 17 genera which occur on the Tinaminae,

14 or 82% are indigenous to this group. In contrast, two of five or 40% and one of three or 33% are restricted to the Rhynchotinae and Eudromiinae, respectively. If the criterion of endemicity is used to indicate primitiveness, then the Tinaminae are a more primitive subfamily. This subfamily also harbors the four most primitive "heptapsogastrine" genera in terms of thoracic structure. Although most of the tinamou genera can be immediately identified once a list of the Mallophaga genera parasitizing them is made, the Mallophaga genera serve best to distinguish host categories of greater than generic rank. This is especially true in respect to the major groups designated by von Boettischer.

DISTRIBUTION OF MALLOPHAGA SPECIES GROUPS ON TINAMOU GENERA

In studying the distribution of species groups of Mallophaga genera which occur on more than a single host genus, definite degrees of relationship may be demonstrated between the tinamou genera.

The species groups of *Rhopaloceras* found on *Crypturellus*, *Tinamus* and *Nothocercus* may each be distinguished by details of the male genitalia

TABLE I
DISTRIBUTION OF MALLOPHAGA GENERA ON THE TINAMIFORMES

MALLOPHAGA GENERA	HOST GENERA								
	Tinaminae			Rhynchotinae				Eudromiinae	
	<i>Tinamus</i>	<i>Crypturellus</i>	<i>Nothocercus</i>	<i>Rhynchotus</i>	<i>Nothoprocta</i>	<i>Nothura</i>	<i>Taoniscus</i>	<i>Eudromia</i>	<i>Tinamotis</i>
<i>Rhopaloceras</i>	X	X	X						
<i>Kelloggia</i>	X	X	X						
<i>Strongylocotes</i>	X	X	X	X		x			
<i>Ornicholax</i>	X								
<i>Lamprocorpus</i>					X		X		
<i>Heptapsogaster</i>	X	X	X	X	X	X	X	X	X
<i>Pectenosoma</i>		X							
<i>Trichodopeostus</i>			X						
<i>Megapeostus</i>	x	X							
<i>Pterocotes</i>	X	x	X						
<i>Physconella</i>		X	X						
<i>Megaginus</i>		X							
<i>Discocorpus</i>		X							
<i>Cuclotocephalus</i>					X				
<i>Nothocotus</i>			X						
<i>Pseudolipeurus</i>	X	X	X						
<i>Pseudophilopterus</i>	y	y							
<i>Tinamolaeicola</i>								X	X
<i>Microctenia</i>	y	y							
<i>Menacanthus</i>	y	y		X	y	y		y	

X—Present on all species of a host genus except for *Cuclotocephalus*, *Lamprocorpus*, *Megaginus* and *Discocorpus* which are restricted to certain species groups.

x—Present on one or two species of a host genus.

y—Present on members of a genus but exact distribution not fully known.

and the internal sclerotized bands of the female genitalia. The female genitalia of the species from *Crypturellus* and *Nothocercus* are more similar than those from *Tinamus*.

Kelloggia was formerly separated into three distinct genera, each on a different host genus. The species groups on *Nothocercus* and *Crypturellus*, previously the genera *Austrokelloggia* and *Hypocrypturellus* respectively, both have conspicuous conia. These are extremely reduced in the species on *Tinamus*. The pterothorax and abdominal segment II are more similar in the species of *Kelloggia* on *Nothocercus* and *Crypturellus*.

The extreme degree of sexual dimorphism exhibited by the males of the genus *Pterocotes* from *Tinamus* was previously noted. A single species is known from *Crypturellus*. *P. cylindricus* (Clay), closely allied to the species groups on *Nothocercus*, is known from *Crypturellus n. noctivagus* and *C. n. zabele*.

Megaepostus, known from all species of *Crypturellus*, is found on a few subspecies of *Tinamus major* in South America. It is undoubtedly a derivative of one of the *Crypturellus* inhabiting species.

Heptapsogaster contains more species than any other tinamou inhabiting genus. It is the only one presently known to parasitize all the host genera of the order. Three closely related groups, *temporalis*, *mandibularis* and *tuxtlae*, are found on *Crypturellus*. *H. minuta*, *parvula* and *grandis* occur on *Tinamus*. They apparently are derived from the same stock as those on *Crypturellus* but are not related to them. Only a single group occurs on *Nothocercus*. This one is closely related to *H. temporalis*. On the remaining tinamous, *Heptapsogaster* has speciated to fill a variety of niches occupied by members of other genera on the Tinaminae. Distinct groups such as *H. tessellata* on *Nothoprocta*, *H. rotundata* on *Rhynchotus*, and *H. dilatata* on *Nothura* show clear affinities to the general "heptapsogastrine" stock. They are all presumed to be inhabitants of the back niche. The *minor* group contains species with an elongated abdomen and narrower heads. It is the only group of *Heptapsogaster* with a body form approximating that of the wing niche dwellers. Representatives occur on *Taoniscus*, *Nothura* and *Nothoprocta*. The single species on *Taoniscus* shows greater divergence than those on the other two host genera. The remaining species on the Rhynchotinae and Eudromiinae appear to form a natural group which has speciated to occupy two niches on most of the host genera. *Rhynchotus* and *Nothoprocta* both contain species living on the head and back, *Nothura* and *Eudromia* both have only head-dwelling species, and *Tinamotis* has apparently just the back-dwelling form. The head niche species on *Nothoprocta cinerascens* shows such a degree of sexual dimorphism in the male that

Carriker placed it in a separate genus *Heteroepostus*.

On the basis of the male genitalia, closer affinities are exhibited between the species of *Pseudolipecurus* on *Crypturellus* and *Nothocercus* than between those on *Crypturellus* and *Tinamus*. *Pseudophilopterus* is recorded from so few species that it is not currently known whether its species on *Crypturellus* and *Tinamus* form two distinct groups.

Tinamolaecola has speciated on *Eudromia* and *Tinamotis*, but unlike *Pseudolipecurus*, has no distinct groups inhabiting each host genus.

Menacanthus is of sporadic occurrence and cannot be divided into species groups. The species of *Microctenia* from *Tinamus* have a pair of tergo-central setae on either side of the midline while those on *Crypturellus* have three tergo-centrals in the same position.

From this brief review of the distribution of the major species groups of Mallophaga, it is seen that they are far more useful than the genera proper in an analysis of the generic relations of the hosts. The overall picture is one of a close conformity to the arrangement by von Boettischer. Only a single change in his dendrogram seems necessary. Most of the species groups on the Tinaminae demonstrate clearer affinities between *Crypturellus* and *Nothocercus* than between *Tinamus* and *Nothocercus* as depicted by von Boettischer. It would be desirable to place *Nothocercus* on the same branch as *Crypturellus*.

DISTRIBUTION OF MALLOPHAGA SPECIES ON TINAMOU SPECIES

Genus *Tinamus*

The described species of *Rhopaloceras* fall into two main groups. The first, typified by *R. oniscus* (Nitzsch), was described from *T. solitarius*. A second closely related species, *R. carrikeri* Eichler, was named for the description of *R. oniscus* by Carriker from *T. tao septentrionalis*. Series of available specimens are too small to distinguish the species on *tao* and *solitarius*. In no event, can they be mistaken for the much smaller species on *T. major*. Carriker has described *R. genitalis* and *R. simplex* from this group, but the material is inadequate for separation. No members of this genus have been found on *T. osgoodi* and a single female has been found on *T. guttatus*. This individual is closer to the species on *T. major* than to that on *T. tao*.

Two main groups of *Kelloggia* occur on *Tinamus*. Carriker placed the first of these, with extreme sexual dimorphism, in a separate genus, *Heptagoniodes*. A pair of closely related species, *K. zgonus* (Nitzsch) and *K. dimorphus* (Carriker), which may be separated only by differences in the proportions of the male genitalia, exist on *T. tao tao* and *T. tao weddelli*. *K. clayi* (Guimarães

and Lane) from *T. solitarius* and *K. mirabilis* (Carriker) on *T. tao septentrionalis* may be readily distinguished from each other and from *K. agonus* and *K. dimorphus* by striking differences in their male genitalia. A species found on *T. tao kleei* is known only from females, so its exact position remains in doubt.

The remaining species of *Tinamus* are parasitized by members of the second group which are not sexually dimorphic. Five species can be distinguished on the basis of male genitalia and slight differences in the measurements of various structures. *T. major* is parasitized by three species. *K. mexicanus* Carriker is on *T. m. percautus* and *T. m. robustus*. *K. brevipes* Carriker, originally described from *T. m. castaneiceps* in Costa Rica, is now known from *T. m. zuliensis*, *m. olivascens*, *m. ruficeps*, *m. serratus* and Brazilian specimens of *m. peruvianus*. The third species, *K. latithorax* Carriker, whose type host was *T. m. peruvianus*, has subsequently been found on *m. fuscipennis*, Panama specimens of *m. castaneiceps*, *m. saturatus*, *m. latifrons*, *m. major* and Bolivian and Peruvian *m. peruvianus*. *K. ruficeps* Carriker from *T. m. ruficeps* and *K. serrati* Guimarães from *T. m. olivascens* appear to be identical with *K. brevipes*. Likewise, *K. chocoensis* Carriker from *T. m. latifrons* and *K. taoi* from *t. tao* (host probably erroneous) are synonyms of *K. latithorax*. Two new species occur on *T. guttatus* and *T. osgoodi*.

The closely related species of *Strongylocotes* are mainly distinguished by size and proportions. Contrary to the situation in most of the genera found on *Tinamus*, it cannot be stated that certain host species are related on the basis of parasite distribution. *S. wernecki* Guimarães and Lane, restricted to *T. solitarius*, is the largest species in this group. *S. taoi* Carriker, *S. weddelli* Carriker and *S. carrikeri* Guimarães have been described from *T. tao septentrionalis*, *t. weddelli* and *t. tao* respectively, but do not seem distinct and probably are synonyms of *S. taoi* Carriker. Several names (*S. cordiceps*, *ruficeps*, *angulocapitis*, and *boliviensis*) have been proposed by Carriker for the species occurring on *T. major*. Due to the limited material available, there seems little reason for this excessive splitting. *T. o. osgoodi* and *o. hershkovitzi* have a species which is very closely allied or identical with the one on the *T. major* group. The undescribed species on *T. guttatus* is considerably smaller than other species on *Tinamus*.

Ornicholax was divided into three main groups by Guimarães (1948). With the study of further material, his categories seem justified. *O. alienus* (Giebel) is found on *T. solitarius*. The populations on *T. tao tao* and *T. tao septentrionalis* have each been treated as separate species or subspecies, *O. taoi* Carriker and *O. carrikeri* Guimarães, respectively. There seem to be no significant differences between any of the populations found

on all the subspecies of *T. tao*. *O. alienus* is possibly identical with *O. taoi*; if this is the case, *O. alienus* has priority. The second group contains three to four species typified by *O. robustus* Carriker which was originally described from *T. m. castaneiceps*. Additional records show this species to occur on possibly all subspecies of *T. major* except *T. m. major*, *peruvianus*, and *serratus*. *O. mexicanus* Carriker, 1944, was described from *T. m. percautus*, but is not distinct from *O. robustus* Carriker, 1903. No males have been observed from *T. m. peruvianus*, the type host of *O. boliviensis* Carriker, so its validity cannot be ascertained. Specimens from *T. m. serratus* may be members of the species. Two new species occur on *T. guttatus* and *T. o. osgoodi*. On the basis of male genitalia and general proportions, the species on *o. osgoodi* and *o. hershkovitzi* show closer affinities to *O. robustus* than the species on *T. guttatus*. *O. olfersi* Guimarães differs considerably from the balance of the species in the male genitalia and shape of the head. Originally described from *T. m. major*, it is now known from *T. m. olivascens*, *m. serratus* and *m. latifrons*. One Colombian individual of *T. m. latifrons* harbored both this species and *O. robustus*. *O. olfersi* is apparently restricted to the South American subspecies of *T. major*.

Heptapsogaster grandis (Carriker) was originally described from *T. major peruvianus*, with further records from *m. saturatus*, *m. olivascens*, *m. serratus*, *m. ruficeps*, and *m. major*. Guimarães and Lane (1937) described *H. oliverioi* from *T. solitarius*, but Guimarães (1942a) later considered it a synonym of *H. grandis* (Carriker, 1936). The few specimens available from *T. tao tao*, *t. weddelli* and *T. solitarius* indicate these two species are validly separated by size differences. Two new species on *T. osgoodi* and *T. guttatus* differ from the former by the relative proportions of the two pairs of "scent glands." A second group consists of *H. minuta* (Carriker) and related species. It was first reported from *T. major castaneiceps*. Subsequently, Carriker (1944) considered the population from *T. m. percautus* to be distinct. Additional material from six other subspecies of *T. major* and two subspecies of *T. osgoodi* have been examined. There is no need to split the species. Guimarães (1942a) described *H. keleri* from *T. tao tao*. *H. parvula* (Carriker) constitutes the last species group. It is on all of the host species and subspecies except *T. osgoodi* and *T. guttatus* and cannot be subdivided.

Two species of *Megapeostus* are known from *Tinamus*. *M. alterus* Clay, described from *T. major latifrons*, was on a specimen of *T. m. olivascens*. Its closest relative may be a species on *Crypturellus obsoletus griseiventris*. *M. ruficipitis* Clay is only known from the male holotype from a Peruvian skin of *T. major ruficeps*. It may be a straggler such as *M. parvigenitalis* which occurs on *Crypturellus noctivagus garleppi*.

Pterocotes is represented by three species. *P. taoi* Carriker, whose type host was *T. tao kleei*, is of general occurrence on *T. tao* and its subspecies. A second species, *P. solitarius* Guimarães and Lane, is restricted to *T. solitarius*. *P. aberrans* (Carriker) is present on all subspecies of *T. major*. In 1944, Carriker described *P. colombianus* and *P. mexicanus* from *T. m. serratus* and *T. m. percautus*. The study of series from most of the subspecies of *T. major* shows that *P. colombianus* and *P. mexicanus* are synonymous with *P. aberrans*. The abdominal chaetotaxy and male genitalia of *P. taoi* and *P. solitarius* show closer relationships to each other than either one with *P. aberrans*. This genus has not been reported from *T. osgoodi* or *T. guttatus*.

Pseudolipeurus exhibits a pattern of host distribution similar to that of other genera. *P. taoi* Carriker and *P. peruvianus* Carriker have been described from different host subspecies of *T. tao*. A single male from *T. tao kleei* has been observed so the validity of both species cannot be determined. Material from *T. solitarius* has been identified as *P. taoi* by Guimarães (1942c) and von Kéler (1939a). The shape and size of mesosomal elements of the male genitalia enable two species to be distinguished from the remaining ones inhabiting *Tinamus*. *P. tinami* (Carriker), originally described from *T. major castaneiceps*, is also present on *m. robustus*, *m. fuscipennis*, *m. saturatus*, *m. latifrons* and *o. osgoodi*. Carriker described *P. ruficeps* from *T. m. zuliensis* in 1944 and *P. saturatus* from *T. m. saturatus* in 1953. These cannot be distinguished from *P. tinami*. *P. serratae* Carriker, described from *T. major peruvianus*, is the second species inhabiting the *major* complex. The illustration by Guimarães (1942c) of the male genitalia of a species of *Pseudolipeurus* from *T. m. major* adds an additional host record to this species.

Pseudophilopterus tinami Carriker is only known from its original description from *T. major zuliensis*.

Four species of *Microctenia* are known from *Tinamus*, namely *M. tibialis* Kéler from *T. solitarius*, *M. major* Carriker from *T. m. major*, *M. guimaraesi* Carriker from *T. m. peruvianus*, and *M. heterocephalus* Guimarães from *T. guttatus*. Only the last named species has been studied.

Two species of *Menacanthus* have been described from this host genus, *M. brachygaster* (Giebel) and *M. latacephalus* Carriker from *T. tao* (ssp. ?) and *T. major saturatus*. Further evidence is needed to ascertain whether these records are due to contamination or whether these species actually parasitize *Tinamus*.

Genus *Crypturellus*

Rhopaloceras is poorly represented in the collection so little can be added to the classification by Carriker. The main groups can be separated by the male genitalia. *R. rudimentarius* Carriker

is known from nine of the 13 subspecies of *C. soui*. A closely related species, *R. undulatus* Carriker, occurs on *C. undulatus*. Two other allied species are also known, *R. brevitemporalis* Carriker on *C. obsoletus punensis*, and *R. pennaticeps* (Paine and Mann) on *C. tataupa* and *C. parvirostris*. *R. almeidai* Guimarães, different from any species in the genus, is found on *C. n. noctivagus*. The final group has a pair of species, *R. spatulata* Carriker and *R. heterogenitalis* Carriker, described from *C. noctivagus idoneus* and *C. b. boucardi*. A pair of males from *C. cinnamomeus goldmani* and *C. noctivagus duidae* belong to one of these two species but cannot be accurately determined until compared with the types. A third male from *C. n. garleppi* appears slightly different and may be a new related species. Females are known from *C. cinereus*, *C. v. variegatus*, *C. strigulosus* and several subspecies of *C. cinnamomeus*, but cannot be determined without associated males.

Carriker (1955b) has proposed the names *R. variegatus* and *R. cinereus* respectively for a single female from *C. variegatus* and three females from *C. cinereus*. Females of many species of *Rhopaloceras* are separated solely by quantitative characters. With such small series as the ones above, and in the absence of associated males, it is unwise to segregate new species merely because they were found on new hosts which theoretically should harbor new species.

The species of the genus *Kelloggia* on *Crypturellus* form an extremely homogeneous group whose members may generally be distinguished only by means of slight size differences and the male genitalia. *C. cinereus* and *C. berlepschi* are parasitized by closely related species, *K. heterurus* (Carriker) and an undescribed one. *K. nigriceps* (Carriker) is distributed on seven subspecies of *C. soui* while *K. inconspicuus* (Carriker) is known from *C. soui inconspicuus*. Males of this latter species have not been studied, but from Carriker's figure it may be related to *K. obsoletus*. Two species with different male genitalia and chaetotaxy are present on *C. obsoletus*. *K. obsoletus* (Carriker), with *C. o. punensis* as its type host, was reported from *C. o. ochraceiventris* and is known from *o. chirimolanus*. *K. ribeiroi* (Guimarães) described from *C. o. obsoletus*, also occurs on *C. o. griseiventris*. It is the only known species with lanceolate setae on the head and body. The two subspecies of *C. variegatus* are parasitized by *K. coniceps* (Taschenberg). A closely related undescribed species, differing chiefly in size, occurs on *C. brevirostris bartletti*. A complex of six species covers almost the entire balance of the genus. *C. undulatus* and its subspecies are parasitized by *K. undulatus* (Carriker). *K. laticeps* (Guimarães) is found on *C. n. noctivagus*. *K. strigulosus* (Guimarães), whose type host is *C. strigulosus*, also occurs on *C. noctivagus garleppi*. *K. idoneus* (Carriker) described from

C. n. idoneus is also found on *C. n. duidae*, *transfasciatus* and *boucardi costaricensis*. Originally described from *C. b. boucardi*, *K. boucardi* (Carriker) is found on all nine subspecies of *C. cinnamomeus*. *K. cinnamomea* (Carriker) from *C. cinnamomeus mexicanus* is indistinguishable from *K. boucardi* (Carriker). One of the two closely related species in the final group has an overlapping host distribution. *K. genitalis* (Carriker) is restricted to Brazilian populations of *C. tataupa tataupa*. In contrast, *K. mendax* (Guimarães and Hopkins) occurs on all of *C. parvirostris* (Brazil, Paraguay, and Bolivia), *C. tataupa lepidotus* (northeastern Brazil), *C. t. inops* (northern Peru), *C. t. peruvianus* (central Peru), and *C. t. tataupa* from Bolivia, Paraguay, and Argentina.

The host distribution of the species of *Strongylocotes* parallels that of *Kelloggia*. A pair of related species, *S. berlepschi* Carriker and *S. abdominalis* Carriker, inhabit *C. berlepschi* and *C. cinereus*. *C. soui* is parasitized by *S. subconiceps* Carriker, or a flock of closely allied forms on different host subspecies. Carriker has described three subspecies of *S. subconiceps* (*S. s. cauae* on *C. s. cauae* and *C. s. soui*, *S. s. felisae* on *C. s. caqueta* and *C. s. harterti*, and *S. s. perijae* on *C. s. mustelinus*), and Guimarães and Lane a single one (*S. s. albigularis* on *C. s. albigularis*). The male specimens observed have been from *C. s. modestus*, *s. meserythrus*, *s. nigriceps*, *s. harterti*, and *s. inconspicuus*. These all conform to *S. subconiceps*. *C. obsoletus* harbors several closely related species. *S. nirmoides* (Carriker) was described from *C. obsoletus punensis*. A probable synonym of *S. nirmoides* is *S. intermedius* Carriker from *C. o. ochraceiventris*; a single male from *C. o. chirimotanus* fits either of these species descriptions.

The second group consists of *S. complanatus* (Piaget), described from *C. o. obsoletus* and also present on *C. o. griseiventris*. Another major group occurs on *C. o. variegatus* and *C. brevirostris bartletti*. *S. variegatus* Carriker (described from subspecies *salvini*) is on the former; *S. setifer* Hopkins and *S. caquetae* Carriker (described from the nominate subspecies) are probable synonyms. An undescribed species is on *C. brevirostris bartletti*. The remaining species, except those on *C. tataupa* and *C. parvirostris*, have been considered subspecies of *S. interruptus* by Carriker (1953b). They do form a closely related complex, but the various components deserve specific rank. *S. limai* Guimarães, whose type host was *C. undulatus vermiculatus*, is also found on the other subspecies of *C. undulatus*. *S. noctivagi* Clay seems to be confined to *C. noctivagus noctivagus* and *C. n. zabele*. *S. interruptus* Carriker, described from *C. n. garleppi*, can also contain the population on *C. n. erythropus*. Species from *C. n. idoneus* (*S. idoneus* Carriker) and *C. columbianus* (*S. columbianus* Carriker) have not been observed.

The populations on *C. cinnamomeus* and *C. b. boucardi* are identical, and *S. fimbriatus* Clay (1937) from the former host has priority over *S. boucardi* Carriker (1944) from the latter. *S. glabrous* (Carriker) on *C. t. tataupa* and *C. t. peruvianus* and *S. orbicularis* (Carriker) on *C. parvirostris* comprise the final species group.

Each of the three species groups of *Heptapsogaster* will be discussed separately. The *H. temporalis* group may be divided into two sections on the basis of the chaetotaxy of abdominal segment VI in the male. *H. feminina* Carriker from *C. cinereus* has two hairs on this pleurite, while the remaining species have one hair and one spine. *H. boliviensis* Carriker and *H. brasiliensis* Carriker have been described from *C. obsoletus punensis* and *C. o. obsoletus*. Although *H. javus* Carriker from *C. v. variegatus* has not been studied, it appears to be valid. Carriker has described *H. temporalis* from *C. u. undulatus*; it is also present on *C. u. adpersus*, *u. vermiculatus*, and *u. yapura*. *H. chinirrii* Carriker and *H. sinuensis* Carriker have only been reported from *C. noctivagus garleppi* and *C. columbianus*. *H. boucardi* Carriker was described from *C. b. boucardi* and later was reported from *C. noctivagus idoneus*. The final species, *H. acutiventris* Clay, described from *C. cinnamomeus mexicanus*, differs from the preceding species (except for *H. boucardi*) in terms of the male pleural chaetotaxy. Materials from nine subspecies of *C. cinnamomeus* have been compared with specimens from *C. b. boucardi*. *H. boucardi* is identical with *H. acutiventris* which has priority. Since no individuals of the *H. temporalis* group have been observed from large series of skins of *C. soui*, *C. tataupa*, and *C. parvirostris*, it is assumed that these Mallophaga species are absent from the aforementioned hosts.

H. tuxillae and its allies (*H. inexpectata* group of Carriker, 1944) form the second group. *H. benii* Carriker, described from *C. soui inconspicuus*, occurs on at least six other subspecies of *C. soui*. *H. insperata* Hopkins, previously known from its type host, *C. obsoletus obsoletus*, is also present on *C. o. griseiventris*. The similarity of the tergopleural chaetotaxy of the females places the remaining species in a concise section. *H. undulata* Carriker is restricted to the subspecies of *C. undulatus*. *H. magdalenae* Carriker, described from *C. noctivagus idoneus* and subsequently recorded from *C. columbianus*, appears closely related to *H. tuxillae* Carriker from *C. b. boucardi*. Males from five subspecies of *C. cinnamomeus* and a single one from *C. transfasciatus* do not appear to be separable from *H. tuxillae*. The recently described *H. potosii* Carriker, 1954, on *C. cinnamomeus mexicanus*, is apparently a synonym of *H. tuxillae*. An undescribed species with conspicuous differences in the shape of the parameres and mesosomal elements occurs on *C. strigulosus*, *C. noctivagus*

spencei (Venezuela), and *C. n. erythropus* (British Guiana). The *H. tuxillae* group is probably absent from *C. cinereus*, *C. berlepschi*, *C. variegatus*, *C. tataupa*, and *C. parvirostris*.

In contrast to other groups whose components may be segregated by abdominal chaetotaxy, members of the *H. mandibularis* group can be separated accurately only by the male genitalia. Carriker has described four subspecies of *H. mandibularis* from *C. soui* (*H. m. tapicollae* from *C. s. meserythrus*, *H. m. nigriceps* from *C. s. nigriceps*, *H. m. albigularis* from *C. s. albigularis* and *H. m. motilonensis* from *C. s. mustelinus*). From the scanty material available, *H. tapicollae* seems a good species containing at a minimum the populations inhabiting *C. s. meserythrus*, and *C. s. modestus*. *H. nigriceps* is likewise a valid species, with additional records from *C. s. inconspicuus*. The recognition of *H. motilonensis* and *H. albigularis* as valid species is questionable. The genitalia of species from *C. obsoletus* are different. *H. crucis* Carriker, from *C. o. punensis*, also occurs on *o. ochraceiventris*. *H. stulla* Clay, a different species, is found on the eastern *C. o. obsoletus*. It was well illustrated by von K  ler (1939a: 240, fig. 13) but was misdetermined as *H. mandibularis*. A single male from *C. o. griseiventris* is close to this species, but may be different. *H. yapurae* Carriker is known from four of the subspecies of *C. undulatus*. *H. idonea* Carriker, *H. garleppi* Carriker, and *H. noctivagi* Clay have been described from *C. n. idoneus*, *n. garleppi*, and *n. noctivagus*. All materials examined from *C. strigulosus*, *noctivagus erythropus*, and *n. spencei* belong to a single species whose genitalia differ from those illustrated for *H. idonea* and *H. garleppi*, but conform perfectly to the figure of *H. stulla* (Clay, 1937: 142, fig. 4b); the figure for the genitalia of *H. noctivagi* had inadvertently been substituted for that of *H. stulla*. It is advisable to refer to the specimens from *C. strigulosus*, *C. n. noctivagus*, *n. erythropus*, and *n. spencei* as *H. noctivagi*. Carriker (1944) described *H. modestae* from *C. b. boucardi*, and later (1954) described *H. cinnamomea* from *C. cinnamomeus mexicanus*. Materials studied from several populations of *C. cinnamomeus* are identical with specimens from *C. b. boucardi*, so *H. cinnamomea* should be considered a synonym of *H. modestae*. The final species group, *H. mandibularis* Carriker, is present on *C. t. tataupa*, and possibly on *C. parvirostris*. Individuals from the latter host are slightly smaller, and may be separable with the study of additional specimens.

Carriker (1944) described two species, *H. costaricensis* from *C. soui modestus* and *H. latacephala* from *C. u. undulatus*, which are supposed to belong to the group of species present on *Tinamus*. Neither of these species has been encountered, and at present these host records should be viewed with suspicion.

In *Pectenosoma* (unlike *Heptapsogaster*) the

genitalia are uniform throughout the genus. Species are distinguished by differences in the numbers and rows of thoracic and abdominal papillae and by minor size differences. Carriker (1944) separated materials from *C. soui* into three subspecies, considering the populations from *C. s. inconspicuus*, *C. s. meserythrus*, and *C. s. nigriceps* distinct. Examination of material from his hosts and from six other subspecies of *C. soui* indicates that all of the populations are a single species, *P. inconspicuus* Carriker. *P. punensis* Carriker is known from *C. o. punensis* and *o. ochraceiventris*; a single male from *C. o. obsoletus* is tentatively placed here. The species on *C. variegatus* form another group comprising *P. verrucosum* (Taschenberg) from Brazilian individuals of *C. v. variegatus*, and *P. salvini* Guimar  es from *C. v. salvini*. Both Guimar  es (1950a) and I have found *P. salvini* on specimens of *C. v. variegatus* from British Guiana. *P. parvum* Carriker and *P. subparvum* Guimar  es and Hopkins are closely related species present on *C. tataupa* and *C. parvirostris*.

The remaining *Pectenosoma* species are all members of a single group. As in other instances, *C. undulatus* and its subspecies are parasitized by one species, *P. yapurae* Carriker. The complex on *C. noctivagus* is difficult to interpret in this genus. *P. noctivagum* Guimar  es, known only from its type host *C. noctivagus noctivagus*, is a distinct species. Carriker has described *P. angustum* from *C. n. garleppi* and *P. boucardi* from *C. b. boucardi*. Specimens examined from these two hosts, with additional series from *C. strigulosus*, *C. noctivagus erythropus*, *n. spencei*, and *n. idoneus*, cannot be clearly divided into species and it may be possible that only a single species is present over this host range. *P. cinnamomeum* Carriker occurs on all the subspecies of *C. cinnamomeus*. One male from *C. transfasciatus* appears to conform to *P. cinnamomeum* rather than to the species on the *C. noctivagus* complex. *P. tinami* Carriker from *Tinamus major percautus* appears to be an instance of contamination from *Crypturellus cinnamomeus sallaei*.

The genus *Megapeostus* can be apportioned into two sections. These have been considered as separate genera, *Megapeostus* and *Heterogoniodes*. An analysis of the characters used to separate them indicates generic separation is not necessary. The *Megapeostus* section contains a range of groups with varying degrees of asymmetry in the male genitalia. The closely related species on *C. soui*, *C. obsoletus*, *C. brevirostris* and *C. tataupa* may be considered as the first main group. *M. soui* and *M. platycephalus* were described by Carriker from *C. soui soui* and *s. inconspicuus*. Examination of over 60 specimens from eight subspecies of *C. soui* indicates that a single species, *M. soui* Carriker, is present on this host. *M. heptarthrogastriiformis* Eichler, described from *C. obsoletus punensis* and also

present on *C. o. ochraceiventris* and *o. castaneus*, is closely allied to the above. An undescribed species, with similar parameres but a different head shape, occurs on *C. o. griseiventris*. The species on *C. o. obsoletus* is different from the former, especially in respect to the male genitalia. It appears close to *M. petersi* (Carriker) from *C. t. tataupa* but its true nature will not be known until specimens have been seen from the latter host. A final undescribed species in the group is present on *C. brevirostris bartletti*.

The second group contains a single species, *M. fuscus* Clay, found on *C. v. variegatus* and *v. salvini*. *M. asymmetricus*, *M. parvigenitalis*, and *M. secundus* form a third species group. *M. asymmetricus* Carriker, described from *C. u. undulatus*, is known from all subspecies of *undulatus* except *u. confusus*. A closely related species, *M. parvigenitalis* Carriker, is only known to occur on *C. noctivagus garleppi*. *C. cinnamomeus* and its subspecies are parasitized by a very distinct species, *M. secundus* Clay.

The final group contains two described species, *M. multiplex* Clay from *C. b. boucardi* and *M. idoneus* Carriker from *C. noctivagus idoneus*. Additional material of this group has been seen from *C. strigulosus*, *C. noctivagus erythropus*, *n. spencei*, *n. duidae*, and *C. boucardi costaricensis*. The differences in the male genitalia of *M. multiplex* and *M. idoneus* mentioned by Carriker (1944) do not appear to be constant. There are significant differences in the measurements of females from *C. b. boucardi* and *C. strigulosus*, but insufficient males are available for comparable study. If only a single species can be recognized from this complex, *M. multiplex* Clay has priority. The second section contains three species. *M. clypeiceps* (Giebel) and *M. heterurus* (Carriker) are found on *C. cinereus* and *C. berlepschi*. *M. arcaeiceps* (Clay), described from *C. cinnamomeus mexicanus*, is also present on *c. sallaiei* and *c. intermedius*.

Pterocotes cylindricus (Clay), the sole species of the genus on *Crypturellus*, occurs on *C. noctivagus noctivagus* and *n. zabele*. Its status has been mentioned previously.

The species of the genus *Physconella* are poorly represented in the material available. *P. cinerea* Carriker, the largest one known from *Crypturellus*, is present on *C. cinereus*. *P. kelloggi* (Paine), on *C. soui*, has striking genitalia. Carriker has described *P. subsimilis* from *C. s. inconspicuus*, but it is indistinguishable from material on seven other subspecies of *soui*. *P. hamata* Carriker has been reported from *C. obsoletus punensis*. Only females of *Physconella* are known from *o. obsoletus* so their relation to *P. hamata* remains unknown. Similarly only females are known from *C. v. variegatus* and *C. brevirostris bartletti*. The balance of the hosts contain species closely allied to *P. genitalis* Carriker from *C. noctivagus garleppi*. *P. emersoni* Carriker, from *C. undulatus adpersus*,

is the only other species yet described in this group. It also occurs on *u. undulatus* and *u. yapura*. Males of species related to the above two have been observed from *C. noctivagus atricapillus*, *n. idoneus*, *C. strigulosus*, *C. cinnamomeus vicinor*, *c. praepes*, *C. b. boucardi* and *b. costaricensis*. A maximum of three specimens has been available from each of these hosts so it has been thought unwise to subdivide the group further.

Megaginus has been recently reviewed by Carriker (1955a). He currently recognizes ten forms. Some of his criteria for separation (markings of paratergal plates, minor size, and male genitalia differences) break down when additional material is studied. *M. sordidus* Carriker and *M. felisae* Carriker from *C. berlepschi* and *C. cinereus* are only known from females and have not been observed. However, all Mallophaga from the above hosts are restricted to them, and so these species are retained. Carriker has described *M. latacephalus* from *C. soui meserythrus*, *M. dissimilis* from *C. s. nigriceps*, *M. excavatus* from *C. s. inconspicuus*, and *M. caquetensis* from *C. s. caquetae*. With the study of both sexes from the above subspecies of *soui*, it seems best to consider all these forms as synonyms of *M. emarginatus* Carriker, described from *C. obsoletus punensis*. *M. quadrithorax* Carriker, unencountered since its description from a single male on *Tinamus major fuscipennis*, appears to be a straggler from *C. soui modestus* and is a synonym of *M. emarginatus*. *M. tessellatus* Carriker, from Venezuelan individuals of *C. tataupa*, has not been observed. The tergopleural chaetotaxy of *M. tataupensis* Carriker from *C. t. tataupa* and *t. peruvianus* readily distinguishes it from *M. emarginatus*.

Discocorpus is rather closely related to *Megaginus* in many respects. It mainly occurs on species of *Crypturellus* that *Megaginus* does not parasitize. If intermediate species occurred, it certainly would be combined with *Megaginus*. An undescribed species is present on *C. o. obsoletus*. *D. microgenitalis* Carriker has been described from *C. t. tataupa*. Figures of this species indicate it is closely allied to the previous one. The remainder of the species exhibit close affinities. *D. cephalosus* Carriker from *C. noctivagus garleppi* and an undescribed species on *C. undulatus yapura* and *u. adpersus* compose one group. *D. intermedius* Carriker has been described from *C. noctivagus idoneus*. No material has been observed from this host so specimens from *C. strigulosus* are assigned to this species with reservations. *D. furculus* Carriker has been described from *C. b. boucardi* from Veracruz, Mexico and has also been observed from *b. costaricensis*. *D. mexicanus* Carriker, described from *C. cinnamomeus mexicanus*, has been found on seven additional subspecies of *cinnamomeus* and *C. b. boucardi* from Oaxaca and

Chiapas, Mexico. Single specimens have been encountered on *C. transfasciatus* and *C. columbianus*. The species on *transfasciatus* seems allied to *D. furculus*. The one on *columbianus* appears related to *D. mexicanus*.

The genus *Pseudolipeurus* is divided into a number of distinct groups. The male genitalia show a wider range of divergence than in most Mallophagan genera. *P. macconelli* Clay is on *C. cinereus*. *P. megagenitalis* Carriker from the same host is identical to Clay's species. Two species occur on *C. soui*. *P. subsimilis* Carriker, whose type host is *C. s. inconspicuus*, is also present on *s. nigriceps*. *P. dubius* Guimarães from *C. s. soui* also occurs on *C. s. meserythrus*, *s. harterti*, and *s. albicularis*. *P. soui* Carriker from *C. s. cauae*, *s. mustelinus*, *s. harterti*, and *s. caquetae* is a synonym of *P. dubius*. Three diverse species inhabit *C. obsoletus*. *P. carrikeri* Hopkins is on *C. o. punensis*, *P. conspicuus* Guimarães on *C. o. griseiventris*, and *P. longipes* (Piaget) on *C. o. obsoletus*. The latter species seems related to *P. plumbeus* (Pessoa and Guimarães) found on *C. talaupa* and *C. parvirostris*. A very distinct species, *P. theresae* Guimarães, occurs on *C. v. variegatus*. Two species have been described from *C. undulatus*. *P. genitalis* Carriker (1936) has been described from the nominate subspecies and also occurs on *C. u. yapura* (Guimarães, 1944b). *P. macrogenitalis* (Monteiro de Barros, 1933), described from *C. u. vermiculatus*, differs only in the shape of the apices of the mesosomal apparatus of the male genitalia. At present, it is advisable to consider these as a single species, *P. macrogenitalis*. *C. n. noctivagus* and *n. zabele* harbor a very distinct species, *P. megaceros* Guimarães. The balance of the genus from *Crypturellus* forms a close group. Four species have been described by Carriker, *P. garleppi* from *C. noctivagus garleppi*, *P. sanctaemariae* from *C. n. idoneus* and later from *C. saltuensis* and *C. columbianus* (1953a), *P. similis* from *C. b. boucardi* and *C. cinnamomeus sallaei*, and *P. robustus* on *Tinamus major percautus*. Adequate series of specimens for comparison have been available only from the hosts of *P. garleppi* and *P. similis*. These two species can be distinguished just by means of details of the male genitalia. A single male from *C. n. duidae* seems to be close to *P. garleppi*. Specimens from *C. strigulosus* cannot be separated from the series of *P. similis* encountered on six subspecies of *C. cinnamomeus* and the two subspecies of *C. boucardi*. The measurements for *P. robustus* Carriker fall within the range of *P. similis* and it is undoubtedly a stray from *Crypturellus cinnamomeus sallaei*.

Little can be said concerning the relations of the species of *Pseudophilopterus*, which are extremely rare in collections. Two main groups of species seem to exist, separated by the presence or absence of the postspiracular setae on abdomi-

nal tegum III. It appears to be present on species from *C. soui*, *C. obsoletus* and *C. variegatus* and absent on the *C. undulatus*, *C. noctivagus*, and *C. cinnamomeus* group. *P. perijanus* Carriker is only known from its type host, *C. soui mustelinus*. *P. obsoletus* Carriker from *C. obsoletus punensis* has been recorded from Brazilian populations of *o. obsoletus* (von Kéler, 1939a and Guimarães, 1944b). A single female from *C. v. variegatus* is a member of the first group. No material has been observed from *C. undulatus yapura* and *C. saltuensis*, the type host of *P. hirsutus* Carriker and *P. grandior* Carriker. Females have been found on *C. n. noctivagus*, the type host of *P. noctivagus* Guimarães, and *C. strigulosus*. The female from *strigulosus* can be referred to the species group lacking post-spiracular seta III. The final species, *P. similis* Carriker, described from *C. cinnamomeus sallaei*, is also known from *c. mexicanus*.

Two species of *Microctenia* have been described from *Crypturellus*, *M. crucis* Carriker from *C. obsoletus punensis* and *M. soaresi* Guimarães on *C. n. noctivagus*.

A single species of *Menacanthus* is known from *Crypturellus*. *M. coniceps* Carriker has been described from *C. soui cauae*. The presence of this genus on *Crypturellus* requires further verification.

Genus *Nothocercus*

Three species of *Rhopaloceras* have been described from this genus. *R. abbreviatus* Carriker on the two subspecies of *N. nigrocapillus* has close affinities to *R. bonapartei* Carriker described from *N. b. bonapartei*. The third species, *R. laticeps* (Piaget), has been found on *N. j. julius* and *N. j. fuscipennis*.

A single species of *Kelloggia*, *K. intermedia* (Carriker) has been described from this genus. Originally reported from the two subspecies of *N. nigrocapillus*, Carriker has also collected the species on *N. b. bonapartei*. Additional specimens have been observed from *N. n. nigrocapillus*, *N. bonapartei frantzii*, *N. b. plumbiceps*, and *N. j. julius*. No further division is currently advisable although the small series from *j. julius* provides indications that this population may show significant size differences.

Strongylocotes is present on the species of *Nothocercus*. Two distinct groups apparently exist. The first contains just *S. spinosus* (Piaget) on *N. j. julius*. The second group contains five species described by Carriker. He records *S. subspinosus* from *N. n. nigrocapillus*, *S. peruvianus* from *N. n. cadwaladeri*, *S. bonapartei* from *N. b. bonapartei*, and *S. intercedens* from *N. b. intercedens*. With the examination of additional specimens from *N. b. plumbiceps* and *b. frantzii*, his forms appear indistinguishable and might all be considered under the name of *S. peruvianus*.

A single species group of *Heptapsogaster* occurs on *Nothocercus*. It is most clearly related to *H. femininus* Carriker on *Crypturellus cinereus*, a member of the *H. temporalis* group. Carriker has described *H. nothocercae* from *N. b. bonapartei*, with *N. nigrocapillus cadwaladeri* also listed as harboring the species. Populations on *N. n. nigrocapillus*, *bonapartei plumbiceps*, and *N. b. intercedens* are also referable to this species. An undescribed species with different chaetotaxy is restricted to *N. bonapartei frantzii*. *H. julius* Carriker from *N. j. julius* is also found on *N. j. fuscipennis*. It shows a greater degree of divergence than either of the preceding members of this species group.

Trichodopeostus can be divided into two main groups on the basis of the male genitalia. The first contains a single species, *T. aculeatus* (Piaget) present on *N. j. julius*. Three species are present in the second group. *T. spinosus* Carriker has been described from *N. n. nigrocapillus*, and *T. incertus* Carriker from an immature female on *N. n. cadwaladeri*. This last species is undoubtedly a synonym of *T. spinosus*. *T. praegracilis* Carriker, whose type host is *N. b. bonapartei*, is also found on *b. plumbiceps*. An undescribed species, related to the preceding, is limited to *N. b. frantzii*.

The species of *Pterocotes* may be separated into two main sections. Each host population possesses members of both groups which often occur on the same individual. Contrary to most instances where two species present on one host differ in many adaptive features as differences in the presence or absence of sexual dimorphism of the antennae, or in the degree of sexual dimorphism (Clay, 1950), these species groups are separated chiefly by size differences. It is possible that the large species inhabits the head niche while the smaller one is restricted to wing and back feather tracts. A single large species, *P. inexpectatus* (Carriker), is assigned to one group. Originally described from *N. b. bonapartei*, it is also found on *N. n. nigrocapillus*, *N. j. julius*, *N. b. intercedens* and *b. frantzii*. Since the genitalia of the specimens appear identical, it does not seem possible to subdivide the group further. The second section with the small species can be segregated into two main groups of closely related species. The first of these, *P. tergalis* (Carriker) was described from *N. n. nigrocapillus*, and is also apparently present on *N. bonapartei intercedens*. A very close undescribed relative of the above differing only in some dimensions of the male genitalia is encountered on *N. j. julius* and *j. fuscipennis*. *P. nothocercae* (Carriker), with rather different genitalia, is found on its type host *N. b. bonapartei* and on *b. plumbiceps*. A close undescribed ally of *P. nothocercae* occurs on *N. b. frantzii*.

Two species of *Physconella*, *P. nothocercae* and *P. julia*, have been described by Carriker from

Nothocercus. In addition to its type host, *N. n. nigrocapillus*, Carriker (1944) has reported *P. nothocercae* from *N. b. bonapartei*. Additional specimens have been observed from his hosts and from *N. b. plumbiceps*, *b. intercedens*, and *b. frantzii*. The closely related *P. julia* is only known from *N. j. julius*.

Nothocotus contains five species, all described by Carriker. *Nothocotus parvithorax*, *N. centralis*, *N. subsimilis*, and *N. genitalis* all form a closely related group. The first two species were described from *Nothocercus b. bonapartei* in different areas, while the latter two species are known respectively from *Nothocercus nigrocapillus* (both subspecies) and *Nothocercus j. julius*. *Nothocotus distinctus*, with a different head shape in the male and unique genitalia, is restricted to *Nothocercus bonapartei frantzii*.

Pseudolipeurus is poorly known on *Nothocercus*. Carriker has described three species, one from each of the main host groups. *P. grandis* was originally described from a single female on *N. n. nigrocapillus*, and the alleged male described by him (1944) was from *N. b. bonapartei*. This latter identification is an instance of contamination, from (possibly) *Crypturellus noctivagus idoneus* from the same locality. A male has been observed from the type host, and its genitalia are quite distinct. Two other species, *P. verendus* Carriker and *P. bonapartei* Carriker, are recorded from *N. j. julius* and *N. b. bonapartei*.

Genus *Rhynchotus*

Strongylocotes lipogonus (Nitzsch) is found on all the subspecies of this monotypic genus. *S. alticola* Carriker, described from a population of *R. rufescens maculicollis*, is found not valid after study of additional specimens. Females from *R. r. rufescens* from Reyes and Buena Vista, Bolivia, and Vaccaria, Brazil may be distinguished from all other populations by the greater length of the vulval hairs.

The remaining Ischnocera belong to the genus *Heptapsogaster* and are members of three species groups. *H. rotundata* (Rudow) is present on all subspecies. No differences exist between any of the populations studied except in the length of the lateral abdominal seta of tergum VI. There is a noticeable difference in the specimens from *R. r. rufescens* and the other two populations, *r. maculicollis* and *r. pallescens*. This does not seem worthy of taxonomic recognition, especially since the specimens of *R. r. maculicollis* are all from a single locality. The second group consists of three species. *H. latithorax* (Carriker) is sympatric with the other two, *H. crenulata* (Carriker) from *R. r. maculicollis*, *r. pallescens*, and *r. catinae*, and *H. sexpunctata* (Piaget) on *R. r. rufescens*. The latter two are large species, separated by genitalia and proportions from the very much smaller *H. latithorax*. The antennae of *H. latithorax* are filiform while those of *H.*

crenulata and *H. sexpunctata* are dimorphic in the male. This indicates a difference in mating behavior which would tend to isolate the species. The last group consists of a single species, *H. sexsetosa* (Piaget), known from all the subspecies except *R. r. calingae*. Carriker (1944) has described a second species, *H. secunda* from *R. r. maculicollis*. His diagnostic features do not hold true and with the small amount of material available subdivision does not seem necessary.

A single menoponid, *Menacanthus arctifasciatus* (Piaget), described from *R. rufescens* (subspecies ?) is known from all subspecies except *R. r. pallescens*.

Genus *Nothoprocta*

Carriker has described two species of the genus *Lamprocorpus* from this host genus. In both instances there has probably been a misidentification of the hosts. *L. spinosus*, described from *N. pentlandii ambigua*, has not been subsequently encountered on the type host or other subspecies of *pentlandii*. Numerous specimens have been found on *N. curvirostris peruvianus* and *c. curvirostris*. Material subsequently collected by Carriker has been from *c. peruvianus*. It seems that *curvirostris* is the true host of this species. *L. hirsutus* was described from *N. ornata branickii* from Lake Titicaca, Peru. The subspecies of *ornata* present at this locality is *ornata*. Additional specimens of *L. hirsutus* are known from *o. ornata* and *o. rostrata*. A single female has been encountered on a skin of *N. taczanowskii*. This is an undescribed species related to *L. hirsutus*.

Four diverse species groups of *Heptapsogaster* occur on *Nothoprocta*. The first group contains three species which appear to occupy the head niche filled by *Lamprocorpus* on *N. ornata*, *N. curvirostris*, and *N. taczanowskii*. *H. teres* (Clay), whose type host was *Nothura maculosa peruviana* and which was also recorded by her from *Nothoprocta p. perdicaria*, definitely does not occur on *Nothura*. It is restricted to *Nothoprocta p. perdicaria* and *p. sanborni*. The remaining species, *H. carrikeri* (Clay) and *H. subteres* (Carriker), are restricted to *N. cinerascens* and *N. pentlandii pentlandii*. The second group consists of a single species, *H. testudo* Clay, described from *Nothura maculosa peruvianus* (1937). In 1944, Carriker described *H. heterura* from *Nothoprocta cinerascens*; it is a synonym of the above species. Materials from the two subspecies of *N. perdicaria* and *N. cinerascens* cannot be distinguished from each other and conform perfectly to *H. testudo* Clay. Evidently a mislabeling of material has occurred, similar to the case of *H. teres* described in the same paper. The third group contains three species, apparently back inhabitants. *H. chacoensis* (Carriker) has been described from *N. cinerascens* and is limited to that host. Specimens from *N. perdicaria* are

very close to *H. chacoensis* but deserve specific rank. An undescribed species on *N. pentlandii pentlandii* and *pentlandii oustaleti* is distinct from the two preceding ones. The final group contains three to four species. *H. truncata* Carriker was originally recorded from *N. ornata branickii* at Lake Titicaca. As with *Lamprocorpus hirsutus*, the type host is actually *N. o. ornata*. *H. ornata* Carriker, later described from *N. o. ornata*, is a synonym of the above species. *H. tessellata* Carriker, described from *N. curvirostris peruviana*, is also found on *c. curvirostris*. The species of the *H. tessellata* group on *N. taczanowskii* is extremely close to *H. truncata* but it may be separable. *H. pentlandii* Carriker is only known from its description from *N. pentlandii pentlandii*. Judgment on the presence of this species on *pentlandii* should be held in abeyance until further specimens have been encountered.

Carriker has divided the species of *Cuclotcephalus* into two groups, *C. extraneus* and *C. secundus*. He believes that species of both these groups coexist on the same host. This current study does not confirm his contention. Three species of the *C. extraneus* group have been described, *C. extraneus* Carriker from *N. ornata branickii* at Lake Titicaca (= *o. ornata*), *C. ornatus* Carriker from *N. o. ornata* at Callipampa, Bolivia, and *C. similis* Carriker from *N. pentlandii pentlandii*. Specimens have been observed from *N. o. ornata* and *N. c. curvirostris* which fit *C. extraneus* perfectly. *C. ornatus* may be considered identical with *C. extraneus*. The second group contains *C. secundus* Carriker from *N. pentlandii oustaleti* and *pentlandii pentlandii*, and *C. incachacae* Carriker from *N. o. ornata*. Only *C. secundus* has been encountered, both times on the two subspecies of *pentlandii* where Carriker found it. From the evidence available, it seems that *C. extraneus* is restricted to *N. ornata* and *N. curvirostris*, and *C. secundus* occurs on *N. pentlandii*.

A single species of *Menacanthus*, *M. nothoproctae* Carriker, has been described from *N. cinerascens*. Members of this genus have also been observed from *N. perdicaria*, *N. pentlandii pentlandii*, and *N. curvirostris*. *Menacanthus* is probably a normal parasite of *Nothoprocta*.

Genus *Nothura*

A single species of *Strongylocotes* occurs on *Nothura*. *S. tinami* (Rudow) is restricted to *N. boraquira* and is distributed on the Bolivia, Brazil and Paraguay populations of the host.

As in *Nothoprocta*, several distinct groups of *Heptapsogaster* are present on *Nothura*. *H. boulloni* Clay constitutes the first group. It has the same host range and distribution as *Strongylocotes tinami*. The wing niche group includes three species. *H. boraquirae* Clay only occurs on *N. boraquira*. The remaining two species are rather closely related to each other and may be

distinguished only by means of the male genitalia and paratergal chaetotaxy. *H. boliviana* (Carriker), described from *N. maculosa oruro* (= *darwinii agassizii*), is known from *N. darwinii agassizii* and *d. boliviana*. *H. minor* Hopkins, a new name for *H. minuta* (Carriker), was described from an Uruguayan specimen of *N. maculosa maculosa*, erroneously identified as *maculosa nigroguttata* (Carriker, 1936). This species has been encountered on *N. maculosa annectens*, *m. maculosa*, *m. paludivaga*, and *m. major*. Only a few specimens from *N. chacoensis* and *N. minor* were available, and at present they are considered as *H. minor*. The final group has a single described species, *H. dilatata* (Rudow) from *N. boraquira*.

A species of *Menacanthus* has been encountered on *Nothura m. maculosa* (Guimarães, 1947b). As additional material is known from two other subspecies of *maculosa*, it seems that this genus is normally found on *Nothura*.

Genus *Taoniscus*

The single species of *Heptapsogaster* known from this monotypic genus has been previously discussed.

Genus *Eudromia*

An undescribed species of *Heptapsogaster* is found on *Eudromia elegans* and its subspecies (*elegans*, *intermedia*, *multiguttata*, *formosa*, *devia*, *albida*, and *patagonica*). Another undescribed *Heptapsogaster* from *E. mira* is significantly smaller and probably represents a second species. Both of these species show affinities with *H. teres* which parasitizes *Nothoprocta*.

Tinamotaecola has at least one undescribed species on *Eudromia*. The material from *E. elegans elegans*, *e. intermedia*, *e. formosa*, and *e. albida* belongs to one species. The single known male from *E. mira* is much smaller than any of the preceding individuals and it may be a separate species.

Menacanthus is present on several of the subspecies of *E. elegans*.

Genus *Tinamotis*

Carriker has described a single species of *Heptapsogaster*, *H. andinae* from *Tinamotis pentlandii*. Specimens indistinguishable from this species have been observed from *T. ingouffi*.

Tinamotaecola andinae Carriker was originally encountered on *T. pentlandii* in Bolivia. Further specimens have been found on skins of this host from Peru and Chile. The few specimens available from *T. ingouffi* are conspicuously smaller in size and may be a separate species.

AVIPARASITOLOGICAL CONCLUSIONS

On the basis of the distribution of Mallophaga species on the genus *Tinamus*, two main groups of the genus may be distinguished. In every

Mallophaga genus, it is noted that one group of related species is found on *T. tao* and *T. solitarius* while the other is found on *T. major*, *T. osgoodi* and *T. guttatus*. Distinct species of *Kelloggia*, *Strongylocotes* and *Pterocotes*, and possibly of *Ornischolax* are found on *T. tao* and *T. solitarius*. There appears to be a sufficient divergence, using the Mallophaga alone, to consider both these birds as distinct species. In the second group, both *T. osgoodi* and *T. guttatus* contain species which are not shared between themselves or with *T. major*. The species present on *osgoodi* are more closely related to those encountered on *major* than on *guttatus*. There seems to be no evidence that *osgoodi* or *guttatus* should be combined with *major*. The distribution of certain species of *Kelloggia*, *Ornischolax* and *Pseudolipeurus* provides evidence that there is some geographical differentiation among the subspecies of *T. major*.

The genus *Crypturellus* can be divided into three main sections on the basis of its Mallophaga fauna. The first group consists of *C. cinereus* and *C. berlepschi*. The second contains *C. soui*, *C. obsoletus*, *C. brevirostris*, *C. variegatus*, *C. tataupa* and *C. parvirostris*. The last section holds the balance of the species—*C. undulatus*, *noctivagus*, *strigulosus*, *transfasciatus*, *colombianus*, *boucardi*, *saltuensis*, and *cinnamomeus*. This pattern of distribution occurs in many genera of Mallophaga. There is no overlap of Mallophaga species on *C. cinereus* and *C. berlepschi*—an indication of their specific status. Although *C. soui* is one of the most widespread of Central and South American birds, ranging from southeastern Mexico to southern Peru and Rio de Janeiro, Brazil, there is little diversity in the Mallophaga fauna found throughout the host range. There are only signs of divergence in the subspecies *inconspicuus* from eastern Bolivia, central and southern Peru, and *nigriceps* from eastern Ecuador and northeastern Peru. A basic dichotomy is exhibited in *C. obsoletus*. One group of Mallophaga species is present on *C. o. punensis*, *o. ochraceiventris*, *o. castaneus* and *o. chirimotanus*, all west South American subspecies, while another group is present on the eastern *C. o. obsoletus* and *o. griseiventris*. In the case of *Megapeostus* and *Pseudolipeurus*, there are even different species on *C. o. obsoletus* and *o. griseiventris*. Unfortunately no Mallophaga were found on the single available specimen of *C. o. cerviniventris* from Venezuela. From the evidence of Mallophaga distribution, *C. obsoletus* would be split into two species. The Mallophaga present on *C. tataupa* and *C. parvirostris* are extremely close to each other and usually differ only in quantitative characters. Most of the species appear to be more closely related to those occurring on the *obsoletus punensis*, *o. ochraceiventris*, etc. section than to any other species of *Crypturellus*. The species on *C. variegatus* are all quite distinct and

no differences exist between the Mallophaga present on its subspecies except for *Pectenosoma*. Two of the three species known from *C. brevirostris bartletti*, from the genera *Kelloggia* and *Strongylocotes*, show very close affinities to *C. variegatus*. The third, a species of *Megapeostus*, resembles the species found on *C. soui*. The third group of *Crypturellus* contains species of birds whose Mallophaga fauna is less diversified than the preceding groups. These birds may be of more recent origin or the environment of the Mallophaga on these birds may be more uniform than that on the other host species. *C. undulatus* possesses a distinct fauna and the species on its six subspecies give no indication that any further subdivision of the species is necessary. The species found on *C. n. noctivagus* and *n. zabele*, with one exception, are different from those encountered on the remaining forms referred to as *noctivagus*. *C. noctivagus garleppi* has a distinctive group of Mallophaga closely related to the homogeneous group found on *C. n. duidae*, *n. idoneus*, *n. erythropus*, and *C. strigulosus*. These last four forms appear to have close affinities to *C. boucardi*. The Mallophaga on *C. cinnamomeus* are distributed throughout its ten subspecies. No differentiation of any sort has been detected. Certain of the species, *Kelloggia boucardi* (Carriker) and *Discocorpus mexicanus* Carriker, on *C. cinnamomeus* appear to have become established on Mexican populations of *C. b. boucardi* from Chiapas and Oaxaca while Veracruz material of this subspecies and *boucardi costaricensis* from Honduras, Nicaragua and Costa Rica show definite relations to the northern South American group of *C. noctivagus* as *n. idoneus*. The available specimens from *C. transfasciatus* are divided in their relations between *C. cinnamomeus* and *C. boucardi*. Lack of sufficient material from *C. saluensis* and *C. colombianus* prevents any further statement than that they show relations to the *cinnamomeus-boucardi-noctivagus idoneus* group. On the basis of the evidence from the Mallophaga, it seems that *C. cinnamomeus* is a distinct species. *C. boucardi*, *C. noctivagus idoneus*, *n. duidae*, *n. erythropus* and *C. strigulosus* form a closely related species. *C. noctivagus garleppi* is probably distinct and *n. noctivagus* and *n. zabele* are definitely distinct.

In analyzing the Mallophaga on *Nothocercus*, two main groups of species are apparent. One is found on *N. julius* and the other on *N. bonapartei* and *N. nigrocapillus*. The differences between the Mallophaga found on *N. bonapartei frantzii* and *b. bonapartei* are of the same magnitude as those found between parasites on different species of *Crypturellus*. By the same criteria used previously, these would be considered distinct. In any event, the subspecies *bonapartei* and *plumbiceps* of *bonapartei* are closely allied in contrast to *b. frantzii*, and appear to exhibit closer affinities

with *N. n. nigrocapillus* than to *N. bonapartei frantzii*. Unfortunately no skins of *N. b. discrepans* have been available to examine for Mallophaga.

Little differentiation has occurred on the bird populations constituting *Rhynchotus rufescens*. This can be considered as a single species.

Two main groups of *Nothoprocta* are discernible. The presence of *Lamprocorpus* and the *Heptapsogaster tessellata* group readily identify the species group containing *N. ornata*, *tanzanowskii*, and *curvirostris*. The second group of *Nothoprocta*, characterized by Mallophaga of the *Heptapsogaster teres* and *H. chacoensis* groups, consists of *N. perdicaria*, *N. cinerascens*, and *N. pentlandii*. In the first group, the study of material from *N. ornata rostrata* and *o. ornata* shows that no great differences exist between them while rather striking differences exist between *N. ornata* and *N. curvirostris*. These are considered as distinct species. The relations between members of the second group are likewise apparent. *N. perdicaria* and *N. cinerascens* are closely related, possibly of less than specific rank, while *N. pentlandii pentlandii* and *N. pentlandii oustaleti* belong to a different species.

Nothura boraquira is a very distinct species. If the genus *Nothura* is divided into groups, *boraquira* would constitute one and the remaining species would compose the other. The distribution of *Heptapsogaster boliviana* (Carriker) on *Nothura darwinii* and *Heptapsogaster minor* Hopkins on *N. maculosa* distinguishes these two bird species. *N. chacoensis* and *N. minor* are closely related to *N. maculosa* but a statement as to their precise relationships requires the study of additional material.

Little can be added to the knowledge of *Eudromia* and *Tinamotis* from the study of the distribution of Mallophaga except to state that two species are definitely recognizable in each genus, *Eudromia elegans* and *E. mira* and *Tinamotis pentlandii* and *T. ingoufi*.

Many of the relationships observed in this present study may not be in agreement with those postulated by ornithologists in their papers on the classification of the tinamous. However, the agreement is remarkably close between the distribution of Mallophaga and that of their hosts. Studies of this sort involving the analysis of interspecific relationships can contribute to a more thorough understanding of the evolution of many groups.

SUMMARY

Several thousand specimens of Mallophaga have been studied from 130 of the 140 known species and subspecies of tinamous. 18 of the 20 Mallophaga genera parasitizing this host order are restricted to it. The generic nomenclature used is that of Hopkins and Clay (1952) with the following exceptions: *Austrokelloggia*

Carriker = *Kelloggia* Carriker, *Heterogoniodes* Carriker = *Megapeostus* Carriker, and *Heptapsus* Carriker = *Pterocotes* Ewing. An analysis of the segmentation of the heptapsogastrid pterothorax and abdomen indicates that the Heptapsogastridae can no longer be considered distinct from the Philopteridae. In this group of Mallophaga, there is a parallel between a primitive pterothorax and abdomen of the parasite and the phylogenetic position of the host.

An analysis of the distribution of Mallophaga genera on their hosts indicates that they can be used to distinguish host categories of greater than generic rank. The inclusion of *Crypturellus*, *Tinamus* and *Nothocercus* in the Tinaminae, *Rhynchotus*, *Taoniscus*, *Nothura* and *Nothoprocta* in the Rhynchotinae and *Tinamotis* and *Eudromia* in the Eudromiinae is justifiable by the parasite data.

The Mallophaga species groups define host genera and provide exact data on their relationships. Von Boettischer's classification (1934) with one exception conforms perfectly to the divisions depicted by the tinamou lice. Parasite distribution indicates that *Crypturellus* and *Nothocercus* are more closely allied than either one is with *Tinamus*.

Data from taxonomic studies of the approximately 200 species of lice parasitizing the tinamou has been used to ascertain the relations of the parasites. These relationships have been compared with an accepted classification (Hellmayr and Conover, 1942) of the host species. The amount of agreement between these lice and their hosts is very high. The usual situation is one of a 1:1 correspondence between host and parasite species. In a few instances, a species of Mallophaga is found on a group of closely related species which may actually be a polytypic species. A section on aviparasitological conclusions serves to present those findings of ornithological significance. By the use of Mallophaga, many of the relationships among species of tinamou which were poorly known or speculative have been confirmed or denied by this technique.

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